Uneven-aged silviculture as a management tool to mitigate biodiversity loss

A case study of beetles in boreal forests

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Cover: Pondering beetle
    Illustration K. Joelsson

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Abstract

Intensive forest management for wood production has altered ecosystem structures and processes, and led to habitat loss and species extinctions. Subsequently, interest in alternative management methods, such as uneven-aged silviculture, has increased. Uneven-aged silviculture maintains a stratified forest with continuous cover and a stable microclimate by low level and more frequent harvesting. Due to preserved forest structures and retained habitat heterogeneity, uneven-aged silviculture may maintain species associated with old growth forest better than current forest management practices. In a large-scale field experiment, I investigated how different silvicultural approaches affected forest beetles, a group of species severely disfavoured by current forest practise. I compared the species richness, abundance and community structure of beetles in an experimental system comprising of five treatments: clear-cutting, thinning (both representing even-aged silviculture), selective felling (representing uneven-aged silviculture), reference, and old growth forest (both representing unmanaged controls).

Selective felling maintained beetle assemblages similar to the reference stands with the exception of cambium consumers. The assemblage of cambium consumers was instead similar to old-growth forests, which suggest that selective felling may add conservation value. In contrast, even-aged silviculture altered the beetle assemblages. Clear-cuts differed from all other stand types, while thinning had beetle assemblages that approached the assemblages of uneven-aged stands, indicating a partial recovery after clear-cutting. However, thinned stands still differed from reference stands. Harvest trails within a selectively felled forest increased openness, resulting in higher temperatures and lower humidity. Beetle assemblages differed between the trails and the retention strips. Both open habitat species and old-growth specialists were among the species associated to harvest trails, which potentially could explain why species assemblage in selective felling did not differ from reference stands or thinned stands.

My results support the hypothesis that uneven-aged silviculture better maintains beetles assemblages associated with semi-natural mature forest than even-aged silviculture. Selectively felled stands could benefit species that are dependent on mature or old growth forest since some of the needed habitat qualities persist. Uneven-aged silviculture might therefore be a better management tool when the conservation of biodiversity is of concern.

Keywords: Beetles, Biodiversity, Boreal forest, Coleoptera, Conservation, Selective felling, Uneven-aged silviculture

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Dedication

To Sven, who taught me to love the forest
and Eva, who taught me to love science.

Everything not saved will be lost.
  Nintendo 'Quit Screen' message

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 Joelsson, K.,* Hjältén, J., Work, T., Gibb, H., Roberge, J-M., Löfroth, T. (2017). Uneven-aged silviculture can reduce negative effects of forest management on beetles. *Forest Ecology and Management*, vol 391, pp. 436-445.

II Hjältén, J.,* Joelsson K., Work, T., Löfroth, T., Roberge, J-M. (2017). Biodiversity benefits for saproxylic beetles with uneven-aged silviculture. *Forest Ecology and Management*, vol 402, pp. 37-50

III Joelsson, K.,* Hjältén, J., Work, T. Uneven-aged silviculture can enhance the stand scale heterogeneity and beetle diversity. (2018) *Journal of Environmental Management* vol 205C pp.1-8 (in press)

IV Joelsson, K.,* Hjältén, J., Gibb, H. Effects of even and uneven-aged silviculture on early and late stage saproxylic beetles: using direct and indirect sampling (submitted)

Papers I-III are reproduced with the permission of the publishers.

* Corresponding author

The contribution of Klara Joelsson to the papers included in this thesis was as follows:

I   Joelsson contributed to the experimental design, main responsible for planning and conducting the field work, all data analysis and main responsibility for writing.

II   Joelsson main responsible for planning and conducting the field work, significant part the data analysis and contributed to the writing.

III Joelsson main responsible for the experimental design, full responsibility for planning and conducting field work, all data analysis and main responsibility for writing.

IV   Joelsson main responsible for planning, conducted the field work, all data analysis and main responsibility for writing.

1 Introduction

1.1 Forest ecosystems in the Anthropocene

A majority of ecosystems across the globe are at present times formed by anthropogenic activities rather than natural disturbances (Hansen *et al.*, 2001). During the last century, humans have extensively modified most of the world's forests often resulting in degraded environmental conditions (Houghton, 1994; Foley *et al.*, 2005). The changes in structures and processes of forest ecosystems have led to habitat loss and species extinctions (Butchart *et al.*, 2010; Ceballos *et al.*, 2015; Newbold *et al.*, 2015).

