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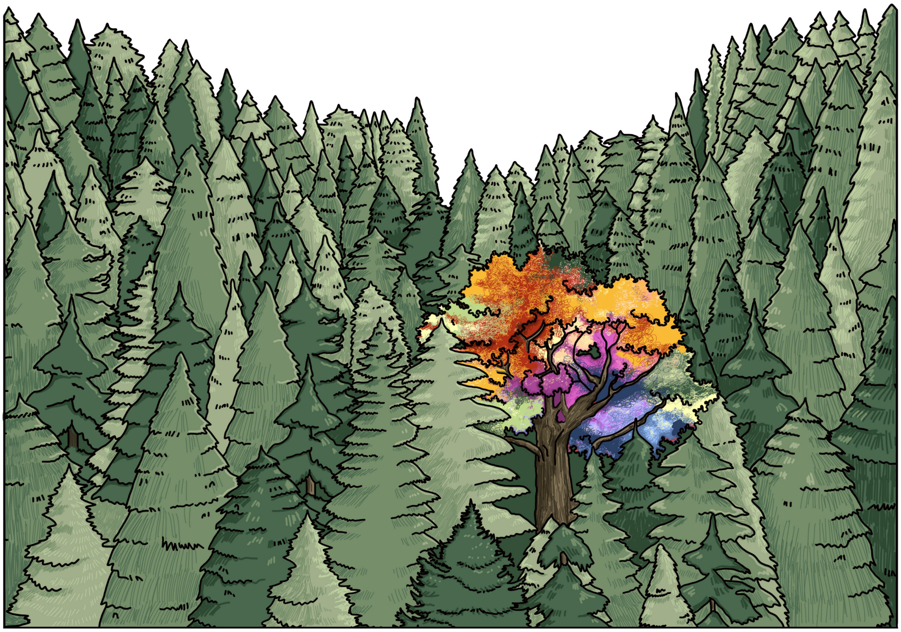
Old trees in young forests

Biodiversity management in planted conifer forests in southern Sweden

Delphine Lariviere



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Errata for

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Page 19
Location: line 17
Is now: “This thesis investigated different aspects of forest management in young planted conifer forests compared to yesterday’s forestry”
Should be: “This thesis investigated different aspects of forest management in young planted conifer forest. The aim was to evaluate how choices in forest management contribute to biodiversity with the example of tree retention in thinning or through the choice of rotation length.”

Page 28
Location: line 16
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Should be: “This includes the retention of deadwood, tree groups, buffer zones, and individual trees that offer potential habitats for plants and animals and may prevent damage in sensitive biotopes (Figure 2).”

Page 34
Location: line 13

Is now: “having fallen from 120 years old, on average (all species included), to about 100 years old from 2004 to 2018.”
Should be: “having fallen from 120 years old, on average (all tree species included), to about 100 years old from 2004 to 2018.”

Page 68
Location: Legend Figure 19
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Should be: “Field retention tree as 5 m buffer (…)”

Paper IV, Page 9
Location: line 12, 13, 14,15
Is now: Figure 5a
Should be: Figure 4a

Paper IV, Page 10
Location: line 9,10,11,14.
Is now: Figure 5b
Should be: Figure 4b

Paper IV, Page 17
Location: line 5
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Should be: performance should be explained by the height

Location: line 24
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Should be: difficult to find individual trees as it makes it harder to delimitate (…)

Old trees in young forests: Biodiversity management in planted conifer forests in southern Sweden

Abstract

Sweden's long history of intensive forest management has made conservation measures in the forest landscape necessary to counteract the loss of biodiversity. Retention forestry has been systematically practiced since 1993 and consists of the preservation of different structures and habitats to create and maintain suitable habitats for species that do not cope well with clear-cutting. Many of these stands are now entering thinning. The aim of this thesis was to evaluate how choices in forest management contribute to biodiversity with the example of tree retention in thinning or through the choice of rotation length. First, gap cutting around old oaks (*Quercus robur*) in a Norway spruce (*Picea abies*) forest was investigated as an example of retention management in southern Sweden (**I** + **II**). We found that oaks contributed to the diversity of the stand due to their specific associated species. The removal of Norway spruce next to the oaks at the time of thinning boosted oak vitality and increased the species richness and abundance of vascular plants and saproxylic beetles due to increased temperature and light exposure, especially oak-associated beetles. In another study, the effect of forest age was investigated on four taxa: birds, bryophytes, lichens, and vascular plants in Norway spruce and Scots pine (*Pinus sylvestris*) stands (**III**). The older stands, both of Norway spruce and Scots pine, had a distinct species community of understorey species and epiphytes. In Norway spruce stands, older stands typically had more deadwood, which could have favoured bryophytes and birds by providing specific habitats and resources. Older Scots pine stands had the highest lichen species richness, but the implementation of other understorey species was impaired by the dominance of a few competitive dominating species. Finally, we explored the potential of using a canopy height model (CHM) to find and map retention trees (**IV**). We concluded that this method is a cost-effective solution to map and characterise past retention efforts to facilitate forest management and ensure that old trees are kept throughout the present and subsequent rotations. Our results indicate that this method can discern retention areas to an accuracy of 66%. The findings in this thesis provide knowledge on how the management of retention trees and the choice of rotation length can support biodiversity and provide guidelines for forest management so that their positive effects on forest biodiversity can be maintained over time.

Keywords: biodiversity, tree retention, *Quercus robur*, conifer, hemiboreal zone, release cutting, thinning, management

Gamla träd i ung skog: Skötsel för mångfald i planterade barrskogar i södra Sverige

Sammanfattning

Sveriges långa historik av intensivt skogsbruk har påverkat förutsättningarna för skogens biologiska mångfald. De negativa effekterna kan dock mildras genom aktiva hänsynsåtgärder, och naturhänsyn i samband med avverkning, och har varit standard sedan skogsvårdslagen reviderades 1993. Genom att bevara och skapa strukturer och miljöer kan arter få hjälp att överleva den kritiska kalhyggesfasen. Många av de bestånd som avverkades på 1990-talet är nu i gallringsfas. Syftet med avhandlingen var att utvärdera hur olika skogsskötselalternativ påverkar den biologiska mångfalden. I en första studie undersöktes hur frihuggning av gamla ekar (*Quercus robur*) i granskog (*Picea abies*) kan bidra till förstärkta naturvärden (**I + II**). Ekarna bidrog till en ökad mångfald i skogen genom sina specifika associerade arter. Frihuggning (gallring) av granar närmast ekarna stärkte ekarnas vitalitet och ökade artrikedomen samt förekomsten av kärlväxter och vedlevande skalbaggar. Framför allt gynnades ekberoende skalbaggar av den högre temperaturen och ljusinsläppet. I en annan studie undersöktes skogens ålder hos fyra artgrupper i bestånd med gran och tall (*Pinus sylvestris*): fåglar, mossor, trädlevande lavar och kärlväxter (**III**). Äldre bestånd, både med gran och tall, hade en välavgränsad artsammansättning i fält- och bottenskikt och bland lavar. Äldre granbestånd hade vanligtvis mer död ved, vilket kan ha gynnat mossor och fåglar genom att tillhandahålla specifika livsmiljöer och resurser. Unga tallbestånd var mer artrika (artrikedom, artdiversitet – Shannon-diversitet, unika arter) än de gamla. Äldre tallbestånd hade visserligen högst mångfald av lavar, men diversiteten av markvegetation tycks ha påverkats negativt av ett fåtal dominanta arter. Slutligen undersöktes möjligheten att använda en trädhöjdsmodell (Canopy height model, CHM) för att identifiera naturvårdsträd som lämnats i samband med tidigare avverkning (**IV**). Metoden visade sig vara ett kostnadseffektivt sätt att kartlägga tidigare naturhänsyn, så att information finns tillgänglig vid planeringen av framtida skogsbruksåtgärder. Resultaten tyder på att metoden kan urskilja hänsynsområdena med en noggrannhet på 66 %. I sammandrag ger avhandlingen kunskap om hur skötsel av naturvårdsträd och valet av omloppstid kan användas för att stärka den biologiska mångfalden, och resultaten kan bidra till riktlinjer för den skogliga planeringen.

Nyckelord: Biologisk mångfald, naturhänsyn, barrträd, södra barrskogsregionen, *Quercus robur*, gallring, skogsskötsel

Dedications

To science and facts.

To all the articles I saved for later, but never read.
To all the reviewers that went through my first painful drafts of research articles.
To all the future reviewers who will probably endure the same.

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. Lariviere, D.*, Holmström, E., Brunet, J. & Weslien, J. (2021) Release of retained oaks in Norway spruce plantations. A 10-year perspective on oak vitality, spruce wood production and ground vegetation. *Forest Ecology and Management*, 480, 118670. https://doi.org/10.1016/j.foreco.2020.118670

II. Lariviere, D.*, Holmström, E., Petersson, L., Djupström, L., Weslien, J. (2023) Ten years after: Release cutting around old oaks still affects oak vitality and saproxylic beetles in a Norway spruce stand. *Agricultural and Forest Entomology*, 1 (11). http://doi.org/10.1111/afe.12563

III. Petersson, L.*, Lariviere, D., Holmström, E., Lindbladh, M., Felton, A. (2023) Potential implications of shortened rotation length for forest birds, bryophytes, lichens and vascular plants: An example from southern Swedish production forests (In review, *Plos One*)

IV. Lariviere, D.*, Westerfelt, P., Ene, L.T, Lindbladh, M., Felton, A., Holmström, E. Using the Canopy height model (CHM) to detect old retention trees and areas before the first thinning. (manuscript)

Paper I and II are open access and published under Creative Commons License. * Corresponding author.

The contributions of Delphine Lariviere to the papers included in this thesis were as follows:

I. The original experiment was designed by MKW. DL, EH, and JW participated in the development of the research question. DL planned and performed the field work with the help of field assistants and staff from the Asa research station. DL analysed the data and wrote the manuscript together with the co-authors.

II. The original experiment was designed by MKW. DL, EH and JW participated in the development of the research question. DL planned and performed the field work with the help of field assistants and staff from the Asa research station. DL analysed the data and wrote the manuscript together with the co-authors.

III. Field work was performed by LP, ML and AF. DL participated in analysing the data and writing the manuscript, which was led by LP.

IV. DL and EH developed the research question and designed the experiment together with the co-authors. The model concept was developed by PW. Field validation data were provided by ML and AF. DL analysed the data. DL wrote the manuscript together with the co-authors.

Delphine Lariviere (DL), Emma Holmström (EH), Jan Weslien (JW), Maria Koch Widerberg (MKW), Lisa Petersson (LP), Matts Lindbladh (ML), Adam Felton (AF), Per Westerfelt (PW).

List of figures

1. Background

1.1 Yesterday's forestry: Forestry and conservation

The establishment of forest conservation measures in Sweden has been a long and gradual process. Forestry is an intrinsic part of Swedish history and has evolved to meet societal, environmental, and economic standards. The way we need forest yesterday is not the same way we need it today, nor the way in which we will need it tomorrow. Many actors have been involved in shaping the forest we see today. The creation of reserves, the integration of environmental considerations in stands, and the development of alternative management strategies came into the picture progressively, together with changes in the political context, as well as the reorientation of forestry policy. Today's forests, and classical forestry approaches are the result of a long history of intensive forest management linked to historical needs and events, which have become increasingly incompatible with today's expectation of our forest and the need to combine economic, environmental, and social objectives.

This thesis investigated different aspects of forest management in young planted conifer forests compared to yesterday's forestry. This first chapter puts my work into the historical context of forestry, which is essential to understanding today's conservation efforts.

1.1.1 1950s to 1993

In southern Sweden, the landscape was dominated by agricultural land until the 1950s. In past agricultural landscapes, forests were mainly used for grazing and viewed as a complement to farmers' agricultural systems, and many small farmers also owned forest land. The landscape was diversified and fragmented into individual properties, with natural forests and arable land separated by forest edges (Svensson et al., 2016). After the Second World War, a phase of structural transformation began. Many small farms disappeared, a lot of arable land was abandoned, and land resources were concentrated in larger units (Jansson and Antonson, 2011). Changes in agricultural practices and mechanisation translated into agricultural intensification and the replacement of horses and hand labour with tractors. The yield of arable land was improved through artificial fertilisers. Grazing decreased as dairy producers developed more efficient indoor production systems. The mechanisation and chemicalisation of agriculture were both a result of the labour shortage and a reason why labour forces were rationalised away from agriculture.

In parallel with the reformation of agriculture, forestry also changed. Prices for timber increased, renewing interest in forestry in southern Sweden (Brunet et al., 2012). After the Second World War, farmers were instructed to plant low-productive areas with forests; thus, many agricultural lands were converted to forests (Lindbladh et al., 2014). Wooded pastures were afforested, and forest cover increased rapidly (Eriksson and Cousins, 2014, Mazier et al., 2015). Plantations have become increasingly common in southern Sweden, particularly in the province of Småland (Cui et al., 2014). In the same way it occurred for agriculture, new forestry methods were introduced, such as mechanised site preparation, forest fertilisation, and aerial spraying of herbicides to control brushwood in clear-cut areas. Altogether, the increased afforestation of agricultural lands and mechanisation led to a dramatic increase in productivity from the 1960s to the 1980s. A measure of how forestry has succeeded is that between 1950 and today, the standing volume has increased 200%, from 1 to 3 billion cubic metres (Kumar et al., 2021).

Between 1960 and 1990, the “even-aged” stand management system became the most widespread forestry practice in Sweden, leaving large areas of cut forest after felling, with some reaching several hundred hectares in the northern part of the country. Large, clear-cut areas were regenerated with planted Norway spruce (*Picea abies*) or Scots pine (*Pinus sylvestris*), and the use of herbicides and insecticides became common practice.

As forestry and agriculture intensified in the 1960s, public opinion began to rise. The increase in Norway spruce plantations on former agricultural lands, as well as the logging of beech forests in southern Sweden, were perceived as a threat to the old cultural landscape (Brunet et al., 2012, Lindbladh et al., 2014). Additionally, the aesthetics of clear-cut systems and the large areas left clear after harvest have been heavily criticised (Lundmark et al., 2013) The 1970s is considered “the decade of confrontation” in Sweden (Simonsson et al., 2014). Scientists and non-governmental organizations (NGOs) started to develop informational support for the negative effect of forestry on biodiversity. The first red list of species in Sweden was a valuable tool for understanding the detrimental effects of conventional forestry on forest organisms (Simonsson et al., 2014). Then came scientific evidence of the negative effects of forestry on several organisms and forest specialists. The intensification and homogenisation of forests leads to habitat loss, habitat degradation, and habitat fragmentation, which are the primary drivers for biodiversity decline (Betts et al., 2017).

Forested ecosystems harbour most of the global terrestrial biodiversity, and forest ecosystems are more diverse than any other ecosystems (Brockerhoff et al., 2017). Conserving forest biodiversity has become crucial not only in Sweden but also around the world. The environmental movement and the fight for forest conservation and protection have spread across the globe. Forest protection guidelines were established at the first European conference on forests in Strasbourg in December 1990. In 1993, a second conference was held in Helsinki, prompted by the Swedish Environmental Code (Miljöbalk, 1998:808). This was preceded by the framework of implementing decisions during the 1992 United Nations Conference on Environment and Development (UNCED) in Rio, with the Rio Declaration relating to forests, biological diversity, and climate change. In conjunction with the country’s internal context, international agreements have gradually influenced Swedish policymaking.

1.1.2 After 1993

In 1993, the Swedish Forestry Act was updated, ensuring that equal importance was given to both production and conservation objectives (1§ Skogsvårdslag 1979:429). This principle is still applied today. However, the details of what and how much should be done remain elusive. Swedish forestry policies are goal oriented rather than action oriented. They have been qualified as “soft/relaxed” policies with weak legal regulations (Nylund, 2009, Simonsson et al., 2014). The law is based on “Freedom under responsibility,” and mandatory management plans have been abolished and replaced with more flexible guidelines (Nylund, 2009). As a result, the forestry act was followed by the creation of non-state governance schemes, such as certification standards, including the Forest Stewardship Council (FSC) in 1995 and the Programme for the Endorsement of Forest Certification (PEFC) in 1999. The implementation of these certification standards was market-driven, i.e. by the consumer´s demand for more “environmentally friendly” forestry products and aspirations for more qualitative and stricter forestry regulations than the current Swedish policy. In 2020, more than 15.4 million ha of forests were certified according to either the FSC and/or PEFC standards (Skogsstyrelsen, 2021).

Certification introduced the concept of “Voluntary set-asides” (VSA). VSA has no formal protection but rather strong informal protection through certification. Nature reserves, national parks, conservation agreements, and biotope protection are the four formal forms of protection and constitute the basis for the Swedish strategy for forest conservation, in which land is set aside to protect forest ecosystems (land sparing). In total, 8.8% of forest land is formally protected (**Figure 1**) (SCB, 2022). The second strategy for forest conservation in Sweden is to reconcile production and conservation goals (land sharing). The retention forestry approach was proposed to achieve this strategy. When a stand is harvested, one way to counteract and buffer the effect of clear-cutting on forest organisms is to retain living or dead trees, single or in groups, for the next rotation (Fedrowitz et al., 2014). Retention covers 0.5 million hectares or 2.1% of the productive land area (**Figure 1**) (SCB, 2022). Retention integrates conservation measures within productive forests.

The management of retention later in stand development is the main theme investigated in this thesis. The implementation of retention forestry after 1993 has defined the way forests look today. Almost 30 years later, we are seeing the results of yesterday’s forestry, and these stands include new features and are now awaiting thinning.

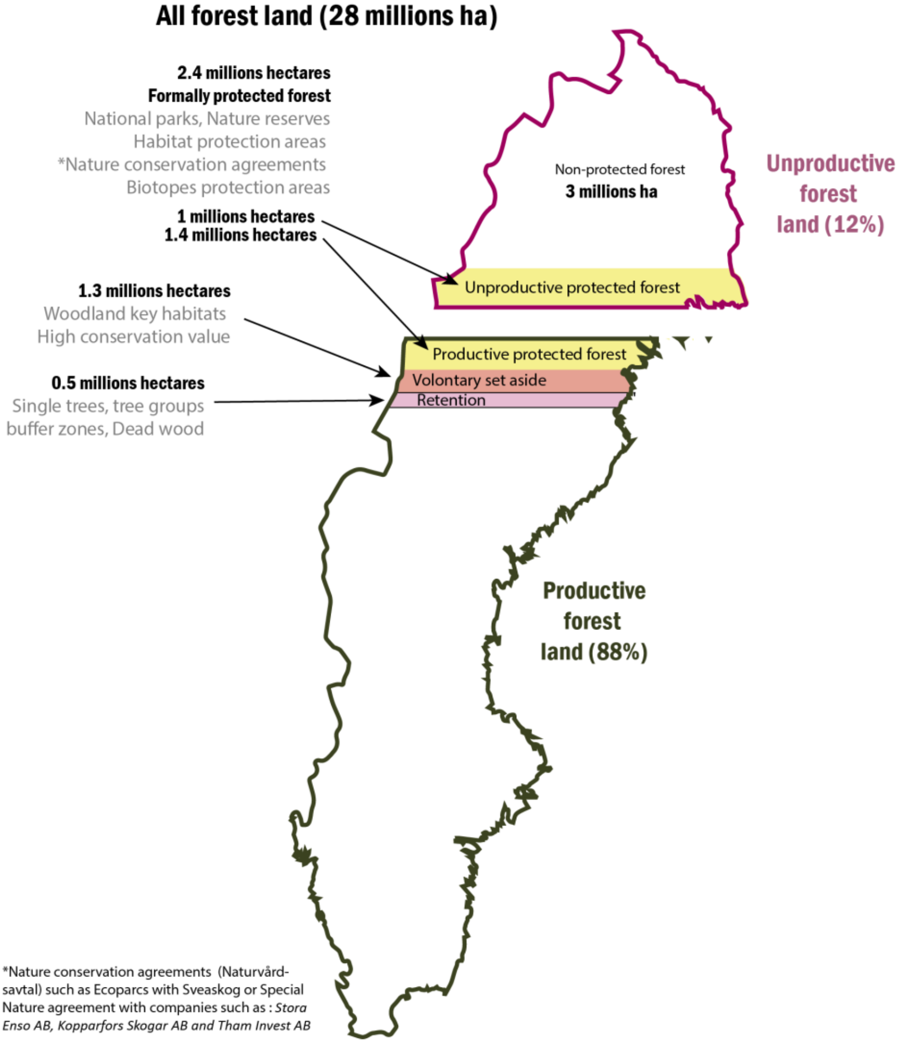

Figure 1. Illustration of formally protected forest land, voluntary set aside, retention, and unproductive forest land in Sweden. Unproductive woodlands (forests that do not produce more than 1 m^3 per hectare per year) are exempt from forestry by the Forestry Act because they provide green infrastructure, biodiversity, and other ecosystem services. *Data source: SCB*

2. Introduction

Anthropogenic activities and a changing climate are putting increasing pressure on forest ecosystems. Forestry intensification has led to large-scale deforestation, degradation, and altered natural disturbance regimes (FAO, 2020). Intensive forest management has resulted in a strong decline in forest biodiversity because of the loss of important structures for forest diversity (Nilsson et al., 2001, Kuuluvainen, 2009). Forests harbour immense terrestrial and aquatic biodiversity and represent the most species-rich habitat type worldwide (Mace et al., 2005, Lindenmayer, 2009). Economic benefits from forests often come at the expense of the environment and the well-being of society, and vice versa (Mönkkönen, 1999, Strengbom et al., 2018).

In recent decades, the challenge has been to find cost-efficient strategies to maximise wood production while accommodating social and environmental goals. Current forest biodiversity conservation strategies rely on sparing and protecting habitats for conservation, and/or managing forests in a more integrated way, sharing the land to meet several objectives (Felton et al., 2020). One way to reconcile wood production and environmental goals is to preserve biologically important features within production stands and recreate disturbances through forest operations (North and Keeton, 2008, Kuuluvainen et al., 2021). Several environmental restoration and conservation efforts have been implemented over the last three decades to benefit biodiversity and mimic natural disturbances (Angelstam, 1998). The retention or creation of key structures, such as deadwood, broadleaf, and old trees, have been implemented to restore habitats and structural diversity in managed landscapes (Fedrowitz et al., 2014). Similarly, silvicultural operations can control or create investments for conservation within a stand

and bring back structural heterogeneity to accommodate goals other than production (Strengbom et al., 2018).

Even though retention has been practised for the last three decades, little information has been gathered over the years. Where and what are these investments? Most importantly, are they still fulfilling their purpose 30 years later and/or are they in need of management? In this thesis, some aspects and possibilities of adapting or evaluating current forestry practices for biodiversity management within a clear-cut system, such as retention, thinning, or rotation length for biodiversity, were investigated.

2.1 Today's forestry

In Sweden, 28 million hectares of the land is covered by forest, about 84% of which is considered to be "productive forest land" (potential tree growth of more than 1 m^3 ha^{-1} $year^{-1}$) (**Figure 1**) (SCB, 2019). Therefore, forestry and forest management are major determinants of forest biodiversity. Today's Swedish forestry is centred on a clear-cut system with planting of seedlings, which leads to even-aged monocultures. The clear-cutting system combines a series of forest operations between two harvests; in southern Sweden, the rotation length is 88 years, on average, depending on the tree species, site fertility, and owner objectives (Skogsstyrelsen, 2018).

The historical exploitation of forests in southern Sweden has generated a homogeneous forested landscape that differs from the natural forest historically found, which is normally dominated by broadleaved or mixed coniferous–broadleaved forests (Björse and Bradshaw, 1998, Lindbladh, 1999). In today's modern production forestry ecosystem, natural disturbances and succession are no longer the primary factors driving the amount, dispersal, and diversity of forest structural elements that contribute to the diversity of habitats and species present in forest ecosystems (Kuuluvainen and Grenfell, 2012). In the case of clear-cutting, harvest, and management operations define the new forest succession (Lindenmayer et al., 2006), and forest conditions are controlled and tailored as agricultural systems to increase wood production and quality (Puettmann et al., 2012).

2.2 Biodiversity in hemiboreal forests

Biodiversity in hemiboreal forests is a direct outcome of forest operations in southern Sweden. The hemiboreal forest is a transition zone between the nemoral and boreal forests (Gustafsson et al., 2015). Due to climatic overlap, this zone has the highest species richness in Sweden for many organism groups, such as insects and fungi (Nilsson et al., 2001). The high species diversity in this zone is due to the larger diversity of tree species (Gustafsson et al., 2015). However, as a legacy of forest land use history (mentioned above in 1.1), today's proportion of planted conifers in production forests in Götaland is high. In recent decades, Norway spruce has been especially popular due to its rapid growth, easy establishment, resistance to browsing, and high demands from the industry (Löf et al., 2012). In conjunction with the homogenisation of the productive forest in favour of Norway spruce, stands are usually cleared of broadleaves and harvested at a rather young age compared to the potential lifespan of crop trees (Curtis, 1997, Andersson and Niklasson, 2004).

Intensive management has led to the destruction of old forest habitats, and forest harvest has a large negative impact on more than 1400 red-listed species in Sweden (Eide et al., 2020). These species are often dependent on old forest structures (e.g., coarse woody debris (CWD) and old trees) and cannot tolerate severe habitat destruction, such as clear-cutting. Forest specialist species are left to rely on fractions of old growth forests spared for conservation and productive forest land, with no prospect of ageing.

Old growth forests and old trees, especially noble broadleaved tree species, are considered important for nature conservation (Gotmark et al., 2006, Price et al., 2020) of both invertebrates and vertebrates. They provide complex structures, unique habitats, and substrates old enough to be colonised by old-growth specialised species (Berg et al., 1994, Andersson and Östlund, 2004, Asbeck et al., 2020). As trees grow old, they develop particular ecological characteristics and micro-habitats (holes, hollow trunk, rough bark).They also can develop various stages of decaying deadwood, which provide important habitats and resources for many species (Kneeshaw and Gauthier, 2003, Ranius et al., 2008, Parmain and Bouget, 2018). Additionally, the canopies of old deciduous trees allow more light to pass through their crowns compared to conifers and offers different environmental conditions

(Andersson and Östlund, 2004, Franklin and Van Pelt, 2004). Therefore, the management and conservation of older broadleaves trees within productive forest land is essential for biodiversity conservation.

2.2.1 Retention forestry

When a stand is regenerated, it is possible to create or preserve features specifically for conservation purposes. To break the trends, and mitigate the negative effect of forestry on biodiversity, the concept of "retention forestry" was introduced in the 1990s and stated in Forestry Act 30 §, as "*retention measures shall be taken in all forestry practices on all forest land eligible under the legislation*."

Retention is an adaption to clear-cutting and is based on the preservation of certain features in the stand that are favourable for certain species (Fedrowitz et al., 2014). This includes the retention of deadwood, tree groups, buffer zones, and individual trees that offer potential habitats for plants and animals and may prevent damage in sensitive biotopes (**Error! Reference source n ot found.**) (Fedrowitz et al., 2014, Beese et al., 2019). The primary aim of tree retention is to promote biodiversity by increasing structural diversity on clear-cuts and in future forest stands (Kruys et al., 2013). Retention is increasingly used in traditionally managed forests. An argument for retention is that the combination of the new planted trees together with retention creates a stand structure that better resembles the complex structure of forests after natural disturbance, helping to maintain ecosystem functions dependent on these structures.

Retention is applicable in different biomes and is adapted in other parts of Europe (Gustafsson et al., 2020), America (Beese et al., 2019), and Australia (Scott et al., 2019). Despite being quite a young practice, many ecological studies have attempted to tackle the perspectives of retention forestry and biodiversity. For example, Lindenmayer et al. (2012) reported more than 450 studies on the link between retention and biodiversity. According to Gustafsson et al. (2020), over 100 papers have been published in Nordic and Baltic countries, examining how flora and fauna respond to retention strategies at clear-cutting. However, due to the short history of the practice, little research has been conducted on how retention practices affect forest structures, biodiversity, and wood production in the long term and if the retained features still contribute to biodiversity in today's young forest (entering the first thinning phase).

