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The forgotten forest

On thinning, retention, and biodiversity in the boreal forest

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Abstract

Fennoscandia has had a long history of intensive forest management. It can therefore be regarded a trial zone for other boreal regions which are still largely unaffected by forestry. In Fennoscandia, forestry has resulted in many threatened species and methods that maintain biodiversity have therefore been called for. Retention forestry, where parts of the forest and structural elements key to biodiversity are retained, have here been introduced to the final felling stage. However, for intermediate stages such as forest thinning, few such methods have been suggested and none have been tested experimentally. I therefore performed empiric and experimental studies investigating the effects of current and alternative forest thinning routines on biodiversity and the breeding success and occurrence of singular species, in two study locations in Sweden. I show that conventional thinning reduces the forests structural complexity and has a strong influence on the species composition and richness of forest-dwelling birds and epiphytic lichens in young managed forests typical for Fennoscandia. This influence was largely negative for forest-dwelling birds at least in the short term, but under certain conditions positive for epiphytic lichens. Adjusting conventional forest thinning towards a retention forestry approach will according to my thesis likely result in a higher biodiversity in these forests compared to what is practice today. This can be achieved if (i) either the understory vegetation below 3-5 m above ground on the whole stand or (ii) entire plots of ca. 1 ha are retained, (iii) an even and rich tree species composition is re-established, and (iv) more large-diameter trees are spared. The Siberian jay is considered indicative of the effect of thinning on bird species relying on a complex forest vegetation. In a habitat suitability model, I provide detailed spatial information on where thinning can increase or decrease the jay's breeding success, based on the distance of a forest to human settlements. These findings help fill the research gap for young managed boreal forests, which in Fennoscandia comprise 60% of all managed stands. Therefore, this thesis adds novel and essential points to the guidelines for managers and policy makers that wish to combine biomass production with environmental commitments in the boreal forest.

Keywords: thinning, forest, boreal, bird, lichen, biodiversity, retention, Bayesian, management, Siberian jay

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Dedication

For my brother Dominic.

> Your life's obstacles impose you with the challenges of a doctoral thesis – daily – and you accept it with a smile.

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. Julian Klein, Paul Haverkamp, Eva Lindberg, Michael Griesser, Sönke Eggers (2020). Remotely sensed forest understory density and nest predator occurrence interact to predict suitable breeding habitat and the occurrence of a resident boreal bird species. Ecology and Evolution, 10 (4), 2238-2252.

II. Julian Klein, Göran Thor, Matthew Low, Jörgen Sjögren, Eva Lindberg, Sönke Eggers (2020). What is good for forest birds is not always good for epiphytic lichens: interactions between structure and species richness in managed boreal forests. Forest Ecology and Management, 473, 118327. (in press)

III. Julian Klein, Göran Thor, Matthew Low, Jörgen Sjögren, Eva Lindberg, Sönke Eggers. Tree species identity and composition shape the epiphytic lichen community of structurally simple boreal forests over vast areas. (manuscript)

IV. Julian Klein, Matthew Low, Eva Lindberg, Jörgen Sjögren, Sönke Eggers. Experimental support for biodiversity retention measures during thinning in boreal forests. (manuscript)

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The contribution of Julian Klein to the papers included in this thesis was as follows:

I. Participated in the development of ideas, assembled and analysed the data, created the figures, and led the writing of the manuscript as well as the review process.

II. Led the development of ideas, designed the study, coordinated and participated in the data collection, assembled and analysed the data, created the figures, and led the writing of the manuscript as well as the review process.

III. Participated in the development of ideas, designed the study, participated in the data collection, analysed the data, created the figures, and led the writing of the manuscript.

IV. Led the development of ideas, designed the study, coordinated the experiment, coordinated and participated in the data collection, assembled and analysed the data, created the figures, and led the writing of the manuscript.

During this doctorate study, Julian Klein contributed to the following papers not included in the thesis:

I. Josefsson et al. (2020). Improving scientific rigour in conservation evaluations and a plea deal for transparency on potential biases. Conservation Letters, e12726. (in press)

II. Paul Haverkamp, Julian Klein, Michael Griesser. Forest management effects on survival of a long-lived bird. (submitted)

1. Introduction

How can we improve the management of natural resources so that the decline in biodiversity on Earth stops?

While the boreal forest belt is one of the few largely intact ecosystems on earth, some regions, especially Fennoscandia have had a long history of intensive forest management (Esseen et al., 1992; Östlund et al., 1997) and it can therefore be regarded a trial zone for forestry in the rest of the boreal region (Naumov et al., 2018). In Fennoscandia, intensive forest management has resulted in a strong decline of forest biodiversity (Kålås et al., 2006; Rassi et al., 2000; SLU Artdatabanken, 2020). However, many threatened species are not decreasing in numbers because the boreal forest is managed, but rather as a result of how it is managed (Holm, 2015). We therefore need to know which management interventions are responsible for the decline, and how these can be altered to function within ecosystem boundaries. In this thesis, I aim at increasing this knowledge with regard to thinning in the boreal forest and provide one piece of the puzzle for answering the introducing question.

1.1 The state of the boreal forest

The boreal forest is the world's largest land biome. It is home to an estimated 100 000 species (Ruckstuhl et al., 2008) and contains 60% of all carbon stored in forests (Kasischke, 2000). The economic value of this and other ecosystem services is ca. 90 billion USD per year for the Canadian part alone (Burton et al., 2010). These large economic values are besides climate change, which is comparatively stronger in this region (Lindner et al., 2010), the reason why the boreal forest ecosystem is threatened today. Here forestry plays the major role, but its environmental impact varies greatly between countries, with 35% of forest land exploited in Canada (Bogdanski, 2008), 76% in Russia (Burton et al., 2003), and at least 90% in Fennoscandia (Linder and Östlund, 1998). This relatively high degree of naturalness in Russia and North America is responsible for the low number of threatened species in this biome as a whole (IUCN, 2020). However, the likelihood of species extinctions will increase if the expansion of forestry in the whole boreal region is to reach the level of that in Fennoscandia (Naumov et al., 2018). In Fennoscandia, species have already become extinct or are at risk of extinction under current environmental conditions (Kålås et al., 2006; Rassi et al., 2000; SLU Artdatabanken, 2020). The reason for this is the fact that forest management in Fennoscandia has replaced natural disturbances and succession as the main drivers of the amount, dispersion, and variety of forest structural elements that shape biodiversity (Angelstam and Kuuluvainen, 2004; Brumelis et al., 2011). Understanding the mechanisms behind the negative consequences of forestry on biodiversity in Fennoscandia is therefore crucial for all boreal nations that wish to reconcile forest management and biodiversity commitments (CBD, 2010).

1.2 Forest structural elements and biodiversity

Biodiversity in forests is driven by the complexity and amount of structural elements that together increase habitat heterogeneity (MacArthur and MacArthur, 1961; Stein et al., 2014). It is, however, difficult to define what exactly these structural elements are from the perspective of a focal species because both its fundamental and realised niche usually comprises a multitude of structural elements (Whittaker et al., 1973). Nevertheless, some structural elements, that are key to either a focal species or biodiversity as a whole, can usually be identified. In the boreal forest these are coarse woody debris (Jonsell, 2008; CWD; Siitonen, 2001), the tree species composition (McMullin et al., 2010; Roberge et al., 2008), the density and vertical distribution of the forest's vegetation (Thompson et al., 2003), and very old trees (Berg et al., 1994; Tikkanen et al., 2006). However, to maintain a high biodiversity, these elements need to be present in sufficient amounts locally, and at the right dispersion in the landscape (Fahrig, 2013) to prevent populations from falling into negative density dependence, ultimately resulting in local extinction (Courchamp et al., 1999). A habitat feature, such as a forest structural element, can be present in the right local amount for individuals of a species to sustain itself for a while. However, if the population is too small and the local habitat too isolated from other suitable habitats, populations can suffer from inbreeding and genetic drift (Lamont et al., 1993), emigration into sink habitats (Amarasekare, 2004), higher parasite pressure (Holmes, 1996), stochastic extinctions (Lande, 1998), or habitat destructions by natural forces (Tilman et al., 1994). In addition, these patches of suitable habitat usually suffer from edge effects due to their strong dispersion in the landscape meaning that the actual habitat amount is often smaller than the patch area (Aune et al., 2005). In Fennoscandia, the amount, dispersion, and variety of key structural elements are greatly reduced in managed compared to natural forests (Brumelis et al., 2011). Even though the importance of these key structural elements for forest diversity and resilience have been recognised, their retention levels during management interventions are often insufficient to support populations at the landscape scale (Rudolphi, Jönsson and Gustafsson, 2014; Johansson, Wikström and Hylander, 2018; Sterkenburg et al., 2019; but see Lundström et al., 2013). In fact, even many completely retained natural forest patches suffer from species extinction debt (Berglund and Jonsson, 2008), most likely due to a lack of key structural elements in the surrounding managed forest landscapes (Aune et al., 2005; Rudolphi and Gustafsson, 2011). It is therefore crucial to find out which forest management practices can retain the amount, dispersion, and variety of these key forest structural elements required to support both a high level of biodiversity in managed stands and provide a green infrastructure for species confined to natural forest patches within the managed forest landscape. There is already a lot of knowledge on how the different structural elements affect biodiversity from complex natural systems. However, these effects might be different or more easily exposed in simple managed systems where small changes in a forest structural element can lead to a relatively larger response in the species community, due to less complex abiotic and biotic interactions.

1.3 The study system

1.3.1 Silviculture in the boreal forest

Even-aged silviculture with a stand replacement every 80-100 years is the dominant form of forestry in the boreal region (Smith et al., 1997). Stands are replaced by clear-felling (in Sweden 1-100 ha, in average 4.5; Swedish Forest Agency, 2014) with subsequent replanting or retention of seed trees. Between planting and felling, several pre-commercial and commercial thinnings occur to promote growth of the most economically valuable trees. During pre-commercial thinning, mostly deciduous trees are cleared and remain on the ground. During commercial thinning, smaller than average trees (thinning from below) and/or larger than average trees (thinning from above) are removed from the forest aged 40-70. Retention forestry, which to some extent preserves key structural elements, has during later years been introduced to clear-felling with the aim to alleviate negative consequences for biodiversity (Gustafsson et al., 2012; Kruys et al., 2013). However, similar methods have hardly been suggested nor studied in regard to their biodiversity conservation efficiency for forest thinning (but see: Eggers and Low, 2014; Lindbladh and Abrahamsson, 2008; Patriquin and Barclay, 2003). This even though 60% of Fennoscandia’s managed forests will be thinned during the coming decade (Swedish Forest Agency, 2017). Knowing which species groups are affected by conventional and alternative forest thinning methods, and understanding which structural elements we need to preserve at what amount to alleviate possible negative effects, is therefore crucial for the development of sustainable forestry in the boreal region.