Prior to extensive human influences, boreal forest landscapes were formed by natural disturbances ranging from large to small scale disturbances (Kuuluvainen, 2002; Shorohova *et al.*, 2011). High to low severity fires, insect outbreaks and storm events have historically created highly variable landscapes where patches of mature forests are interspersed with early successional habitats, with large quantities of standing and downed deadwood. When forest management in Fennoscandia intensified in the second half of the 19th century, selective cutting was the most common silvicultural practice, where the highest valued trees were harvested, leaving a more or less continuous forest cover behind (Lundmark *et al.*, 2017). During the early and middle part of 20th century, even-aged silviculture (e.g. clear-cutting) began replacing selective cutting, and in 1950, selective cutting was prohibited (Axelsson & Östlund, 2001; Simonsson, 2016). Over the last 60 years, even-aged silvicultural practices have intensified in parallel with technical developments (Lundmark *et al.*, 2013). Today, more than 90% of the Swedish forest is managed with even-aged silviculture (Skogsstyrelsen, 2014).

Negative effects of even-aged silviculture on forest biodiversity have been linked to simplification and homogenization of forest structure (Paillet *et al.*, 2010). Since the 1950s deadwood volume in the landscape has decreased to one-tenth of what would occur in a natural forest and less than 12% of the

forest exceeds an age of 140 years (SLU, 2016). Throughout a forest rotation, even-aged silviculture maintains a single-layered, even-aged forest through cleaning and thinning. Stands are then clearcut, often before trees gets old and senescence has started, leaving the even-aged forests poor in deadwood and old trees (Felton *et al.*, 2017). Retention forestry is a modified form of clear-cutting that, by retaining important elements (deadwood, tree groups, single trees) during harvest, could integrate the conservation of biodiversity with timber production (Gustafsson *et al.*, 2012; Simonsson *et al.*, 2015). However the economically viable levels of retention may not be sufficient for all forest species to persist (Johnson *et al.*, 2014).

With increasing conversion to even-aged forests, forest species associated with older, more heterogeneous forest habitats are often restricted to small remnants (Esseen *et al.*, 1997; Bernes, 2011). Semi-natural forests that have eluded clear-felling are important refuges for old-growth favoured species as well as a source of biodiversity for more intensively managed surrounding stands, since biological legacies such as dead wood, old trees and microclimatic conditions have been preserved (Berg *et al.*, 1994; Stenbacka *et al.*, 2010; Hjältén *et al.*, 2012; Johansson *et al.*, 2016). About 2000 forest species are currently red-listed in Sweden and approximately half of them live in old-growth forest. For these species, even-aged silviculture is thought to be the biggest threat (Tikkanen *et al.*, 2006; Westling, 2015).

1.1.1 Natural-disturbances based management approaches

Alternative forest management approaches, based on natural disturbance regimes, including uneven-aged management, might prevent further loss of biodiversity (Pommerening & Murphy, 2004; Drever *et al.*, 2006). The underlying hypothesis of natural disturbance-based management (NDBM) is that many aspects of biodiversity can be protected and ecosystem resilience secured if forest management maintains habitats and habitat structures that are consistent with those found in landscapes dominated by natural disturbances (Angelstam, 1998; Drever *et al.*, 2006; Kuuluvainen & Grenfell, 2012).

In boreal Fennoscandia, stand-replacing disturbances have been historically less widespread compared to boreal North America (Franklin, 2007). Smaller-scale disturbances that cause single-tree or localized mortality may therefore have played a significant role in forming the Fennoscandian forest (Ohlson & Tryterud, 1999; Kuuluvainen, 2002). These smaller-scale disturbances maintained stratified, old-growth, uneven-aged forests with continuous forest cover and high deadwood volumes.

Uneven-aged silviculture aims to mimic small-scale natural disturbances through more frequent but less intensive harvesting interventions. Single-tree