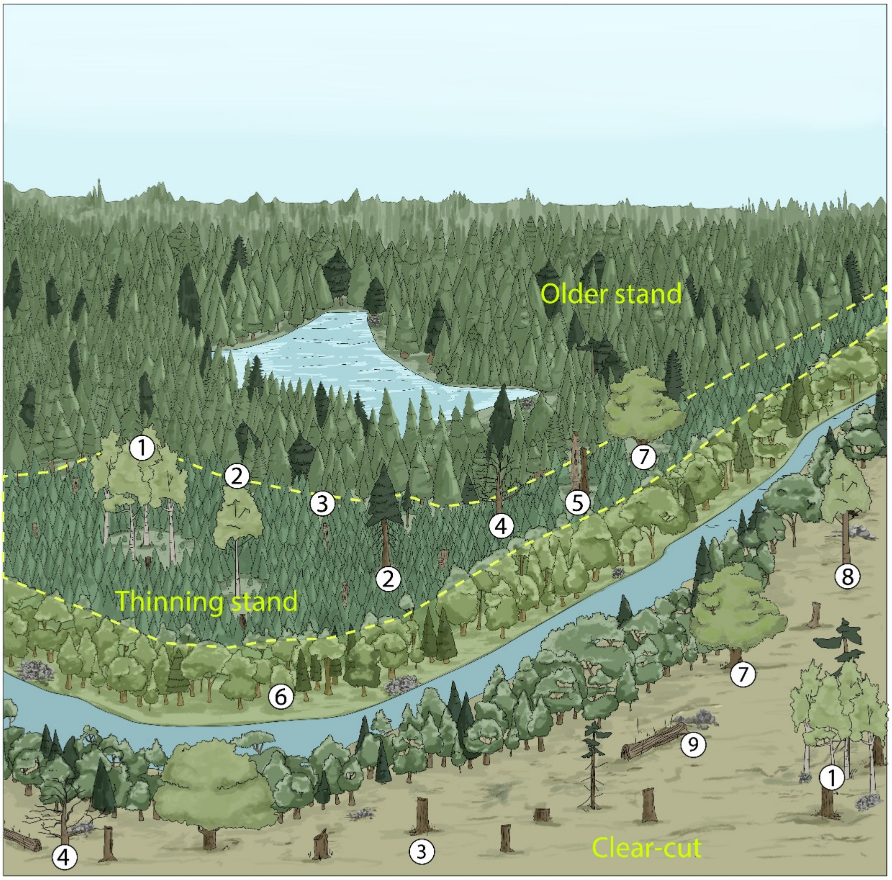

Figure 2. Representation of the retention forestry approach in Sweden at clear-cut (foreground) and thinning phase (middle ground). The background represents an older stand without retention that is soon to be harvested. The different numbers represent the most common type of retention present in the stand. **1**. Group of trees, **2**. Single tree (broadleaf or conifer), **3**. Low stump, **4**. Standing dead tree, **5**. High stumps, **6**. Buffer zones with broadleaves, **7**. Older broadleaves (oak), **8**. Other broadleaves (aspen, willow, rowan), **9**. Lying deadwood.

2.2.2 Retention of oak in southern Sweden

Retention is widely practiced in Sweden; on average, in 2021, about 8% of the clear-felled area was retained (SCB, 2022). The most common type of retention is done during clear-cutting by leaving single trees or tree groups from the previous stand (**Figure 2**), but it can also be done when crop trees are planted on open land with scattered old trees. For example, oak retention is commonly practiced in southern Sweden when afforesting pastures. The mechanisation and intensification of forestry (mentioned above in 1.1) has led to the conversion of many oak pastures into production forest stands by planting Norway spruce (Lindbladh et al., 2014).

In Sweden, oaks have a long natural and cultural history. A long time ago, oaks were declared the property of the crown and used by the navy for ship production (Eliasson and Nilsson, 2002). In the Middle Ages, the oak tree, regardless of its place of growth, was considered state property. Their felling was prohibited, and farmers were stuck with giant trees, shadowing and impacting their crop land. Many of the good oaks were selectively cut down for the construction of ships, and the remnant oaks were mostly dead, decaying, and hollow trees (Eliasson and Nilsson, 2002, Naturvårdsverket, 2006). From the mid-19th century onwards, legislation gradually changed. Those who owned land gained equal property rights, and social equality increased. Consequently, the oak tree stopped being perceived by the common people as an object of oppression and injustice. Nowadays, oak trees represent “diversity and landscape richness” rather than a symbol of social injustice causing disagreement and division (Eliasson and Nilsson, 2002).

For cultural and political reasons, as well as for its importance to biodiversity, many oaks have been preserved despite the afforestation of the land. This has led to the creation of what is called an “old retention tree” or “eternity tree” within production forests. Oak is a light-demanding tree species with long longevity and a coarse trunk. Oaks harbours diverse flora and fauna and have the highest number of associated species in Sweden (Sundberg et al., 2019, Artdatabanken, 2020). One of the reasons is that because of its longevity, it can provide a wide variety of decaying deadwood and habitats. Species associated with oaks usually have a high dependence on the tree and are tree-specific species (Jonsell et al., 1998, Mitchell et al., 2019). Without proper care, the retention of the oak at the beginning of the rotation may be affected by the development of a new productive stand. This raises concerns regarding long-term survival and the contribution of these retention trees to biodiversity.

The release of oaks, or gap cutting, has been proposed to improve conditions for biodiversity in managed forests. The release consists of the removal of trees around the retained oak and can be practiced in conjunction with thinning operations. Studies have shown that the release improves oak vitality and habitat quality for associated species (Paltto et al., 2008, Götmark, 2009). It can also mimic natural disturbances and affect ecological processes through gap dynamics (Muscolo et al., 2014). By increasing habitat diversity and structural complexity, gap cutting creates new niches and stimulates the species diversity of both fauna (Widerberg et al., 2012, Gran and Götmark, 2019) and flora (Gálhidy et al., 2006, Widenfalk and Weslien, 2009). These changes may affect saproxylic beetles' assemblages (Widerberg et al., 2012, Mason and Zapponi, 2015, Hjältén et al., 2017, Hägglund et al., 2020) but also ground layer diversity and abundance (Goldblum, 1997, Gálhidy et al., 2006, Fahey and Puettmann, 2007, Kelemen et al., 2012). However, little information is available about the long-term and persistence of the effects of the release. Additionally, maintaining both wood production and biodiversity in stands with old retained oaks poses challenges to forest management in Sweden. Keeping oaks will decrease the area for crop tree production and may also affect the growth of crop trees. Lindén (2003) has shown that retention may come at the cost of production benefits.

2.2.3 Biodiversity management in thinning

Studies have shown a clear increase in the number of retention objects in the Swedish forestry landscape since the 1990s (Kruys et al., 2013, Holmström et al., 2019, Kyaschenko et al., 2022). Under ideal circumstances, retention forestry has the potential to create a network of smaller old-growth forest patches, as well as single older trees, which can complement larger set-aside forest areas and increase forest landscape connectivity (Angelstam et al., 2020). However, little information is available regarding how many, what, and where retention measures have been implemented, and no digital or archived data exist in a systematic way. Private owners are still not required to report the location of retention areas. Only a few larger companies have started to implement spatial registration of retention to be created in the planning before clear-cuts. Without knowing where the retention trees are, there are risks that they will be harvested or neglected during subsequent thinning.

The Swedish Forest Agency provides spatial open-source information on forest data based on aerial laser scanning. Airborne laser scanning (ALS), also commonly known as Light Detection and Ranging (LiDAR), is a remote sensing method that provides three-dimensional information on vegetation structures. The Swedish LiDAR data, or more precisely, the 3D point cloud, have been processed into a tree height raster, also called the canopy height model (CHM). The Canopy Height Model (CHM) dataset is a high-resolution 1 × 1 metre raster layer that maps tree height as a continuous surface. The accuracy and quality of a CHM improves with higher point density LIDAR data. The CHM provides highly accurate and detailed measures of forest height, cover, and canopy structure estimates, hence offering high-quality information regarding the presence and location of otherwise unregistered and potentially higher retained trees over large forest areas. Remote sensing may present a cost- and time-effective solution to map and characterise retention trees.

ALS cloud point data has been used to detect individual trees' crowns within a stand with good accuracy (Hyyppä et al., 2012, Luo et al., 2018, Douss and Farah, 2022). Height estimates generated from LiDAR data have been found to be of similar or better accuracy than corresponding field-based estimates (Næsset and Økland, 2002). Studies have demonstrated that the LiDAR measurement error for individual tree heights (of a given species) could be less than 1.0 m (Holmgren and Persson, 2004). Retention trees can be detected on clear-cut areas (Holmström et al., 2019, Hardenbol et al., 2022, Lindbladh et al., 2022) via visual cues. However, visual interpretation of orthophotos is a subjective way to find trees, and trees retained in clear-cut areas may not be present at thinning. Currently, there is no way to acquire this information automatically and objectively for large areas. Thus, there is a need for tools that can facilitate and monitor these features throughout the stand by first locating them and then enabling follow-up work over subsequent decades. The tree height raster provided by the Swedish Forestry

Agency is freely available and represents a great and accessible way for forest owners to locate retention areas. Registered localisation will increase the probability that these structures and patches will be considered in all subsequent forestry measures, ensuring their preservation in the present and subsequent rotations. It can also offer opportunities for forest research, planning, and operations to locate and manage retention areas on a landscape scale. However, such a method does not yet exist. This thesis provides guidelines on how to use the tree height raster to locate retention trees and areas just before thinning.

2.2.4 Gap cutting in thinning

In Sweden, Norway spruce-dominated stands include one or two pre-commercial and one or several commercial thinning operations, depending on site productivity. Thinning is done primarily to reduce competition and select the best crop trees for valuable wood production during the next phase of rotation (see 2.1). In 2022, 40% of Swedish forests were defined as "thinning forests." In terms of area, thinning is the most common harvest (annually 306,000 hectares) (Nilsson et al., 2022). If well planned, thinning is also a management measure that can increase the structural complexity of young planted forests, mimic natural disturbances, and consequently potentially increase species diversity (Dieler et al., 2017, Klein, 2020). Therefore, it is obviously a great opportunity to couple thinning with conservation management.

Thinning is the first heavy operation involving a harvester. It usually consists of the harvest of c. 30% of the tree volume and is carried out with the help of strip roads. During thinning, strip roads are a practical route used by the harvester to reach the trees within the stand. Once thinning is completed, the stem density reduction within the stand and the strip road results in increased light availability below the canopy and increased availability of soil water and nutrients (Muscolo et al., 2014, Sohn et al., 2016), affecting fauna, flora (Thomas et al., 1999, Widenfalk and Weslien, 2009, Duguid and Ashton, 2013), and even fungal communities (Wu et al., 2019, Tomao et al., 2020) below the canopy. However, thinning can also reduce the forest's structural variety and has a strong influence on species living in young managed forests. Its effect is generally positive or neutral on the diversity and abundance of many taxa (Ares et al., 2010, Verschuyl et al., 2011). Thinning influences species richness by altering the stages of succession and has a similar effect to that created by gap cutting. Adapting the thinning programme to retention is essential to preserve and create conservation value within the stand and to maintain it throughout the rotation. Adaptation can occur through the management of broadleaves (old retained oaks) or through the direct conservation management of certain zones through thinning.

2.2.5 Rotation length

In conventional forestry, after one or several thinnings, it is time to harvest. In practical forestry, one of the basic principles for defining the length of the rotation time is to maximise profitability and harvest the stand when the mean annual increment growth culminates (Curtis, 1997, Brukas and Weber, 2009). In Sweden, rotation length has become shorter (Skogsstyrelsen, 2018), having fallen from 120 years old, on average (all species included), to about 100 years old from 2004 to 2018. This shortening is mostly explained by an earlier harvest due to associated risks with more mature stands.

In the context of climate change, there are now threats associated with older planted Norway spruce stands. Because of their flat root system and large crown, Norway spruce are at risk for storm damage (Valinger and Fridman, 1999, Wallentin and Nilsson, 2014) and are also sensitive to European spruce bark beetle (*Ips typographus*) attacks (Långström et al., 2009). The decision regarding rotation length has shifted (Schlyter et al., 2006) and instead of letting the rotation length be determined by the culmination of increment growth, stands are now more often harvested with the purpose of minimising the risk of losing value due to stand damage (Brukas and Weber, 2009).

At the time of harvest, forest age is one of the most simple but ecologically important key values that may be controlled by forest management (Lindenmayer et al., 2006). Increasing the stand age allows the development of older trees and structures and creates a wider range of age classes, tree sizes and structures, and greater spatial heterogeneity (Curtis, 1997). Prolonged rotation ages promote other habitats by creating specific tree microclimates and allowing features connected to old trees to develop, such as dead branches and coarse bark, promoting the abundance of more common old-growth species (Lindenmayer et al., 2006, Felton et al., 2017).

Prolonged rotation length also provides a longer time for ecological succession, e.g. of fungi and insects in deadwood and of ground vegetation, and time for tree mortality and input of deadwood (Jonsson et al., 2005). Today, forest-associated species outside conservation areas fully rely on the time between clear-cutting, which may not give enough time for late successional plant species to colonise, deadwood volumes to accumulate, or old forest structures to develop (Jonsson et al., 2005, Nordén et al., 2014).

Shortening the rotation length impacts many aspects of biodiversity in forest ecosystems (Roberge et al., 2016, Felton et al., 2017). By shortening the rotation length, crucial key habitat features are lost, as well as late successional species that only thrive in the old forest with a steady microclimate and in the absence of early successional species (Lindenmayer et al., 2006, Felton et al., 2010). The colonisation and establishment of forest-specialist species may thus be impaired. Koskela et al. (2007) showed that biodiversity benefits can be expressed as a sum of the benefits accumulating from the age of the stand becoming harvested and the retention trees, which reach their biological maturity and decay during the next rotation period. Prolonged rotation age and green tree retention can become key means of promoting biodiversity in commercial boreal forests in Scandinavia.

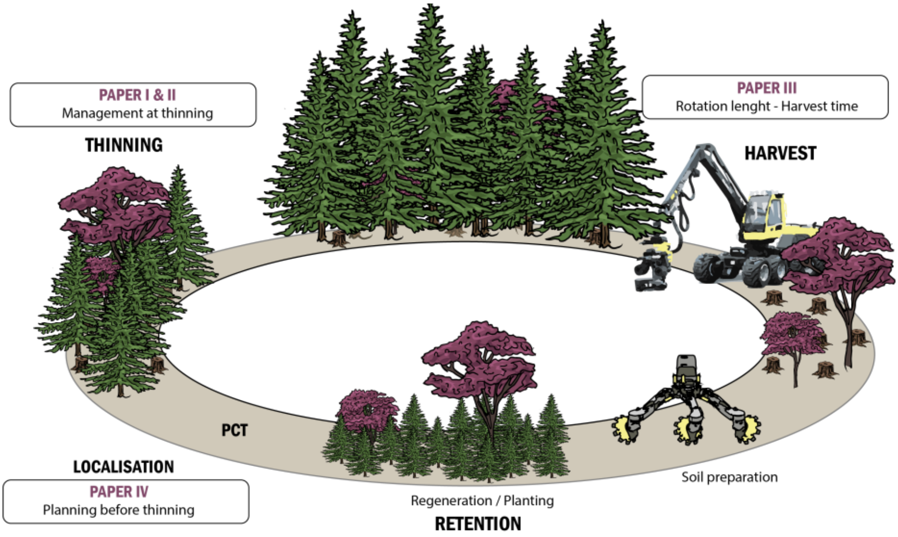

Figure 3. Conceptual framework of this thesis. The study system is a productive forest harvested by clear-cutting. This illustration places each paper in context with a clear-cutting cycle. Papers I and II deal with the retention of oak at regeneration and their management at thinning. Paper IV deals with the planning and localisation phase pre-thinning. Paper III deals with the last phase of the clear-cutting system, the harvest, and how rotation length impacts biodiversity. Pre-commercial thinning (PCT) is not discussed in this thesis but still represented in the illustration.

3. Aim of the thesis

This thesis dealt with different aspects of conservation management for planted forests established after 1993 applying retention forestry (**Figure 3**). The goal was to broaden the knowledge about the management of these new types of stands that are today entering the first thinning phase. In this doctoral thesis, the following main objectives were addressed:

Papers I & II addressed whether the release of old retained oaks during the thinning phase in a planted Norway spruce stand is an efficient conservation management method to preserve important biodiversity values while accommodating production goals. The effect of the release was investigated by evaluating the changes that occurred within a 10-year timeframe on vascular plants and saproxylic beetles, as well as oak vitality and the potential effect of Norway spruce removal on production objectives.

Paper III studied the conservation value of conventionally managed stands that had undergone a conventional thinning programme and described communities of birds, vascular plants, bryophytes, and lichens. The study contrasted species communities in younger (55 ± 5 years old) and older (80 ± 5 years old) Norway spruce and Scots pine stands.

Paper IV aimed to evaluate how efficiently green tree retention from the previous generation can be found using a spatial model based on tree height raster. We studied stands in time of the first commercial thinning, which was among the first clear-cuts made with retention forestry management initiated in 1993.

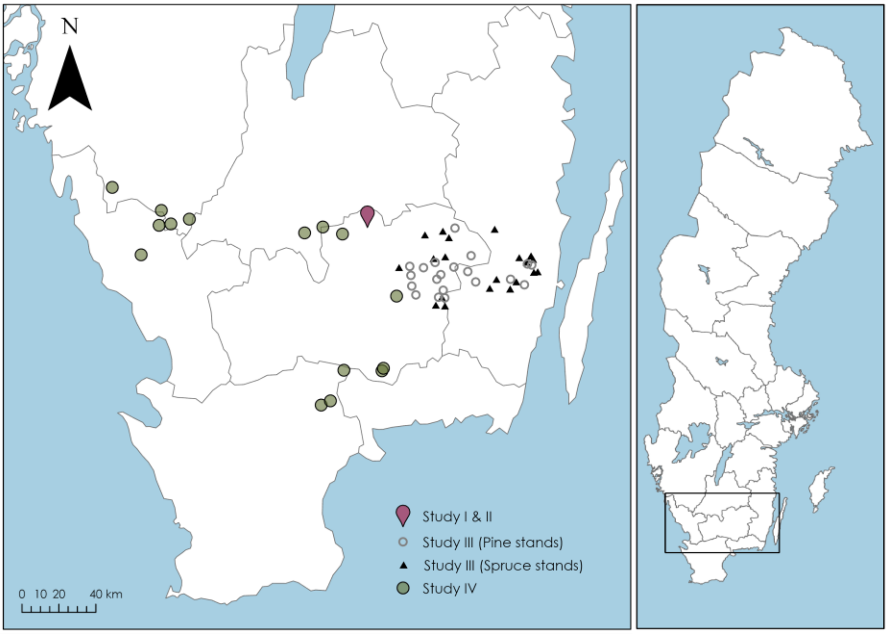

Figure 4. On the right side is the delimitation of the thesis study area in southern Sweden (Götaland). On the left side is the location of the stands used for each paper. For Papers I and II (purple). Stands used for Paper III, Scots pine stands (black triangles) and Norway spruce stands (white circles). Stand used for Paper IV (green circles).

4. Methods

4.1 Study area

The data collected for this thesis were obtained from stands located in southern Sweden. Papers I and II used data collected from an experimental stand in Asa (county of Kronoberg), 40 km north of Växjö. Paper III used 40 stands located in Småland, within the two adjacent counties of Kalmar and Kronoberg. Finally, for Paper IV, the 15 stands were located in Skåne (3), Kronobergs (4), Hallands (2), Västra Götaland (4), and Jönköpings (2) counties (**Figure 4**). This part of Sweden is characterised by a mixture of agricultural lands, meadows, mires, and forest landscapes.

4.2 Oak retention and release (Papers I–II)

Both studies focused on the 10 years effects of the release of old oaks retained in a commercially planted Norway spruce forest. Paper I focused on the effects of the release on vascular plants, oak vitality, and Norway spruce production surrounding the oak, while Paper II focused on saproxylic beetles.

Both papers were follow-up studies of Koch Widerberg (2013) in Asa and used the exact same location, oaks, and experimental design. The stand used for the experiment is a 5.5-hectare Norway stand planted in 1975. The stand was thinned in 2008, and during thinning, three different release treatments were applied to 33 selected oaks. Oaks were evenly selected over the stand and clustered into 11 blocks containing 3 focal oaks, each undergoing one treatment (**Figure 5**). The three treatments were defined as High release

(HR), where all Norway spruces were removed under the crown of the oaks and extended in a two-metre zone; Medium release (MR), where all Norway spruces were removed directly under the crown of the oaks only; and No release (NR), where no Norway spruces were removed, except for occasional trees harvested in conventional thinning.

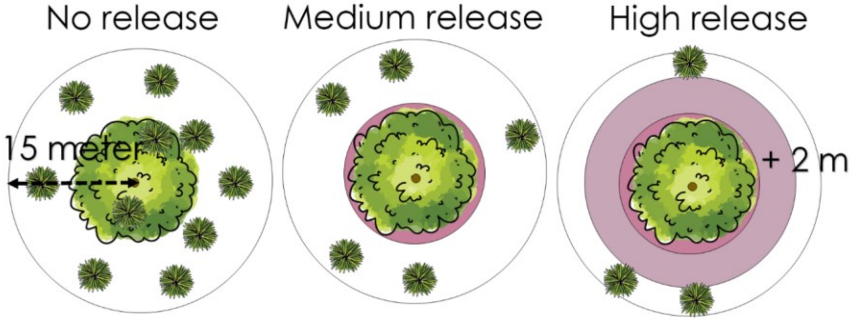

Figure 5. Illustration of the three different release treatments. On the left is the control, where no Norway spruces were removed. In the middle is the medium release, where all Norway spruces below the oak crown were removed. On the right is high release, where all Norway spruces were removed under the crown of the oaks and extended in a two-metre zone.

Widerberg et al. (2012) inventoried saproxylic beetles in the different treatment and found that three years post-treatment, the diversity of oak-associated saproxylic beetles was positively affected by the release. We repeated the initial measurements 10 years later to evaluate the potential long-lasting effects of the release. To do so, various variables were investigated, such as the diversity and abundance of vascular plants (Paper I) and saproxylic beetles (Paper II), as well as the effect of the release on oak vitality (deadwood, diameter at breast height (DBH), and crown development). Paper I also determined how the retention of oaks affected the production of Norway spruce in terms of diameter and basal area increment (Paper I).

In 2018 and 2019, the same 33 oaks were investigated, and the same circular sample plots (15 m radius from the focal oak) were used around each focal oak to collect data on all trees located within the sample plots. Data such as tree species, DBH, height, and distance from the oak were collected. Additionally, each focal oak crown length was measured from the trunk to the end of the crown in 4 cardinal directions, as Koch Widerberg (2013) did in 2010. Finally, hemispherical pictures of each focal oak were taken to quantify canopy openness (**Figure 6**).

In August 2018, a vascular plant survey was carried out in the form of qualitative and quantitate inventories with transects under the oak crown in 4 cardinal directions. Vascular plant species richness and abundance for each focal oak were calculated (**Figure 7**) and vascular plants were categorised according to Heinken et al. (2019) and to their affinity with the habitat (forest specialist, generalist, or open land) (Paper I).

In both 2018 and 2019, from May to September, window traps located 5 m high on the south side of each focal oak trunk were used to sample saproxylic beetles (**Figure 8**). The traps were emptied every 3 weeks, and all saproxylic beetles (Coleoptera) were identified to the species level by taxonomist Bengt Jan-Olof Andersson (Nybro, Sweden), as well as Hans Erik Wanntorp (Brottby, Sweden). All saproxylic beetle species found were classified according to their affinity to oak and Norway spruce:

- **Group I** saproxylic species associated with oak AND Norway spruce.
- **Group II** saproxylic species associated with oak but NOT with Norway spruce.
- **Group III** saproxylic species not associated with oak.
- **Group I + II** saproxylic species associated with oak.

Species richness, abundance, and composition were computed for each focal oak and beetle group. Temperature and light were recorded at each of the two extreme treatments (high release and no release) with a total of 22 oaks using loggers placed on the top right corner of the window traps (**Figure 8**).

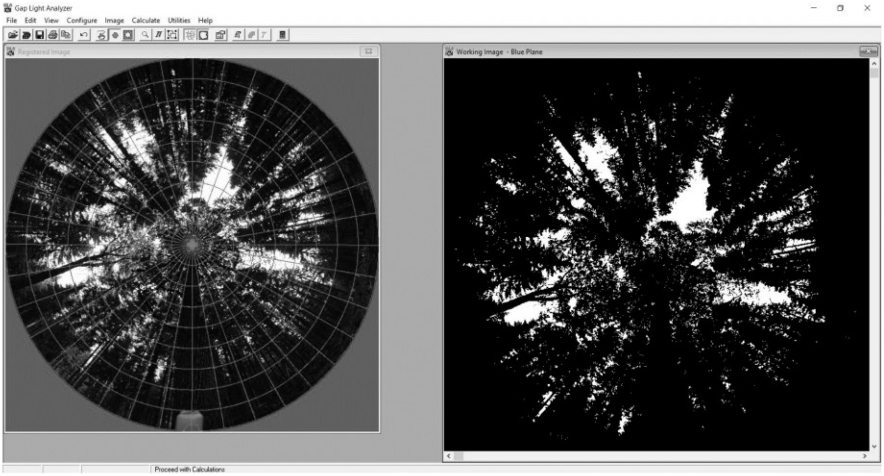

Figure 6. Print screen from the software Gap light analyser (Frazer et al., 1999). Hemispherical pictures were analysed to assess the amount of canopy openness around each oak. The software transforms the pixels from the picture into a black and white representation to obtain a percentage of canopy openness (white pixels, visible sky). Canopy openness was defined as the amount of visible sky between the oak and Norway spruce canopies.

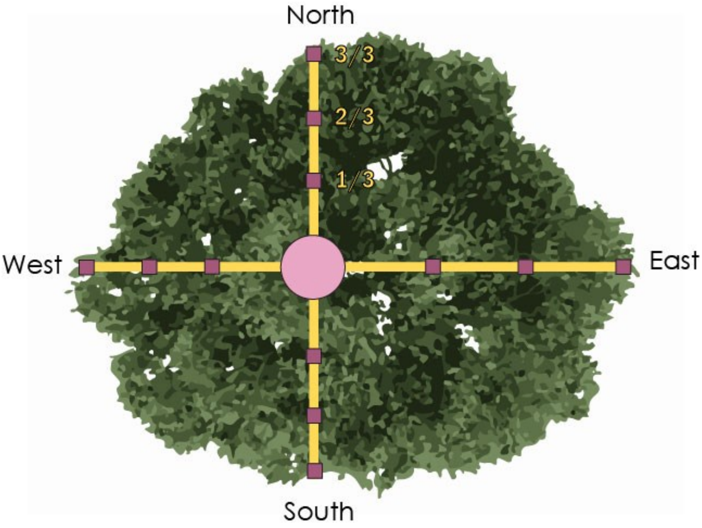

Figure 7. Vascular plant plot inventory design. A transect was defined for each cardinal direction (yellow) for each focal oak crown. Three 1 × 1 m square plots (purple) were placed at each third of the crown length in each cardinal direction of the focal oak following the transect. The crown length was defined as the distance between the trunk of the focal oak and the end of the crown. In total, 12 plots were inventoried per focal oak.

Figure 8. Picture of a window trap used to catch saproxylic beetles during the experiment. The trap was pulled up to 5 metres above the ground via a rope system. The wood pole holding the Plexiglas® was inserted into the white container via holes, which also served as drainage holes in case of heavy rain. At the top-right corner of the trap, a light and temperature logger can be seen in the picture (the round green object).

4.3 Rotation length (Paper III)

Twenty Scots pine and twenty Norway spruce-dominated forest stands were used in this study. The dominant tree species, either Scots pine or Norway spruce, constituted at least 80% of the standing volume, and the stands were randomly selected but only from stands in the database that matched intermediate fertility site properties that could be used for both tree species (Petersson, 2019). This restriction was made to avoid Norway spruce sites with high fertility or Scots pine sites with low fertility. Two different stand age categories were chosen. The 80-year-old (±5) stands (older stands) represent an approximation of the average time of stands being harvested in southern Sweden today, whereas the 55-year-old (±5) stands (younger stands) matched the lower baseline for when a stand was allowed to be harvested according to Swedish legislation. This resulted in 10 stands of each category, i.e. older (Spruce 80) and younger Norway spruce (Spruce 55) and older (Pine 80) and younger Scots pine (Pine 55).

Vascular plants and bryophytes were surveyed within ten 100 m^2 circular sample plots located in the centre of each stand (**Figure 9**). The first four plots were placed in the centre of the stand and decided using a Geographic Information System (GIS) beforehand; the remaining 6 were added in a random direction and placed > 25 metres from the stand edge, and never closer than 25 metres to each other. The presence of all vascular plants and bryophyte species were inventoried using 2 × 2 m quadrats, placed in the centre of each sample plot. Epiphytic lichens were inventoried on the living crop tree closest to the centre of each circular sample plot. The presence/absence of lichen species was surveyed up to 2 m on the tree trunk and on branches up to the same height. Finally, birds were surveyed four times during spring 2017 from late March/early April to late May. Four 40 m radius circular plots were placed in the central parts of the stands. Each centre of the plot was used for point counting and surveyed for five minutes.

The species found during the inventory were categorised according to their habitat affinity using the classification by Bernhardt-Römermann et al. (2018), Schmidt et al. (2011) and Heinken et al. (2019). “Forest” species refer to species that prefer forests, glades, and forest edges. “Open land” species refer to species that prefer open land but may occasionally occur in the forest. Finally, “generalist” species refers to species that occur across closed forest and open land. Generalists are defined in terms of having no preference for shaded and open environments. To classify birds into forest, generalist, and open land species, we used information from the Birds of the World (https://birdsoftheworld.org/bow/home) preferences for open and forest land.