1.3.2 Conventional- and alternative thinning methods

Conventional forms of thinning (pre-commercial- as well as commercial thinning from above and below) in the boreal forest is suspected to (i) simplify the tree species composition with especially deciduous trees becoming fewer (Swedish National Forest Inventory (NFI), 2019), (ii) decrease the amount of coarse woody debris, and (iii) decrease the density of the forest vegetation in the understory and overstory (Eggers and Low, 2014; Joelsson et al., 2017). As mentioned above these changes are expected to result in a lower biodiversity and alternative commercial thinning methods have therefore been suggested. This even though the effect of conventional thinning (ConvT, Fig. 1) on the amount and variety of forest structural elements and biodiversity has not yet been tested experimentally in the boreal forest. One alternative thinning method, understory retention thinning (UstRetT, Eggers and Low, 2014) retains at least 250 Norway spruces *Picea abies* per hectare with living branches below 2 m above ground. Another method is the complete retention (CplRet) of entire patches while the surrounding forest is thinned conventionally. This method is often applied during final felling (Gustafsson et al., 2012) but has neither been tested for its efficiency in retaining biodiversity during thinning, nor for which areal extent is required to have an effect. Moreover, how these thinning methods affect the structural elements in the boreal forest remains largely unknown.

Figure 1. Conventional thinning in a managed boreal forest in Sweden.

1.3.3 Why forest-dwelling birds and epiphytic lichens?

In this thesis I studied forest-dwelling birds and epiphytic lichens to evaluate the effect of thinning on biodiversity. Forest-dwelling birds and epiphytic lichens can have opposing habitat demands, due to one being mobile and the other sessile. They are therefore a good choice for evaluating the effect of different thinning methods on biodiversity, and whether the effects diverge across taxa. Especially birds are expected to react strongly to the thinning induced changes in the density and vertical distribution of the forest's vegetation (Müller et al., 2010). Forests with a dense understory give protection from predators during foraging (Griesser and Nystrand, 2009) and a larger variety of nesting sites (Chisholm and Leonard, 2008). However, whether a dense overstory is beneficial to birds is more unclear. The reduced light penetration through the upper vegetation layers will result in a colder nest microclimate during breeding and possibly in a lower amount of food for nestlings (especially insects; Hedwall et al., 2013; Williams, 1961). The willow tit *Poecile montanus* and the Siberian jay *Perisoreus infaustus* are species that can show decreased reproductive success and adult survival in forests with a more open understory (Eggers and Low, 2014; Griesser et al., 2007). These species' response to thinning could therefore be indicative of how thinning affects other understory dependent organisms. Well studied bird species like the Siberian jay can, in this context, be used to evaluate whether the effect of understory cover is unconditional, or whether it depends on the presence of predators from which nestlings and parents are protected (Eggers et al., 2005). Because if the effect of a forest structural elements on biodiversity or a life history trait interacts with other biotic or abiotic variables with a spatial distribution, habitat suitability models can be produced that guide management geographically.

Figure 2. The Siberian jay *Perisoreus infaustus* can react strongly to forest thinning.

Epiphytic lichens are often used as biodiversity indicators in the boreal forest (Jonsson and Jonsell, 1999). Epiphytic lichens are expected to respond positively to a more open forest vegetation due to their light-dependence for photosynthesis (Palmqvist, 2000). In contrast to most birds, they are often dependent on the abundance of different host tree species (McMullin et al., 2010; Müller et al., 2010) meaning epiphytic lichen diversity is usually higher in mixed-wood forests (Dettki and Esseen, 1998). Exactly how the tree species composition affects epiphytic lichens in young managed boreal forests is however unclear. A larger stem diameter could further improve managed forests as a epiphytic lichen habitat by providing microstructures (bark crevices) usually associated with very old trees (Thor et al., 2010).

Figure 3. The lung lichen *Lobaria pulmonaria* is an epiphyte.

2. Objectives

My objective with this thesis was to explore how the amount and composition of the structural elements in managed boreal forests, that are altered by conventional commercial thinning, affect the diversity and well-being of forest organisms, as well as to test whether alternative thinning methods (UstRetT & CplRet) and better spatial planning can alleviate possible negative effects. To achieve this, I posed the following questions in the indicated papers:

(1) Which forest structural elements are to what extent affected by conventional thinning and alternative methods (**paper II & IV**)?
(2) Is the species richness of epiphytic lichens and forest-dwelling birds affected by the density and vertical distribution of the forest's vegetation, and if so are the effects diverging (**paper II)?**
(3) How is the species occurrence and richness of epiphytic lichens related to the host tree species' identity and stand level alpha and beta lichen diversity to the forest's tree species composition (**paper III**)?
(4) Can a certain setup of the structural elements in questions 2 and 3 optimize the richness of both taxa in a forest stand (**paper II & III**)?
(5) How are different bird species, guilds, and population trend groups affected by conventional thinning (**paper IV**), and can alternative methods and improved spatial planning of thinning interventions alleviate previously known, and in this study exposed, possible negative consequences (**paper I & IV**)?
(6) How do my findings fit with previous studies on the effect of forest thinning, or the structural elements it affects, on biodiversity in managed boreal forests, and can I synthesize general recommendations?

3. Methods

3.1 The study sites

All data used for this thesis stems from within the boreal forest belt of Sweden (Fig. 4). The study site of **paper I** is located in the northern boreal region near Arvidsjaur (65.67, 19.17, AYT = -1°C; SMHI, 2020), while the study site of **paper II, III & IV** is located at the southern edge near Uppsala (59.84, 17.96, AYT = 5°C). The most abundant tree species in the study sites are Norway spruce *Picea abies* and Scot's pine *Pinus sylvestris*. Birch *Betula* spp. is the most abundant deciduous species, followed by aspen *Populus tremula*, alder *Alnus glutinosa*, and few oaks *Quercus robur* in the southern site. The study sites are dominated by stands that are managed mainly for the production of pine, with the Arvidsjaur site containing all stages of a forestry rotation period and the Uppsala site containing 40-70 year old stands, subject to commercial thinning. Both sites also include nature reserves, where no forestry has been performed for ca. 200 years (Arvidsjaur site) and ca. 100 years (Uppsala site). While the Arvidsjaur site is part of a long-term study providing data on Siberian jay reproductive success, the Uppsala site was newly established, specifically to experimentally test the effects of commercial forest thinning and retention measures on epiphytic lichens, forest-dwelling birds, *Coleoptera*, *Diptera*, and the reproductive performance of hole nesting birds.

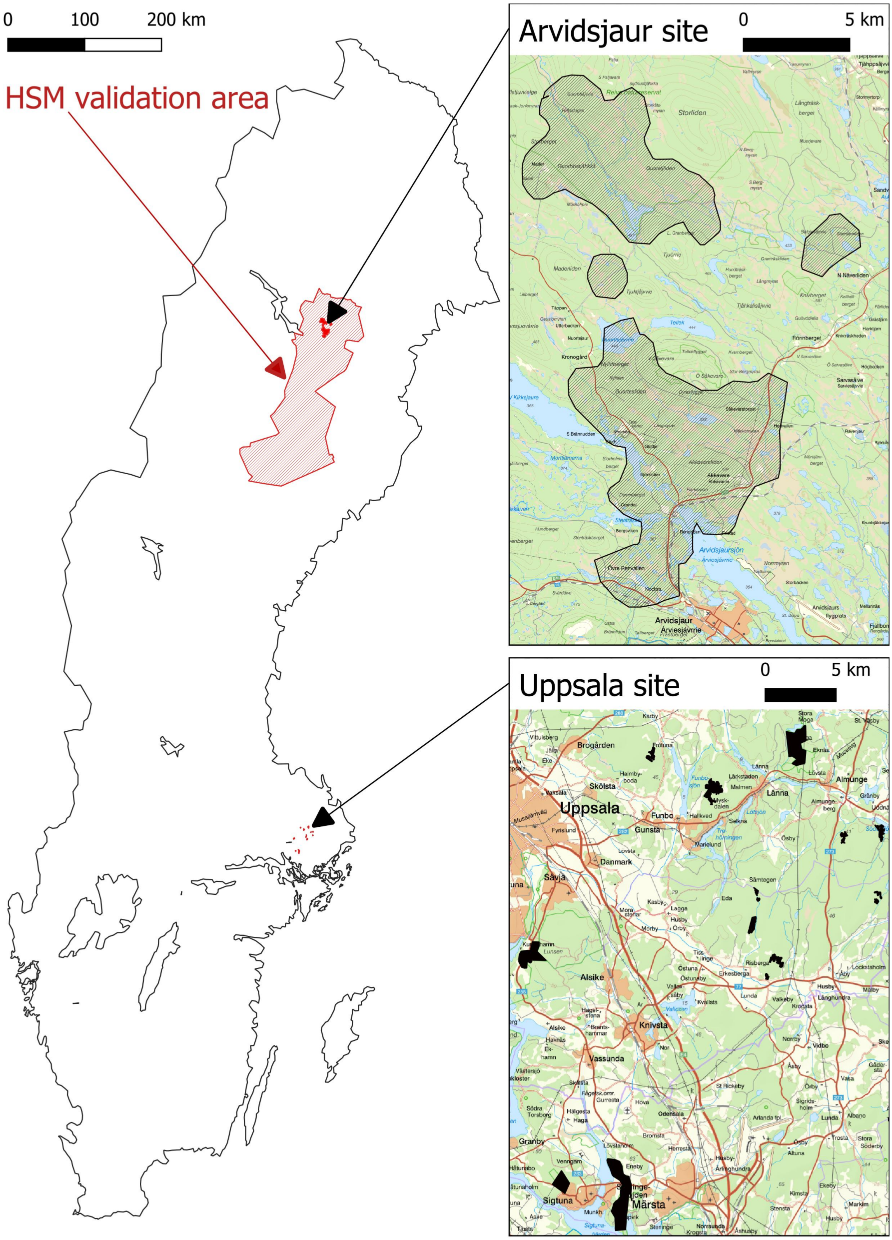

Figure 4. The map shows the locations of the two study sites and the area used for the validation of the Siberian jay habitat suitability model.