selection felling (hereafter 'selective felling') is the most commonly used uneven-aged silvicultural method for spruce forests in Sweden. Selective felling maintains a stratified, uneven-aged forest by repeated harvesting of individual large-diameter trees. Approximately 70% of the standing volume is retained at each of the felling events, which occurs at 15-30 year intervals. The initial harvest event opens up harvest trails, spaced approximately 20 m apart. In subsequent interventions, the same harvest trails are used and single trees are extracted from the forest in-between. The harvesters are only driven in the harvest trails to minimize impacts on vegetation, forest recruitment and deadwood in the 20 m strips separating the machine corridors(Oleskog *et al.*, 2008; Lundqvist *et al.*, 2009).
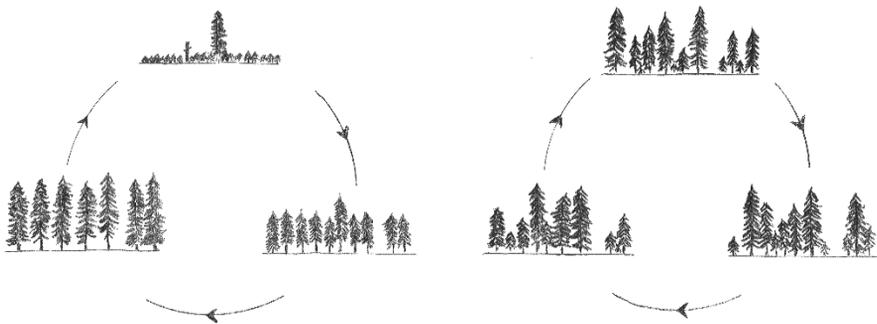
Figure 1. Schematic picture over the two silvicultural systems, even-aged silviculture on the left and uneven-aged silviculture on the right hand side, visualizing the change in forest structure change over time under the different management regimes.

The rationale for uneven-aged silviculture is that, by mimicking small-scale disturbances, a continuously forested stand with uneven-aged tree structure, stratified canopy and stable microclimate will be retained. Retention of these habitat qualities within the managed stand is expected to maintain associated biodiversity (Kuuluvainen et al., 2012). Uneven-aged silviculture may therefore provide an opportunity to combine biodiversity and production, and preserve temporal continuity of forests within the managed landscape by avoiding clear-cutting. However, maintaining structures and processes important for biodiversity while meeting timber management goals is a balancing act (Franklin, 2007) and it is therefore crucial to evaluate how uneven-aged silvicultural methods affect forest species assemblages.

1.2 Deadwood, diversity and silviculture

Deadwood is a key component in natural forest ecosystems. It influences soil formation, nutrient cycling and provides resources and habitat for a vast number of species (Siitonen, 2001; Rondeux & Sanchez, 2010; Seibold *et al.*, 2015a). About one fourth of all forest species and half of the beetles in Fennoscandia are saproxylic, i.e., dependent on deadwood (Siitonen, 2001). This dependence can be a direct need of the woody substrate itself, or indirect through dependence on other saproxylic organisms. Thus saproxylic organisms can include fungivores, predators or parasitoids feeding on organisms restricted to the wood (Speight, 1989).

Deadwood decomposes over time, and saproxylic species face particular challenges related to changes in resource quality. As decay advances, chemical composition of wood as well as nutrient availability change until most structural components are disintegrated and the remaining nutrients integrate with the soil (Ulyshen *et al.*, 2016). Preferences for particular decay stages may vary among species, however, eventually, all deadwood becomes inhabitable. The ephemeral nature of deadwood habitats means that there is limited time for colonization, reproduction and dispersal and the reproductive success of saproxylic populations depends not only on current, but also on future supply of suitable habitat (Stokland *et al.*, 2012). Saproxylic species often specialize on particular deadwood substrates and the communities shift with factors such as tree age, tree species, sun exposure, log size and decay stage (Hjältén *et al.*, 2007; Seibold *et al.*, 2016). Thus, effective conservation of saproxylic diversity will necessitate diversity of deadwood.

However, even-aged silviculture reduces the volume and diversity of deadwood. Managed forests tend to have low volumes of deadwood with poor representation of large dead trees in later decay-classes (Kruys *et al.*, 1999). If green-tree retention is left following harvesting, there will likely be recruitment of future deadwood in the stand. After this initial input of deadwood following harvesting, it might take up to 70 years before new deadwood recruitment begins, which will quickly be met with the next cycle of clearcutting (Ranius *et al.*, 2003). This causes large temporal variation of deadwood, both in quantity and quality. Species with limited dispersal capacity are highly sensitive to this break in continuity (Nilsson & Baranowski, 1997; Siitonen & Saaristo, 2000). Since uneven-aged forests have a multi-layered tree cover, continuous input of deadwood is theoretically possible and a higher variation in decay-classes might be achieved.

1.2.1 Forest beetles

Beetles (*Coleoptera*) constitute a significant portion of forest biodiversity and perform important ecological functions, including decomposition of deadwood and nutrient cycling (Grove, 2002). However they are sensitive to silvicultural practices and changes in habitat quality (Siitonen, 2001; Boucher *et al.*, 2012). Beetle diversity is known to increase with increasing structural complexity of the stand, such as numbers of microhabitats, higher tree species diversity and deadwood diversity (Esseen *et al.*, 1997; Siitonen, 2001; Bouget *et al.*, 2013; Gibb *et al.*, 2013). Approximately 20 % of Swedish beetles are red-listed and current forest management practices remains an important contributing factor for threatened and endangered beetles (Westling, 2015).