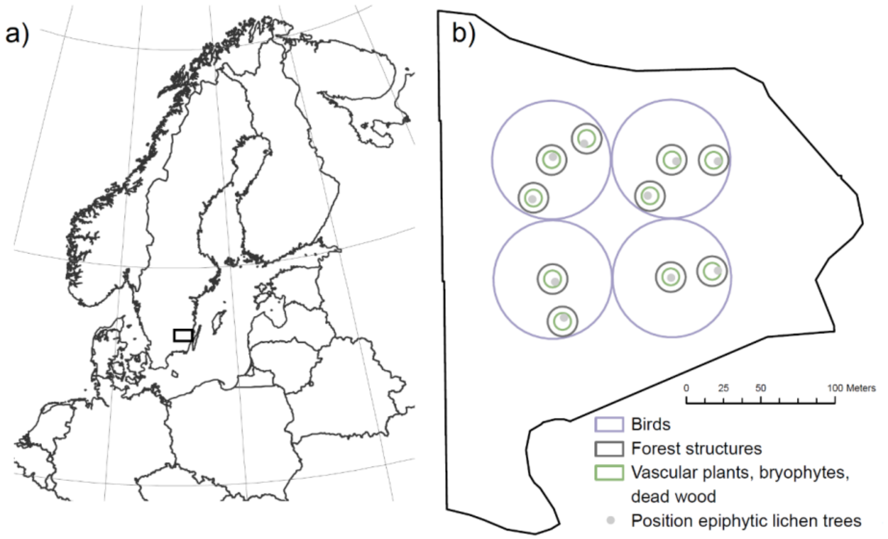

Figure 9. a) Location of stands in south-eastern Sweden used for study III. b) Survey data from 40 Norway spruce- and Scots pine-dominated stands used in this study. In the stands, four bird plots of 40 m radius (purple) were placed in the central parts of the stand. In the very centre of the bird plots, understorey vegetation plots of 100 m^2 (green) were placed. Another six understorey vegetation plots were placed in random directions from the four central plots, resulting in 10 understorey vegetation plots. In each of the 10 plots, the crop tree (Norway spruce of Scots pine) closest to the plot centre was selected for the epiphytic lichen survey (light-grey markers). Forest structures were measured in 10 plots of a 10-m radius (dark grey).

4.4 Mapping of retention (Paper IV)

We investigated the possibility of locating retention trees or areas within planted Norway spruce stands before thinning using the first national tree height raster produced from the first Swedish laser scanning (2009–2016) with a resolution of 1 m × 1 m. The study was inspired by Westerfelt et al. (2017) and was integrally translated into R statistics software (R Core Team, 2022). Fifteen stands from Lindbladh et al. (2022) were selected to investigate our method. All stands were inventoried from the ground for retention trees in 2018. All retention trees found during the field inventory were characterised, measured (DBH and height), and then GPS marked. The stands were visited in 2020 to collect data at the sample plot level (6 sample plots of 10 m radius per stand) (**Figure 10**), and the Norway spruce mean height (from the sample plots in 2020) was calculated for each stand.

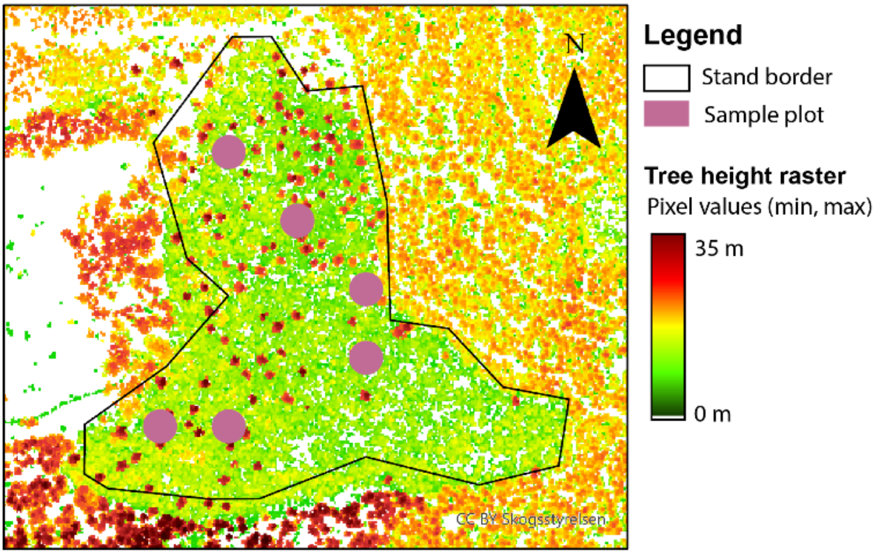

Figure 10. Stand border example with six sample plots and the tree height raster layer. Each pixel is a 1 × 1 m representation of a height. Pixels with a value of 0 are represented by transparency.

The height of the retention tree recorded in the field (2018) and the height of the Norway spruce trees from the sample plots from (2020) were compared as a foundation for our method and tested to see if the retention trees within the stands were higher than the planted Norway spruce before the first thinning. Then, the method was based on the assumption that the overall height distribution of the planted Norway spruce stand should fit a normal distribution over time. Hence, all pixel values that were very unlikely under the normal distribution of that population of planted trees were assumed to be retention trees. From that statement, all trees above a certain height value were potentially considered retention trees from the previous generation (**Figure 11**). The height value/threshold that separates planted trees from retention trees can be determined subjectively by visual inspection of the pixel height distribution histogram, but we tested different thresholds based on the mean and standard deviation of the Norway spruce height to objectively find single retention trees or retained areas within a stand before the first thinning. Mean height, standard deviation, and the interquartile range method (IQR) or the mean from an unconstrained clustering method (UCM) were used as individual height thresholds to model and delimitate the potential retention tree or retained areas for each stand (**Figure 11**). For each stand, we tested each threshold and calculated the probability of identifying retention trees, as well as the proportion of overestimation, and evaluated which threshold was best. The following thresholds were used:

- **Threshold 1**: Mean + 1.2*SD
- **Threshold 2**: The interquartile range (IQR) measures the spread of the middle half of the pixel data. This is the range for the middle 50% of all pixels within a stand. The IQR was used to assess the variability where most of the values lie. The interquartile range was the region between the 75th and 25th percentiles (75 – 25 = 50% of the data). The upper limit, where 25% of the data lies, was used as threshold 2.
- **Threshold 3**: The UCM method allows for comparisons of the quality of discrimination among clusters based on Bayesian information criteria (BIC). It is a model-based clustering, classification, and density estimation based on finite Gaussian mixture modelling. To extract the average height of the crop at the time of laser scanning, the pixel data from each stand were extracted, and an unsupervised clustering method (UCM) was used to distinguish Gaussian distributions and their parameters.

- **Threshold 4**: Intersection of the two Gaussian distributions found by the UCM.

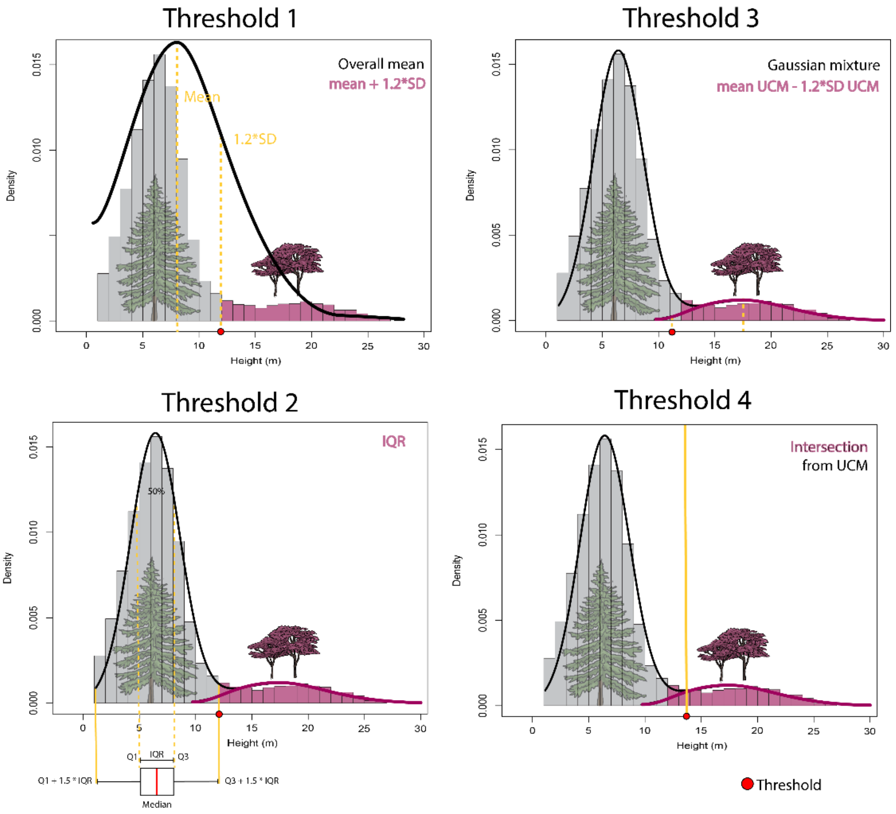

Figure 11. Illustration of the thresholds used to detect retention trees within planted Norway spruce stands. Threshold 1 is based on the overall mean and standard deviation of the pixel height distribution (including both Norway spruce and retention trees). Threshold 2 was based on the IQR method, where the upper limit was used as the separation of retention trees and Norway spruce. Threshold 3 was based on the separation of both Gaussian distributions through the UCM method; parameters for both distributions were extracted, and the threshold was based on the mean and standard deviation of the potential retention tree distribution from the UCM. Finally, threshold 4 was the intersection between the two distributions obtained from the UCM method.

5. Results and discussion

5.1 Oak retention and release (Papers I & II)

5.1.1 Competition, tree growth, and retention tree

Paper I showed that after 10 years, the release had a positive effect on the vitality of the focal oaks, which is expressed by a lower proportion of deadwood and an increased crown size for the high-release oaks (**Figure 12**). However, the gap created by the treatment was closed, as canopy openness did not differ between treatments at the time of my studies, suggesting that the oak may have colonised the surrounding canopy opening through crown growth. In contrast, control oaks strongly suffered from aboveground competition by the Norway spruce, leading to an increasing number of dead branches in the crown and reduced canopy expansion, which is in line with other studies (Runkle, 1981, McCarthy, 2001). Oaks (*Quercus* spp.) are known to be a shade-intolerant species, with high crown plasticity but usually with lower competitive ability when growing with other species (Le Due and Havill, 1998). The aboveground competition in the control potentially negatively affected the photosynthetic ability and overall tree vitality. This experiment presents strong evidence that crowding causes crown irregularities and an unclear pattern of growth among directions (**Figure 12**). Our findings strongly indicated that with increasing crown encroachment by neighbouring Norway spruce, portions of the crown slowly die, and eventually the entire tree will die if not released, which is in line with earlier studies (Harrington and Warren, 2006, Longuetaud et al., 2013).

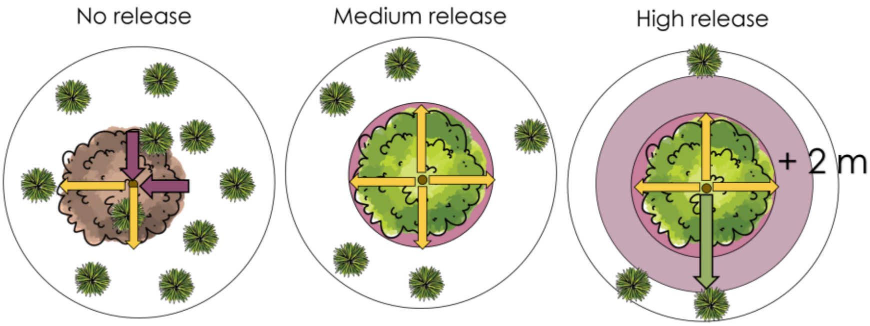

Figure 12. Effect of the treatment on oak vitality. The crown of the control is smaller and represented in brown, illustrating a higher amount of deadwood, and the arrow shows the growth (green) or shrink (purple) of the crown length in the four-cardinal directions. The yellow arrows indicate no change.

Despite being a shade-tolerant species, Norway spruce was overruled by the shade-intolerant oak, probably due to its size, both at the time of forest regeneration 45 years ago, as well within the time frame of these studies. Apart from aboveground competition, oaks may initiate belowground competition because of their large and well-established root system (Mauer et al., 2017). Most oak tree roots lie only half a metre under the soil, and may spread to occupy a space four to seven times the width of the tree's crown, generally forming a circle with a diameter two or more times the height of the tree (Stone and Kalisz, 1991). The presence of mainly small and suppressed Norway spruce seedlings within, and dominant Norway spruce trees almost exclusively outside a five-metre radius from oaks suggests that belowground competition occurred (**Figure 13**).

Tree growth and competition play central roles in forest dynamics. Competition is an important factor to consider when managing retention trees within a stand. Trees compete for space and the availability of sunlight, nutrients, and water (Sands and Mulligan, 1990, Barbier et al., 2008). Studies about inter- or intra-species competition between trees have been extensively studied (Palik et al., 2003, Barbier et al., 2008, Pretzsch et al., 2017). Papers I and II provide new insights that oaks left as retention trees have certain competitive advantages when released at the time of the first thinning. If not released, its vitality will decrease (**Figure 12**). Active release at the time of thinning is an effective management measure that will have a positive effect over time and may allow old retained oaks to survive and stay vital at least throughout the current Norway spruce rotation.

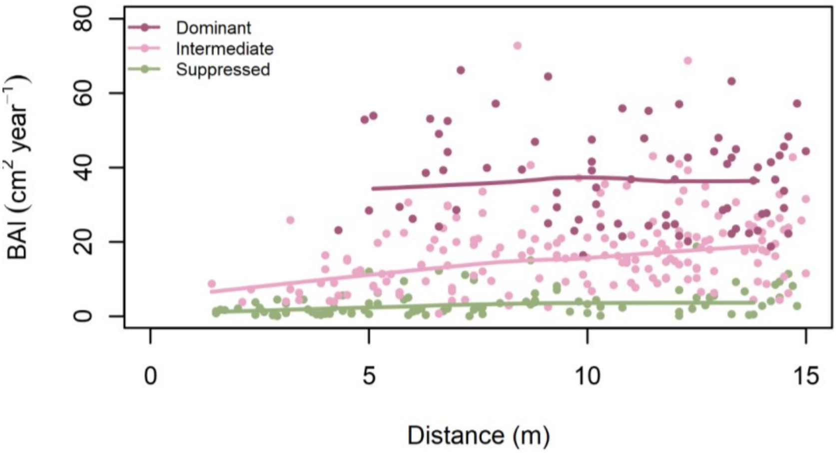

Figure 13. Basal area increment (BAI) among dominant, intermediate, and suppressed Norway spruce trees within a 15-metre radius around the control oaks. Each circle represents a Norway spruce tree, and the classification is based on the basal area. The smoothed lines are the predicted values from the model for the groups (Lariviere et al., 2021).

5.1.2 Retention, biodiversity, and ecological successions

The release of the oaks showed positive effects on the species diversity of saproxylic beetle species, especially for oak-associated beetles, while vascular plant species richness and abundance generally increased under the released oaks. Ten years post release, a total of 62 vascular plant species and 157 saproxylic beetle species were found in the 33 oaks investigated.

Saproxylic beetles

Higher beetle species richness, higher abundance (for certain groups), and different species composition of saproxylic beetles were found in the released oaks compared to the control (**Figure 14**). The higher species richness and abundance of the oak specialist saproxylic beetle group (Group I + II, saproxylic species associated with oak) was especially interesting. The positive response was in line with other studies showing that saproxylic species, such as beetles, generally react positively to gap creation (Widerberg et al., 2012, Jokela et al., 2019) and thinning (Gran and Götmark, 2019). A possible explanation could be that, still 10 years after treatment, the amount of light reaching the oak trunks and the temperatures were greater for released than for the non-released oaks despite the canopy having been closed. The colonisation of the canopy by the oak crown differs from the dense Norway spruce, as it allows greater insolation and temperature through its multi-layered crown (Andersson and Östlund, 2004). The higher temperature and amount of light reaching the oak can affect the microclimate in the oak crown, bark, trunk, and other structures that are important for saproxylic beetles. The amount of deadwood has been shown to be important for the diversity of saproxylic beetles (Müller et al., 2015b). However, in Papers I and II the importance of sun exposure seemed to be even more important, as the amount of deadwood in the oak crowns was higher in the non-released treatments while species diversity was lowest. As oaks are shade-intolerant trees, their specific associated saproxylic species are likely to be adapted to similar open, light, and warm conditions, as supported by our findings of higher numbers of oak specialists in the release treatments.

Vascular plants

The cover and species richness of vascular plants were significantly higher in the release treatments compared to the control (**Figure 15** a & b). These results are in line with other studies showing that plant species diversity often responds positively to forest thinning (Widenfalk and Weslien, 2009, Ares et al., 2010). Gap cutting has similarities with thinning, and its effect can initiate different ecological processes that affect the habitat and the occurrence of species through gap dynamics and ecological succession. The creation of a gap in the canopy can be seen as a simulation of natural disturbances on a local spatial scale. This gap impacts the understorey through the alteration of important resources for plant growth (Muscolo et al., 2014). Our studies confirm that these effects remained after 10 years because of the more open conditions created by the release. Light availability is known to be an important driver for plant growth, facilitating vegetative reproduction, as well as species diversity (Dai, 1996, McEwan et al., 2014, Muscolo et al., 2014). Shade-tolerant species can survive when there is very little light but also grow better with increasing light (Gaudio et al., 2008). Therefore, the release can be positive for both forest specialist and generalist species and consequently sustain higher abundance and species richness. This was confirmed by our findings, as high released oaks in general had a higher number of species, as well as a higher vegetation cover for all three groups of generalist woody, true forest herbaceous, and general herbaceous species compared to the controls. Many of the vascular plant's species found in the release were habitat generalists, whereas none of those disturbance-tolerant species were found in the control. The control was characterised by a low cover of true forest species and/or species with low light requirements.

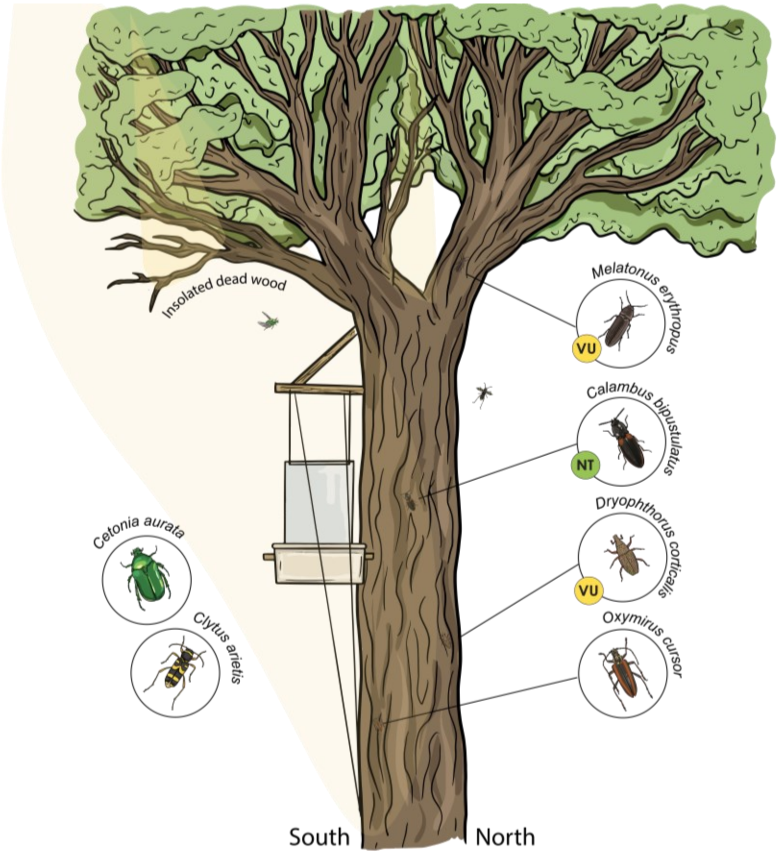

Figure 14. Representation of a window trap on a released oak. The trap is located 5 meters high on the south side of the oak. High released oaks had higher temperature and insolation. Caught Near threatened (NT) and Vulnerable (VU) species according to IUCN are illustrated. *Cetonia aurata* and *Clytus arietis* were species associated with released oaks.

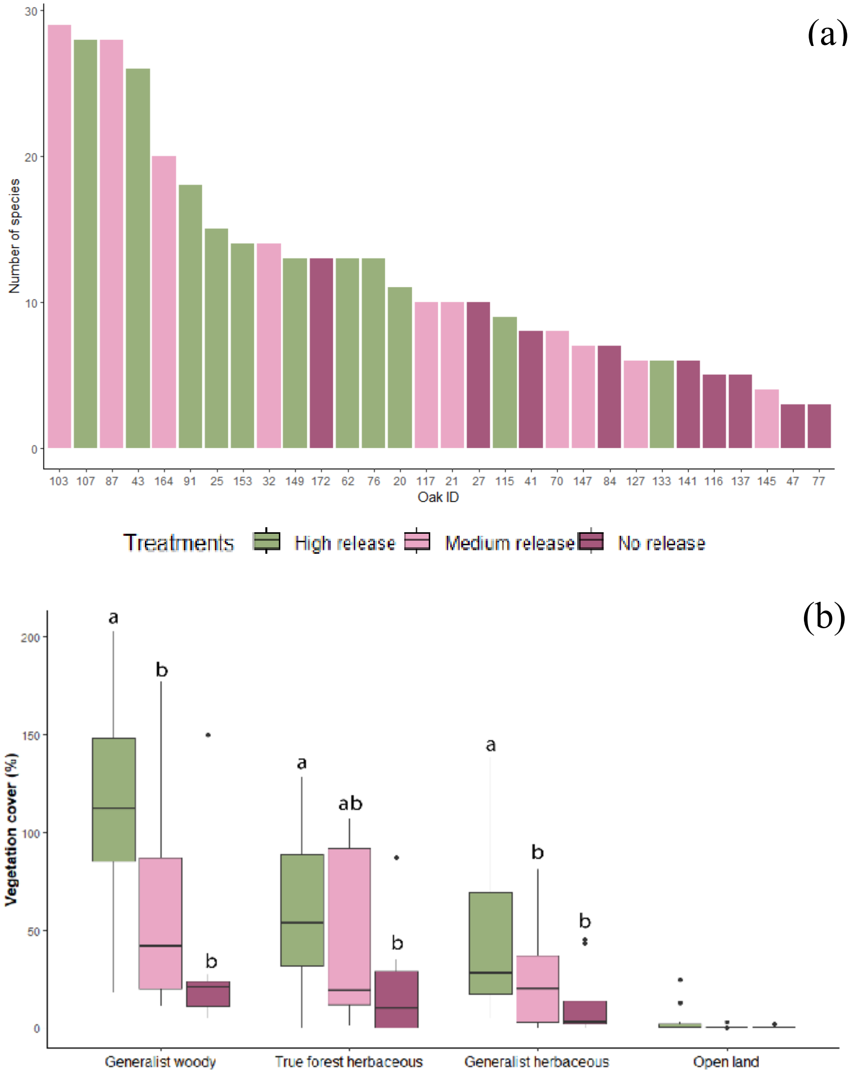

Figure 15. Vascular plant species richness (a) and abundance (b). Species richness is expressed by the number of species found at each focal oak (Oak ID) belonging to the different treatments (high release, medium release, no release). Species richness is sorted from high (left) to low (right). The control (NR) is mostly represented on the right of the graph and characterised by a low number of different species. Abundance is expressed by the mean percentage cover for each of the different habitat's categories used in Lariviere et al. (2020) for each treatment (HR, MR, NR). The means sharing a letter do not significantly differ from each other.

Overall effect

Knowing that coniferous forests generally provide less diversified vascular plant understories than broadleaved and mixed forests (Barbier et al., 2008, Hedwall et al., 2019), this study highlights the importance of considering understorey dynamics and competition in forest management practices. Papers I and II clearly show the positive effects of high release around previously retained oaks (**Figure 16**). The effects remained even 10 years after treatment; however, this is not a guarantee for the long term, as recolonisation of a strong competitive pioneer generalist species may occur. Through succession, the regeneration of woody species, including Norway spruce, can be favoured by release cutting, and the cover of the herbaceous species may gradually decrease again until a new release cut is done. As the gap closes in the future, species richness may decrease. But it has also been documented that it can take more than a decade for management legacies to disappear, and that they can sometimes even be permanent (Dupouey et al., 2002, Cuddington, 2011).

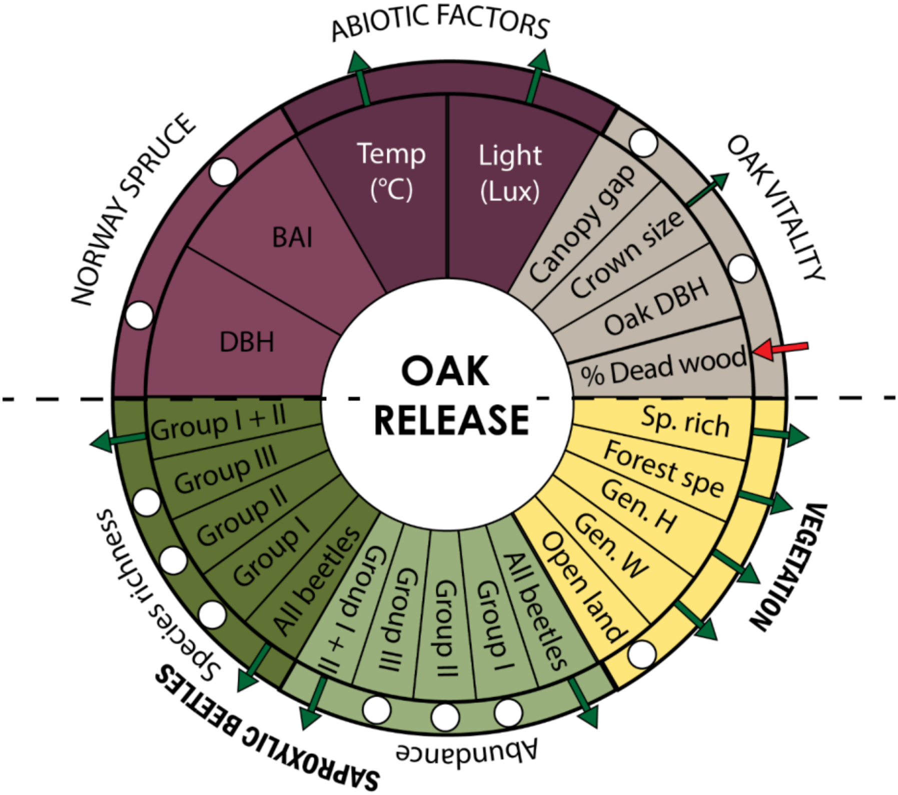

Figure 16. Overall effect of the release of the oak on the different variables studied and described in Papers I & II. The green arrows represent a positive effect, the red arrows represent a negative effect, and the white circles represent no effect.

Explanatory variables: The Norway spruce basal area increment (BAI), diameter at breast height (DBH), temperature (Temp), and insolation (light). The gap size within the 10-metre radius (canopy gap). The size of the focal oak crown in m2 (crown size). The diameter at breast height of the focal oaks (Oak DBH) and the proportion of deadwood in the focal oak crown (% deadwood).

Response variables: "Sp. rich" refers to the species richness of all vascular plants found under oak crowns in a 15-metre radius. "Forest spe" refers to the abundance of vascular plants belonging to the forest specialists, "Gen. H" generalist herbaceous, "Gen. W" generalists woody, and open land groups. The saproxylic groups refer to Group I saproxylic species associated with oak and Norway spruce, Group II saproxylic species associated with oak but not with Norway spruce, Group III saproxylic species not associated with oak, and Groups I + II saproxylic species associated with oak.

5.2 Rotation length (Paper III)

Overall, the species found during the inventory were dominated by species with generalist requirements for forest and open land environments (**Figure 17**), and these species are known to tolerate multiple thinning events and unstable environmental conditions. The older Norway spruce stands had the largest number of unique species (**Table 1**). The reason for this may be that the older Norway spruce stands had more variations in microhabitat structures due to the significantly larger supply of deadwood compared to Scots pine stands and younger stands of Norway spruce (**Table 1**).

The overall species diversity (all taxa) was slightly higher between older and younger Norway spruce stands, but the difference was only significant for bryophyte and vascular plants, where older stands had a higher Shannon index. Overall, the community differed greatly between the younger and older stands of Norway spruce, except for birds (**Table 1**). For Scots pine stands, the basal area increased in older stands but not the amount of deadwood. Younger Scots pine stands had higher overall species richness (all taxa) compared to older Scot pine stands. Younger Scots pine stands had a specifically higher species diversity of bryophytes and vascular plants compared to older Scot pine. Finally, both lichen and bryophytes had significantly different species communities between older and younger Scots pine stands (**Table 1**).

Table 1. Environmental variables, overall Shannon diversity and number of unique species (upper part of table), and Shannon diversity and species composition (community) by taxon (lower part) in the different stand types.

NS55 = Norway spruce, 55 years old, NS80 = Norway spruce, 80 years old, SP55 = Scots pine, 55 years old, SP80 = Scots pine, 80 years old. A positive effect is represented by a "+", a negative effect by "-", and no effect by a "0". For species communities, similar communities share the same letter. The "." represents the near significance to a 0.05 threshold. The unique species are expressed in terms of the number of species unique to the stand category.