3.2 Study designs

The Uppsala thinning study
To find out how the forest's structural elements that are affected by thinning in turn affect epiphytic lichens and forest-dwelling birds (**paper II & III**), and experimentally test the bird community's response to conventional and alternative thinning methods (**paper IV**), a regional forestry company (Holmen AB) provided us with originally nine experimental forest stands of totally 250 ha near Uppsala, Sweden. The company also thinned the forests in the winters of 2017-2019 according to three experimental treatments. On these nine forest stands, I placed as many 50 m radius circular plots as was simultaneously possible, when linear elements, clearings, and wetlands were excluded. From the resulting 117 plots, I randomly chose 58 plots, and randomly assigned one of the three experimental treatments; conventional thinning (ConvT), understory retention thinning (UstRetT), and complete retention (CplRet), with at least one of each treatment in each of the nine forest stands. These 58 experimental plots were surveyed *before* the thinning experiment was performed (with some exception in the lichen survey: see section 3.3.1.), to find out how the forest's structural elements simultaneously affect epiphytic lichens and forest-dwelling birds in **paper II & III** (Fig. 5). For the thinning experiment in **paper IV**, I placed an additional 20 plots across the study area where no forestry (NoFor) occurs in the plot's surroundings. These plots were placed semi-randomly within the experimental stands, in similar managed forests and in nature reserves, because I wanted to ensure the intactness of at least some NoFor plots for 20 years post thinning (Fig. 5). 10 out of the 58 experimental plots were later also assigned to NoFor, as one experimental forest stand was downed by Storm Alfrida in December 2018 (SMHI, 2019) before thinning could take place, and another was never thinned (Fig. 5). In the experiment in paper **IV**, I used these resulting 30 NoFor plots as control plots to see if and how the remaining 16 CplRet and 16 ConvT plots affect the bird community of young managed boreal forests. In this experiment, I further compared the 16 UstRetT plots to CovT plots with CplRet plots as controls, to see if UstRetT is an efficient retention method (For details on the experimental design see Box 1, **paper IV**). CplRet can serve as controls in this context, because i) no thinning occurred on CplRet plots and ii) because ConvT, UstRetT, and

CplRet plots were equally affected by conventional forest thinning which was performed on the entire experimental stands, including ConvT plots but excluding UstRetT and CplRet plots (Fig. 5). This design fulfils the criteria for a block-level semi-randomised before-after control-impact design (BACI; Underwood, 1997).

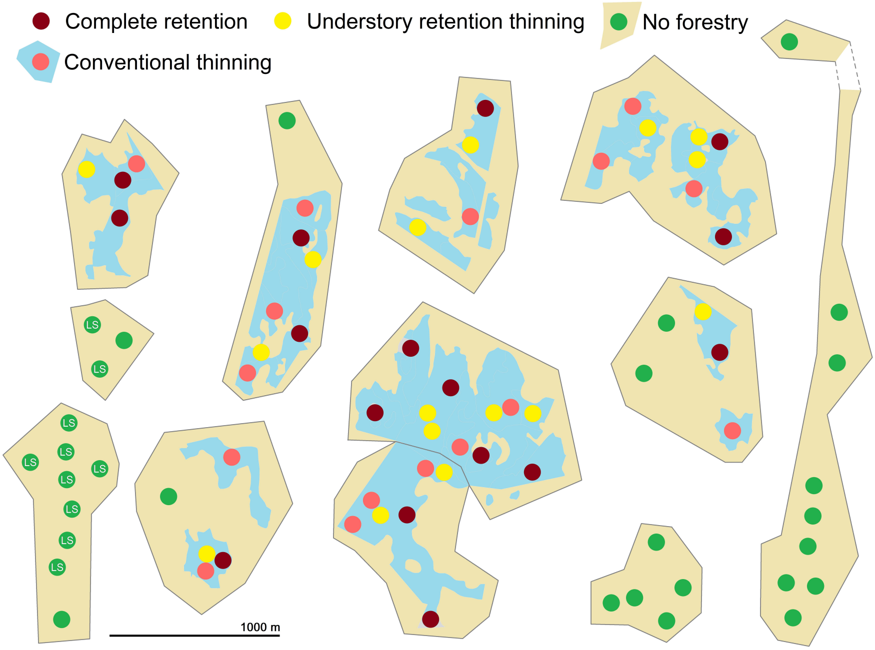

Figure 5. The design of the thinning study in **paper II, III & IV**. I show the study blocks, the treatment plots and how the treatment plots' surroundings were affected during the experiment. Lichen surveys were performed on all impact treatment plots (ConvT, UstRetT, and CplRet) as well as on the NoFor plots indicated with *LS* (Lichen Survey). The distance between blocks is not actual, but it is within the blocks. For actual geographical location of the blocks see Fig. 4.

The habitat suitability model for the Siberian jay

To build the habitat suitability model (HSM) for the Siberian jay in **paper I**, I used long-term data on Siberian jay breeding success and the distance of the nest to the closest human settlement (a proxy for nest predator occurrence; see section 2.3 in **paper I** for detailed reasoning and proof) in interaction with nest concealment at various radii around the nest. To validate the HSM, I compared its predictions of breeding success with independently collected occurrence data on a regional scale (18 290 km^2, Fig. 4).

3.3 Data collection

On the Arvidsjaur site (**paper I**), the data collection was connected to where Siberian jays built their nests. However, I also used data on human settlements (SCB, 2014) to calculate the distance of the nest to the closest human settlement as well as independently collected Siberian jay occurrence data (Bradter et al., 2018) for the HSM verification. For the collection of ground forest data and for the epiphytic lichen survey on the Uppsala site (**paper II, III & IV**), I placed three 10 m radius subplots within every plot, one in the centre, one 25 m to the east and one 25 m to the west (Fig. 6). All data this thesis employs is, or will be, freely available (See papers for specific links).

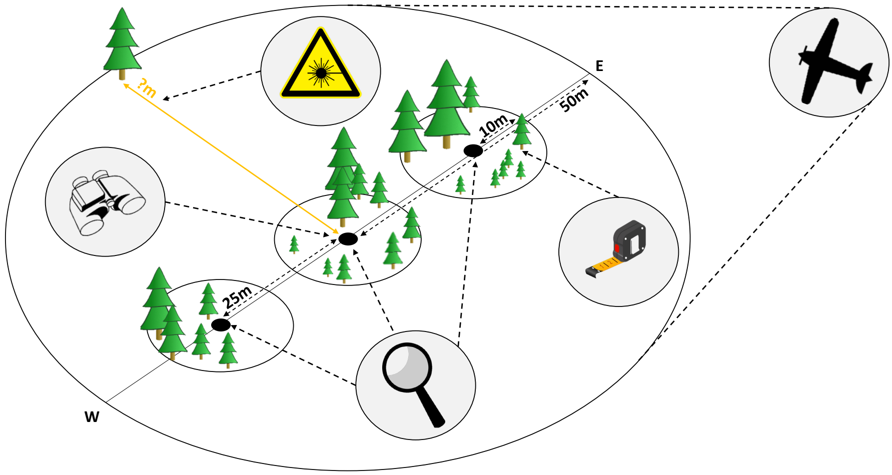

Figure 6. The design and the measurements performed on each plot of thinning experiment (Epiphytic lichen survey only on 58/78 plots).

3.3.1 Species data

The Uppsala thinning study

To measure bird species occurrence in **paper IV** and bird richness in **paper II**, another ornithologist and I performed point counts where we noted the occurrence of all species heard or seen (no flyby birds) within the plot boundaries (50 m radius, Fig. 6). Every plot was always visited (3-5 visits per season) by the same observer earliest 30 minutes before and latest six hours after sunrise between April 1st and June 21st. All 78 plots were surveyed in 2017 and 2018 while only the plots that were thinned during winter 2018/2019 as well as their paired NoFor plots were visited in 2019. At each visit, two five-minute sessions were performed. The break between sessions was 20 minutes in 2017 and 5 minutes in 2018 and 2019. After 2017, I decreased the break to 5 minutes since we almost exclusively made the first observation of a species during the first 15 minutes in 2017 (See **paper IV**). The resulting number of survey sessions varied with the migration behaviour of the focal species. I excluded some bird species because their occurrence cannot be associated to the forest structure on the experimental stands (For more details, see **paper II & IV)**. For **paper II,** only the plots on which the lichen survey was performed were included (The 58 original experimental plots). For the epiphytic lichen survey in spring 2018, I randomly chose one of the three subplots (Fig. 6) and a lichenologist noted the species occurrence of all epiphytic lichens on the stem and branches of all living trees with a diameter breast height (DBH) of at least 10 cm. The lichenologist (Göran Thor) only surveyed the lowest 2 m of the tree, but this is representative for lichen occurrence on the whole tree (See **papers II & III**). Among the 58 surveyed plots, 22 had already been thinned four months prior to the survey. However, within this time frame, the lichen occurrence on the remaining trees could still be associated with the pre-thinning forest structure (Johansson et al., 2018). A reference collection of the majority of species observed in this study can be found at the UPS herbarium in Uppsala, Sweden. I provide a complete species list of epiphytic lichens and forest-dwelling birds (including guild identity) in the appendix of **paper II**.

The habitat suitability model for the Siberian jay

To build the HSM in **paper I**, I made use of nesting data which was collected from 1998-2004 and 2011-2013 from a colour-ringed population on the Arvidsjaur site. Each March, nests were located during egg incubation and followed until breeding success could be determined (For details on field methods see Griesser et al., 2017).

3.3.2 Forest data

On ground data

On the Uppsala site, my field assistants measured the DBH and noted the species of every tree with a DBH above 5 cm on each subplot (Fig. 6). They further noted whether the tree was alive and in case it was a spruce, whether it had living branches down to below 2 m above ground (understory spruce). Understory spruces were counted even if the DBH was below 5 cm. In the plot centre, I measured the visibility in the forest with a laser device (Leica DISTO™ A5; for details see **paper IV**). These measurements were performed to correlate the tree species composition with the vegetation densities in **paper II**, to relate the host tree identity and DBH, as well as the plot's tree species composition to epiphytic lichen occurrence and diversity in **paper III**, and to compare the forest structure (basal area, tree species composition, visibility, no. understory spruces per hectare, and coefficient of variation of the DBH) between the different thinning treatments before and after the experiment as well as compare the before-after changes on ConvT and UstRetT plots in **paper IV**. No on ground forest data was collected for **paper I**.

Airborne LiDAR data

I used LiDAR (light detection and ranging) data as a measurement of forest vegetation density in **paper I & II**. I did this to quantify nest concealment in **paper I**, and to explore the relative importance of understory- and overstory density for epiphytic lichens and birds in **paper II.** LiDAR is a remote sensing technology which relies on laser beams emitted from aeroplanes that are reflected back to the plane by the forest vegetation or the ground (Lefsky et al., 2002). The point of reflection is calculated from the 3D coordinates, speed, and flying angle of the plane. From the resulting point cloud, I calculated the percentage of laser returns below and above different height breaks as a metric for vegetation density (Fig. 7). LiDAR data is available for the entire forest area of Sweden (Lantmäteriet, 2016). For details on the LiDAR measurements consult the appendix of **paper I**.