Beetles are a well-studied group and we have relatively good knowledge about their habitat preferences, feeding guilds and decay stage preferences for many of the saproxylic species (Gossner *et al.*, 2013; Thorn *et al.*, 2014). The beetle community depends on deadwood composition and microclimatic conditions and tend to change if those conditions are altered. How beetle species respond to silviculture may vary depending on their traits. The initial phases of decomposition are relatively fast. Saproxylic beetles using early decay stages are adapted to a quickly changing habitat and are therefore are among the first colonizers to arrive in deadwood (Gibb *et al.*, 2006a; Stokland *et al.*, 2012). For later decay stages, decomposition phases are typically longer, thus these habitats may present more prolonged opportunities for colonization by saproxylic organisms (Nilsson & Baranowski, 1997; Lee *et al.*, 2014). Later decay stages of deadwood take longer to develop, it can take up to 50 years for a spruce log to reach the advanced stages of decay (Storaunet & Rolstad, 2002). Thus, species using the later decay stages of deadwood might be more susceptible to the impact of silviculture.

1.3 Aim

The aim of my thesis is to compare the effect of even-aged and uneven-aged silviculture on beetle communities and to identify potential mechanisms by which different silvicultural methods affect beetle communities. My study focused on the stand-scale effects of even-aged and uneven-aged silviculture on beetle diversity. A particular focus is to evaluate whether uneven-aged silviculture can be used as a conservation tool to maintain biodiversity or to reduce the loss that traditional management causes. The specific objectives of my thesis are to:

I   To compare the effect of uneven-aged silviculture and traditional even-aged silviculture on beetle communities.

II   Evaluate if there are additional conservation benefits from uneven-aged silviculture- in particular whether selective felling can function as a habitat for old-growth associated species.

III   Study how small-scale habitat dynamics within selectively felled forests affects microclimate and beetle assemblages.

IV   Compare how habitat requirements influence obligate saproxylic beetles response to different forest management approaches and compare whether different sampling methods show a comparable result

2 Methods

2.1 Study sites (Paper I-IV)

My study area was located in the boreal forest of central Sweden, in the provinces of Jämtland and Medelpad (63.0–62.3 N, 15.2–16.4 W). Annual temperature in the region averages 2° C (ranging from -10 to +15° C) and yearly precipitation is 600 mm (SMHI, 2013). Forest cover about 77% of the total land area in those provinces and is to large extent managed for timber production (SLU, 2016). Five different stand types are included in this thesis; (1) recently clear-cut stands that were uneven-aged prior to harvesting but became even-aged as a direct consequence of clear-cutting ('Clear-cut'); (2) older, even-aged stands regenerated after clear-cut 50–60 years ago that recently have undergone commercial thinning ('Thinning'); (3) mature stands originating from uneven-aged, stratified stands which recently have undergone uneven-aged silviculture ('Selective felling'); (4) mature stands originating from uneven-aged, stratified stands without recent history (50 year) of management, resembling selective felling stands prior to management ('Reference') and (5) uneven-aged, old-growth forest with confirmed high conservation values ('Old-growth'). The harvest operations (clear-cut, thinning and selective-felling) occurred 2-15 years prior to the study.