Variables	**NS55**	**NS80**	**SP55**	**SP80**
Deadwood	-	+	0	0
Basal area	0	0	-	+
Stem density	0	0	0	0
Canopy cover	0	0	0	0
All taxa				
Shannon	-	+.	+	-
Unique species	27	70	41	30
Bryophytes				
Community	a	b	a	b
Shannon	-	+	+	-
Lichens				
Community	a	b	a	b
Shannon	0	0	0	0
Vascular plants				
Community	a	b	a	b
Shannon	-	+	+	-
Birds				
Community	a	a	a	a
Shannon	0	0	0	0

Bryophytes

The community composition of bryophytes was significantly different when comparing younger and older stands of Norway spruce (**Table 1**). This may be due to the longer continuity (time since clear-cut) of forest cover in older Norway spruce stands. Another reason for the shift in bryophyte communities in the older stands could be the larger amount of deadwood in older Norway spruce stands (22.4 m·$^{\mathrm{ha}^{-1}}$, compared to the other stand types (4.1–6.2 m·$^{\mathrm{ha}^{-1}}$). Many species of bryophytes, especially small low-competitive species and hepatic species, are specialised for growing on deadwood (Dittrich et al., 2014, Müller et al., 2015a). In Scots pine stands, there was also a significant shift in bryophyte communities when comparing younger and older stands. However, in contrast to Norway spruce stands, the species richness of bryophytes was lower in older Scots pine stands than in younger stands. While deadwood did not differ between stand ages, this shift in both species community and the lower species richness in older Scots pine stands may be caused by the dominance of a few competitive understorey species, such as weft-forming mosses *Pleurozium schreberi* and *Hylocomium splendens*, which may form an effective barrier preventing less competitive species of bryophytes from establishing and reducing species diversity (Tonteri et al., 1990, Petersson, 2019).

Lichens

The species richness of lichens was similar in all stand types (**Figure 18**). However, community composition significantly differed between younger and older stands for both Norway spruce and Scots pine. These results suggest that lichen community differences between stands of varying ages may result more from community shifts than an accumulation of species in older stands. The species present on older trees usually differs from those on younger trees (Gustafsson and Eriksson, 1995, Ranius et al., 2008, McDonald et al., 2017), with the main reason being that lichens have special preferences for growing substrates, such as bark structures, or are limited by pH, both of which are often more favourable on older trees (Wolseley and James, 2000, Fritz et al., 2009). In addition, different species of lichens may respond differently to the interior forest climate (Belinchón et al., 2007), and variations in stand structures can have an impact on species composition (Klein et al., 2020). Older Scots pine stands usually have particularly open conditions due to their high canopy and the lack of small trees and shrubs, which are often removed during thinning. In our study, stem density was particularly low in the older Scots pine stands (611 stem ha^{-1}), which is in accordance with the management templates for thinning. The open conditions found in our study may have been beneficial for the development of diverse lichen flora and explained the highest species richness of epiphytic lichens found in the 80-year Scots pine stands.

Vascular plants

In Norway spruce stands, vascular plant diversity increased in older stands, and community composition was significantly different between younger and older stands (**Figure 18**). The differences in understorey communities between older and younger Norway spruce stands may be due to the longer forest cover continuity (time since the last clear-cut), promoting a more stable environment for forest specialists. Neither diversity nor community composition differed between younger and older Scots pine stands. In Scots pine stands, there was a significant difference in species richness when comparing younger and older Scots pine stands. As explained for bryophytes, the older stands may be characterised by the dominance of a few competitive understorey species, such as the dwarf shrub *Vaccinium myrtillus* and weft-forming bryophyte species. These species may form an effective barrier preventing less competitive species of bryophytes and vascular plants from establishing and reducing species diversity (Tonteri et al., 1990, Petersson, 2019). In addition to preventing the establishment of new plant species, the dominating species in the ground vegetation could also have outcompeted other species. Over time, communities will be dominated by a few competitively superior species, in our case, weft-forming mosses and dwarf shrubs, driving pioneer species to extinction. Younger Scots pine stands are closer to recent disturbances, and this process is also illustrated by the intermediate disturbance hypothesis, which states that the highest species richness (and diversity) will occur at moderate levels of disturbance (Cordonnier et al., 2006).

Birds

Bird species richness was highest in the 80-year-old Norway spruce-dominated stands. However, no significant difference in species communities or species richness was found for birds between the stand ages (**Figure 18**). Additionally, birds were the only taxonomic group in which generalist species were not dominant. Instead, forest species were the most common type of bird species recorded. This difference, compared to the other species groups, might be because birds are mobile organisms. Hence, birds can select suitable habitats and move between environments after habitat changes. Additionally, the presence of vertical structures is preferred by many birds spending time in forests (Müller and Bütler, 2010, Klein et al., 2020), and in our case, the lack of structures below the canopy may have caused the lower bird diversity in Scots pine stands, and especially in the older Scots pine stands.

Insects

Even though insects were not included as a taxon in the study, interesting results were found that could indicate how saproxylic insects might respond to a shortening of rotation length. A rich supply of decomposed woody debris is known to be essential for hosting abundant saproxylic fauna (Jonsell et al., 1998, Bouget et al., 2013, Seibold et al., 2016), and saproxylic beetles are an important resource for insectivorous birds, such as woodpeckers (Lindenmayer et al., 2006, Summers, 2010). In this study, the deadwood supply was low in all types of stands but considerably higher in older Norway spruce stands. However, the available deadwood mostly consisted of recently dead standing trees or wind throws. The very sparse presence of broadleaves in all stand types, in combination with a general sparse supply of deadwood suitable for saproxylic insects, is not optimal for supporting saproxylic insects. However, *Vaccinium* spp., the dominant species in older Scots pine stands, is considered a keystone species, and a valuable resource for insects (especially *Lepidoptera* spp., *Bombus* spp.) (Ritchie, 1956, Olsen et al., 2022), although not part of the scope of this study. Potentially, we may have missed a rich and diverse part of Scots pine forest-associated biodiversity.

Overall

This study shows that stand age is an important factor in the species diversity and composition of vascular plants, bryophytes, and lichens. However, it also shows that the investigated species can have contradictory responses to both age and tree species. While increasing age is likely to have positive effects on species of bryophytes and vascular plants in Norway spruce stands, this cannot be said for the Scots pine stands in this study. Where species in Norway spruce forests seemed to accumulate with age, driven by the preference for stable microclimates, species richness in Scots pine stands seemed to be affected by the competition of some dominating understorey vegetation species. Importantly, the scope of our study was to compare the diversity of the different stands within the rotation length of the production stands. It could be discussed that Scots pine stands would develop deadwood and old structural qualities if the stands were left for free development. In general, species diversity was highest in the older Norway spruce stands, except for lichens, where the Scots pine stands had higher diversity, especially older Scots pine stands. Birds did not show a clear response on either stand age or tree species. In contrast to lichens, bryophytes, and vascular plants, they do not have to persist in disadvantageous changes but can often fly to a new area to find a suitable habitat.

Possible impact on the landscape level

At the landscape level (pooling all stands and taxa together), generalist species were the most common category of species, followed by forest species and open land species. Since our stands are a selection of monocultures resulting from a conventional forestry system without retention, it is a representation of today's stands awaiting harvest. On a landscape level, the length of forest rotations determines the variation of stand age distributions, and the general shortening of rotation length has major socioecological implications. Roberge et al. (2016) stated that if rotation lengths were shortened, at some point the proportion of younger stands would increase, causing repercussions on the availability of resources and habitats due to more frequent clear-cutting events, and a larger proportion of forest belonging to the clear-cut and younger forest phase. Alternatively, longer rotations imply smaller proportions of the landscape in the clear-cut and young forest phases, as well as the presence of post-mature forest stands in the landscape. One scenario that has been proposed in several studies is a landscape with a mosaic of rotation length providing a variety of different aged stands, which means a wider range of age classes, tree sizes, and structures (Curtis, 1997, Didion et al., 2007, Roberge et al., 2018, Angelstam et al., 2020), with a shortening of rotation in part of the landscape while extending them elsewhere to achieve multiple goals. Stands that are subjected to longer rotations provide older trees and are also more likely to provide a larger supply of deadwood (Ranius et al., 2003, Weslien et al., 2009), both important for rare and threatened forest species. Adapted thinning regimes, tree retention, and deadwood can help alleviate the effect of shorter rotations.

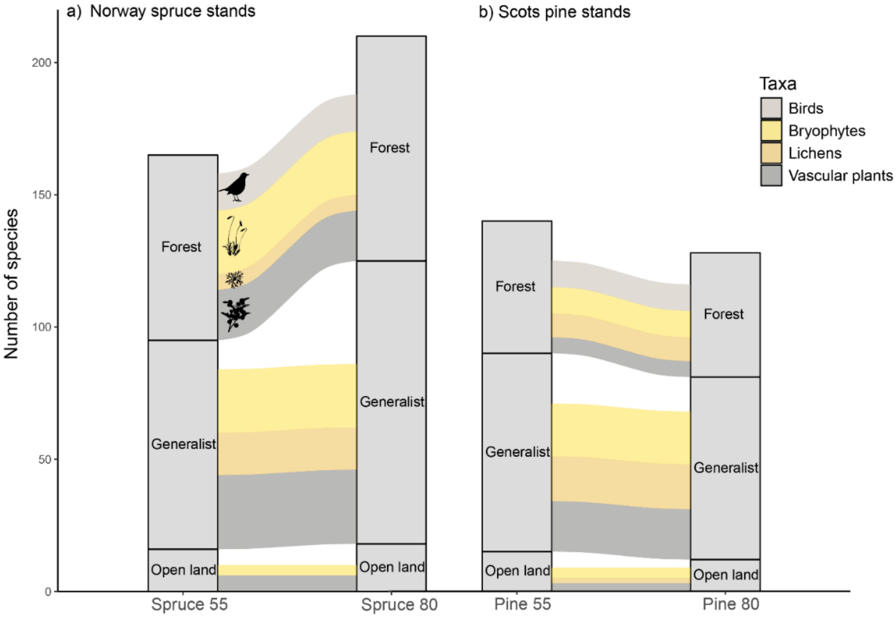

Figure 17. Proportion of different species groups at the landscape level (all stands pooled together). Bars show the different stand ages, and flows between bars illustrate the number of species occurring in both younger and older stands.

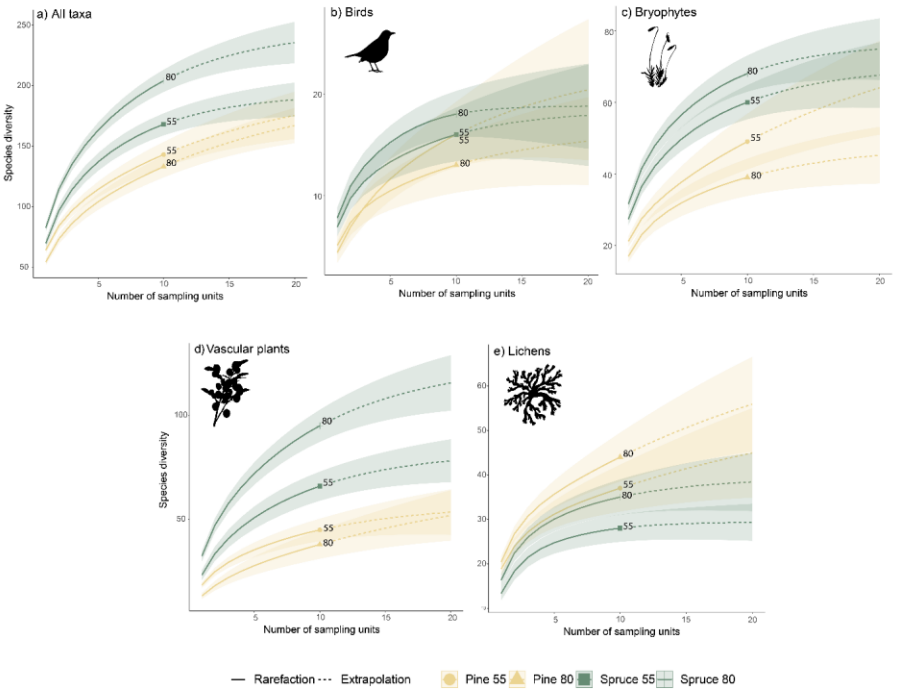

Figure 18. Illustration of species diversity through coverage-based rarefaction and extrapolation (R/E). The sampling curves correspond to each age (55 vs 80) and tree species (Norway spruce (green) and Scots pine (yellow)) for each of the taxon a) birds, b) bryophytes, c) lichens, and d) vascular plants) at stand level. Species diversity is based on Hill's numbers qΔ with q = 0 (species richness). The plots show the randomised interpolated accumulation curves (solid lines) for each of the 10 younger and older Norway spruce and Scots pine stands. The results were extrapolated to double the amount of stand inventoried.

5.3 Mapping of retention (Paper IV)

We found that retention trees were generally higher than the planted crop tree before the first thinning phase. Our results also indicate that the best of the tested methods could discern retention areas to an accuracy of 66%, but trade-offs between area overestimation and the number of trees identified may occur. In addition, individual trees may be hard to detect, particularly birch, beech, and oak (**Figure 19**).

Today, to ensure that the retention trees or areas are not felled, they need to be marked with tape before each final felling. Digitalisation and technical advancement can increase cost effectiveness and ensure that retention objects are permanently localised. This advancement may thus provide an unparallel data source that can be used for biodiversity conservation. Many studies have successfully located and characterised retention trees using point clouds from ALS (Næsset and Økland, 2002, Holmgren and Persson, 2004, Hardenbol et al., 2022). However, the use of the canopy height model is sparser (Mustonen et al., 2008, Zielewska-Büttner et al., 2016) and not necessarily targeted for biodiversity conservation management. We believe that the canopy height model increases the accessibility of the data and is a great opportunity for wider application among forest owners. This methodology presents a foundation that can benefit both forest management and ecological research.

Thinning is the most common forest operation in terms of area in Sweden. In 2022, 40% of the forest was defined as a “thinning forest.” In terms of area, thinning is the most common felling measure (annually 306,000 hectares) (Nilsson et al., 2022). There is a lack of analyses at the landscape level and spatial studies about previously created retention, such as deciduous trees and old trees. This tool can be used for planning and thinning operations and build on already known aspects or nature values to increase connectivity between habitats for forest-dwelling species at the landscape level.

There is ongoing debate about the quantity of retention needed to sustain biodiversity (Fahrig, 2001, Söderström, 2009, Gustafsson et al., 2020). However, it is quite difficult to quantify and give explicit thresholds for which level of biodiversity is to be sustained without any information about their spatial distribution or quantities. Patterns differ according to the species targeted, for example, between mobile and sessile organisms (Fahrig, 2001, Lindenmayer et al., 2015). This method opens research possibilities and can, to some extent, provide information about the location and quantity of retention at the landscape level and ensure continuity in retention measures previously made.

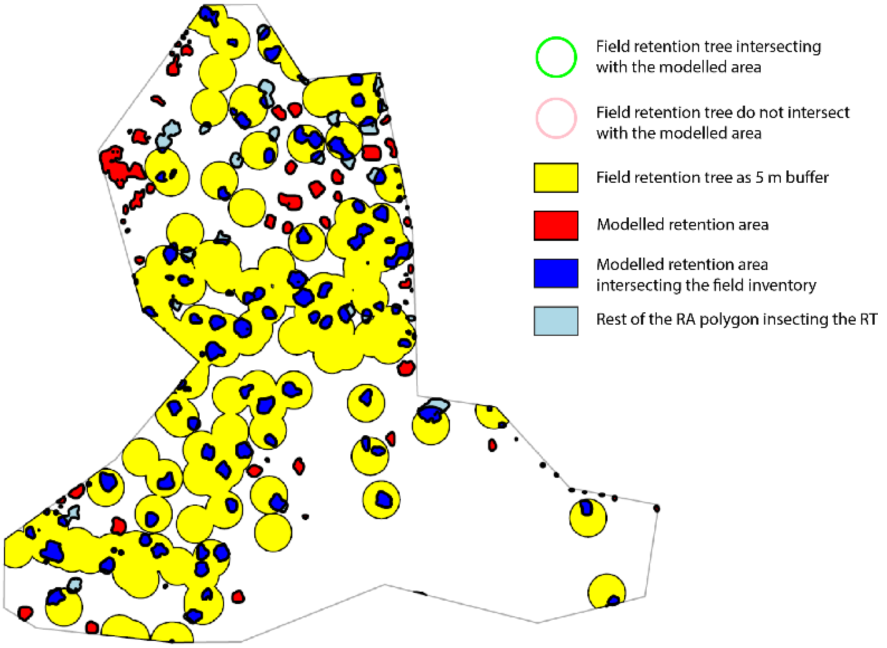

Figure 19. Example of output, with validation in terms of area (right). The yellow polygons represent the area inventoried in the field, whereas the blue represents the expected retention area from our method that matches the field inventory (dark and light blue) or perfectly matches the field inventory (dark blue). The leftover red areas are defined as overestimation, i.e. predicted retention areas that do not match the field inventory.

6. Main conclusions from each paper

Papers I & II illustrate the possibility of boosting old broadleaf trees' biological values by integrating a release procedure within the thinning programme that decreases interspecies competition within the stand and boosts oak growth and vitality. Oak release is a management procedure that is still efficient even after 10 years and benefits the diversity of plants and saproxylic beetles but also oak vitality without losing wood production in crop trees. Retention is a way to reconcile production and environmental goals. It allows us to keep features that are beneficial for organisms that do not cope well with clear-cutting. Old oaks are a wise choice for retention because they harbour a wide diversity of species, and many organisms are attached to oaks. The retention and management of old oaks and other deciduous broadleaf trees can ensure the survival and development of some species, but further research is needed to study the extent of the long-term effects in this specific setting. More actions may be needed in the future to maintain wood production, oak vitality, and species diversity. The oaks that are present in productive Norway spruce stands need management to ensure their survival and long-term contribution to biological diversity. As thinning is the first heavy forest operation with a harvester conducted in a stand, it should be seen as an opportunity to initiate or improve the conservation value. Oak release at the time of thinning is one management possibility for old retained oaks.

Paper III provides basic knowledge of the biological values of conventionally managed Norway spruce or Scots pine stands that have undergone a conventional thinning programme. By comparing 55- and 80-year-old stands, we illustrate the consequences of harvesting age on the forest's biological value. The effect of shortened rotation length would be most notably negative for lichen communities in both Norway spruce- and Scots pine-dominated stands. Bryophytes and vascular plant communities would also be strongly negatively affected by a shortening of rotation length in these stands since late successional species will disappear. Norway spruce and Scots pine stands differ in their species composition, stand dynamics, and ecological succession, which are essential for biodiversity. The stands in this study are good examples of forests soon to be harvested, and this study stresses the need to adapt their management for biodiversity conservation. By not shortening the rotation length, there is a possibility of retaining quality structures, habitats, and species in the next rotation. Koskela et al. (2007) expressed the biodiversity benefits from longer rotation lengths as a sum of the benefits accruing from the age of the stand becoming harvested, and the retention of older structures or trees, which will reach their biological maturity and decay during the next rotation period. Shortened rotation lengths result in losses in the development of habitat features that are key to biodiversity conservation in the next rotation. The 80-year-old forest stands we examined may be considered old with respect to production forest rotation lengths in Sweden but are young with respect to natural life spans for both tree species. Considering that stand-forming trees of Norway spruce can reach an age of 500–600 years and solitary Scots pine trees can become over 700 years old (Andersson and Niklasson, 2004, Castagneri et al., 2013), current rotation lengths are short. Our results indicate that shortening the rotation length of Scots pine and Norway spruce in this part of Sweden from 80 to 55 years could have important consequences for forest biodiversity.

Paper IV shows that the tree height raster can be used to detect retention trees with an accuracy of 66%. This is important information, both as an input for practical planning in forest management and for monitoring biodiversity trends. Clearly, retention trees are at risk of disappearing or being harvested during thinning if information about their location is not provided in the instructions and operational harvest plan. Consequently, knowledge of the spatial distribution of former conservation efforts increases the possibility of preserving forest structures that are important for biodiversity and enhances the possibilities for active management to keep species in the stand across rotations. More research is needed to improve the level of accuracy and higher resolution for tree-level detection while still using accessible data.

All papers deal with how species assemblages change over time, the common denominator being ecological succession. Gap cutting around old oaks will disrupt the succession, where open land species, such as herbs and grasses, are released instead of being dominated by the typical Norway spruce forest understorey of mosses and dwarf shrubs. Gaps could be a significant contribution to flora conservation since many open land species are decreasing in southern Sweden, possibly to some extent due to denser and darker forests (Hedwall et al., 2019). Ecological succession is also highlighted in Paper III, which suggests that shortening the rotation length will disrupt the succession before late successional species arrive. Tree retention at final felling can compensate but probably not counteract the negative effect of decreasing rotation length, leading to increasingly younger forest stands in the landscape. Paper IV demonstrates that although several decades have passed since trees were retained at final felling, retained trees can be spotted by digital techniques just before thinning. Localisation and characterisation of retention trees over the rotation of the stand may ascertain that they keep growing old and provide successional habitats both as living and dead.

Forestry operations coupled with conservation strategies are the keys in creating and shaping biological values within productive stands. Tree retention and retention areas are conservation strategies that can play an important role in the survival, dispersal, and re-establishment of species from multiple taxa. Together, the papers indicate that the past way of regenerating forests by clear-cutting without retention combined with the present trend towards shorter rotation lengths is a threat to biodiversity. Forest management that provides increasing numbers of old trees is probably essential for many species, and retention forestry probably plays an essential role. With modern technology, previous measures done in forest operations can easily be detected and can be protected in future forest operations. Adaptation of forest operations, such as thinning and rotation length, is important for creating and managing biological values.

7. Tomorrow's forestry

Since 1993, despite the amount of forest clear-cut and thinned every year, conservation values have been created over time through retention (Kruys et al., 2013, Holmström et al., 2019, Kyaschenko et al., 2022). These stands include new features that will evolve together with the crop tree. Within the clear-cut system, throughout the planning of future operations and management in today's forests, there are ways to adapt forest operation strategies for goals other than production. As presented in this thesis, the location and management of retained trees and the maintenance or prolongation of rotation length are existing tools to boost the conservation value of a productive stand.

The Swedish integrated management strategy combines large-scale protected forest areas, such as national parks, intermediate-scale reserves set within the forest production matrix, and at the smallest scale, the retention of key habitat features within production stands (Lindenmayer et al., 2006, Simonsson et al., 2014). The goal is to create a multiscale and multifunctional forest that combines economic, social, and environmental goals (Triviño et al., 2017, Felton et al., 2020, Eggers et al., 2022).

The dedication of reserves and areas explicitly set aside for conservation are important for species that require space and stability (Rolstad, 1991, Honnay et al., 2005). However, in heavily managed, fragmented landscapes, protected areas may not be sufficient to conserve forest biodiversity (Driscoll et al., 2013). Angelstam et al. (2020) stated that the current forest ecosystem representation by "off production" forests is "insufficient" and problematic to fulfil criteria such as spatial continuity that some forest species need. The majority of Sweden's protected forests are in the northwest part of the country and are called the mountain “green belt” (Svensson et al., 2020). Only a few remnants of intact forest landscapes and the multitude of set asides present inland (within productive stands) lack spatial coherence to form a working network of conservation areas to support viable metapopulations of both rare and common species (Hanski and Ovaskainen, 2000, Lindenmayer et al., 2006).

Therefore, the implementation of conservation actions within the current Swedish silvicultural system is essential to increase representativity and connectivity and reconcile production and environmental goals. Research on how to combine biodiversity and timber production has rapidly grown in recent years (Eyvindson et al., 2018, Naumov et al., 2018, Díaz-Yáñez et al., 2020, Eggers et al., 2020, Moor et al., 2022). Clear-cutting coupled with retention forestry is an interesting approach; however, it is not the only approach. Recently, it has been suggested that coordinated efforts, appropriately assessed sites, and carefully planned management using a diversity of strategies can make a significant difference in wildlife habitats, native plants, animal biodiversity, and aesthetics (Triviño et al., 2017, Díaz-Yáñez et al., 2020, Eggers et al., 2020). Eggers et al. (2022) pinpointed the obvious trade-offs occurring while trying to reconcile these objectives, and they stressed the need for further research with case management guidelines, which may vary according to region and type of forest. To make sustainable forest management operational, we must improve data collection and collaborate with managers and scientists. There are no simple solutions for managing forest ecosystems sustainably. Researchers and foresters must remain humble about their ability to predictably control these complex systems in the face of unprecedented global changes and continuous societal norm changes.

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Popular science summary

Tree retention, then what?

Forest is a place to produce wood but also a home for thousands of species of plants and animals. About 30 years ago, we started to leave trees at final felling for conservation and biological diversity purposes. “Retention trees” became a new concept. Such trees are sometimes easy to recognise, e.g. old oaks in a young spruce forest, but sometimes the differences are not so noticeable, and there is a risk that these trees will be cut down during forest operations such as thinning or final felling. A lot of research has been done on the benefits of retention trees for biodiversity right after final felling when trees are left still standing on the clear-cut, but almost nothing has been found on the ecological benefits they provide in the denser surrounding new grown forest. There is also a lack of knowledge about how much management should be done for these retention trees when it is time for thinning. There is also a clear trend that rotation length, i.e. the time between two final fellings, is getting shorter and thus the forest is getting younger on average. There are too few studies that have investigated what a shorter rotation length means for biodiversity.

I studied two specific aspects of forestry conservation in southern Sweden: retention and rotation. I looked at how to find retention trees or areas right before the first machine-operated operation—thinning. I used digital height maps to locate retention trees and areas to ease the planning of forestry operations and forest conservation. I also specifically studied the retention of old oaks in a Norway spruce stand and how to manage them properly for biodiversity conservation while still looking at production aspects. I provided results on a 10 years’ time frame and showed that the removal of Norway spruce around the oak will boost its vitality and the plants and oak-associated beetles' richness and abundance. Then, I investigated the effect of rotation length on different species groups, such as birds, plants, mosses, and lichens, and how rotation length can influence which species are found and how rich/poor the forest can become.

My results showed that retention forestry is one piece of the puzzle towards more integrated management of productive forests, considering both economic and environmental goals. Remote sensing techniques are an easy way to locate and plan for the management of retention trees before the first thinning. Retention trees are higher than crop trees (Norway spruce), and their height will stand out from the stand. The current Swedish production forest of Norway spruce and Scots pine has the potential to be "boosted" for biodiversity conservation through forest operation and management. More precisely, the removal of Norway spruce (release) around old oaks improves their vitality and chances of survival over time. Additionally, the release freed the oaks from competition for light, and the underneath fauna and flora were positively impacted by the warmer and lighter local climate. Going hand-in-hand with retention, the rotation length is essential to create quality structures. Older stands harbour a different diversity of plants, moss, and lichens than younger stands. We also found differences in species communities for younger and older production stands, depending on tree species.

These findings provide more knowledge, practical examples, and guidelines of what can be done to sustain biodiversity in managed conifer forests when it is time for thinning. From planning to management until harvest, this thesis provides novel empirical and long-term data that highlight the importance of integrating retention features in younger forests to sustain more diverse and functioning forest ecosystems in productive stands.

Populärvetenskaplig sammanfattning

Den brukade skogen är inte bara en virkesproducent, den är också hem för tusentals växt- och djurarter. Efter den omläggning av skogspolitiken som gjordes i mitten av 1990-talet har det blivit standard att lämna enskilda träd, trädgrupper och strukturer som död ved i samband med avverkning. De hänsynsträd som lämnas är avsedda att stå kvar för evigt. Forskningen om naturhänsynens effekter på biologisk mångfald har framför allt varit inriktad på kalhygges- och ungskogsfasen, medan hänsynsträdens långsiktiga betydelse i den uppväxande skogen är väldigt lite studerad. Det saknas dessutom kunskap om hur hänsynsträden ska skötas i samband med till exempel gallring, och ibland är det svårt att identifiera den tidigare lämnade hänsynen. En annan viktig fråga är den skogliga omloppstiden, som tenderar att bli allt kortare i den brukade skogen. Få studier har undersökt vilken inverkan olika omloppstider i den brukade skogen har för den biologiska mångfalden.

Min avhandling ger kunskapsbidrag till två specifika frågor om biologisk mångfald i den brukade skogen: hänsynsträdens långsiktiga betydelse och skötsel samt omloppstidens roll.

Hänsynsträd och hänsynsområden som lämnades vid 1990-talets slutavverkningar är nu omgivna av virkesproducerande skog. En av uppgifterna var att undersöka om hänsynsträden kan lokaliseras med hjälp av digitala höjdkartor. Om positionerna är kända kan de användas i planeringen av kommande skogsbruksåtgärder. Resultaten tyder på att hänsynsområdena kan urskiljas med en noggrannhet på 66 % om kartläggningen görs innan produktionsbeståndet vuxit förbi hänsynsträden. En annan fråga rör skötsel av hänsynsträden. Här studerade jag gamla ekar, insprängda i granskog i gallringsfasen, och hur deras skötsel kan bidra till ökad biologisk mångfald. Genom att gallra bort granar närmast ekarna ökade ekarnas vitalitet, och dessutom gynnades skalbaggsarter som är särskilt knutna till ek. Gallringen (frihuggningen) gynnade också markfloran, i och med att mer ljus släpptes ner till marken. Frihuggning runt ekarna påverkade inte beståndets totalproduktion nämnvärt.

Skogens ålder är en nyckelfaktor för många ekologiska processer. Ökad ålder leder i normala fall till ökad mängd gamla träd, fler strukturer och en mer heterogen skog som gynnar olika artgrupper. Åldern i sig förbättrar också etableringen av arter som är beroende av uppvuxen skog. I avhandlingen undersöktes hur skogens ålder påverkade fåglar, mossor, trädlevande lavar och kärlväxter i brukade gran- och tallskogar, antingen 55 år (”yngre”) eller 80 år (”äldre”). Skogarna dominerades av generalister, arter som normalt är tåliga mot olika störningar. I den äldre granskogen fanns dock fler unika arter. Äldre granbestånd hade vanligtvis mer död ved, vilket gynnade mossor och fåglar. Kärlväxter gynnades av högre ljusnivåer efter gallring. Yngre tallbestånd var däremot mer artrika än de äldre. Äldre tallbestånd hade visserligen högst mångfald av lavar, men övriga artgruppers diversitet påverkades negativt av ett fåtal dominanta arter. Även om skillnaderna var relativt små kan en högre omloppstid i den brukade skogen få stor ekologisk betydelse på landskapsnivå, med en mindre andel av skogsmarken i kalmarks- och ungskogsfasen.