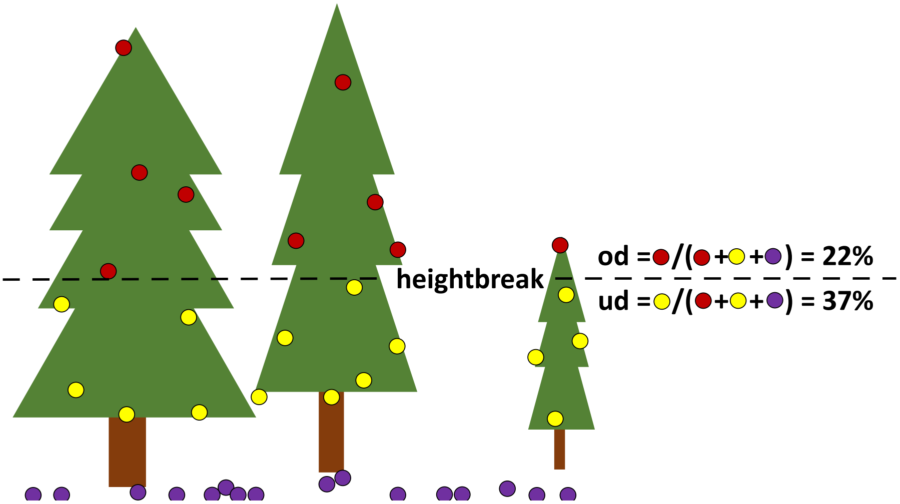

Figure 7. The coloured dots represent LiDAR laser reflections on the vegetation or the ground. The figure shows how the density in the forest understory and overstory is calculated. The heightbreak defining the under- and overstory was 5 m in **paper I** and 3, 5, and 7 m in **paper II** (Reproduced from Klein et al., 2020b).

3.4 Data analysis

I used generalized linear mixed-models (Bolker et al., 2009) in **paper I** to see if the variation in breeding success in the Siberian jay can be explained by an interaction between nest concealment and predator occurrence, in **paper III** to see if the epiphytic lichen occurrence and richness on a tree differs between host tree species, and in **paper IV** to evaluate whether the experimental thinning treatments affected the occurrence of forest birds. I used linear regression models (LM) in **paper II** to see if the stand level richness of epiphytic lichens and birds is differentially affected by the forest understory/overstory density, in **paper III** to evaluate whether the variation in stand level alpha and beta diversity of epiphytic lichens can be explained with the tree species composition and average DBH, and in **paper IV** to compare all the forest metrics among the thinning treatments, before and after the experiment. In **paper II & IV**, Multi Species Occupancy Models (MSOM; Iknayan et al., 2014) were used to estimate the unobserved true occurrence of bird species, and a simplified MSOM in **paper III** to estimate species level occurrences of lichens on trees. I used species accumulation curves (SAC; Gotelli J. and Colwell K., 2001) in **paper II & III** to correct for a sampling bias in epiphytic lichen diversity as plots with a different number of sampled trees were compared. In **paper IV**, I made use of novel indicators, designed to evaluate before-after control-impact (BACI; Chevalier et al., 2019) experiments, to find out to how likely the response of birds can be causally attributed to the experimental thinning treatments. To build these models, I used the statistical computing program R (R Development Core Team, 2019) including a long list of extension packages (see papers for details) and the software JAGS (Plummer, 2003) for the hierarchical Bayesian models in **paper II, III & IV**.

3.4.1 What is a Generalized Linear Mixed-Model?

The GLMM is one of the principle methods to detect if the variation in one measured variable can be explained by one or a combination of many other measured variables. The relationship between the explained and explaining variable is described with a mathematical function, which in turn is the formal description of a proposed hypothesis (Bolker et al., 2009). The terms in this mathematical function are estimated by an algorithm (typically MLE, but see below), which finds the value for the function term that maximises the likelihood for the explained variable to take on the measured data points. From these maximised values and the associated likelihood of all function terms, we can then infer whether to accept or dismiss our hypothesis. The reason why GLMM's have become so popular, and why I use them in **paper I**, **III & IV**, is because they allow for great flexibility when it comes to the data distribution of the explained variable. Moreover, they allow us to define whether the relationship between an explaining- and the explained variable is deterministic (fixed effects) or stochastic (random effects). The linear regression models, which I used in **papers II, III & IV**, are simplifications of a GLMM.

3.4.2 Why the Bayesian philosophy?

The Bayesian statistical philosophy which I apply in **papers II, III & IV**, as opposed to the Frequentist philosophy which I used in **paper I & IV**, is equally old historically, but has only found wider spread application with the recent development of high computing power (Robert and Casella, 2011). In frequentist statistics a hypothesis is accepted or dismissed based on the likelihood (P(Data|Hypothesis) in Eq. 1) of taking the same decision over and over again if the scientific study at hand were to be repeated an eternal times. Typically, we dismiss the null hypothesis if the expected frequency of taking a different decision in all these eternal repetitions is lower than 1 in 20. In Bayesian statistics however, we estimate the probability for a hypothesis to be true, given the measured data (P(Hypothesis|Data) in Eq. 1; Kruschke and Liddell, 2018). This seemingly small difference allows to directly calculate the probability of different scenarios. For example in **paper IV,** I calculated the probability of birds to respond positively or negatively to the thinning treatments, which directly answers my question and requires no choice of reasonable frequencies of false hypothesis acceptance (Type 1 Error). However, the Frequentist and Bayesian philosophy are related. If we know the universal likelihood of measuring the data at hand P(Data), and if we include our prior knowledge of the study system P(Hypothesis), we can use P(Data|Hypothesis) from above and Bayes' theorem (Eq. 1; Bayes, 1763) to calculate the posterior probability P(Hypothesis|Data) on which we then base inference.

$$\mathrm{P}(Hypothesis|Data) = \frac{\mathrm{P}(Data\,|\,Hypothesis)\times\mathrm{P}(Hypothesis)}{\mathrm{P}(Data)} \qquad (Eq.1)$$

The inclusion of prior knowledge in data analysis is an advantage of the Bayesian over the Frequentist philosophy, as it is rare that we know nothing about the system we study. P(Data) however, is unknown and has to be estimated. To do this, I used the Markov chain Monte Carlo algorithm (MCMC; Robert and Casella, 2011).

3.4.3 Multi Species Occupancy Models

MSOMs (Iknayan et al., 2014) are hierarchical community models which are often implemented in a Bayesian framework and most widely used in the study of birds (Kéry and Royle, 2008). A MSOM is essentially a classical hierarchical model, which is applied to all species in a community at once. At the first hierarchical level, the observed occurrence frequency of every species is explained by the unobserved true occurrence of this species and its probability of detection by the observer (not implemented in the MSOM in **paper III**). At the second hierarchical level, this unobserved true occurrence is then explained with the variables of interest, for example the thinning treatments before and after the experiment in **paper IV** or a lichen species' host tree in **paper III**. Implementing an MSOM in a Bayesian framework allows the extraction of various community metrics, such as species richness, which can then be integrated into another Bayesian model. I made use of this in **paper II**, where I combined the extracted species richness of forest birds with the species richness of epiphytic lichens, which in turn had been extracted from a Bayesian species accumulation model, to test if the taxa's response to forest vegetation densities differed.

3.4.4 Species accumulation curves

SAC are traditionally used when species richness between different sampling locations is compared, but the number of sampling units differs (Gotelli J. and Colwell K., 2001). To create an SAC, all sample units are reshuffled *n* times and the cumulative species richness across all sampling units is calculated for each n. The asymptotic species richness (an additional sampling unit does not add a new species), which is expected if we were to sample an eternal number of units, is then calculated using a saturation function. I here use the Michaelis-Menten function, because its half-saturation parameter is an index for beta diversity (Kluth and Bruelheide, 2004), and alpha and beta diversity can therefore be explained simultaneously in the manner of a GLMM (For details on this newly developped modelling approach see **paper II & III**).

3.4.5 The Before-After Control-Impact indicators

I used a set of indicators to evaluate whether the experimental thinning treatments resulted in a change in the occurrence of forest birds (Fig. 8). These indicators are especially useful when evaluating and comparing many species at once, as I do for birds in **paper IV**. The BACI-contrast (Eq. 2) shows whether an observed changed in the impact site (in **paper IV**; ConvT, UstRetT & CplRet) is directionally different to the observed change in the control site (NoFor or CplRet).

$$BACI_{contrast} = (ImpactAfter - IBefore) - (ControlA - CB) \quad (Eq. 2)$$

However, Underwood (1997) suggests that an observed change in the impact site can only really be attributed to the impact treatment, if the magnitude of change is larger on impact than control sites, and impact sites therefore contribute more to the observed BACI-contrast than control sites (CI-contribution, Eq. 3; Chevalier et al., 2019).

$$CI_{contribution} = |IA - IB| - |CA - CB| \qquad (Eq.3)$$

Chevalier *et al.* (2019) further suggest an indicator measuring the magnitude of divergence between impact and control sites during the course of an experiment (CI-divergence, Eq. 4). If a BACI-contrast is non-zero, CI-divergence reveals how similar (positive values) or dissimilar (negative values) control and impact sites were before the experiment, and thereby expose the comparability among experimental sites.

$$CI_{divergence} = |IA - CA| - |IB - CB| \qquad (Eq.4)$$

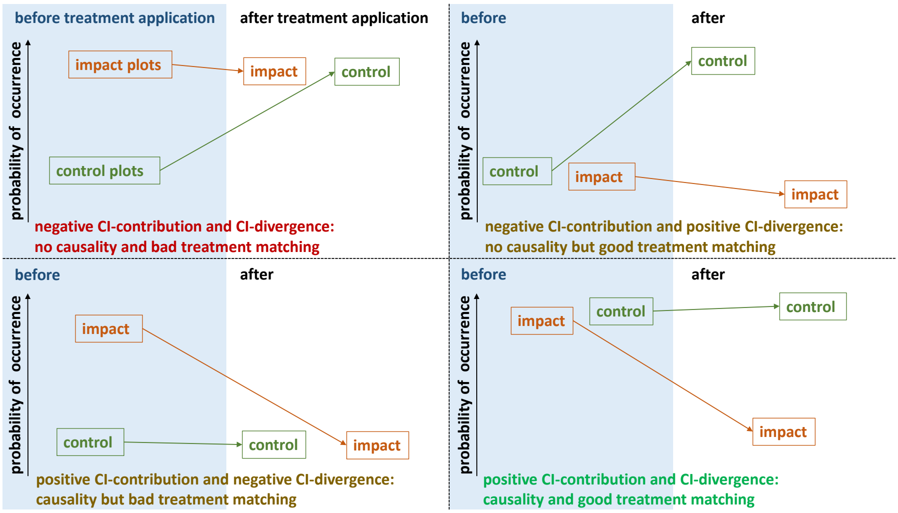

Figure 8. The BACI-contrast tells whether an observed change in the impact site is directionally different to the observed change in the control site. However, a negative/positive BACI contrast can arise from eight different scenarios. Here, the CI-contribution and the CI-divergence indicators assist in identifying which scenario. Only the scenarios resulting in negative BACI contrasts and how they are calculated are shown (Conceptually adapted after Chevalier et al., 2019).