De skogar som föryngrats de senaste 30 åren innehåller en mosaik av virkesproducerande träd och lämnad hänsyn. Det är viktigt att denna hänsyn bibehålls även i det fortsatta brukandet, och att nya strukturer skapas som ytterligare förstärker naturvärdena. Avhandlingen ger ett bidrag till detta genom att den visar hur hänsynsträden kan identifieras och skötas. Den visar också att en ökad omloppstid kan gynna vissa artgrupper.

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Release of retained oaks in Norway spruce plantations. A 10-year perspective on oak vitality, spruce wood production and ground vegetation

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ABSTRACT

This study explores the decade-long effects of release cutting around old retained oaks (*Quercus robur* L.) in a Norway spruce (*Picea abies* L. Karst) stand that was 33 year old when thinned. The impacts on both nature conservation values and spruce wood production were evaluated in a randomized block design. To release oaks from competition, stems of Norway spruce were cut around 33 oaks, in three different treatments: high release (HR), medium release (MR) and no release (NR). Trees within a circular sample plot (15 m radius from the oak) were measured at time of treatment and 10 years after. The treatment effects on stand development, oak vitality and understory vegetation were evaluated after ten years, using tree diameter, height measurements, oak crown and tree structure estimates as well as ground vegetation surveys. Release cutting did not impact spruce production within the sample plot, and given that there were no other obvious sources of spruce suppression in the stand, we speculate that release cutting has little to no impact at the stand scale. Oak crowns in the control plots (NR) became smaller after ten years, while the crowns expanded and colonized the gap in the release treatments. Simultaneously, the amount of dead wood in the crown increased among oaks in the control treatment, indicating dieback. Cover and species richness of vascular plants in the understory were significantly higher in the HR and MR treatments compared to NR. These results suggest that the creation of relatively wide gaps (greater than 2 m) around retained oak crowns is one efficient approach to maintain their conservation values in a spruce-dominated stand on a longer time frame. This will allow oaks to expand their crowns, increase their vitality and increase species richness and diversity of plants under the canopy. The economic loss of creating large gaps instead of no gaps may be negligible since the overall spruce production was not affected within 15 m of each oak.

1. Introduction

In northern Europe, intensive forest use and expansion of coniferous plantations has led to dramatic changes in the structure and composition of boreal and semi-boreal forests (Anderberg, 1991, Lindbladh et al., 2014). Old-growth and secondary deciduous forests, meadows and open woodland pastures have been reduced to a small part of their original coverage, replaced by homogeneous productive forests mostly lacking deadwood, old growth trees and other important features for biodiversity (Kuusela, 1994, Lindbladh et al., 2014, McGrath et al., 2015). The decline in old deciduous trees has diminished several species' habitats and populations, especially among insects and cryptogams (Artdatabanken, 2020).

Improving conditions for biodiversity is needed in managed forests. The retention of older deciduous trees, or retention forestry, is a practice used in clear-cut systems which are applied in most European forests (Vanha-Majamaa and Jalonen, 2001, Gustafsson et al., 2019, Gustafsson et al., 2020). This approach to harvesting retains important structures, safeguards habitat continuity and thus positively affects biodiversity compared to clear felling (Gustafsson et al., 2010, Fedrowitz et al., 2014, Gustafsson et al., 2020).

Old oaks (*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.) are frequently left as "retention trees" in conifer-dominated production forests. They provide valuable habitats and contribute to the diversity of

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many species groups, as solitary trees in the open landscape (Buse et al., 2007, Horak et al., 2014) or in forests (Tews et al., 2004, Widerberg et al., 2012, Parmain and Bouget, 2018). This is mainly due to the long lifespan of the oaks, and the fact that they provide a variety of habitats for epiphytic and saproxylic species on bark, in hollows and on dying and dead branches (Johansson et al., 2009, Lassauce et al., 2011). In northern Europe, many oak-associated species are on the Red List (Skarpaas et al., 2011, Mitchell et al., 2019, Mölder et al., 2019, Artdatabanken, 2020), including many beetles (Jonsell et al., 1998, Jonsell et al., 2007, Carpaneto et al., 2015, Mitchell et al., 2019), fungi and lichens (Thor, 1997).

Maintaining both wood production and biodiversity in stands with old retained oaks poses challenges to forest management in Sweden. For example, release cutting during thinning may play a crucial role in preserving old oaks and their associated species as well as maintaining plant diversity on the ground. Release cutting around single trees improves oak vitality and habitat quality (Paltto et al., 2008, Götmark, 2009) by reducing competition from surrounding trees and bushes (Read, 1996). It can also mimic natural disturbances and affect ecological processes through gap dynamics (Muscolo et al., 2014). By increasing habitat diversity and structural complexity, release cutting create new niches, and stimulate the species diversity of both fauna (Widerberg et al., 2012) and flora (Gálhidy et al., 2006, McEwan et al., 2014).

Ground vegetation is an essential component of forest ecosystems because of its importance for soil processes, nutrient cycling, litter decomposition, forest succession, food chains, and ecosystem services like berry production (Nilsson and Wardle, 2005, Gilliam, 2007, Shields and Webster, 2007). Previous studies have shown the positive effect of gap creation on both ground layer diversity and abundance (Goldblum, 1997, Gálhidy et al., 2006, Fahey and Puettmann, 2007, Grandpré et al., 2011, Kelemen et al., 2012). The size of the gaps, soil characteristics and site history are important drivers of species composition. The development of the oak crown will affect gap dynamics and related ecological processes, making it important to understand how understory plant communities change as the canopy closes (Tsai et al., 2018).

This study explores effects of release cutting in a Norway spruce (*Picea abies* L. Karst) plantation on the vitality of old retained oaks (*Quercus robur* L.), the growth of the surrounding Norway spruce and the diversity and abundance of surrounding ground vegetation over a ten-year period. To our knowledge, no previous study has simultaneously examined the decade-long effect of release cutting on oak vitality, the diversity of understory plants and conifer wood production. The overall objective of the study was to collect information to help improve management schemes for spruce stands with old retained oaks. Here we compare two different degrees of release cutting around old oaks in a dense Norway spruce stand. We hypothesize that release cutting will reduce spruce wood production within experimental plots around the oaks (H1). Release cutting will increase oak vitality, indicated by less dead wood in the oak crown and positive crown development (H2). Release cutting will also lead to higher ground vegetation cover compared to the control and a greater diversity of understory vascular plants species (H3).

2. Material and methods

2.1. Study area

The experiment is located in a 5.5 ha forest stand in the Asa Experimental forest in Sweden (57.138° N, 14.756° E). The site was planted with Norway spruce in 1975 with a 2 × 2 m spacing. Various deciduous trees that were present at the time of planting were retained and these constitute a part of the current overstorey. Pedunculate oak (*Quercus robur* L.), European aspen (*Populus tremula* L.) and Norway maple (*Acer platanoides* L.) are the most common broadleaved species in the stand. Retained oaks were, on average, 153 years old in the winter of 2018 (Drobyshev et al., 2019). According to historical pictures, the stand is an old wooded pasture. The site is quite fertile, with a site index of G39, which corresponds to a projected mean dominant height of the Norway spruce at the stand age of 100 years of 39 m (Hägglund and Lundmark, 1977). The site is located at around 220 m above sea level with an annual mean temperature of 6.6 °C and mean annual precipitation of 458 mm (reference years 1990–2019 from climate data from the SITES Asa research station). The site is located on a 10% slope facing west. Soil conditions are predominantly mesic (90% of stand area) and soil texture is sandy silt (80%) (Lindén, 2003).

The stand was first measured in 2003 by Lindén (2003) using a grid of sample plots to investigate how scattered large deciduous tree affected Norway spruce production. Therefore, all deciduous tree identifications were from this year. Thereafter the stand was thinned in 2008 and simultaneously a release cutting experiment was established by Koch Widerberg (2013) using oaks from Lindén (2003) broadleaved data. Koch Widerberg (2013) studied the effect of release cutting around retained oaks on saproxylic insects, and measured the focal crowns previous to thinning in 2007. In 2010, Altmäe (2012) investigated the effect of retained trees on the growth of Norway spruce, and some of the Norway spruce stand data was measured following Koch Widerberg (2013) sample plot method.

2.2. Experimental design

Eleven clusters of large oaks were identified from Lindén (2003), and were used as blocks in the experiment, evenly distributed over the entire stand. The study was designed as a randomized block experiment with three release cutting treatments, each treatment containing one focal oak, in total 33 focal oaks (Koch Widerberg, 2013). The treatments were created during the thinning of the stand in 2008, and defined as: 1) High release (HR), where all spruces were removed under the crown of the oaks and extended in a two meter zone; 2) Medium release (MR) where all spruces were removed directly under the crown of the oaks only; and finally 3) No release (NR) where no spruces were removed (Fig. 1). There was supposed to be no overlap between the 15 m radius plots within blocks. However, we discovered some overlap (ca 6 m) between two NR plots in different blocks and between a HR and MR plot from the same block. These overlaps were not corrected for in the analyses.

The crown radii sizes ranged from 2 to 10.3 m depending on the direction; therefore a sampling plot with a 15 meter radius was established around every one of the 33 focal oaks (corresponding to 0.07 ha, in total 42.4% of the total stand area). The individual focal oaks were considered as the center of the sample plot and marked with a permanent stick. Unfortunately, two oaks (111 & 166) were mismarked and thus excluded from the 2018 study, which left 31 plots (Appendix A). No further harvest of spruce or other tree species has been undertaken since the experimental treatments were applied.

2.3. Stand development

All trees above 1.3 m height within the sample plots were measured, including their distance to the focal oak stem, two years after the treatment in 2010 and eight years later, 2018. Diameter at breast height (DBH), 1.3 m above ground was recorded using a caliper. In addition, the heights of six sample trees of Norway spruce were measured systematically in each plot (two with the largest diameter and four in each of the smaller diameter groups). All Norway spruce trees were assigned an estimated height from the diameter-height function (Näslund, 1936) based on the measured sample trees.

In total our analysis includes 1294 trees, of which 1088 (84%) were Norway spruce and the rest broad-leaved species: Aspen (*Populus* sp.), Alder (*Alnus* sp.), Maple (*Acer* sp.), Oak (*Quercus* sp.), Lime (*Tilia* sp.), and Birch (*Betula* sp.) (Appendix B.1 and B.2). Of the 1294 trees, 1195 were also present in the 2010 inventory. DBH and basal area in 2010 and 2018 of missing (n = 49) and new Norway spruce trees (n = 42)

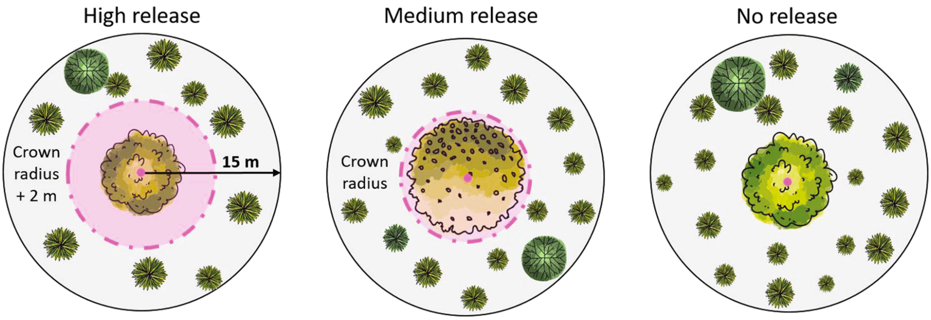

Fig. 1. Release cutting experiment. The left image shows the High Release (HR) treatment, the middle image shows the Medium Release (MR) treatment, and the right image shows the control No Release (NR). In dotted pink-line is the delimitation for the release cutting according to the treatment, and in light grey is the 15 m sample plot with a pink dot, or focal oak stem as the center. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

respectively were reconstructed using linear regression (Appendix B.3). For every sample plot, dominant height (Appendix B.4), mean height, and mean DBH of Norway spruce were calculated. Basal area increment (BAI, $m^2 ha^{-1}$), DBH increment (DBHI, cm year $^{-1}$) were calculated using 2010 and 2018 values.

Treatment effects on Norway spruce DBH and BA for both years as well as DBHI and BAI were tested in R studio 3.4.3 (R development core Team, 2018) using REML linear mixed models (LMMs). The p-values were obtained using Satterthwaite's approximation using the 'lme4' and 'lmerTest' R packages (Bates et al., 2011, Kuznetsova et al., 2015) and interpreted based on a 0.05 critical alpha threshold. For DBHI and BAI the initial 2010 DBH, or initial BA, were included as a covariate in the model in order to capture the variability in growth linked to initial stand values.

The interaction of tree size and competition from the focal oak, and how it is affecting the annual basal area growth of the tree was investigated, in a subset of the data only including the Norway spruce trees in the control plots (where trees from 1 to 15 m distance from the oak were present). The individual tree growth in terms of annual basal area growth (BAI) was tested in a mixed model using the plot as random variable.

$$\log(BAI_{ij}) = \mu + \beta_0 BA_{ij} \times \log(Distance_{ij}) + \beta_1 BA_{ij}^2 + \varepsilon_{ij}, Plot_j N(0, \sigma_{ij}^2) \quad (1)$$

Where BAI is the annual basal area growth, BA the initial basal area, Distance is the distance from the focal tree to the tree for tree 1 to *i* in each plot 1 to *j*. Transformations were made to reduce heteroscedasticity, and model selection was based on lowest AIC and smallest mean standard error. For model interpretation and visualization the trees were divided into three size classes: suppressed (smaller than mean DBH-1 standard deviation); dominant (larger than mean DBH + 1 standard deviation) and intermediate (in between).

2.4. Oak vitality

The focal oaks stem circumference was measured at breast height both in 2010 (Altmäe, 2012) and 2018 with a measuring tape and DBH (cm) was deduced (Appendix A). The focal oak's crown width from the stem to the edge of the crown was measured in four cardinal directions both in 2007 and 2018 (Fig. 2). Crown changes within this period were calculated by using the treatment mean crown width differences in each direction (crown growth) (Fig. 2). The crown area (i.e. the sum of all 4 triangles areas) for each focal oak (Fig. 2) was calculated for 2007 and compared to make sure the focal oaks did not have significantly different areas between treatments.

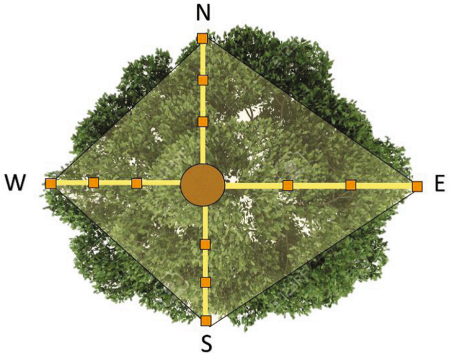

Fig. 2. Vegetation sampling design. Transects (yellow), area (shaded yellow) and quadrats (orange) are found up to the crown width limits in each cardinal direction. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Canopy openness was estimated as the amount of visible sky between the oak and the Norway spruce canopies using hemispherical pictures in a circle 1-meter from each focal oak stem. Eight photos were taken in the four cardinal and four intercardinal directions at the height of 1.8 m from the ground to capture the degree of canopy openness around each focal oak. Pictures were analyzed in the software Gap light analyzer (GLA) (Frazer et al., 1999) which transforms the pixels into a black and white representation in order to derive the percentage openness of the canopy (white pixels indicating visible sky). Each focal oak had a canopy openness value for each of the eight directions, and then the mean canopy openness per focal oak was computed to compare each treatment (with and without direction as a covariate).

Finally, the quantity of dead branches in the crown was assessed and used as an indicator of oak vitality. Dead wood was measured with the help of 2-dimensional tree architecture drawings (Appendix C). Each drawing was created in relation to the total tree height, which was measured with a Vertex IV ultrasound instrument system. In addition, an eight-meter reference stick was placed against the stem of each measured focal oak as an "eye-reference" for the drawings. For each focal oak, the total length of dead and living wood was calculated and related to the length of all branches on the tree drawing to obtain the proportion of dead wood. Oak 172 was not considered in this analysis and considered as an outlier value. The removal of this oak reduced the standard deviation of the data by 35% within the NR treatment. This may be explained by the fact that the focal oak was located on the edge of the stand in an open area and not representative of a NR tree.

The impacts of retention level on oak vitality were tested by comparing the oak response variables (DBH both years, DBHI, crown width growth, mean canopy openness per oak, or dead wood proportion in the crown per oak) among treatments (HR, MR or NR) using REML linear mixed models (LMMs) (R studio 3.4.3 (R development core Team, 2018). For each model, "block" was used as a random variable and for DBHI, the initial size (DBH 2010) was included as a covariate. The p-values were obtained using Satterthwaite's approximation using the 'lme4' and 'lmerTest' R packages (Bates et al., 2011, Kuznetsova et al., 2015) and interpreted based on a 0.05 critical alpha threshold. Pairwise comparisons between the groups were computed using Tukey's post hoc test (function emmeans in package 'lsmeans' (Lenth and Lenth, 2018)). For all models, the assumptions were verified from inspection of plots of the residuals, and if necessary, transformation of the response variable was performed before statistical testing.

2.5. Vegetation inventory

The vegetation inventory was conducted in August 2018. For vegetation cover, north, south, east, and west cardinal directions were used to delimit four transects from the oak center. Three quadrats of 0.5 × 0.5 m were placed one third of the total distance apart along every transect, with the last plot being at the edge of the oak crown (Fig. 2). Each quadrat was inspected by a single experienced observer and percentage cover was visually estimated for each species within each quadrat. Sometimes species were layered and the total coverage can exceed 100%. In total 30 focal oaks were inventoried as one individual was dead (oak 68) and we discarded the two mismatched oaks (111 & 166). To be able to interpret edge effect, the distance between each oak and the edge of the stands were included as a covariate in the model. For tree seedlings, the percentage cover per seedling was set to 1% of a square plot area.

The percentage cover of each species in each of the 12 sample plots was summarized to one value per focal oak (oak level sum). A supplementary qualitative inventory was carried out by walking the plot in a circular spiral toward the oak. If a species was found within the 15 m radius of the sample plot during the qualitative inventory, but not in any of the 12 sample plots, it was listed with 0.001% total cover at the oak level. The species were classified into the following four habitat groups according to Heinken et al. (2019):

- *True herbaceous forest species* (1.1 & 1.2) (all taxa largely confined to forest): Including group 1.1 which contains taxa that are predominantly found in closed forests, as well as group 1.2 which are mainly species found on forest edges and in forest clearings.
- *Herbaceous generalist species* (2.1), herbaceous species and dwarf shrub species common in both forest and open land. A large proportion of the species of group 2.1 probably had their original habitat in forests and have migrated from here into the open habitats.
- *Woody generalist species* (2.1), Tree and shrub species (excluding dwarf shrubs confined to the herbaceous layer).
- *Open land species* (2.2) are only occasionally found in the forest, and mainly occur in open habitat (dwarf shrub heaths, lime and sand-poor grasslands, wet meadows, etc.). Most species of group 2.2 are shade-intolerant.

The cover sum for each functional group was then calculated for each oak plot. Finally, the mean cover of each functional group per treatment was compared. Each species cover data was transformed into a binary presence/absence (1/0) to indicate how many species were associated with each oak. The impact of retention level on the mean number of species found at each oak was tested in R studio 3.4.3 (R development core Team, 2018) using REML linear mixed models (LMMs) to compare among treatments (HR, MR or NR). In the model, distance to the edge was added as a covariate to see if edge effect had an impact on species diversity, and then block was defined as a random effect. The p-values were obtained using Satterthwaite's approximation using the 'lme4′ and 'lmerTest' R packages (Bates et al., 2011, Kuznetsova et al., 2015) and interpreted based on a 0.05 critical alpha threshold. Pairwise comparisons between the groups were computed using Tukey's post hoc test P (function emmeans in package 'lsmeans' (Lenth and Lenth, 2018)). For all models, the assumptions were verified from inspection of plots of the residuals, and if necessary transformation of the response variable was performed before statistical testing.

3. Results

3.1. Stand development

The basal area (m^2ha^{-1}) for the Norway spruce adjacent to the focal oaks (15 m radius) was not significantly different among treatments (HR, MR, NR) directly after release cutting (Table 1). However, the arithmetic mean of Norway spruce DBH was smaller in NR compared to HR and MR (Table 1). The release cutting treatment had no effect on total stem growth of the Norway spruce around the focal oak in our sample plots, resulting in no significant difference in DBH, DBH increment, BA or BAI (Table 1).

For individual trees in the control plots, there was a significant increase in annual basal area growth with increasing distance to the focal oak treatment (F-value = 29.502, df/dendf = 1/333.31, **p < 0.000**) which interacted with initial tree size (F-value = 7.074, df/dendf = 1/334.89, **p < 0.008**). Including the squared initial basal area improved model fit (Fig. 3, Appendix E). Using the initial tree size classification for visualization of model behavior also highlighted the result that intermediate sized trees showed more growth dependency to the focal oak than suppressed trees (Fig. 3). Dominant trees were more or less absent in the nearest five meters from the focal oak.

Table 1

Effect of "Treatment" on the different Norway spruce variables at plot level (n = 31). The table shows means ± standard errors of the mean (SE) for each treatment (High release HR, Medium release MR and no releases NR). It also shows the F-value, degrees of freedom (df), denominator df (dendf) and p-values. P-values in bold are significant (p < 0.05). Means sharing a letter are means that are not significantly different from each other. *Growth variables (BAI, DBHI) all have respective initial measurement as covariates.

	Mean ± SE					
Response variable	HR	MR	NR	F	df, dendf	p
Stand BA 2010 (m^2/ha)	17.56 ± 1.31	17.89 ± 1.31	19.11 ± 1.45	0.40	1, 16.164	0.674
Stand BA 2018 (m^2/ha)	25.27 ± 1.96	25.86 ± 1.96	27.60 ± 2.17	0.43	1, 16.707	0.653
Mean DBH 2010 (cm)	21.69 ± 0.69 (a)	21.89 ± 0.69 (a)	18.92 ± 0.78 (b)	4.98	1, 28	**0.014**
Mean DBH 2018 (cm)	25.85 ± 0.89 (a)	26.19 ± 0.89 (a)	22.54 ± 1.00 (b)	4.43	1, 28	**0.021**
BAI (m^2/ha $year^{-1}$)*	1.37 ± 0.19	1.60 ± 0.19	1.61 ± 0.21	0.69	2, 17.791	0.516
DBHI (cm $year^{-1}$)*	0.49 ± 0.018	0.51 ± 0.019	0.52 ± 0.022	0.45	2, 18.978	0.646

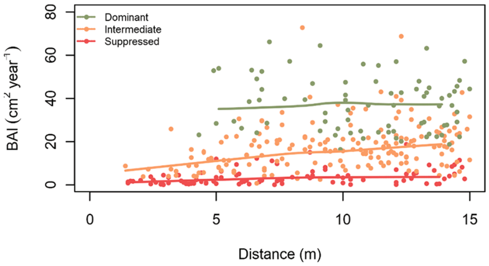

Fig. 3. BAI, annual basal area increment for Norway spruce trees at the different distance from the focal oak. The trees are grouped in colors based on suppressed, intermediate and dominant trees. The smoothed lines are predicted values from the model for the groups respectively (Eq. (1)).

3.2. Oak vitality

The stem diameter increment (DBHI) of the focal oaks did not differ among treatments neither did the initial DBH and the 2018 DBH (Table 2). The 2007 mean crown area did not differ between treatment (F-value = 0.119, df/dendf = 2/28, p = 0.888). The mean crown area in HR treatment (47.23 m^2 ± SE 5.73) did not differ compared to the mean crown area in MR (44.15.23 m^2 ± SE 5.73) or NR (Mean 43.39 m^2 ± SE 6.42). In addition, the crown length in the different direction was not significantly different between treatment (F-value = 0.274, df/dendf = 3/111.52, p = 0.761).

Mean crown width growth was about ten times higher in HR and MR treatments than in the NR treatment. The treatment effect was highly significant (Table 2). The canopy openness (open sky gaps) around the focal oaks did not differ among treatments eight years after release cutting (Table 2). Finally, the mean proportion of dead branches was affected by treatment (Table 2) with the highest proportion of dead branches in the NR treatment and the lowest in the HR treatment.

3.3. Vegetation

3.3.1. Cover data

The understory vegetation had a significantly different cover among treatments; with higher coverage in HR compared to MR and NR (F-value = 5.019, df/dendf = 2/114.632, **p = 0.008**). True forest herbaceous species mean cover is about three to four times higher in HR (76.86% ± SE 15.15) compared to NR (21.24% ± SE 16.07). The mean ground cover of generalist herbaceous species in the HR treatment (90.29% ± SE 41.02) was almost twice as high compared to NR (57.77% ± SE 41.44). The mean ground cover of generalist woody species was around three times higher in HR (113.57% ± SE 15.80) compare to NR (36.48 ± SE 17.50) and doubled in MR (62.77 ± SE 16.37) compared to NR. Finally, the differences in open land species cover among treatments are marginally non-significant. All habitat groups, except open land species, had higher cover in HR and MR treatments compared to NR treatment. The difference was statistically significant for HR vs NR (Fig. 4). The plot location in relation to the edge of the stand only affected open land species (F-value = 4.970, df/dendf = 1/11.293, **p = 0.047**).

Quercus sp. seedlings were observed adjacent to 11 of the sample plots out of the 30: four times in HR and four times in MR with a respective mean cover of 4.0% ± SE 1.2 and 1.3% ± SE 1.2, and three times in NR with a mean cover of 2.0% ± SE 1.4. Norway spruce seedlings were observed adjacent to 29 oaks, 11 times in HR with a mean cover of 19.4% ± 3.7, 10 times in MR with a mean cover of 8.6% ± SE 3.9 and finally eight times in NR with a mean cover of 6.6% ± SE 4.4.

3.3.2. Plant species richness

In total, 62 different species were inventoried, 45 species were found during the quantitative inventory in the quadrats and an additional 17 species were detected inside the full 15 m radius sample plots during the qualitative inventory (species list in Appendix D). In the HR treatments, 50 different species were found, in the MR treatments 50 species and in NR, 21 species. Some species were more frequent, such as *Oxalis acetosella*, which was found in all plots and treatments, compared to *Calamagrostis canescens*, *Solidago virgaurea*, and *Lysimachia vulgaris* which were only found in HR plots. All NR species were also found in MR treatments.

There was a significant difference in the mean number of species found in the three treatments (F-value = 6.4853, df/dendf = 2/18.022, **p = 0.007**). HR and MR treatments had significantly more species compared to NR (Fig. 5). HR had a mean number of species of 15.5 ± SE 2.0, compared to 13.3 ± SE 2.1 in MR and 7.2 ± SE 2.2 in NR. Distance was not a significant predictor of species diversity (F-value = 2.0654, df/dendf = 1/19.302, p = 0.167). The highest and lowest number of species found around a single oak was 29 and 3, respectively.

4. Discussion

This study generated novel information that can be applied to improve management of young conifer stands with old deciduous trees. The experiment shows that release cutting, including removal of commercially planted Norway spruce trees around large oaks, has positive effects on oak vitality and increase plant diversity and abundance. The release cutting had no detrimental effects on total Norway spruce wood production within a 15 m radius of the focal oak and over nine growing seasons. This indicates that releasing retained oaks during commercial thinning may be a way to balance production goals and conservation values.

4.1. Spruce wood production

This study demonstrates that removal of Norway spruce trees around old oak trees during the first thinning does not reduce growth or standing volume at the plot level over a 10-year period. The most obvious explanation of these results is that spruce trees under the oaks

Table 2
Effect of the different treatments on the different focal oak variables. The table shows means ± standard errors of the mean (SE) for each treatment (High release HR, Medium release MR and no releases NR). It also shows the F-value, degrees of freedom (df), denominator df (dendf) and p-values. P-values in bold are significant ($p < 0.05$). *For DBHI, initial DBH was used as a covariate in the model. Means sharing a letter are means that are not significantly different from each other.

	Mean ± SE					
Focal oak variables	HR	MR	NR	F	df, dendf	p
DBH 2010 (cm)	63.75 ± 3.39	61.53 ± 3.59	56.62 ± 3.81	1.017	2, 27	0.375
DBH 2018 (cm)	67.33 ± 3.64	65.92 ± 3.84	60.69 ± 4.08	0.807	2, 27	0.456
DBH increment (cm)*	3.47 ± 0.87	4.41 ± 0.91	4.23 ± 0.98	0.180	2, 16.49	0.836
Crown width growth (m)	1.12 ± 0.26 (a)	0.72 ± 0.26 (a)	0.10 ± 0.26 (b)	6.1223	2, 119	**0.003**
Canopy openness (%)	16.11 ± 0.81	15.83 ± 0.83	15.55 ± 0.82	0.8683	2, 228.38	0.421
Dead wood proportion (%)	23.84 ± 2.95 (a)	27.88 ± 3.11 (b)	38.85 ± 3.54 (b)	5.640	2, 26	**0.009**

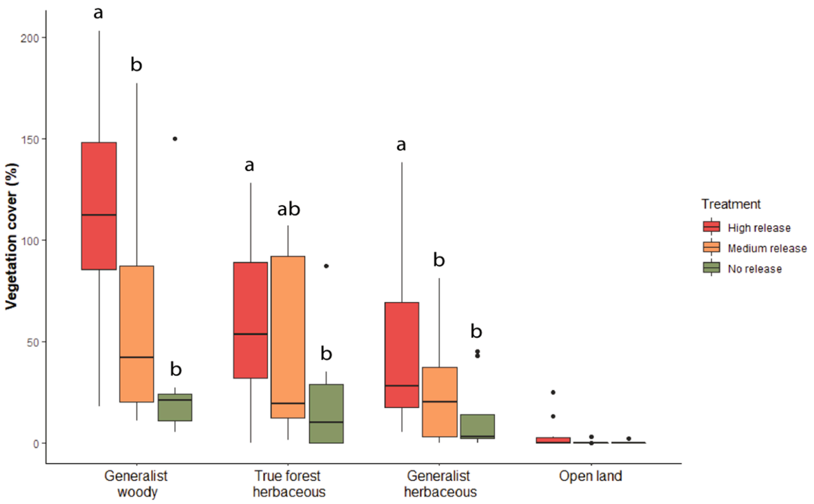

Fig. 4. Distribution of the ground vegetation cover (in percentage) per habitat group and treatment. The boxplot shows the distribution of the data and the black line shows the median values among blocks in the data set. The letters indicate the pairwise comparisons of means. Boxplots sharing a letter have means that are not significantly different from each other.

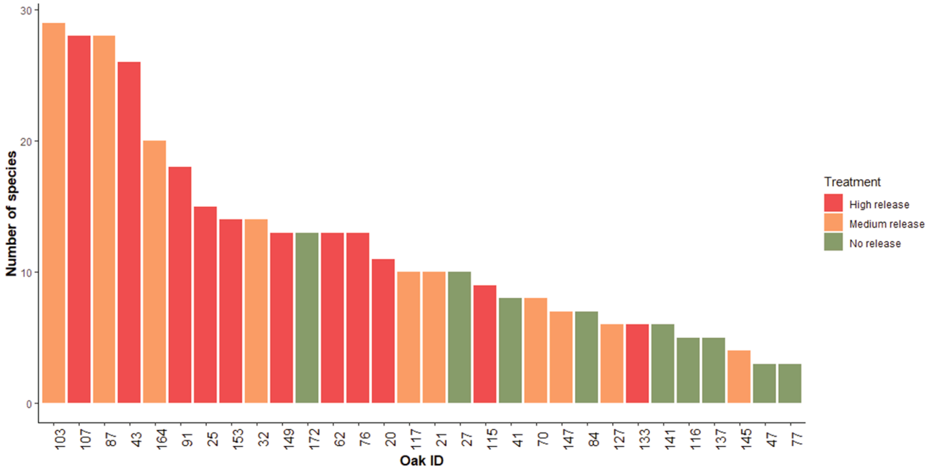

Fig. 5. Species richness for each focal oak (n = 30), represented by its oak ID on the × axis and treatment (HR, MR, NR). Species richness is ordered from the richest oak on the left to the poorest oak on the right. The richest oaks on the left are mostly red (HR) and orange (MR). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

were small and suppressed and contributed very little to the overall growth in the plots. This is reinforced by the fact that control plots had significantly smaller mean Norway spruce DBH compare to the other treatments. Our study is in agreement with results by Lindén (2003) who studied the same stand 10 years prior to the release cutting. When comparing oak retention to the alternative of clear-cutting, Lindén (2003) reported that substantial growth losses in Norway spruce stands can be anticipated, depending on density and size of retained oaks. Our study indicates that growth losses can be anticipated within 5 m from the retained oaks. Our results are in line with the results by Elfving and Jakobsson (2006), who found that Scots pine (*Pinus sylvestris* L.) volume was decreasing within a 5–10 m competition zone depending on fertility. Spruce is a shade tolerant species (Kantola and Mäkelä, 2006) and belowground competition could be an explanation to the reduction of growth. In our data the effect of oak competition was significantly decreasing with distance to the oak and size of the tree basal area, which was primarily visible on the intermediate trees. This may be explained by suppressed trees being outcompeted also by the other Norway spruce trees throughout the stand. Dominant trees were missing in the nearest five meter radius of the oaks, which corresponds to an area of c. 80 m^2 in which Norway spruce production is severely reduced meaning that at a density of e.g. 10 large oaks per ha, about 8% of the area for effective spruce wood production is lost. This exemplifies a significant cost in keeping oaks within spruce production stands.

4.2. *Oak vitality*

Release cutting increased vitality of the focal oaks. Crowns were small in the control plots while they expanded and colonized the space made available in the release treatments. Simultaneously, the amount of dead wood in the crowns increased among oaks in the control treatment, indicating dieback. In a similar experiment conducted by Götmark (2009) with oaks in broadleaf-dominated conservation forests in Sweden, openness around oaks was a positive predictor of oak vitality and similarly he used the amount of dead wood in the crown as a negative predictor of growth vitality. Götmarks and our findings confirm an earlier finding that *Quercus* sp. is shade intolerant, have high crown plasticity, but low competitive ability when growing with other species (Le Due and Havill, 1998, Pretzsch et al., 2013). Control oaks in our study probably suffered from competition and crowding with the surrounding trees, leading to increasing amount of dead crown and reduced crown expansion, which potentially affected photosynthetic ability and the overall tree vitality. Götmark (2009) also mentioned that release cutting increased the mean relative basal area growth of large oaks after four growing seasons. Such an increase was not found in our study, as treatments had no effect on diameter increment of the focal oaks.

4.3. *Vegetation*

Overall, mean plant cover increased with treatment in order NR, MR and HR for all species groups. The creation of a gap in the canopy can be seen as simulation of natural disturbances at a local spatial scale impacting the understory through the alteration of important resources for plant growth (Muscolo et al., 2014). The alteration of the horizontal structure of the forest (including small gaps or thinning) will most importantly change the light environment and according to the theory of gap dynamics, changes in ground vegetation cover occur quite quickly after the creation of the gap since open conditions facilitate vegetative reproduction (Dai, 1996, McEwan et al., 2014, Muscolo et al., 2014). Tree cutting increases not only light but also nutrient and often soil moisture availability for understory plants, which usually boosts their abundance (Matula et al., 2020). However, as also regeneration of woody species, including Norway spruce, was favored by release cutting, the cover of herbaceous species may gradually decrease again until a new release cut is done.

The removal of spruce favoured the growth of both true forest species with low light requirements (e.g. *Oxalis acetosella, Maianthemum bifolium, Lactuca muralis)*, generalist species with higher light requirements and even some indicators of the historical land use (pasture) (e.g. *Veronica chamaedrys, Anthoxanthum odoratum, Alchemilla acutiloba, Ranunculus repens, Hypericum maculatum*) (Tyler and Olsson, 2013, Milberg et al., 2019). These findings are in accordance with previous studies on effects of partial cutting which showed positive effects on a majority of species (Brunet et al., 1996, Götmark et al., 2005). Many of the species found in both the HR and MR treatments are habitat generalists, whereas none of those disturbance-tolerant species were found in the control. Instead, the control was characterized by low cover of true forest-species or/and species with low light requirements.

We also found a higher number of species in the MR and HR treatments compared to NR, including both light demanding generalists and shade tolerant forest species. This may be explained by the fact that shade tolerant species are able to survive where there is very low light availability, but also grow better with increasing light (Gaudio et al., 2008). However, the observed gradient of treatment effect (HR > MR > NR) may indicate that, as the gap closes in the future, species richness may decrease again (Dai, 1996, McEwan et al., 2014, Muscolo et al., 2014). Previous studies have found that grassland species can survive as small remnant populations in forested areas, and that this can facilitate colonization of new sites after canopy opening (De Graaf and Roberts, 2009, Jonason et al., 2016). The extent of this establishment over time remains unknown. It has been documented that it can take more than one decade for management legacies to disappear and they can sometimes even be permanent (Dupouey et al., 2002, Cuddington, 2011). Repeated release cutting could be a suitable management strategy for long-term conservation of a diverse forest ground vegetation in conifer-dominated production forests. Knowing that coniferous forests generally provide less diversified vascular plant understories than broadleaved and mixed forests (Barbier et al., 2008, Felton et al., 2010), this study highlights the importance of considering understory dynamics in forest management practices.

5. Conclusions and management implications

In plantation forestry, the creation of gaps influences a considerable number of biological processes and will provide habitat and new structures that will enhance the vegetation cover and species richness in a long-term perspective. Leaving more space around retention trees when conifers are being planted or releasing the oaks at the time of the first commercial thinning will reduce the competition with Norway spruce and increase oak vitality and conservation value. The felling of the suppressed spruce trees will increase harvesting costs but the impact on spruce wood production is negligible. We suggest that release cutting practices could be developed to support plant diversity, for example, by the creation of larger gaps in early thinnings where old trees are present. The retention and management of old oaks and other deciduous broadleaf trees can ensure the survival and development of some species of the ground vegetation, but further research is needed to study the extent of the long-term effect in this specific setting. More actions may be needed in the future to maintain wood production, oak vitality and plant diversity.

Declaration of Competing Interest

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

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Appendices. Supplementary material

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Supplementary material Paper I

APPENDIX A: Per plot summary of the minimum distance to the focal oak (Min distance to FO (m)), Norway spruce (NS) stem density, Broadleaves species (BS) stem density, Oak (excl. focal oak) stem density, all-tree species stem density. The basal area (BA) for Norway spruce and BA for all trees (NS+BS+FO) for both years. The mean Norway spruce DBH for both years, the mean spruce height for both years, and the focal oak height for both years.

PLOT ID (Focal oak)	Treatment	Block	Min dist. to FO (m)	NS density	BS density	Oak density	All Trees sp. density	2010 NS BA (m^2/ha)	2010 total BA (m^2/ha)	2018 NS BA/ha	2018 total BA (m^2/ha)	Mean NS DBH 2010 (cm)	Mean NS DBH 2018 (cm)	2010 mean NS predicted height (m)	2018 mean NS predicted height (m)	2010 FO height (m)	2018 FO height (m)
103	MR	11	4.6	16	2	4	22	9.26	26.75	13.30	32.41	21.85	26.24	19.4	21.3	25.2	23.2
107	HR	11	5.9	18	6	5	29	9.19	30.75	12.28	33.69	20.42	23.62	18.8	20.2	26.6	20.5
115	HR	8	5.8	36	5	0	41	19.45	26.05	28.46	41.02	21.30	25.61	19.4	21.2	19	19
116	NR	8	2.9	36	3	3	44	14.79	18.11	20.94	44.03	18.42	21.64	18.2	19.3	24.7	20.8
117	MR	8	5.4	46	4	1	51	21.79	37.05	33.47	49.65	19.94	24.50	18.9	20.7	24.1	24.1
127	MR	4	5.0	42	2	0	44	21.24	26.75	31.45	39.68	20.77	25.13	19.3	21.1	18.3	17.7
133	HR	3	5.9	29	7	0	36	14.73	25.61	21.98	44.97	20.83	25.27	19.4	21.2	23.5	22
137	NR	1	1.7	48	10	0	59	22.95	27.90	32.53	40.23	19.00	22.32	17.7	18.8	20.2	20.6
141	NR	3	6.8	39	1	2	42	21.15	29.18	30.80	46.75	21.68	26.08	19.7	21.7	21.3	21.8
145	MR	3	4.6	30	3	3	36	14.60	24.27	21.00	45.48	20.44	24.33	19.2	20.9	22.5	25.2
147	MR	5	5.4	44	1	1	46	23.76	31.54	34.09	48.05	21.61	25.79	19.7	21.6	22.4	23.5
149	HR	5	6.0	43	2	0	45	23.23	27.80	34.81	43.60	21.45	26.11	19.5	21.5	21	21.2
153	HR	9	4.4	32	3	1	37	19.74	27.56	29.00	37.70	22.66	27.25	19.8	21.7	21.7	20.6
164	MR	9	5.4	13	11	2	28	9.93	34.14	15.10	40.75	25.22	30.88	20.6	22.9	25.2	22.5
172	NR	5	2.6	33	0	2	35	18.38	29.58	27.24	40.01	21.61	26.21	19.5	21.5	23.6	24.4
20	HR	2	1.4	45	2	0	47	24.71	33.13	33.90	42.09	21.27	24.71	19.1	20.5	25	25
21	MR	6	4.5	31	2	1	34	19.08	25.07	28.25	38.75	22.27	27.13	19.3	21.4	23.9	20.1
25	HR	6	6.0	35	12	2	49	17.17	36.28	23.95	44.81	19.34	22.61	17.7	18.9	28.6	28.8
27	NR	6	1.4	39	7	2	48	14.52	28.30	20.48	35.76	16.78	19.62	16.8	17.6	21.9	22.4
32	MR	10	5.0	28	4	4	36	13.04	37.22	17.95	43.52	19.29	22.33	18.3	19.4	20.2	20.1
41	NR	10	1.6	63	5	3	71	20.78	36.38	29.56	47.07	16.04	18.69	16.7	17.3	23.7	21.9
43	HR	10	8.2	21	0	3	24	14.67	35.55	21.09	44.03	24.35	29.19	20.4	22.6	26.5	27.6
47	NR	2	2.1	40	5	0	45	15.71	32.53	23.22	41.41	18.18	21.88	18.2	19.6	25.1	21.8
62	HR	1	6.5	29	3	6	38	12.14	38.85	16.80	44.85	18.38	21.47	18.0	19.1	24.5	21.7
68	MR	1	3.0	32	2	1	35	23.27	30.53	33.15	46.84	25.04	29.90	20.7	22.9	20.8	21.4
70	MR	2	3.3	43	3	1	47	18.39	25.34	26.75	43.81	18.94	22.71	18.4	19.9	19.7	22.5
76	HR	4	6.4	36	1	0	37	19.90	24.96	29.38	38.09	21.50	26.04	19.4	21.3	23.1	21.7
77	NR	4	1.0	52	7	0	59	21.99	32.14	32.78	44.22	18.66	22.44	18.2	19.6	20.4	20.9
84	NR	7	2.3	41	3	2	48	14.81	29.11	21.21	41.52	17.14	20.43	17.4	18.6	23	21.4
87	MR	7	5.3	28	3	2	33	18.21	27.25	23.51	34.22	23.00	26.06	19.6	21.1	21.6	21.3
91	HR	7	3.8	20	4	1	25	16.17	24.99	23.26	33.04	26.55	31.72	21.2	23.6	22.6	23.8

APPENDIX B: Density table (B.1), mean stand data in each treatments (B.2), Data selection (B.3), basal area calculation (B.4).

APPENDIX B.1: Original 2010 tree density (stems) per species in each treatment. The density is the number of stem sum for each plot for each treatment. The focal oak row also represent the number of plots as each focal oak represent the center of the sample plot. Broad-leaved species include Aspen, Alder, Maple, Oak, Lime, and Birch but excludes Oaks, which can be found in a separate class. This Table shows the evenness of the sample plots in term of tree species distribution.

Tree density	HR	MR	NR	Total
Norway spruce	344	353	391	1088
Focal oak	11	11	9	31
Broad-leaved species	45	37	41	123
Oak	18	20	14	52
Total	401	403	446	**1294**

APPENDIX B.2: Mean ± SD of the trees' distance to the focal oak for all tree species included (all trees) or only Norway spruce (NS). Mean density in terms of stems per ha and Norway spruce mean height as well as dominant height (two dominant trees) in the different treatments and periods. ***from predicted height model**

	High release		Medium release		No release	
	2010	**2018**	**2010**	**2018**	**2010**	**2018**
Mean distance (m) all trees	11.00 ± 3.12		10.30 ± 3.28		9.50 ± 3.86	
Mean distance (m) Only NS	11.38 ± 2.51		10.52 ± 2.87		9.48 ± 3.70	
Mean density per plot (stems)	31.36 ± 8.98		32.27 ± 10.69		44.00 ± 9.18	
Mean density per plot (stems/ha)	443.65 ± 127.04		456.53 ± 151.23		622.47 ± 129.87	
Spruce height (m)*	19.3 ± 0.98	21.1 ± 1.38	19.4 ± 0.74	21.2 ± 1.06	18.0 ± 1.05	19.3 ± 1.51
Mean dominant height (m)*	23.2 ± 0.25	26.7 ± 0.22	23.5 ± 0.12	27.0 ± 0.17	23.1 ± 0.01	26.4 ± 0.15
Mean focal oak height (m)	22.90 ± 3.10	22.9 ± 3.10	22.2 ± 2.30	21.0 ± 2.10	22.7 ± 1.80	21.8 ± 1.10

APPENDIX B.3: In total, 1451 trees of all species were recorded. Due to difficulties with re-establishing the exact center of the sample plot from the 2010 measurements, two entire plots had to be removed from the dataset (oak 166 (NR) & 111 (NR), n=118) because it was impossible to link any of the 2018 trees with the 2010 data. In addition, four individual trees with highly incoherent distances for 2018 and 2010 were discarded. Norway spruce with basal area increase (BAI) between 2010 and 2018 greater than 0.06 m^2 (n=26) were considered to be outliers compared to the data set and discarded. In total 1294 trees were retained for the analyses, among these 1088 were Norway spruce.

APPENDIX B.4:

For the <u>missing Norway spruce</u> in 2018, their DBHs were calculated using the following models:

$$BAI = \beta_0 + \beta_1 \times BA_{2010} - \beta_2 \times HR - \beta_3 \times MR \qquad (Model\ I)$$

Where the Intercept $\beta_0 = -0.0009072$, $\beta_1 = 0.4767368$, $\beta_2 = -0.0006304$, and $\beta_3 = -0.0004569$. Then the model was applied to the 49 missing 2018 Norway spruce basal areas to finally obtain their BA (Model Ia) and DBH (Model Ib). “Model I” was constructed based on the 1005 spruces with measured variables.

$$BA_{2018} = BA_{2010} + BAI \qquad (Model\ Ia)$$

$$DBH_{2018\ missing\ tree} = \sqrt{\frac{BA_{2018}}{0.00007854}} \qquad (Model\ Ib)$$

For <u>new trees in 2018</u>, their initial 2010 BAI was calculated as:

$$BAI = \beta_0 + \beta_1 \times BA_{2018} - \beta_2 \times HR - \beta_3 \times MR \qquad (Model\ II)$$

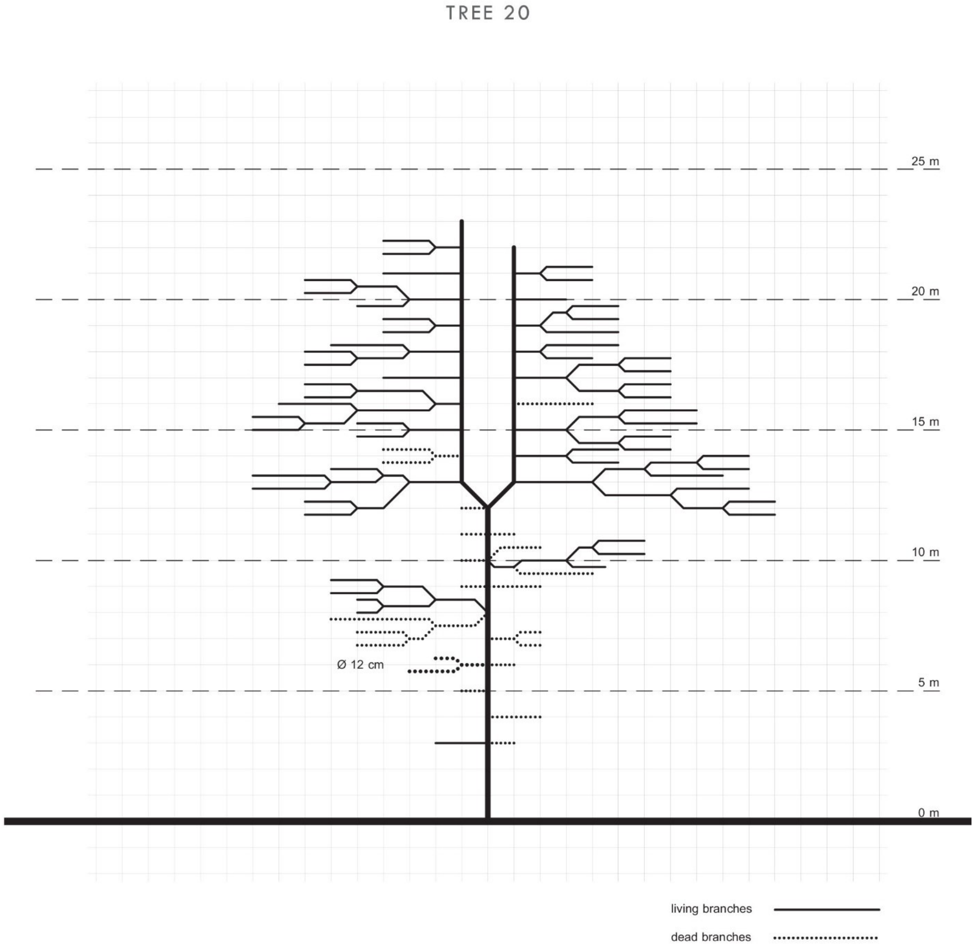
Where the Intercept $\beta_0 = -0.0024122$, $\beta_1 = 0.3641594$, $\beta_2 = -0.0009270$, and $\beta_3 = -0.0007597$. Then the model was applied to the 49 missing 2018 basal areas to finally obtain their BA (Model IIa) and DBH (Model IIb). “Model II” was constructed based on the 1005 spruces with measured variables.

We first constructed a model based on the 1005 spruces that were measured on both occasions, then predicted the 2010 basal areas of the 42 new trees based on model (IIa), to finally obtain their DBH (IIb).

$$BA_{2010} = BA_{2018} - BAI \qquad (Model\ IIa)$$

$$DBH_{2010\ New\ tree} = \sqrt{\frac{BA_{2010}}{0.00007854}} \qquad (Model\ IIb)$$

APPENDIX C: Example of 2D drawing used to determine dead wood proportion in the crown of the focal oaks. Dotted lines represent dead branches and black lines living branches. The drawing has a scale of 1 cm = 1m.



LENGHT OF THE LIVING BRANCHES:	182 m
LENGHT OF THE DEAD BRANCHES:	43 m
PERCENTAGE OF THE DEAD BRANCHES:	19 %

APPENDIX D: List of the species found either in the quantitative plot sampling (Plot species), or the qualitative inventory (New species). Each species is affiliated to a category and a habitat group according to Heinken (2019) (Forest, n=16; Generalist herbaceous, n=29; Generalist woody, n=13; Open land species, n=4). Trees and shrubs among generalists (2.1.) are thus indicated, and analyzed as a separate group. All other species are herbaceous (or dwarf shrubs *Vaccinium spp*.). Species are ordered in terms of overall cover sum through the entire stand.

Species name	Category	Habitat group	Type of inventory	Total ground cover
Rubus idaeus	2.1	Generalist woody	Plot species	960
Corylus avellana	2.1	Generalist woody	Plot species	635
Oxalis acetosella	1.1	Forest	Plot species	634
Agrostis capillaris	2.1	Generalist herbaceous	Plot species	588
Carex pallescens	2.1	Generalist herbaceous	Plot species	504
Picea abies	2.1	Generalist woody	Plot species	352
Calamagrostis arundinacea	1.1	Forest	Plot species	202
Viola riviniana	1.1	Forest	Plot species	186
Juncus effusus	2.1	Generalist herbaceous	Plot species	172
Athyrium filix-femina	1.1	Forest	Plot species	153
Populus tremula	2.1	Generalist woody	Plot species	133
Lactuca muralis	2.1	Generalist herbaceous	Plot species	98
Deschampsia cespitosa	2.1	Generalist herbaceous	Plot species	82
Veronica officinalis	2.1	Generalist herbaceous	Plot species	78
Viola palustris	2.1	Generalist herbaceous	Plot species	77
Luzula pilosa	1.1	Forest	Plot species	66
Phegopteris connectilis	1.1	Forest	Plot species	63
Ranunculus repens	2.1	Generalist herbaceous	Plot species	57
Gymnocarpium dryopteris	1.1	Forest	Plot species	57
Avellana flexuosa	2.1	Generalist herbaceous	Plot species	54
Dryopteris carthusiana	1.1	Forest	Plot species	47
Potentilla erecta	2.2	Open land	Plot species	43
Maianthemum bifolium	1.1	Forest	Plot species	40
Veronica chamaedrys	2.1	Generalist herbaceous	Plot species	36
Quercus robur	2.1	Generalist woody	Plot species	27
Carex leporina	2.2	Open land	Plot species	27
Fragaria vesca	2.1	Generalist herbaceous	Plot species	25
Acer platanoides	2.1	Generalist woody	Plot species	22
Sorbus aucuparia	2.1	Generalist woody	Plot species	22
Betula pendula	2.1	Generalist woody	Plot species	16
Vaccinium myrtillus	2.1	Generalist woody	Plot species	16
Stellaria media	2.1	Generalist herbaceous	Plot species	8
Carex remota	1.1	Forest	Plot species	8
Hypericum maculatum	2.1	Generalist herbaceous	Plot species	7
Stachys sylvatica	1.1	Forest	Plot species	7
Epilobium montanum	2.1	Generalist herbaceous	Plot species	6
Calamagrostis canescens	2.1	Generalist herbaceous	Plot species	5
Molinia caerulea	2.1	Generalist herbaceous	Plot species	5
Galeopsis tetrahit	2.1	Generalist herbaceous	Plot species	4
Lathyrus linifolius	2.1	Generalist herbaceous	Plot species	3
Carex canescens	2.1	Generalist herbaceous	Plot species	2
Solidago virgaurea	2.1	Generalist herbaceous	Plot species	2
Chamaenerium angustifolium	1.2	Forest	Plot species	2
Lysimachia vulgaris	2.1	Generalist herbaceous	Plot species	1
Equisetum sylvaticum	1.1	Forest	Plot species	1
Melica nutans	1.1	Forest	New species	0,004
Dactylis glomerata	2.1	Generalist herbaceous	New species	0,003

Poa nemoralis	1.1	Forest	New species	0,002
Campanula persicifolia	1.2	Forest	New species	0,002
Anthoxanthum odoratum	2.1	Generalist herbaceous	New species	0,001
Cirsium palustre	2.1	Generalist herbaceous	New species	0,001
Dryopteris filix-mas	2.1	Generalist herbaceous	New species	0,001
Geum rivale	2.1	Generalist herbaceous	New species	0,001
Melampyrum pratense	2.1	Generalist herbaceous	New species	0,001
Polypodium vulgare	2.1	Generalist herbaceous	New species	0,001
Vaccinium vitis-idaea	2.1	Generalist woody	New species	0,001
Crataegus monogyna coll.	2.1	Generalist woody	New species	0,001
Frangula alnus	2.1	Generalist woody	New species	0,001
Pinus sylvestris	2.1	Generalist woody	New species	0,001
Salix caprea	2.1	Generalist woody	New species	0,001
Alchemilla acutiloba	2.2	Open land	New species	0,001
Tussilago farfara	2.2	Open land	New species	0,001

APPENDIX E: Output from the mixed model for individual trees in the control plots. The model output shows the annual basal area growth in relation to the initial basal area, distance from the focal oak, and the interaction of the distance and initial tree size. The table present coefficient estimates for each variable, standard error, t-value and p-value. P-values in bold are significant ($p<0.05$).

	Estimate	**Std. Error**	**t value**	**p-value**
Intercept	-0.799	0.213	-3.747	**0.000**
Initial basal area	113.222	8.325	13.601	**0.000**
Distance from the focal oak	-0.567	0.104	-5.431	**0.000**
Initial basal area squared	-620.164	63.336	-9.792	**0.000**
Basal area growth * Distance	9.582	3.602	2.660	**0.008**

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ORIGINAL ARTICLE

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Ten years after: Release cutting around old oaks still affects oak vitality and saproxylic beetles in a Norway spruce stand

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Abstract

1. It is often suggested to release oaks (*Quercus robur*) from competition, to ensure their survival and boost their conservational value. However, few studies have explored how long-lasting this effect is and how it affects saproxylic beetles.
2. Ten years after cutting, we investigated effects of different release cutting levels (high, medium, and no release) around 140-year-old retained oaks in a commercial forest with Norway spruce (*Picea abies*).
3. We evaluated oak vitality using crown and dead wood measurements. Saproxylic beetles were caught in window traps, identified to species level, and grouped according to their association with oak and/or Norway spruce.
4. Released oaks had more light, higher temperatures, greater crown growth, and less dead wood in the crown compared to the no-release control.
5. After 10 years we still found a higher abundance of oak-associated beetles and higher overall species richness of saproxylic beetles in the released oaks. Beetle species composition significantly differed between released oaks and control.
6. We suggest avoiding planting trees beneath retained oaks when regenerating conifer forests and to proceed with conservation management during subsequent thinning by removing regeneration under the oak crowns. We emphasize the benefits of monitoring the retained oaks to maintain tree vitality, habitat quality, and insolation.

KEYWORDS
biodiversity, *Picea abies*, *Quercus robur*, release cutting, saproxylic beetles, tree retention

INTRODUCTION

Many species of beetles specialize in specific microhabitats that can mainly be found on ancient trees. Old, hollow oaks trees (*Quercus robur*) in forests can serve as a habitat for a particularly rich fauna, including many rare and red-listed beetles, and host a high proportion of threatened species (SLU Artdatabanken, 2020; Sundberg et al., 2019). These forest oaks can live for hundreds of years and provide crucial resources and dead wood of different decay stages and diameters (Lassauce et al., 2011; Parmain & Bouget, 2018; Sverdrup-Thygeson et al., 2010). Many species are tightly associated with forest oaks, and free-standing oaks seem to be particularly important because they harbour special communities of beetles (Sverdrup-Thygeson et al., 2010; Widerberg et al., 2012).