4. Results & Discussion

4.1 Thinning and structural complexity in boreal forests

In the thinning experiment in **paper IV**, conventional thinning (ConvT) and understory retention thinning (UstRetT) resulted in a 40% lower basal area (BA) and a slightly lower variation in the trees' stem DBH. However, the percentage of the total basal area attributed to the different tree species and dead wood did not change with thinning and did not differ between the treatments. The tree species richness did not decrease during thinning, irrespective of the treatment, even though the basal area of deciduous trees was reduced. This is most likely because foresters purposefully spare rarer deciduous species such as alder and oak (Gustafsson et al., 2010). The proportions of dead wood and deciduous trees, two key structures for biodiversity (Nilsson et al., 2001), were comparable to what Joelsson *et al.* (2017) measured in thinned stands, but low compared to proportions found in natural forests, across all treatments before and after thinning (Siitonen, 2001). Thinning decreased the number of understory spruces by 50%, resulting in an average of ca. 250 trees per hectare on ConvT and ca. 500 on UstRetT plots. This shows that (i) UstRetT as suggested by Eggers & Low (≥ 250 spruces with live branches below 2 m above ground) is already implemented in ConvT thinning routines in the study region and (ii) that the UstRetT treatment as applied in the thinning experiment in **paper IV** in fact retained twice as much understory foliage as suggested by Eggers & Low. As a consequence of thinning, visibility increased by 60% on UstRetT and ConvT plots, which show that the structural complexity of the forest vegetation was greatly reduced. LiDAR data from after thinning is unfortunately not available. However, the clear decrease in understory spruces and the increase in visibility points towards a general decrease in understory density. The overstory is generally more open in stands with a lower basal area, given the stands are as old (Fig. 9). Thus, since thinning decreases the basal area, also the overstory will be likely more open after thinning.

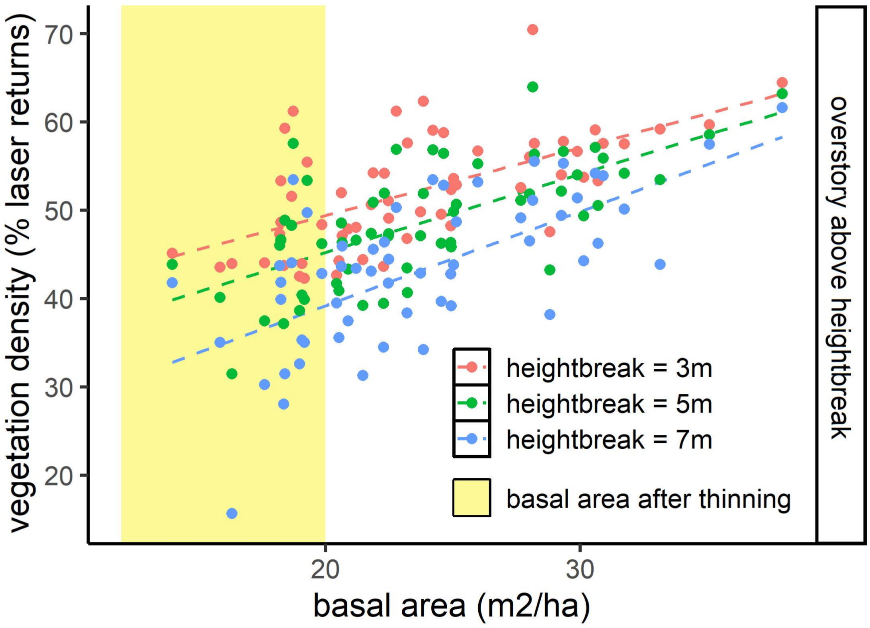

Figure 9. Overstory density in relation to the basal area. The basal area which a thinned forest should have after the intervention according to the Swedish forest agency is indicated (p. 66; Agestam, 2009). The overstory is calculated for the three height breaks used in **paper II** (This figure was modified from Fig. S.5 in Klein et al., 2020b).

These results indicate that ConvT and UstRetT reduce the amount but not the composition (except for the vegetation density, which is to a larger extent preserved in UstRetT) of structural elements found in young managed forests typical of Fennoscandia. However, the results also experimentally confirm what others have pointed out, namely that the amount of key structural elements for forest biodiversity is already very low before thinning (Joelsson et al., 2017) and that ConvT, but also UstRetT to a large extent, miss the opportunity to increase the proportion of deciduous trees and dead wood during thinning.

4.2 On vegetation density and tree species composition

The species richness of forest-dwelling birds was positively related to a denser understory below 3 and 5 m in **paper II** and to thinning methods that to some extent retain the understory in **paper IV** (Fig. 10). That the density in the forest understory affects the species richness of mobile organisms such as birds (Lindberg et al., 2015) and mammals (Carey and Johnson, 1995) is not new. A higher number of species can find suitable nesting sites and protection from predators while foraging on or close to the ground in a dense and complex understory.

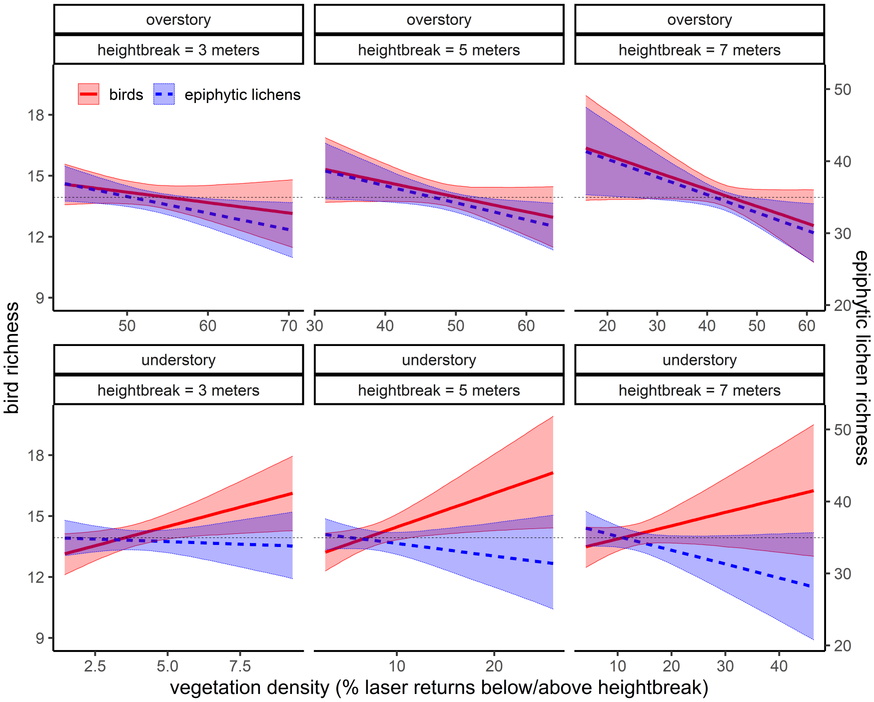

Figure 10. Forest-dwelling birds and epiphytic lichens react to the forest's understory in a divergent way but similarly to the overstory density (Reproduced from Klein *et al.*, 2020b).

Epiphytic lichen richness on the other hand was not (3 m height break) or only marginally affected (negative, 5 and 7 m height break) by a denser understory. An open overstory above all height breaks had a strongly positive effect on lichen richness (Fig. 10). This diverging relationship is most likely because epiphytic lichens (Vondrák et al., 2019) alike vascular plants (Hedwall et al., 2019; Tonteri et al., 2016; Widenfalk and Weslien, 2009) profit from increased light-radiation for photosynthesis in open forests. There is also experimental evidence that more open forests can be positive for epiphytic lichens as long as there is a continuity of essential structural elements such as old trees and hardwood tree species (Root et al., 2010).

In **paper II**, bird richness was also slightly higher when the overstory was open above 7 m, possibly owed to a higher insect abundance in this warmer microclimate (Koivula, 2002). The summed across taxa species richness of forest-dwelling birds and epiphytic lichens was therefore highest in forests with a dense understory below 3 m and an open overstory above 7 m (Fig. 10). The results of **paper II & IV** confirm the idea from previous studies that the effect of the vertical distribution and density of the forest vegetation on bird diversity is likely caused by the actual structural complexity and not by the species identity of the trees species per se (MacArthur and MacArthur, 1961; Müller et al., 2010). In contrast, the vegetation density's effect on epiphytic lichens is most probably not independent of the forests tree species composition (Bäcklund et al., 2016; Jüriado et al., 2003; Kuusinen, 1996). I confirm in **paper III** that lichen richness per tree strongly varies among host tree species with for example Norway spruce hosting in average twice as many species as a Birch tree. How the composition of host tree species further affects epiphytic lichen richness and beta diversity at the stand level in managed boreal forests has however been unclear. I show in **paper III** that twice as many lichen species and twice the beta diversity can be expected in forests that consist of four different tree species compared to a monoculture. To maximise lichen diversity, I show that Norway spruce, Scot's pine and deciduous trees must also exist at relatively even mixtures and that the lowest diversity is expected when a tree species group exists at either very low (< 15%) and high (> 70%) frequencies (Fig. 3 & 4 in **paper III**). Such correlations between a forest's tree species richness and epiphytic lichen richness are known from temperate (Király et al., 2013) and tropical (Frisch et al., 2015) systems but are new for managed boreal forests. A forest with four different native tree species can in Fennoscandia only be achieved with deciduous trees and the results of **paper III** thus pinpoint their crucial role in shaping epiphytic lichen diversity also for managed boreal forests (as compared to natural systems: Kuusinen, 1996; McMullin et al., 2010). Here aspen trees play a central role. Even though epiphytic lichen richness was lowest on aspens among all host tree species in **paper III**, it is expected to be a major contributor to stand level beta diversity since it hosted twice as many uncommon, but not extremely rare species compared to the other tree species. The same role was also attributed to aspens in natural forests of Estonia (Jüriado et al., 2003).