In the hemi-boreal zone of northern Europe, there has been a decline in wooded pastures, which started during the 20th century with urbanization and the intensification of agriculture (Dahlstrom et al., 2008; Eliasson & Nilsson, 2002; Eriksson et al., 2002; Scb, 2019). Especially during the last century, intensive forestry, in combination with a change in farmland management, has changed the structure and composition of the landscape. This has led to the homogenisation of the forest towards even-aged monocultures of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies* (L.) H. Karst.) (Dahlstrom et al., 2008; Lindbladh et al., 2014). Old broadleaved deciduous trees became scarce along with their array of specific microhabitats (deadwood, cavities, bark structure) that benefit many specialist species (SLU Artdatabanken, 2020; Siitonen & Ranius, 2015; Stokland et al., 2012). Numerous saproxylic or epixylic invertebrates, fungi and lichens have declined, and many are currently threatened (Clavel et al., 2011).

To mitigate the effects of the decline of broadleaved trees in Sweden, the strategy during the last decades has been to promote green tree retention in final harvest, meaning retaining individual or clustered broadleaf trees belonging to the previous tree generation (Fedrowitz et al., 2014; Gustafsson et al., 2012; Gustafsson et al., 2020). These retention trees are then surrounded by more recently planted trees (Drobyshev et al., 2019; Koch Widerberg, 2013). One purpose of the retention trees is that they may act as “lifeboats” and provide valuable refuge habitats for plants and animals, and promote the conservation of rare and red listed species (Jonsell et al., 1998; Mitchell et al., 2019; Parmain & Bouget, 2018). Green tree retention can also be practiced when old pastures are converted to Norway spruce plantations, and old trees are retained for the first rotation of the stand. This has been common practice in low-production former agricultural areas in Sweden, where many pastures and former croplands have been converted into production forest stands by planting Norway spruce (Kardell & Henckel, 1994; Koch Widerberg, 2013). Current legislation in Sweden does not forbid planting under the crown of retention trees, even though Norway spruce can rapidly shade and compete with the retained trees. Light can become a limiting factor and have repercussions on other ecological processes, and ultimately local biodiversity. Norway spruce plantations in southern Sweden usually have a 50–80-year rotation, whereas the age of retained oaks may be several hundred years. Therefore, adequate long-term management is crucial to preserve the oaks and the species associated with it.

The release of retention trees—by removing the crop trees around the retained tree—is suggested as a solution for preserving some of the open forest environment that is often associated with high conservation values. Releasing, or “gap cutting” also promotes tree vitality and survival through multiple rotations, especially for tree species that are shade-intolerant such as oaks (Andersson et al., 2011; Götmark, 2009; Shifley, 2004; Widerberg et al., 2012). If early-stage plantations are dense and shaded, a release cutting in the first commercial thinning may be recommended. Such an opening reduces surrounding competition (Lariviere et al., 2020; Lindén, 2003) and increases insolation on the retained tree (Widerberg et al., 2012). It also changes the environment surrounding the tree, resulting in altered light intensity to the forest floor, and changes in soil humidity and soil biological properties (Muscolo et al., 2014). In turn, this may also favour other organisms associated with more open forest conditions, such as understorey vegetation (Gálhidy et al., 2006; Kelemen et al., 2012; Lariviere et al., 2020; Majasalmi & Rautiainen, 2020) or light-dependent beetles (Horak et al., 2014). The surrounding environment, including dead wood availability and temperature, are also important factors for beetle communities (Bouget et al., 2013; Müller et al., 2015). In some circumstances, an increase in temperature may compensate for poor habitat conditions in production forests, especially because shade-intolerant trees like oaks usually also support species adapted to open, light, and warm conditions (Horak et al., 2014; Jonsell et al., 1998).

One common denominator for beetle diversity and oak vitality is the amount of light entering the gap, which directly increases after release and causes an immediate response by saproxylic beetles (Widerberg et al., 2012). However light may gradually decrease with time as the released trees grow and fill the gap (Lariviere et al., 2020). There are no studies that explore the longer-term effect of gap creation on beetle diversity in planted conifer forest. In this study, the objective was to examine 10-year-effects of releasing old oaks on the richness, abundance, and composition of saproxylic beetle communities in a Norway spruce plantation.

The study is based on a thinning experiment established by Koch Widerberg (2013) in a stand a where Norway spruce trees were planted around oaks in 1975. In the experiment, during thinning in 2008, Norway spruce were removed under and around the oak crown at three levels of intensity (high-released oaks (HR); medium-released oaks (MR), and non-released oaks (NR)). Widerberg et al. (2012) found that the short-term effect (first 3 years) of releasing oaks was a higher species richness and abundance of oak-associated beetles compared to the non-released oaks. In this study, we re-examined the same stand 10 years after treatment, using the same experimental design and classification to test two hypotheses:

- The gap cutting still has a measurable effect on oak vitality and abiotic (light and temperature) variables 10 years post-treatment.
- The gap-cutting still has a measurable effect on oak-associated saproxylic beetles in terms of species richness, abundance, and composition.

METHODS

Study site

The study was conducted in 2018 and 2019 as part of an experiment located in the Swedish University of Agricultural Sciences (SLU) experimental forest at Asa (57.138°N, 14.756°E) in Kronoberg County, Sweden (Figure 1). The site elevation is around 220 m with a mean annual temperature of 6.6°C and mean annual precipitation of 458 mm (reference years 1990–2019 from Asa Reference climate data (Langvall, 2021)). The site is located on a 10% slope facing west. The soil conditions are predominantly mesic (90% of stand area), and

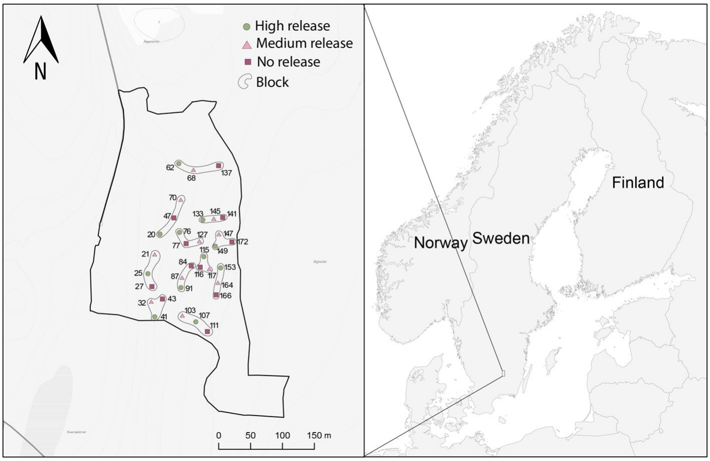


FIGURE 1 Map of the location of the stand used for the release experimentation near Asa. The map on the left shows the 33 focal oaks and the treatment they received: high release (green), medium release (light pink) or the control/no release (dark pink). The total stand area is 5.5 hectares.

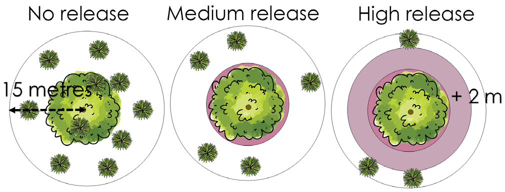


FIGURE 2 Representation of the different treatments in the release cutting experiment. The focal oak is the centre of the sample plot. The left image shows the control, or no release treatment (NR), where no Norway spruce were removed. The middle image shows the medium release (MR) where all Norway spruce were removed under the crown of the oak (dark pink area). The right image shows high release (HR) where all Norway spruce were removed under the crown of the oak (dark pink area) and 2 m beyond the crown area (lighter pink area).

the soil texture is sandy silt (80%) (Lindén, 2003). The experimental area is a 5.5 hectare which was originally a wooded pasture. Norway spruce (*Picea abies*) was planted in 1975 between the 84 pedunculate oaks (*Quercus robur*) and various retained deciduous trees, such as European aspen (*Populus tremula*) and Norway maple (*Acer platanoides*) distributed throughout the area.

Experimental design

The experiment was initially established in 2008 and was described by Koch Widerberg (2013) in further detail. Thirty-three oaks out of 84 were selected across the stand as "focal oaks" to undergo three different degrees of release cutting. On average, the oaks were 140 years old in 2018 (Drobyshev et al., 2019). The distance between the oaks was an average of 24.5 m from trunk to trunk, and the focal oak crown length was in average 4.7 m across all treatments and directions. The experiment was set up as a randomized block design with three treatments, each containing one focal oak, replicated in 11 blocks (Figure 1). Due to the death of one oak and one wrongly match oak from 2008 (Lariviere et al., 2020), we had to discard two oaks so our analyses included only 31 oaks.

In 2008, Norway spruce were removed at different intensities around each focal oak within a 15-m radius from each focal oak. High release (HR) consisted of removing all Norway spruce under and 2 m beyond the crown of the oak; medium release (MR) consisted of removing the Norway spruce directly under the oak's crown; and no release (NR) received no treatment other than normal thinning (Figure 2). Normal thinning was a removal of approximately 25% of the Norway spruce basal area, including strip roads. Most of the other retention trees (if not directly in the strip road area) were retained without any specific gap cutting surrounding them. The mean Norway spruce density (stems per plot) and treatment was 31 ± 9 SD in HR, 32 ± 11 in MR, and 44 ± 9 in NR, corresponding to 440, 450, and 623 stems per hectare, and representing a mean gap size of 8.8, 6.9, and 0 m radius. More details about the Norway spruce production aspects are found in Lariviere et al. (2020).

Insect sampling

Beetles were sampled in 2018 and 2019 using window traps placed approximately 5 m above the ground on the southern side of each focal oak stem, exactly as was done in 2008. Each window trap

FIGURE 3 Window trap used to catch beetles during the experiment. The trap was pulled up to 5 m above the ground using a rope system. The wood pole holding one 30 × 40 cm Plexiglas was inserted into the white container via two holes (one on each side) which also serve as drainage holes in case of heavy rain. At the top-right corner of the trap, a light and temperature logger can be seen (arrow).

consisted of a 40 × 17 × 14 cm white plastic container mounted with a single 30 × 40 cm Plexiglas transparent panel perpendicular to the stem (Figure 3). The containers were filled with 1.5 L of uncoloured monopropylene glycol (30%) and water (70%) solution to which a few drops of detergent were added to remove water surface tension. Traps were emptied every 3 weeks from May to September (six times per year). All saproxylic beetles (Coleoptera) were identified to the species level by entomologists Bengt Jan-Olof Andersson (Nybro, Sweden) and Hans Erik Wanntorp (Brottby, Sweden). The total number of individuals of each species was counted for each year. Only species characterized as saproxylic beetles (facultative and obligate saproxylic) included in Dahlberg and Stockland (2004) classification were used in the analysis.

Koch Wideberg (2013) assessed the beetles' association to oak and Norway spruce on the basis of their ability to use the wood of these tree species for at least some part of their life-cycle (Widerberg et al., 2018) following the classification by Dahlberg and Stokland (2004). We used the same non-nested beetle groups, as done in Koch Widerberg (2013), Widerberg et al. (2018). The four groups were:

- **Group I** saproxylic species associated with oak and Norway spruce.
- **Group II** saproxylic species associated with oak but NOT with Norway spruce.
- **Group III** saproxylic species not associated with oak.
- **Group I+ II** saproxylic species associated with oak.

Both oak- and spruce-associated beetles may also use other tree species present in southern Sweden.

Oak vitality and abiotic variables

A series of data were previously collected for Lariviere et al. (2020). For the present study, we used information about focal oak, such as diameter at breast height (DBH) measured with a calliper, height (metres), and crown area-growth in 10 years (m^2). The focal oak crown area-growth was calculated from the crown length, which was measured from the trunk of the focal oak to the end of the crown in four cardinal directions (north/south/east/west), then transcribed into a crown area in square metres. The crown area growth of the oak was calculated as the difference between the second (2018) and the first measurements (2008). We were also interested in dead wood characteristics, such as the percentage of dead wood in the crown and the diameter of the thickest dead branch on each focal oak. Dead wood was measured once in September 2018 before the leaves had fallen, which allowed easy detection of dead branches. The percentage of dead wood was estimated by counting the number and length of dead and alive branches on each oak. We used 2-dimensional tree architecture drawings (Appendix 2). Each drawing was scaled in relation to the tree's total height, which was measured with a vertex height-measuring instrument and an 8-m reference stick placed on the stem of the tree. Widerberg et al. (2012) found a positive correlation between species richness and the diameter of the thickest dead branch per oak, and therefore we also estimated the diameter of the thickest dead branch by holding a reference stick of 10, 20, 25, or 30 cm beside the branch on a long pole.

Light and temperature were recorded with HOBO Pendant MX Temperature/Light Data loggers, which were installed on the top right corner of the window traps (Figure 3). We used 22 loggers which were placed on focal oaks in the "no release" and "high release" treatments, representing the two extreme treatments. These recorded both light (lux) and temperature (°C) every hour from May to September in 2018 and 2019.

Data analyses

The analyses were conducted in R studio 3.4.3 (R Core Team, 2022). We investigated treatment differences for species richness, abundance, and species composition of saproxylic beetles. We also investigated difference between treatments for oak vitality variables, light, and temperature.

Beetle abundance and species richness

Abundance was calculated as the total number of saproxylic beetles captured at each focal oak for each year. Abundance data can often be overdispersed due to clusters of individuals (variance greater than the mean). For this reason, we used a negative binomial generalized linear mixed model (GLMM) using the function glmer.nb from the R package MASS by Ripley et al. (2013) to determine whether saproxylic beetle abundance differed between treatments.

Species richness was calculated as the total number of beetle species found at each focal oak in each year. We used generalized linear mixed models (GLMMs) with a Poisson distribution and log-transformed data to determine whether the total number of species per oak differed between treatments.

To assess the effect of different treatments, we used either beetle abundance or beetle species richness per oak for each year as the response variable. Treatment and sampling year were used as fixed factors, and block was set as a random factor. Species richness and abundance are often positively correlated in ecological data (Chao & Chiu, 2016). In our analyses, we controlled for this by including abundance as a covariate in the analysis of species richness.

Results for the general linear mixed models (GLMMs) were obtained from Wald Chi-Square Tests and interpreted based on a 0.05 critical alpha threshold. If an independent variable was significant, post-hoc pairwise comparisons between treatments were computed using estimated marginal means (function emmeans in packages lsmeans (v1.8.2; Lenth 2022) and multcomp (v1.4-20; Hothorn et al., 2022)). For all models, the assumptions were verified by inspecting the plots of the residuals, and if necessary, transformation of the response variable was performed before statistical testing. The analyses were conducted separately for each specific group of saproxylic beetles.

Species composition

We assessed the differences in species composition based on dissimilarity using a permutational multivariate analysis of variance (perMANOVA), using the adonis2 function in the vegan package (Oksanen et al., 2019). This model included treatment and block as random variables. To examine differences in beetle species composition between the different treatments, we used non-metric multidimensional scaling (NMDS), which is an unconstrained method. We used the metaMDS function from the R package vegan (Oksanen et al., 2019) with the Bray–Curtis dissimilarity index and interpreted the stress level according to Dexter et al. (2018) where a value of <0.3 is used as the threshold for a good fit and a reasonable interpretation. The analysis was conducted on the full beetle species dataset, with species aggregated per oak.

To see the effect of treatment on species composition we used a canonical correspondence analysis (CCA). We started by running a detrended correspondence analysis (DCA) with the decorana function from the vegan package (Oksanen et al., 2019). The DCA including treatment showed that the length of the first axis is equal to two SD units, and we therefore proceeded to a unimodal test with a CCA (Borcard et al., 2011; Lepš & Šmilauer, 2003). The species data set was used as the dependent variable, and treatment (the three factorials, HR, MR, and NR) was set as the explanatory variable. To obtain the total explained variation for each axis, we compared eigenvalues with the total inertia. The full CCA model and each axis were tested using ANOVA. Ordination plots were produced from the ggplot2 package by extracting the CCA axis values (v3.4.0; Wickham, 2016) and with the basic R plotting function from the vegan package (Oksanen et al., 2019). Plotting all species in the graph made the plot too hard to read. This was solved by using the function orditorp, which automatically adds labels, prioritizing species with higher frequencies.

Oak vitality and abiotic variables

Vitality variables for each oak were averaged at the treatment level and the means were compared in a linear mixed model (LMM) with treatment (fixed) and block (random) as explanatory variables. The proportion of dead wood followed a sigmoidal distribution and was then square root and arcsin transformed for the analyses. The abiotic variables (air temperature and light) were measured and calculated for the two extreme treatments, High Release and No Release. The mean values per oak were calculated, then averaged per treatment for each year. Treatment-related differences in the response variables light and temperature per oak each year were tested using a linear mixed model (LMM) with year as a fixed factor and block as a random factor.

RESULTS

Insect sampling

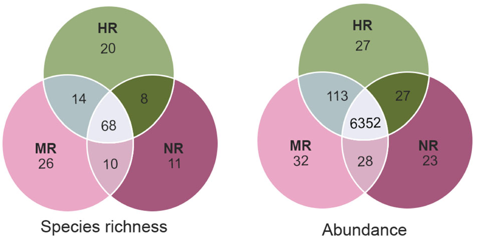
A total of 6602 saproxylic beetles representing 157 different species were sampled across both years, where 2285 individuals were found in high release (HR), 2215 in medium release (MR), and 2102 in no release (NR) trees. A total of 4249 beetles were found in 2018 and 2353 in 2019, belonging to 120 and 115 different species, respectively (Figure 4). In 2018, the most abundant species was *Quedius mesomelinus*, a facultative saproxylic beetle from group II (associated with both on oak and Norway spruce), with a total of 1803 individuals. In 2019, the most abundant species was *Cychramus luteus*, a facultative saproxylic species from group III (not associated with oak), with 647 individuals. Forty-three species (27% of all species) were represented by only one individual (Appendix 1).

Abundance, species richness, species composition

The abundance was similar in all treatments when all species were included (Table 1). When host tree association was considered, two groups showed treatment-related differences in abundance, Group I (both oak and spruce) ($p < 0.001$; Table 1) and group I + II (associated with oak) ($p < 0.05$; Table 1), whereas group II (associated with oak but not Norway spruce) and group III (species not associated with oak) showed no significant difference between treatments (Table 1).

The mean number of different species found at each oak differed significantly between treatments ($p < 0.001$; Table 2). The released oaks had more species than the control. When considering each group separately, only group I + II (associated with oak), had significantly more species at HR and MR compared to NR ($p < 0.05$; Table 2, Appendix 3).

Species composition significantly differed between HR and NR treatments (PERMANOVA, $F_{2/28} = 1.844$, $p = 0.009$, $r^2 = 0.116$). The analysed species composition at the individual oak level in the NMDS resulted in a stress level of 0.24. The NMDS ordination of the saproxylic beetles for the three treatments revealed a cluster for NR sample plots, indicating similarities in species composition among these oaks (Appendix 4). In contrast, HR and MR stands were more widely distributed, indicating less distinctive community compositions separating these treatments. There was a larger variation in the communities in HR and MR compared to NR, as they take up more of the ordination space (Appendix 4).



Species richness Abundance

FIGURE 4 The left Venn diagram shows the number of different species appearing in each treatment. It shows the number of species of saproxylic beetles unique to a treatment or shared by two or three treatments, HR (High release), MR (Medium release), and NR (No release). The right Venn diagram shows the number of individuals in each pool of species. For example, in MR, there are 26 exclusive species only appearing in that treatment, and altogether they represent 32 individuals. In HR, there are 20 exclusive species only occurring in HR, altogether representing 27 individuals. Dataset includes both years (2018 and 2019). In total, 6602 individuals of 157 different saproxylic beetle species were sampled.

The detrended correspondence analysis (DCA) showed that the length of the first axis is equal to two SD units (Appendix 5); we therefore proceeded to a unimodal test with a canonical correspondence analysis (CCA). The constrained axes (treatments) of the CCA explained 8.3% of the variation in the model, and 91.15% of the variation was explained by unconstrained axes (ANOVA, $\chi^2 = 0.123$, $p = 0.009$) (Appendix 5). The ordination diagram (Figure 5) shows the species association with the different treatments. It indicated that a larger proportion (CCA1, 5.98%, $F = 1.837$, $\chi^2 = 0.083$, $p = 0.007$) of variation in species communities was explained by differences between communities in these treatments compared to the MR treatment, which was mainly explained by the y-axis (CCA2, $F = 0.880$, $\chi^2 = 0.040$, 2.98%, $p = 0.717$).

Some beetle species were clearly associated with the NR treatment (right/bottom), such as *Denticollis linearis* (3 ind.), *Trypodendron lineatum* (11), and *Trypodendron domesticum* (38). The other species aggregated at the bottom left of the ordination, including *Dasytes niger* (29), *Calambus bipustulatus* (3), a near threatened (NT) species, *Cetonia aurata* (6), and *Clytus arietis* (5) were associated with the HR treatment. Some species were clearly associated with the MR treatment such as *Hapalarea melanocephala* (3), *Polygraphus poligraphus* (5), and *Soronia punctatissima* (7). However, some beetle species located in the centre of the plot were not clearly distinguished between the treatments. These beetle species were recorded at a high or relatively high frequency throughout the survey. The pool of common species was similar in all three treatments and dominated by *Quedius mesomelinus*, *Cychramus luteus*, *Anaspis rufilabris*, *Cryptophagus scanicus*, and *Dasytes plumbeus*. A total of 57 species were found in only one of the treatments (Figure 4, Appendix 1).

TABLE 1 Results from the negative binomial generalized linear mixed model (GLMM) of saproxylic beetle abundance, as well as the mean and standard error (SE) per oak in each treatment for each beetle group

ABUNDANCE	Year			Treatment			High release			Medium release			No release		
Beetles	Chisq	DF	*p*	Chisq	DF	*p*	Mean	SE	Group	Mean	SE	Group	Mean	SE	Group
All	82.66	1	**0.000**	4.09	2	0.129	97.2	7.3	-	92.3	7.1	-	83.8	6.5	-
Group I	5.18	1	**0.023**	13.50	2	**0.001**	15.8	1.8	**a**	10.9	1.3	**b**	9.6	1.2	**b**
Group II	166.27	1	**0.000**	2.89	2	0.236	52.1	4.3	-	48.6	4.2	-	43.7	3.8	-
Group III	13.65	1	**0.000**	0.28	2	0.870	25.7	2.6	-	27.0	2.7	-	27.0	2.7	-
Group I + II	139.64	1	**0.000**	6.00	2	**0.050**	68.7	5.5	**a**	60.4	5.1	**b**	54.3	4.6	**c**

Note: High release (HR) consisted of removing all Norway spruce under and 2 m beyond the crown of the oak; medium release (MR) consisted of removing the Norway spruce directly under the oak's crown; and no received no treatment other than normal thinning and used as control. "All" included all individuals found during the experiment. Significant p-values are shown in bold. If significant, the results of the Kenward–Roger post-hoc test are illustrated with letters. Means sharing a letter are not significantly different from each other at $p \leq 0.05$. Group I saproxylic species associated with oak and Norway spruce. Group II saproxylic species associated with oak but NOT with Norway spruce. Group III saproxylic species not associated with oak. Group I+ II saproxylic species associated with oak.

TABLE 2 Results from the Generalized Linear Model (GLM) with saproxylic beetles species richness and the mean and standard error (SE) per oak in each treatment High release (HR) consisted of removing all Norway spruce under and 2 m beyond the crown of the oak; medium release (MR) consisted of removing the Norway spruce directly under the oak's crown; and no treatment other than normal thinning and used as control

SP. RICHNESS	Year			Abundance			Treatment			High release			Medium release			No release		
Beetles	Chisq	DF	*p*	Chisq	DF	*p*	Chisq	DF	*p*	Mean	SE	Group	Mean	SE	Group	Mean	SE	Group
All	0.04	1	0.837	13.09	1	**0.000**	10.49	2	**0.005**	23.50	1.17	a	23.30	1.21	a	19.20	1.09	b
Group I	6.18	1	**0.013**	31.14	1	**0.000**	2.99	2	0.224	6.62	0.56	-	7.50	0.62	-	6.07	0.57	-
Group II	3.23	1	**0.072**	7.21	1	**0.007**	2.97	2	0.226	9.39	0.74	-	9.31	0.77	-	7.94	0.70	-
Group III	2.14	1	0.143	3.91	1	**0.048**	3.64	2	0.162	6.56	0.55	-	6.55	0.57	-	5.27	0.51	-
Group I + II	0.85	1	0.356	12.70	1	**0.000**	6.97	2	**0.031**	16.90	0.99	a	16.70	1.02	a	13.90	0.92	b

Note: "All" included all species found during the experiment (157 species). Significant *p*-values are shown in bold. If significant, the results of the Kenward–Roger post-hoc test are illustrated with letters; means sharing a letter are not significantly different from each other. Group I saproxylic species associated with oak and Norway spruce. Group II saproxylic species associated with oak but NOT with Norway spruce. Group III saproxylic species not associated with oak. Group I+ II saproxylic species associated with oak.

Oak vitality and abiotic factors

The oak crowns grew 16–17 times more when released (HR and MR) compared to the non-released treatment (NR) (Table 3). The highest proportion of dead branches was in the NR treatment (39% ± 3.26 SE) and the lowest was in the HR treatment (23.8% ± 3.09 SE). Both the mean proportion of dead branches and canopy growth were affected by treatment ($p < 0.01$; Table 3). The thickest dead branch size did not significantly differ between treatments ($p = 0.149$; Table 3).

Temperature differed between treatments (Table 3) and sampling years (ANOVA, $F_{1/29,141} = 3557.07$, $p < 0.001$). The temperature was higher in HR oaks than NR oaks, and the year 2018 was warmer than 2019 (Table 3). Light differed significantly between treatments, with double lux values for HR versus NR (Table 3). Light did not differ significantly between 2018 and 2019 (Table 3).

DISCUSSION

In this study, we tested two main hypotheses concerning the long-lasting effects of gap creation on (1) oak vitality and abiotic factors and (2) abundance, species richness, and species composition of saproxylic beetles. Both main hypotheses were supported by the data. Ten years after the release, tree vitality was slightly higher in released oaks than in unreleased oaks, and it was warmer and lighter around the released oaks. More beetle individuals and more species of oak-associated saproxylic beetles were trapped on released versus unreleased oaks and species composition differed between treatments. These results are novel and have important implications for management of beetle diversity with different light preferences over time in planted conifer stands.

Different indices of vitality have been used to document that gap cutting improves oak vitality (Gálhidy et al., 2006; Götmark, 2009; Harrington & Warren, 2006; Lariviere et al., 2020; Shifley, 2004). We used crown growth and proportion of dead branches and showed that the oak crown was growing and colonizing the gap when released, while unreleased oaks had higher proportion of dead wood. Götmark (2009) used dead wood in the crowns as a negative predictor of growth and also found that the openness around the oak crown was a positive predictor for oak growth. In addition, he showed a positive effect of release on oak basal area, which we did not find. However, these external cues for oak vitality still cannot address the complete picture of the oaks' response to the release. Other studies are emphasizing the potential negative effects thinning may have on oak vitality (Bergquist & Isacsson, 2002; Drobyshev et al., 2019). Drobyshev et al. (2019) used dendrochronological methods to show that oak growth is negatively correlated with the amount of dead oak crown but is positively related to oak age. They argue that summer drought could potentially be a negative factor for older oaks. Oak responses to thinning are generally positive and gap cutting will reduce the risk of mechanical damage to the tree from potential regrowth as well as reduce competition for water, light, and nutrients, which are factors that can trigger oak death (Andersson et al., 2011).

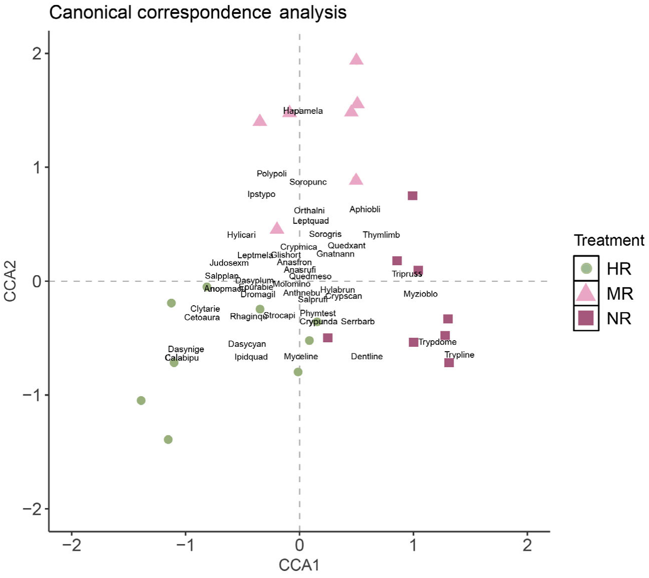


FIGURE 5 Biplot from the canonical correspondence analysis (CCA) of saproxylic beetle composition around 31 oaks in different release treatments. The plot shows the two first axes from the CCA and specific species association with three different gap treatments around the oaks (HR, high release; MR, medium release and NR, no release). The biplot only represent oaks that are within the x and y limit. Only species with the highest overall frequency are presented in the plot. Singletons were therefore excluded. The full species list is available in Appendix 1.