Forest stands with a larger average stem DBH were generally associated with a higher species number of forest-dwelling birds and of epiphytic lichens especially (**paper II & III)**. The potential of a forest to host a high diversity of several taxa is often dependent on the time since stand replacement (McGarigal and Fraser, 1984; Nordén and Paltto, 2001). For taxa that depend on complex tree bark structures, such as epiphytes and many insects (MacFarlane and Luo, 2009), this is especially important in early successional stages, as in the young managed forests I have studied, where this positive correlation of time and the complexity of micro-structures (e.g. bark crevices) is mainly linked to a wider DBH (Brassard et al., 2008).

In **paper II, III & IV**, I only take a snapshot of the relationship of birds and epiphytic lichens with the structural elements in managed boreal forest. The described relationships may interact with other biotic (Klein et al., 2020a) or abiotic (Hedwall et al., 2019) factors, which in turn may vary with time. In fact the association of birds with forest structural elements can be highly stochastic in the strength of the relationship but tends to be directionally constant over time (Yegorova et al., 2013). For epiphytic lichens however, this association is strong and usually constant over time, due to the fact that they are sessile and strongly substrate dependent organisms (Ellis, 2012). There is therefore evidence that the relationships above consistently exist but that they may vary in strength.

A further question, which one might pose in this context, is whether the relationship between composition of structural elements and epiphytic lichens also holds for other organisms. A high lichen diversity is often considered indicative of habitats in which also other organism groups thrive (Jonsson and Jonsell, 1999; McCune, 2000). However, I show in **paper II** that such relationships can in fact be conditional on the composition of structural elements and that one must be careful when drawing conclusions for unstudied taxa based on the well-being of a studied one.

4.3 Thinning detrimental for birds but retention works

The thinning experiment clearly shows that conventional thinning (ConvT) has a negative short term effect on forest-dwelling birds across all guilds, habitat association types, and population trend groups (Fig. 2 in **paper IV**). Five species showed to be especially negatively affected and not a single species showed a clear positive response (See Fig. 3 in **paper IV** for species level effects). The negative impact of ConvT on birds was more pronounced if no forestry (NoFor) as compared to complete retention (CplRet) was used as control, indicating that conventional thinning in a survey plot's surroundings affects the occurrence probability of bird species more negatively than conventional thinning on the plot itself does. It is also highly likely that the observed changes in bird occurrence on ConvT plots were causally related to this treatment (positive CI-contribution values) and that impact and control sites were a good match (positive CI-divergence values; Chevalier et al., 2019). CplRet and understory retention (UstRetT), as applied in this study, did not result in the broad decline in bird occurrence that ConvT resulted in. It is surprising that ConvT negatively affected bird species of all guilds. I show in **paper II** that an open overstory, which is associated with thinned stands, can result in a higher bird richness. Therefore, I expected that birds living in the canopy would be less affected than ground nesters and foragers, who to a larger extent, rely on the cover in the understory which ConvT removes. Equally surprising was the converging response to ConvT of species related to trivial, deciduous, and complex forests. This, despite the fact that ConvT led to a reduction in structural complexity; namely an increased visibility and a reduction in understory tree numbers and in the forest's basal area. An explanation for this decline in species occurrence across habitat association types could be that the observed very large reduction in total tree biomass (reduced basal area) reduces ecosystem productivity (Scheiner and Willig, 2005), with less food and nesting opportunities for all bird guilds and habitat association types as a consequence. However, even though the decrease in tree biomass was the same on UstRetT and ConvT plots, UstRetT did not affect the bird community. Because the reduction in understory spruce numbers was the only difference between ConvT and UstRetT (two times higher on UstRetT after thinning), this forest structural element seems an important factor for many bird species in young managed forests. This result gives experimental support for my findings in **paper II**, that maintaining a dense vegetation below 3 or 5 m above ground is important for bird richness in boreal forests (supported also by Griesser et al., 2007; and Lindberg et al., 2015) and that UstRetT, as applied in this experiment, could be the tool to achieve this. However, even though more than twice as many understory spruces as suggested by Eggers & Low (2014) were spared on average on UstRetT plots in the thinning experiment, CplRet had a more positive effect than UstRetT, when compared to ConvT. This could both be a consequence of the fact that UstRetT in general is not as dissimilar from the conventional thinning practices in the study region as suspected (see 4.1), and that UstRetT in contrast to CplRet lacks a mechanism that promotes forest structural elements known to be elementary to biodiversity like deciduous trees (**paper III**) and dead wood (Nilsson et al., 2001). Even if CplRet was largely able to alleviate the pronounced negative effects of ConvT, it did not fully succeed with birds that require suitable habitat in large amounts to reproduce and survive, such as hole-nesters and birds relying on structurally complex forests (Martin, 1993). The size of CplRet plots (ca. 1 ha) is therefore likely insufficient for some bird species in these nesting guilds (see section 4.4). Aspects related to habitat amount, dispersion and fragmentation which I have introduced in chapter 1.2 most certainly play a prominent role in retention methods such as UstRetT and CplRet. I tested neither how the area of CplRet plots relative to the stand area affects birds in this experiment, nor how the distance of a CplRet plot to the closest structurally intact forest affects my conclusions. It is for example a likely scenario, that UstRetT on the whole stand is more suitable than a single CplRet plot surrounded by large areas of conventionally thinned forest or if the stand to be thinned is only slightly larger than a CplRet plot of 1 ha. The fact that I only measured short term effects (one year post thinning) could also further be why neither of the alternative thinning methods completely retained bird occurrence. The treatments’ effect on the bird community might differentiate with time as for example the amount of deciduous trees increases on ConvT and UstRetT due to more light (Bartemucci et al., 2006) and coarse woody debris increases on CplRet due to higher competition induced tree mortality (Kuuluvainen, 2002).

4.4 How and where? Ask willow tits and Siberian jays

The willow tit *Poecile montanus* and the Siberian jay are two species that are known for their sensitivity to forest thinning (Eggers and Low, 2014; Griesser et al., 2007). I confirm this in **paper I & IV**, but show that thinning can also increase the breeding habitat quality for Siberian jays under specific circumstances. In the thinning experiment, the willow tit was the only species that was clearly negatively affected by ConvT and CplRet plots (Fig. 3 in **paper IV**). Even if causality was not entirely certain in this relationship (neutral CI-contribution values), this result suggests that this hole-nester has a higher demand on the amount of structurally complex forests than any other tested bird species. It is therefore likely that thinning is a strong contributor to why the willow tit is on the Swedish red-list. However, willow tit occurrence was not affected by either UstRetT or ConvT with CplRet as the control (Fig. 3 in **paper IV**). CplRet might not have been a good control in this particular case, since the willow tit declined strongly even on CplRet plots. Any inference on the benefit of UstRetT for willow tits is therefore very uncertain. Lindbladh *et al.* (2020) recently questioned the use of the willow tit as an indicator species for forests with high nature values. While my results can neither support nor challenge this claim, they propose that this species is indeed a suitable indicator for structurally complex forests, independent of stand age. The willow tit's persistence on thinned stands can therefore be taken as a confirmation that the applied thinning method has retained the structural elements important for a large number of bird species.

While the willow tit occurs in all parts of the European boreal region, the Siberian jay is confined to the north, and it's well-being is indicative of a habitat which also supports other Taiga specialists (Versluijs et al., 2019). In **paper I**, I present a habitat suitability model (HSM) which is based on a previously identified biotic interaction between nest predator occurrence (mostly corvids) and nest concealment. Breeding success was highest in forest stands with an open understory (0 - 5 m above ground) 15 – 80 m around the nest if this forest stand was far (> ca. 1.5 km) away from human settlements (proxy for predation pressure, see **paper I** for detailed reasoning and proof), but lowest if this forest stand was close to human settlements. Breeding success was independent of the distance to settlements in forests with a dense understory 15 – 80 m around the nest. This finding supports the theory that the grade of nesting cover is a compromise between higher thermoregulatory costs due to a colder microclimate in denser vegetation and more protection from predators in this denser vegetation (Eggers et al., 2006; Marzluff, 1988; Wiebe and Martin, 1998). Alternative thinning methods, such as CplRet and UstRetT are therefore expected to lead to an increase in breeding success in Siberian jay territories close to human settlements, but will not have an effect far away. In contrary, thinning of young dense stands far away from human settlements will likely increase Siberian jay breeding success. But how well do these recommendations hold across regions? The predictions for breeding success, which were based on this HSM, agreed well with independently collected occupancy data in the region (40 km) around the study site. However, the HSM overestimated breeding success in the southern and the eastern sections of the validation area where the climate is milder. This milder climate is likely related to a generally higher abundance of other more temperate corvid species (Artdatabanken, 2019; Valkama et al., 2011), probably also occurring further away from humans than ca. 1.5 km during the Siberian jay's breeding season. According to my results, this decreases the breeding success of Siberian jays and calls for the retention of dense patches within larger distances of human settlements in milder areas. Better data on the occurrence of corvid nest predators in the whole distribution range of the Siberian jay would therefore make the HSM of **paper I** also applicable to areas with a different climate than the study area. The relevance of forests with a rich understory will probably increase with climate change, when corvid predators are expected to occur in higher abundances further north and inland (Thomas, 2010).

By changing thinning interventions from being uncoordinated in relation to human settlements towards strategically applying the above recommendations according to this HSM (see Fig. 11 for an example of strategic planning of forest thinning), the breeding habitat of the Siberian jay and other taiga specialist birds in managed forests of northern Europe could be improved.

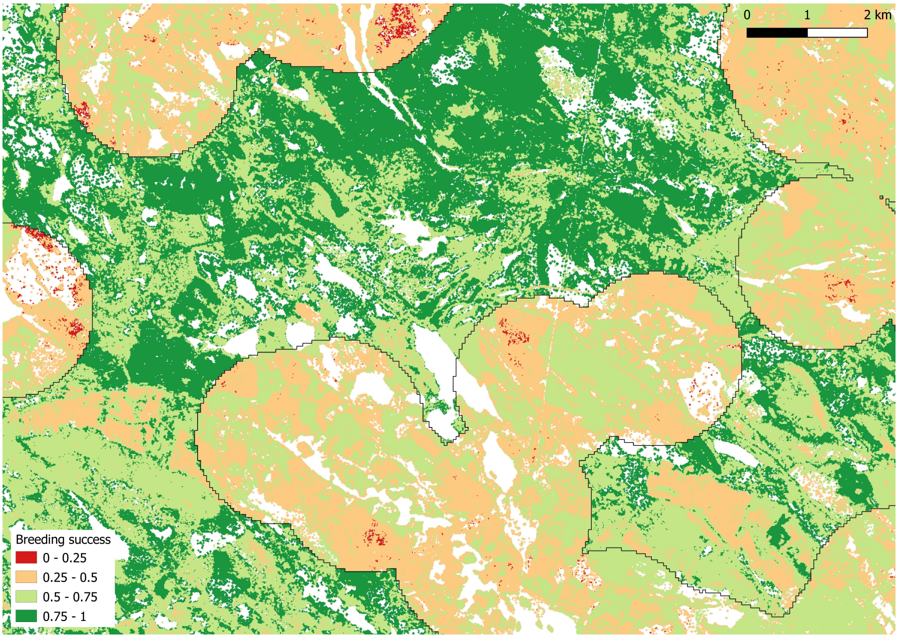

Figure 11. HSM predicted breeding success for Siberian jay. Reducing thinning on reddish pixels inside the circles and increasing thinning on reddish pixels outside the circles will likely increase the breeding success of the Siberian jay at the landscape scale.

4.5 Thinning in other coniferous forests

There are only a limited number of studies that specifically link forest thinning to changes in biodiversity or to the well-being of focal species in the boreal forest (but see section 5.). However, the structural elements and the dynamics in boreal forests are comparable to coniferous forests in other geographical regions. While this also includes Alpine forests in central and southern Europe, the silviculture in these regions does not usually involve clear-cutting and even-aged stands (Nascimbene et al., 2010) and its effect on forest organisms is therefore less comparable. Along the north western coast of North America, however, forest structures and forest thinning methods in Douglas fir *Pseudotsuga menziesii* stands are relatively similar to those in Fennoscandia (Angelstam and Kuuluvainen, 2004; Compare: Franklin et al., 2002). In these forests, both short and long term effects of various thinning intensities on bird diversity were generally positive (Hayes et al., 2003). The higher light penetration after thinning was responsible for a swift increase in structural complexity, which according to the authors led to a higher bird richness. The reason why structural complexity and birds were largely negatively affected by conventional thinning in **paper IV**, could be that I only assessed them immediately after thinning, which does not capture a possible change in structural elements and the species-structure association during the coming years (Yegorova et al., 2013). However, in the studies that assessed the effect of thinning on birds in Douglas fir forests, only the magnitude, and not the direction of the effect, changed over a course of seven (Hayes et al., 2003) and ten years (Yegorova et al., 2013). In a meta-analysis of how pre-commercial and commercial thinning affect birds across North America (excluding boreal forest), responses were only negative when short term effects were considered, while neutral to positive responses were reported otherwise (Verschuyl et al., 2011). These results strongly point out the need for a long term evaluation of how ConvT, UstRetT, and CplRet affect forest-dwelling birds in the boreal region. For epiphytic lichens, my findings were more consistent with those from managed Douglas fir forests, where even rare old-growth associated lichen and moss species profited from an opening of the overstory during thinning (Muir et al., 2006). While this study used transplants to test this, Root *et al.* (2010) showed that thinning while leaving old trees, hardwood gaps, and open grown trees can increase the presence of cyanolichens and alectorioid species that are otherwise uncommon in managed Douglas fir stands. Also the diversity of vascular plants in the understory was increased by several thinning treatments with various retention levels (Ares et al., 2010).

5. Summary, Synthesis & Outlook

The purpose of this thesis was to give recommendations on how to reconcile forest thinning with environmental commitments. These recommendations are for practitioners and stake holders that formulate market certification (Angelstam et al., 2013), as well as to policy makers which must fulfil national and international agreements (CBD, 2010; SEPA, 2007). I now (1) summarise the findings of this thesis in relation to its aims and objectives, (2) put them into the perspective of what is previously known about the effect of forest thinning, or the structural elements it targets, on other organism groups in boreal forests, (3) synthesise recommendations on how forest thinning methods can better combine biomass production with the boreal countries' environmental goals, and (4) provide an outlook of which questions should be answered next.

(1) In **paper IV**, I show that conventional thinning (ConvT) and understory retention thinning (UstRetT) reduce the basal area of all tree species and dead wood, the spread of the stem DBH, the number of understory spruces (less so on UstRetT), but not the tree species composition, and that UstRetT as suggested by Eggers & Low might already be implemented in the thinning routines in the study region. In **paper II & IV**, I showed in correlative and experimental analyses that a denser forest understory below 3-5 m above ground is associated with a higher richness of forest-dwelling birds. In **paper II & III,** I showed that an open under- and overstory as well as an even and rich tree species mixture is expected to lead to a higher alpha and beta diversity of epiphytic lichens and that the summed richness of birds and epiphytic lichens in young managed stands is maximised in a forest with four or more evenly mixed tree species, a larger stem DBH, a dense understory below, and an open overstory above 3 m. In **paper IV**, I reveal in a BACI

experiment that UstRetT with twice the retention level as suggested by Eggers & Low and completely retained (CplRet) forest patches of ca. 1 ha to a large extent alleviate the negative effects which ConvT has on all forest bird guilds, population trend groups, and many bird species in particular. In **paper IV,** I show that the willow tit is especially negatively affected by ConvT, but also CplRet plots and that the willow tit can be an indicator of structurally intact boreal forests, independent of stand age. In **paper I**, I found that ConvT on young dense stands further than ca. 1.5 km away from human settlements (a proxy for predator occurrence) and UstRetT or CplRet on stands closer than ca. 1.5 km will improve the breeding habitat of Siberian jays and possibly other taiga specialists in managed forests. The HSM on which these suggestions are based showed good agreement with independent occurrence data ~40 km around the study site. In this region, it can be used to identify where in the landscape thinning intensity should be increased or decreased to increase breeding success. However, the HSM overestimated breeding success in regions with a milder climate, with likely higher predator occurrence.

(2) In boreal forests, conventional thinning can maintain the peak in vascular plant richness which occurs in the early successional stage after clear cutting by opening up the forest vegetation (Lindgren et al., 2006; Widenfalk and Weslien, 2009). Hedwall *et al.* (2019) confirm this positive effect of open forests on vascular plants and add that this effect is further strengthened if the forest consists of several tree species. However, in the same study the opposite was found for Bryophytes which thrived in spruce dominated and denser stands. These differential responses to forest density was also found for bats in boreal Canada (Patriquin and Barclay, 2003), which suggests that a mosaic of dense and open vegetation will suit many species across taxa, just as I show in **paper I, II & IV**. Mixed-wood forestry generally leads to higher biodiversity across many taxa (Cavard et al., 2011; Felton et al., 2010). However, whether retaining a few life-boat trees is enough (Franklin et al., 1997) or whether tree species need to be well mixed and monocultures prevented, like I show in **paper III** is more unclear. An argument for mixed-wood forestry, beyond its benefit for biodiversity, is the fact that carbon storage, wood biomass and human food production is increased in such forests (Gamfeldt et al., 2013; Jonsson et al., 2019). Conventional thinning does not seem to affect non-saproxylic beetles, while saproxylic species,

especially red-listed ones, are largely absent from thinned forests of the type I studied in **paper II, III & IV** (Stenbacka et al., 2010). This difference clearly illustrates a short-coming of current thinning methods for biodiversity, namely that the amount of coarse woody debris is very low. Lindbladh & Abrahamsson (2008) show that creating high stumps during thinning of Norway spruce can improve the habitat suitability for some saproxylic beetles. Also wood-decaying fungi as well as rare bryophytes and lichens depend strongly on large amounts of dead wood (Santaniello et al., 2017; Svensson et al., 2016). Unfortunately, I cannot present data on any taxa that are specifically indicative of coarse woody debris amounts. The wood-pecker species that are here used as indicators (Mikusiński et al., 2001) were never observed and epixylic lichens were not studied because of a lack of dead wood in the experimental stands. However, CplRet which in **paper IV** was successful in retaining birds during thinning could also benefit dead wood dependent species groups in the long term. CplRet plots could increase the amount of coarse woody debris by retaining what is present before thinning and through self-thinning (Reyes-Hernández and Comeau, 2014). Moreover, a constant and high humidity which is important for many cryptogams (Gauslaa and Solhaug, 1996) might be maintained on complete retention plots. UstRetT, which can maintain both bird and epiphytic lichen richness, is not able to provide the specific habitat types that CplRet does and the benefit of UstRetT for taxa beyond those tested might therefore be limited. Thompson *et al.* (2003) summarised possible consequences of implementing more intensified forest management, such as pre-commercial and commercial thinning, on a large number of taxa in boreal Ontario. They concluded that the effects would be mixed, depending largely on both the proportion of the landscape covered by natural forests and the different management stages. For species relying on large amounts of suitable habitat, such as species depending on coarse woody debris, they foresaw a negative response to thinning. I conclude from this study that the frequency and dispersion of CplRet plots on a thinned stand will be decisive for this thinning method's efficacy in retaining biodiversity in managed forests of Fennoscandia.

(3) The results of my thesis, and of the studies discussed above, indicate that forest thinning in boreal forests can maintain the habitat suitability for many species present before thinning, if (i) one creates a mosaic stand of open

forest through ConvT for light craving organisms and of dense forest through CplRet patches of 1 ha for organisms in need of shady, humid, dense and structurally complex forests, (ii) an even and rich tree species composition is restored on the whole stand mainly by sparing small deciduous trees during pre-commercial and all deciduous trees during commercial thinning until a share of ca. 30% is reached (today 10-15%; **paper IV**, Swedish National Forest Inventory (NFI) 2019), (iii) large diameter trees are spared, and (iv) dead wood is spared already during final felling to, together with CplRet plots, provide higher amounts of coarse woody debris after thinning. Remote sensing tools such as LiDAR are at present widely used in forestry planning (Wulder et al., 2012) and their application in identifying suitable CplRet patches by measuring the vertical distribution and density of the forest vegetation before thinning like in **paper II** should therefore be a formality.

(4) The studies on the effect of different thinning methods on forest-dwelling birds from Oregon show that the magnitude of the response of birds to ConvT, UstRetT, & CplRet will likely change with time. To reassess the thinning experiment of **paper IV** within the coming decade is therefore an obvious next step. In my thesis, I only studied how the amount of suitable habitat affects the efficiency of retention measures in **paper I**. Naturally, it will matter a lot which proportion and dispersion CplRet plots make up on a conventionally thinned stand. To investigate this for several taxa and to also compare CplRet to other suggested thinning methods, such as variable density thinning (Pukkala et al., 2011), would be the next step in investigating methods that combine environmental and biomass production goals. It is also important to state here that rare and threatened species have not been the focus of this thesis or of most of the referred studies and that specific management interventions and conservation programs are needed to prevent them from extinction (Hansson, 2001). I therefore call upon others to investigate how such management interventions can be introduced into thinning routines. In order to prevent carbon loss from forest soils (Kulmala et al., 2014; Pumpanen et al., 2004), silviculture in the boreal forest might have to move from clear-cut retention forestry to continuous cover retention forestry. In such a scenario, my thesis can give insight into how environmental and biomass production goals can be combined, since all forestry in continuous cover forestry resembles commercial thinning (Holm, 2015).