TABLE 3 Relationship between release treatments and different environmental variables

					High release		Medium release		No release		ANOVA		
Variable	*n*	Transf.	Year	Unit	Mean	SE	Mean	SE	Mean	SE	*F*	Df, dendf	*p*
Thickest DB (cm)	31	NT	2018	cm	17.50	1.80	19.00	1.91	22.70	1.91	2.038	2/28	0.149
Dead wood (%)	31	Arcsin(sqrt)	2018	%	23.80	3.09	27.90	3.26	39.00	3.26	5.6216	2/28	**0.007**
Crown area 2018	31	log	2018	m^2	66.10	10.27	63.70	10.44	40.20	6.59	3.278	2/19.54	0.059
Crown growth	31	NT	2018	m^2	24.46	5.12	22.86	5.40	1.43	5.40	6.065	2/19.64	**0.009**
DBH	31	log	2018	mm	624.00	38.30	607.00	39.30	546.00	34.40	1.278	2/18.21	0.303
Height	31	NT	2018	m	23.80	0.83	22.30	0.87	22.90	0.87	0.953	2/19.31	0.403
Temperature	44	NT	2018/2019	°C	16.10	0.08			15.80	0.08	26.201	1/29.52	**0.000**
Light	44	log	2018/2019	Lux	842.00	145.90			399.00	71.30	24.689	1/29.97	**0.000**

Note: The table shows the mean and its standard errors (SE) for three different release treatments of retained oak trees in a Norway spruce stand (high release, HR; medium release, MR; and no release, NR). Temperature and light were only measured in the two extremes treatment HR and NR. Transformed variables are mentioned in the Transf. column where NT = Not transformed, Arcsin(sqrt) = Arcsine square root transformed and log = log10 transformed. The table also shows the *F*-value (*F*), degrees of freedom (df), denominator df (dendf) and *p*-value (*p*). *p*-values from the ANOVA in bold are significant ($p < 0.05$). Thickest DB = diameter of the thickest dead branch (cm), Dead wood = proportion of dead wood in the oak, Crown area = size of the crown in square metre, Crown growth = difference in crown area between 2008 and 2018, DBH = diameter at breast height (mm), Height = height of the focal oak (m).

In our study, the amount of dead wood was lower in the released than unreleased oaks, whereas the species richness and abundance of certain beetle groups were higher. This indicates that dead wood quantity is not always a good predictor or the only predictor of saproxylic beetle diversity. Müller et al. (2015) concluded that dead wood indeed plays a crucial role in saproxylic beetle diversity, but that temperature was also an important driver. Increasing temperature may even compensate for poor habitat conditions in production forests (Bouget et al., 2013; Müller et al., 2015).

We showed that still 10 years after gap-cutting the amount of light reaching the oak trunks was greater for released compared to the non-released oaks. The amount of light reaching the oak is a key factor for saproxylic oak-associated beetles. It promotes the development of a microclimatic variability within the oak crown, bark, trunk, and other structures that are important for saproxylic beetles (Ranius & Jansson, 2000; Seibold et al., 2018). Active management, such as release cutting, can modify these environmental variables to the benefit of the oak itself and its attached conservation value (Gough et al., 2014). Several studies have shown that light is essential for many species associated with oak trees (Bouget et al., 2013; Härdtle et al., 2003; Horak et al., 2014; Jonsell et al., 1998). Shade-intolerant trees, like oaks (*Quercus* spp.), will support species adapted to open, light, and warm conditions and appear to harbour more beetle species dependent on high levels of insolation than more shade-tolerant tree species (Horak et al., 2014; Jonsell et al., 1998; Ranius & Jansson, 2000). Lindhe et al. (2005) showed that high oak stumps have much larger proportions of species favoured by exposed conditions than Norway spruce, which is in accordance with the positive effect of release we found for beetle groups associated with oak. Gran and Götmark (2019) found more saproxylic beetles species following thinning in an oak-dominated mixed forest. This increase was likely due to both increased sun exposure and the addition of new dead wood from the oak. In agreement with Gran and Götmark (2019), we speculate that together with higher insolation, the released oaks provide a more continuous supply of sunny substrates than unreleased oaks. Widerberg et al. (2012) found a positive relationship between the diameter of the thickest dead branch and species richness of oak-associated beetles, which we did not find. Their study did not have an experimental setup with treatments, but instead used a gradient from small to large gaps where the large gaps extended 3–8 m outside the crown edge. They, thus, had much larger gaps than in our study, possibly allowing for high amounts of sun-exposed coarse dead wood.

There were clear differences in temperature between the two sampling years, with 2018 being warmer than 2019. In fact, 2018 was one of the warmest summers ever recorded in southern Sweden (Langvall, 2021). The abundance, species richness, and species composition of beetles differed between years. The higher abundance in 2018 was probably due to higher flight activity and more days with temperatures above the flight threshold, which can increase the number of beetles trapped in a season. Faster insect development, leading to multiple generations of some species might have also played a role (Ratte, 1984; Zaslavski, 1988). The differences in species composition between years were an effect of longer species lists and more year-specific species in 2018 than in 2019. Temperature, as a result of differences in insolation, differed between treatments, and consequently, the window traps on the warmer and sunnier released oaks had a higher flight activity than shaded control oaks. Thus, the trap catches do not only depend on the number of beetles attracted to an oak but also the amount of time they spend flying there (Bouget et al., 2014). In our analyses, we controlled for this by including abundance as a covariate in the analysis of species richness, and found that control oaks (NR) still had lower species richness compared to released oaks for the group I (both oak and spruce) and group I + II (using oaks during at least part of their life cycle).

The species composition differed clearly between the HR and NR treatments. We found patterns in species composition that relate to the life history of some species. For instance, *Trypodendron* spp. probably have an affinity for NR oaks; they are so-called ambrosia beetles that depend on a sufficiently moist microclimate to cultivate ambrosia fungus for their larvae. The HR treatment was characterized by the presence of species that breed in the wood of broadleaf trees and visit flowers for pollen or nectar. For example, *Clytus arietis* is a wasp-mimicking longhorn beetle with adults that visit flowers. Adults of the scarabid *Cetonia aurata* feed on pollen and nectar and were only found in the released treatments. We also found red listed species in the released oaks, such as *Dryophthorus corticalis* (Vulnerable (VU)) and *Calambus bipustulatus* (Near Threatened (NT)), which are associated with broadleaf trees. We did not further explore any possible causal links between species composition among trapped beetles and the local stand structure, but it is clear that the creation of a gap in the forest alters many biotic and abiotic factors, which may affect species composition even at a small spatial scale.

Our findings add to those by Widerberg et al. (2012), who showed that even 3 years post-treatment the diversity and abundance of oak-associated beetles was positively affected by the release (Widerberg et al., 2012). We found that 10 years after there was still a positive effect of the release treatment on the diversity and abundance of oak-associated beetles, and a change in beetle species composition. We added a temporal dimension to the efficiency of oak release and showed a long-lasting targeted effect of release management over time. In contrast, Toivanen and Kotiaho (2010) found that the positive effect of partial cutting on saproxylic beetles in coniferous forests had disappeared after 2 years, probably because the dead wood resource was rapidly exhausted. If the oaks remain healthy, they may provide long-lasting habitats (crown, trunk) for saproxylic beetles. The present study, together with Koch Widerberg (2013) and our earlier study (Lariviere et al., 2020), contributes to the understanding of how saproxylic beetle species richness, abundance, and assemblages are linked to environmental conditions over time.

Since our study was only done in one site, general conclusions should be made carefully. We have avoided to draw any conclusions on effects on beetle populations at a larger scale than the local stand. However, we argue that the experiment was appropriate for evaluating the long-term effect of gap-cutting since the stand is a good representation of a fertile mixed oak/Norway spruce forest typically found in southern Sweden. There is a possibility that the oaks we studied responded quickly because of high site fertility, enabling the trees to fill the gaps faster than oaks would have done on a poorer site. Therefore, more studies conducted on less fertile sites are needed. No other study has addressed this question with an experimental design similar to ours and long-term studies on ecological succession are relatively rare. A space-for-time substitution (chronosequence) is often used, which is handy, but has several disadvantages compared to long-term studies and may even lead to incorrect conclusions (Walker et al., 2010).

CONCLUSIONS

Healthy oaks provide dead branches and hollow wood for a longer time than suppressed dying oaks, and if well managed, a high proportion of the dead wood will be sun-exposed and serve as a valuable habitat for saproxylic beetles. Thus, it is important to maintain and conserve oaks through several rotations in commercial plantations. Forest management practices, for instance thinning, can create favourable conditions for retained trees and species associated with them. Even only moderate release (MR), removing a few trees growing underneath the oak crown, can sustain biological values within the stand. It is important to consider not only the overall quantity of dead wood but also the quantity of sun-exposed dead wood in conservation measures directed towards saproxylic oak beetles. We suggest to avoid planting crop trees beneath retained oaks when regenerating conifer forests and to proceed with conservation management during subsequent thinning by removing regeneration under the oak crown. We emphasize the benefits of monitoring the retained oak to maintain tree vitality, habitat quality and insolation.

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CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

DATA AVAILABILITY STATEMENT

Data available on request from the authors

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Supporting Information

How to cite this article: Lariviere, D., Holmström, E., Petersson, L., Djupström, L. & Weslien, J. (2023) Ten years after: Release cutting around old oaks still affects oak vitality and saproxylic beetles in a Norway spruce stand. *Agricultural and Forest Entomology*, 1–11. Available from: https://doi.org/10.1111/afe.12563

Supplementary material Paper II

APPENDIX 1: List of saproxylic beetle species found in 2018 and/or 2019. The lists show the family they belong to, their IUCN classification (if any), their abundance and their group (Gr.). Group I species are associated with both oak and spruce, Group II species are associated with oak and not spruce and Group III beetles are not associated with oak. HR = High release, MR= Medium release and NR= No release. Species are ordered by group and abundance (the number of individuals found). The HR, MR and NR columns indicate the total number of individuals captured in each treatment. A X in the column Pic indicate that the species has occured on Norway spruce according to Dahlberg and Stokland. A X in the column Que indicate that the species has occured on Oak according to Dahlberg and Stokland.

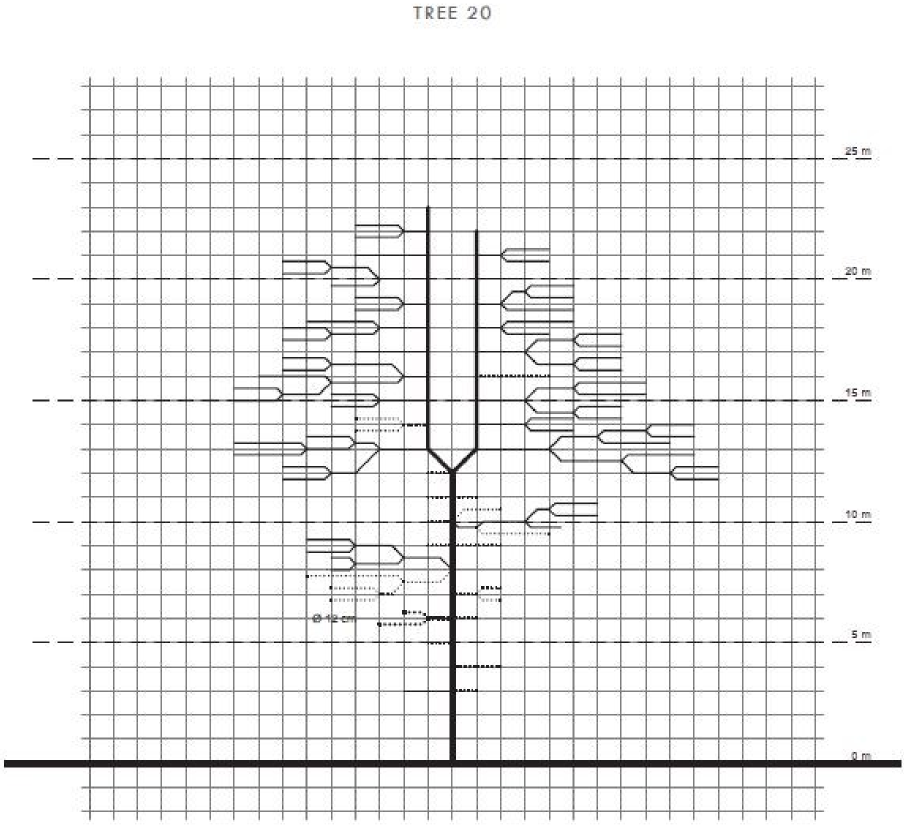
Latin	**Family**	**UICN**	**Gr.**	**HR**	**MR**	**NR**	**Pic**	**Que**
Strophosoma capitatum	Curculionidae		I	107	44	120	X	X
Dromius agilis	Carabidae		I	50	22	16	X	X
Anaspis frontalis	Scraptiidae		I	27	28	20	X	X
Enicmus rugosus	Latridiidae		I	22	23	12	X	X
Anoplodera maculicornis	Cerambycidae		I	22	9	1	X	X
Salpingus ruficollis	Salpingidae		I	17	11	16	X	X
Anthribus nebulosus	Anthribidae		I	16	11	16	X	X
Alosterna tabacicolor	Cerambycidae		I	11	13	11	X	X
Schizotus pectinicornis	Pyrochroidae		I	10	5	3	X	X
Rhagium inquisitor	Cerambycidae		I	8	2	2	X	X
Melanotus erythropus	Elateridae	VU	I	7	6	7	X	X
Ampedus nigrinus	Elateridae		I	6	7	0	X	X
Leptura melanura	Cerambycidae		I	6	5	1	X	X
Quedius xanthopus	Staphylinidae		I	5	20	15	X	X
Thanasimus formicarius	Cleridae		I	4	6	4	X	X
Rhizophagus bipustulatus	Monotomidae		I	4	4	7	X	X
Megatoma undata	Dermestidae		I	4	3	3	X	X
Rhyncolus sculpturatus	Curculionidae		I	3	5	1	X	X
Rhagium mordax	Cerambycidae		I	3	4	2	X	X
Gabrius splendidulus	Staphylinidae		I	3	2	1	X	X
Glischrochilus quadripunctatus	Nitidulidae		I	3	1	2	X	X
Ipidia quadriplagiata	Nitidulidae		I	3	0	1	X	X
Orthocis alni	Ciidae		I	2	6	2	X	X
Leptura quadrifasciata	Cerambycidae		I	2	5	2	X	X
Dorcatoma dresdensis	Ptinidae		I	2	2	0	X	X
Orchesia micans	Melandryidae		I	2	0	2	X	X
Cerylon ferrugineum	Cerylonidae		I	1	5	2	X	X
Aplocnemus nigricornis	Melyridae		I	1	2	2	X	X
Rhizophagus dispar	Monotomidae		I	1	2	2	X	X
Hylobius abietis	Curculionidae		I	1	2	0	X	X
Corticaria rubripes	Latridiidae		I	1	0	2	X	X
Denticollis linearis	Elateridae		I	1	0	2	X	X
Bibloporus bicolor	Staphylinidae		I	1	0	1	X	X
Cartodere constricta	Latridiidae		I	1	0	0	X	X
Dromius fenestratus	Carabidae		I	1	0	0	X	X
Dryophthorus corticalis	Dryophthoridae	VU	I	1	0	0	X	X

Grynocharis oblonga	Trogossitidae		I	1	0	0	X	X
Oxymirus cursor	Cerambycidae		I	1	0	0	X	X
Aphidecta obliterata	Coccinellidae		I	0	3	2	X	X
Latridius hirtus	Latridiidae		I	0	2	0	X	X
Agathidium nigripenne	Leiodidae		I	0	1	1	X	X
Cerylon histeroides	Cerylonidae		I	0	1	0	X	X
Hallomenus binotatus	Tetratomidae		I	0	1	0	X	X
Leptusa pulchella	Staphylinidae		I	0	1	0	X	X
Quedius plagiatus	Staphylinidae		I	0	1	0	X	X
Rhizophagus nitidulus	Monotomidae		I	0	0	2	X	X
Agathidium seminulum	Leiodidae		I	0	0	1	X	X
Quedius mesomelinus	Staphylinidae		II	588	694	636		X
Dasytes plumbeus	Melyridae		II	210	125	48		X
Anaspis rufilabris	Scraptiidae		II	202	199	159		X
Cryptophagus scanicus	Cryptophagidae		II	124	124	226		X
Dasytes niger	Melyridae		II	28	1	0		X
Scolytus intricatus	Curculionidae		II	17	8	3		X
Dasytes cyaneus	Melyridae		II	14	2	4		X
Cryptarcha strigata	Nitidulidae		II	12	9	5		X
Glischrochilus hortensis	Nitidulidae		II	12	14	11		X
Conopalpus testaceus	Melandryidae		II	11	11	1		X
Pachygluta ruficollis	Staphylinidae		II	9	10	10		X
Dacne bipustulata	Erotylidae		II	8	3	1		X
Leiopus nebulosus	Cerambycidae		II	7	5	3		X
Malthinus flaveolus	Cantharidae		II	7	3	2		X
Phymatodes testaceus	Cerambycidae		II	7	3	7		X
Anaspis thoracica	Scraptiidae		II	6	6	5		X
Cryptarcha undata	Nitidulidae		II	6	2	7		X
Cryptophagus dentatus	Cryptophagidae		II	5	7	0		X
Cychramus variegatus	Nitidulidae		II	5	8	7		X
Enicmus testaceus	Latridiidae		II	5	23	12		X
Clytus arietis	Cerambycidae		II	4	1	0		X
Gnathoncus nannetensis	Histeridae		II	4	9	8		X
Mycetochara linearis	Tenebrionidae		II	4	0	3		X
Orchesia undulata	Melandryidae		II	4	7	6		X
Calambus bipustulatus	Elateridae	NT	II	3	0	0		X
Trichius fasciatus	Scarabaeidae		II	3	2	0		X
Agrilus biguttatus	Buprestidae		II	2	0	0		X
Ctesias serra	Dermestidae		II	2	1	3		X
Lordithon lunulatus	Staphylinidae		II	2	2	2		X
Mycetochara flavipes	Tenebrionidae		II	2	0	0		X
Quedius brevicornis	Staphylinidae		II	2	1	2		X
Salpingus planirostris	Salpingidae		II	2	1	0		X
Soronia grisea	Nitidulidae		II	2	5	5		X
Trypodendron domesticum	Curculionidae		II	2	2	34		X
Attagenus pellio	Dermestidae		II	1	0	1		X

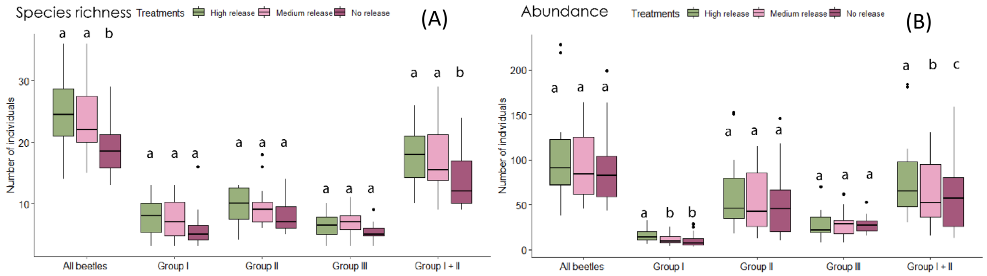
Cis micans	Ciidae	II	1	0	1		X
Dromius quadrimaculatus	Carabidae	II	1	0	0		X
Hapalarea floralis	Staphylinidae	II	1	0	0		X
Quedius scitus	Staphylinidae	II	1	0	0		X
Rabocerus foveolatus	Salpingidae	II	1	4	1		X
Saperda scalaris	Cerambycidae	II	1	1	0		X
Sinodendron cylindricum	Lucanidae	II	1	5	0		X
Soronia punctatissima	Nitidulidae	II	1	5	1		X
Velleius dilatatus	Staphylinidae	II	1	2	1		X
Agathidium confusum	Leiodidae	II	0	1	0		X
Agathidium pisanum	Leiodidae	II	0	1	0		X
Agathidium varians	Leiodidae	II	0	0	1		X
Ampedus pomorum	Elateridae	II	0	2	0		X
Anisotoma axillaris	Leiodidae	II	0	1	1		X
Anobium nitidum	Ptinidae	II	0	0	1		X
Diaperis boleti	Tenebrionidae	II	0	2	0		X
Dorcatoma chrysomelina	Ptinidae	II	0	1	0		X
Epuraea guttata	Nitidulidae	II	0	1	0		X
Hapalarea melanocephala	Staphylinidae	II	0	3	0		X
Haploglossa villosula	Staphylinidae	II	0	1	0		X
Leptusa fumida	Staphylinidae	II	0	0	1		X
Magdalis cerasi	Curculionidae	II	0	0	1		X
Nemadus colonoides	Leiodidae	II	0	1	0		X
Prionocyphon serricornis	Scirtidae	II	0	1	1		X
Thymalus limbatus	Trogossitidae	II	0	2	2		X
Triplax russica	Erotylidae	II	0	1	2		X
Cychramus luteus	Nitidulidae	III	216	287	277		
Molorchus minor	Cerambycidae	III	121	88	77	X	
Athous subfuscus	Elateridae	III	83	84	72	X	
Hylastes brunneus	Curculionidae	III	57	62	99	X	
Melanotus castanipes	Elateridae	III	25	18	13		
Polydrusus cervinus	Curculionidae	III	18	9	6		
Cryptophagus micaceus	Cryptophagidae	III	16	24	13		
Judolia sexmaculata	Cerambycidae	III	11	7	0	X	
Hylis cariniceps	Eucnemidae	III	8	9	1	X	
Cetonia aurata	Scarabaeidae	III	5	1	0		
Pityogenes chalcographus	Curculionidae	III	5	3	1	X	
Aleochara moerens	Staphylinidae	III	4	1	1		
Epuraea abietina	Nitidulidae	III	4	2	1	X	
Cryptophagus abietis	Cryptophagidae	III	2	1	3	X	
Ernobius angusticollis	Ptinidae	III	2	0	0	X	
Pityophagus ferrugineus	Nitidulidae	III	2	0	0	X	
Sericus brunneus	Elateridae	III	2	0	0	X	
Serropalpus barbatus	Melandryidae	III	2	2	4	X	
Ampedus tristis	Elateridae	III	1	0	0	X	
Anaspis flava	Scraptiidae	III	1	0	0		

Anidorus nigrinus	Aderidae	III	1	0	0	
Anthrenus museorum	Dermestidae	III	1	0	0	
Cortinicara gibbosa	Latridiidae	III	1	3	0	X
Ips typographus	Curculionidae	III	1	2	0	X
Nemozoma elongatum	Trogossitidae	III	1	0	0	
Polygraphus poligraphus	Curculionidae	III	1	3	1	X
Rhyncolus ater	Curculionidae	III	1	4	2	X
Triplax aenea	Erotylidae	III	1	0	0	
Anatis ocellata	Coccinellidae	III	0	1	1	
Anobium thomsoni	Ptinidae	III	0	1	0	X
Bolitophagus reticulatus	Tenebrionidae	III	0	1	0	
Corticaria foveola	Latridiidae	III	0	1	1	X
Cryphalus abietis	Curculionidae	III	0	0	2	X
Dorcatoma robusta	Ptinidae	III	0	1	0	
Dryocoetes autographus	Curculionidae	III	0	0	1	X
Epuraea aestiva	Nitidulidae	III	0	2	0	
Euplectus sanguineus	Staphylinidae	III	0	0	1	
Hapalarea linearis	Staphylinidae	III	0	1	0	X
Hylis procerulus	Eucnemidae	III	0	1	0	X
Magdalis ruficornis	Curculionidae	III	0	1	0	
Malthinus biguttatus	Cantharidae	III	0	1	0	
Microrhagus lepidus	Eucnemidae	III	0	1	0	
Mycetochara axillaris	Tenebrionidae	III	0	1	0	
Myzia oblongoguttata	Coccinellidae	III	0	1	3	X
Phloeotribus spinulosus	Curculionidae	III	0	1	1	X
Silvanoprus fagi	Silvanidae	III	0	0	1	X
Tetropium castaneum	Cerambycidae	III	0	1	0	X
Thanasimus femoralis	Cleridae	III	0	1	0	X
Trypodendron lineatum	Curculionidae	III	0	0	11	X

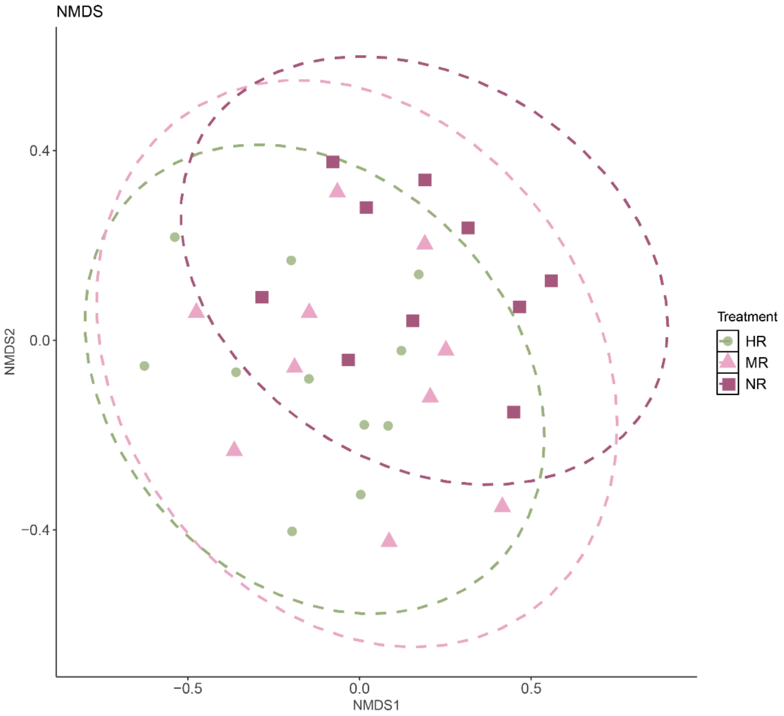
APPENDIX 2: Example of a 2D drawing used to determine dead wood proportion in the crown of the focal oaks. Dotted lines represent dead branches and black lines represent living branches. The drawing is not to scale.



APPENDIX 3: Median (black lines) species richness (A) and abundance (B) per oak per year (n = 66) according to treatment for different beetle group. The boxplot shows the distribution of the data and the black horizontal line shows the median value among blocks in the data set. Whiskers above and below the boxes indicate the 10th and 90th percentiles. Points above and below the whiskers indicate outliers outside the 10th and 90th percentiles. The letters indicate significant pairwise differences of means among treatments within beetle groups (Kenward-roger post-hoc test).

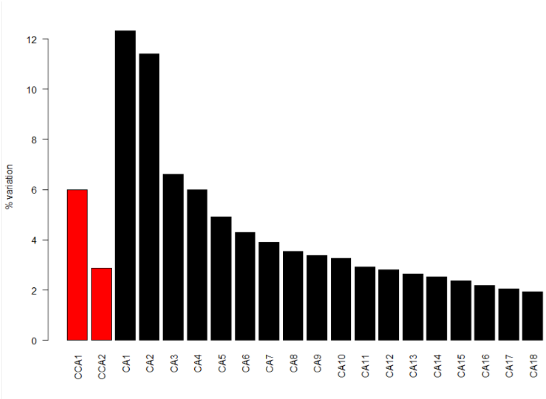


APPENDIX 4: NMDS plots of the 31 oaks surveyed in the experiment. The plot shows the delimitation of the beetle community according to each treatment (HR: High Release, MR: Medium Release and NR: No Release). The stress value was 0.238.



APPENDIX 5: Results from the canonical correspondence analysis (CCA) with treatments as explanatory variables. Inertia is mean squared contingency coefficient. "Total Inertia" is the total variance in species distributions. "Constrained Inertia" is the variance explained by the environmental variables."Proportion" represent the percentages of variance of species distributions explained by Constrained and Unconstrained variables. Eigenvalues of constrained and unconstrained axes represent the amount of variance explained by each CCA axis. The graphic below shows the amount of variation explained by both constrained (red) and unconstrained axes (black).

CCA	**Inertia**	**Proportion**	**Rank**				
Total	1.38743	1.0000					
Constrained	0.12273	0.08846	2				
Unconstrained	1.26470	0.91154	28				
Eigenvalues for constrained axes	CCA1	CCA2					
	0.08300	0.03973					
Eigenvalues for unconstrained axes	CA1	CA2	CA3	CA4	CA5	CA6	CA7	CA8
8/28	0.17091	0.15815	0.09175	0.08300	0.06807	0.05971	0.05405	0.04910



ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

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This thesis aimed to evaluate how choices in forest management can contribute to biodiversity, with the example of tree retention in thinnings or through the choice of rotation length. The release of old oaks while thinning a Norway spruce stand increased oak vitality and species richness of both plant and saproxylic beetles without impacting stand production. Age of conventionally managed conifer stands without tree retention, affects the number of unique species, species richness, and species composition. This thesis also includes the exploration of a remote sensing method to locate retention trees in pre-thinning conifer stands to help planning forest operations and maintain retention through multiple rotations.

Delphine Lariviere received her first MSc in Ecology and Biodiversity Management from Montpellier University, France, and second MSc in Conservation Biology from Lund University, at the department of Ecology in Lund, Sweden. Her undergraduate degree is from Lille University, France.

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