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Popular science summary

Why did I do the research that has led to this thesis?

The multitude of species on Earth is declining at an unprecedented rate. The reason for this is the fact that we humans have been replacing the natural world with an anthropocentric one, one that is managed for our own needs. To change this course, we need to find new ways of using our environment. The boreal forest, which is the largest forest on Earth, is in many of its corners still unmanaged. In Fennoscandia, this is very different. Here, many forest species are declining in numbers and today's forestry practices are not ecologically sustainable. Forestry methods that maintain biodiversity have consequentially been called for. One such methods is Retention Forestry where parts of the forest and the structures that are important for biodiversity are left untouched in the forest. However, few retention methods have been suggested for conventional thinning in boreal forests, and none have been tested in experiments, and experiments are vital for drawing solid conclusions.

What did I do?

In conventional forest thinning, economically less valuable structures like deciduous trees, dead wood, and small undergrowth trees are removed. Through empirical and experimental studies in Sweden, I wanted to find out how conventional and alternative thinning methods affect the diversity and occurrence of forest birds and tree-living lichens, as well as the breeding success of the Siberian jay.

What did I find out?

My results show that conventional thinning reduces the forest's structural variety and has a strong influence on which and how many bird and lichen species can live in the young managed forests typical of Fennoscandia. This effect was mostly negative for birds, but under certain conditions positive for tree-living lichens. I show that biodiversity in these young managed forests would probably increase, if (i) either the undergrowth on the whole forest stand or (ii) entire plots of ca. 1 ha are spared during thinning, if (iii) many tree species at an even mixture are left standing, and (iv) more large-diameter trees are spared. The Siberian jay is considered and indicator of the effect of thinning on bird species relying on forest with both dense and open vegetation. I found out that Siberian jays have a higher chance of breeding successfully in open forests, far away from humans, where nest predators are rare. Close to humans however, their breeding success was higher in denser forests where the nest is protected from predators. Based on these results and with the help of remote sensing data, I provide detailed maps that show where in the landscape thinning can increase and where it can decrease the jay's breeding success.

What is the contribution of the thesis?

All of these findings help fill the research gap for young managed boreal forests, which in Fennoscandia make up 60% of all managed stands. Therefore, this thesis adds novel and essential points to the guidelines for managers and policy makers that wish to combine biomass production with environmental commitments in the boreal forest. Ultimately, the implementation of this thesis' findings would be small step forward towards a more sustainable use of the planets resources.

Populärvetenskaplig sammanfattning

Vad var syftet med denna doktorsavhandling?

Den biologiska mångfalden på Jorden minskar som aldrig förr. Orsaken är att vi människor har omvandlat den naturliga världen till en antropocentrisk värld, en värld som vi brukar för enbart våra behov. För att ändra den inslagna riktningen behöver vi nya sätt att bruka naturen. Den boreala skogen är världens största skog och är på sina håll fortfarande intakt i sitt ursprungliga tillstånd. I Norden ser det dock väldigt annorlunda ut. Här är många skogslevande organismer hotade och dagens skogsbruk är inte hållbart. Skogsbruksmetoder som bibehåller den biologiska mångfalden har därför efterlysts. En sådan metod är till exempel ett skogsbruk där strukturer som har en särskild betydelse för mångfalden lämnas orörda. Få sådana metoder har emellertid föreslagits för gallring, och inga alls har prövats i experiment, vilket dock är mycket viktigt för att kunna dra välgrundade slutsatser.

Vad har jag gjort?

Nuvarande gallringsmetoder leder till att ekonomiskt mindre värdefulla strukturer såsom lövträd, död ved och underväxt huggs bort. Genom empiriska och experimentella studier i Sverige ville jag ta reda på i vilken utsträckning nuvarande och alternativa gallringsmetoder påverkar mångfalden och förekomsten av skogsfåglar och lavar på träd, samt häckningsframgången hos lavskrikan.

Vad har jag tagit reda på?

Mina resultat visar att nuvarande gallringsmetoder minskar olikartade strukturer i skogen, och att det har en stark inverkan på vilka och hur många fågel- och lavarter som kan existera i dem unga brukade skogarna som är typiska för Norden. Inverkan var i huvudsak negativ för fåglar, men under vissa förhållanden positiv för lavar. Jag kan visa att den biologiska mångfalden i gallringsskogarna skulle sannolikt öka om (i) antingen underväxten på hela skogsbeståndet eller (ii) hela ytor på ca. 1 ha sparas under gallringen. Likadant, om (iii) många olika trädslag i en jämn blandning får stå kvar, och (iv) fler grova träd sparas. Lavskrikan anses vara en signalart för gallringens påverkan på fåglar som är beroende av en välskiktad skog. Jag kan visa att lavskrikan har en högre häckningsframgång i öppna skogar om skogarna ligger långt ifrån bebyggelse, där fåglar som är boplundrare är färre. Nära människor var lavskrikornas häckningsframgång emellertid högre i tät skog, där lavskrikans bo är skyddad från predatorer. Baserad på dessa resultat och med hjälp av fjärranalysdata kan jag tillhandahålla en karta som i detalj visar vart i landskapet gallring förväntas höja eller minska lavskrikans häckningsframgång.

Vad bidrar den här avhandlingen med?

Alla mina upptäckter hjälper till att fylla forskningsglappet för unga brukade boreala skogar, som i Sverige utgör 60% av den brukade skogens areal. Därför bidrar denna avhandling med nya råd till skogsförvaltare och beslutsfattare som önskar att jämställa produktion och miljö. I grunden är avhandlingens upptäckter, om så tillämpat, små steg mot ett mer hållbart brukande av planetens resurser.

Populärwissenschaftliche Zusammenfassung

Aus welchem Grund habe ich diese Forschungsarbeit geschrieben?

Die Vielfalt der Lebewesen auf der Erde verschwindet in nie dagewesenem Tackt. Der Grund dafür ist die Tatsache, dass wir Menschen unsere natürliche Umwelt durch eine anthropozentrische ersetzt haben, eine Welt, die wir nach unserem Belieben bewirtschaften. Um diese Entwicklung aufzuhalten, müssen wir neue Bewirtschaftungsmethoden finden. Der boreale Nadelwald ist der flächenmässig grösste Wald der Erde und in vielen Gebieten noch in seinem ursprünglichen Zustand. Nicht so in Fennoskandien. Hier ist die gängige Forstwirtschaftspraxis nicht nachhaltig, wodurch das Überleben vieler waldlebender Arten bedroht ist. Alternative Forstwirtschaftsmetoden, welche die Artenvielfalt erhalten, sind deshalb dringend notwendig. Bei einer dieser Methoden, werden Strukturen, welche für die Artenvielfalt im Wald essentiell sind, bei Kahlschlägen nicht abgeholzt. Wenige solche Methoden sind jedoch für dem Kahlschlag vorhergehende Bewirtschaftungsschritte, wie zum Beispiel dem Waldausdünnen vorgeschlagen, und keine experimentell getestet worden, obwohl experimentelle Studien wichtig sind, um solide Schlusssätze zu ziehen.

Was habe ich gemacht?

Beim konventionellen Waldausdünnen werden wirtschaftlich minderwertige Strukturen wie Laubbäume, Totholz und Unterwuchs entfernt. Anhand empirischer und experimenteller Studien in Schweden wollte ich herausfinden, wie die konventionelle und alternative

Waldausdünnungsmethoden die Vielfalt und das Vorkommen waldlebender Vögel und Flechten sowie den Bruterfolg des Unglückshähers beeinflussen.

Was habe ich herausgefunden?

Meine Ergebnisse zeigen, dass konventionelles Waldausdünnen die Vielfalt der Strukturen im Wald reduziert und dadurch stark beeinflusst, welche und wieviele Vogel- und Flechtenarten in den typischen jungen Wirtschaftswäldern Fennoskandiens vorkommen. Dieser Einfluss war grösstenteils negativ für Vögel, jedoch unter gewissen Bedingungen positiv für Flechten. Ich kann aufzeigen, dass die Biodiversität in diesen jungen Wirtschaftswäldern höchstwahrscheinlich steigt, wenn (i) entweder der Unterwuchs im gesamten Waldbestand oder (ii) ganze Flächen von ca. 1 ha nicht ausgedünnt werden, wenn (iii) so viele Baumarten wie möglich in ausgewogenem Verhältnis und, (iv) grossstämmige Bäume in grösserer Anzahl stehen gelassen werden. Der Unglückshäher dient als Zeigerart für Vogelarten, welche auf einen Wald mit variationsreicher Vegetation angewiesen sind. Ich kann aufzeigen, dass der Unglückshäher einen höheren Bruterfolg hat, wenn er weit weg von menschlichen Siedlungen, wo Nesträuber selten sind, in offenen Wäldern brütet. In der Nähe von Siedlungen ist der Bruterfolg jedoch höher in dichteren Wäldern, wo das Nest vor den zahlreicheren Nesträubern bei Siedlungen geschützt ist. Basierend auf diesem Ergebnis und mit der Hilfe von Fernerkundungsdaten, konnte ich detaillierte Karten herstellen, welche aufzeigen, genau wo der Unglückshäher von einem allfälligen Waldausdünnen profitiert und wo es seine Chancen erfolgreich zu brüten senkt.

Wie trägt meine Arbeit zur bestehenden Kenntnislage bei?

Alle Forschungsergebnisse dieser Studie helfen die Wissenslücke bei jungen borealen Wirtschaftswäldern, welche in Fennoskandien 60% der gesamten Wirtschaftswaldfläche ausmachen, zu füllen. Diese Arbeit unterstützt Förster und Politiker mit essentiellen Ratschlägen dabei, Biomasseproduktions-Ziele und Umweltschutz-Vereinbarungen im borealen Nadelwald gleichermassen zu erfüllen. Schlussendlich, sind die Erkenntnisse dieser Arbeit in kleiner Schritt vorwärts in Richtung einer nachhaltigen Nutzung unserer planetaren Ressourcen.

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This thesis was written here

Ouu…and thanks to the tax-payers of Sweden which granted me a generous salary during these four years. Without you, life would have been so much harder.

Those and the one, I am really thankful for in life, know of it.

ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

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Forestry has led to many threatened species in boreal Fennoscandia. This thesis shows that conventional thinning, the removal of economically inferior trees, negatively impacts birds, but can positively impact epiphytic lichens under specific conditions. Retention methods, where the understory on the whole forest stand or entire plots of ~1ha are spared during thinning, can together with a diverse tree species composition improve the post-thinning habitat for both taxa, and the reproductive habitat for the Siberian jay, an indicator species for Taiga-specialists.

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