The stands are evenly distributed in the landscape and not closer than 1000 m apart (Figure 2) and selected to be as similar as possible in terms of stand size, altitude, tree species composition and soil conditions. Norway spruce (*Picea abies* (L.) Karst) dominated all study sites (>70% of the volume) and the ground vegetation was mainly bilberry (*Vaccinium myrtillus L.*).
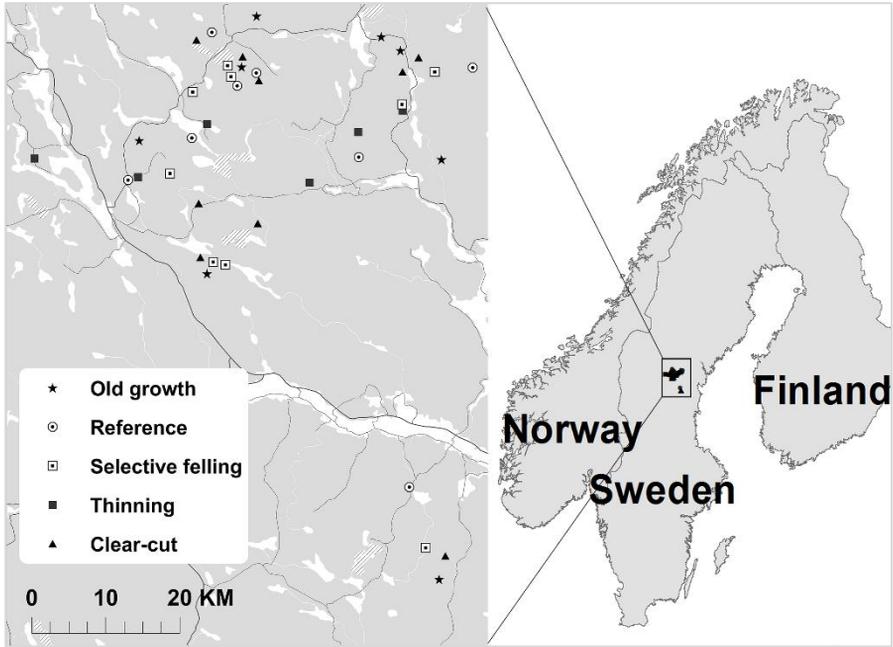
Figure 2. Map over the distribution the included stands.

To evaluate biodiversity benefits of uneven-aged silviculture compared to traditional even-aged silviculture (Paper I), I compared species richness, abundance and beetle assemblages in four treatments; 1) clear-cutting, 2) thinning, 3) selective felling and 4) reference stands. By comparing species richness, abundance and assemblage of beetles in selective felling, reference and old-growth forest with high conservation values, I aimed to evaluate additional conservation benefits with uneven-aged silviculture (Paper II). I addressed small-scale habitat dynamics within stands subjected to uneven aged silviculture through a study comparing microclimate and beetle community the open habitat on harvest trails with closed forest in-between (Paper III). To study how sampling techniques and habitat requirements influences obligate saproxylic beetles response to different forest management practices I compared early and late successional saproxylic beetle assemblages in all five stand types using two different sampling techniques (Paper IV).

2.2 Beetle sampling

I used two different trapping methods for sampling beetles for this thesis; one method that collects beetles broadly associated with a given stand-type (window-traps) and one to sample specific to individual deadwood substrate

(bark sieving). Window traps are a general trapping method, highly efficient in ensuring large samples of flying insects (Hyvarinen *et al.*, 2006). Although window traps have been shown to reflect beetle assemblages of the local features around the trap (Sverdrup-Thygeson & Birkemoe, 2008), there are concerns regarding the extent to which trapped beetles represent transient visitors that may not necessarily be related to local stand conditions (Jonsell & Weslien, 2003; Wikars *et al.*, 2005). By using direct sampling of a deadwood substrate, one can be assured that all captured beetles were actually produced in the stand within specific deadwood substrates. Sieving the bark from experimental logs is one example of direct sampling of a standardised habitat (Alinvi *et al.*, 2007), but this trapping method restricts the sampled species to a subgroup with similar habitat preference. A combination of window traps and bark sieving of experimental logs is often recommended (Müller *et al.*, 2015) to measure beetle responses at both the stand and substrate level. I compared the results from the two trapping methods in paper IV.

All beetles were determined to species level by taxonomic expert B. Andersson, with the exception of the genera *Epuraea*, *Acrotrichi* and *Gabrius*. Nomenclature and taxonomy of the beetles follows the Swedish taxonomic database (Dyntaxa version 1.1.6102.24188, 2015) from the Swedish Species Information Centre. Beetle species were classified as either saproxylic or non-saproxylic (Stokland *et al.*, 2012) and into feeding guilds. Feeding guilds are not mutually exclusive, so species can occur in more than one group. Feeding preferences for individual species were largely based on Koch *et al.* (1989) volume 1-3 and Palm (1959). These designations were then expanded to include species found in northern parts of Sweden (Hilszczański, J., Pettersson, R. and Lundberg, S. pers. comm.) and verified against ecological information provided by leading taxonomic experts at the Swedish Species Information Centre. In addition, the obligate saproxylic beetles were assigned to wood decay classes, using the data available from Thorn *et al.* (2014).

2.2.1 Window traps on stand scale level (Paper I, II and IV)

From late May to September 2014, three window traps (Polish IBL2 traps, CHEMIPAN, Warsawa, Poland) were placed in each stand in all stand types, at 25 m distance from the centroid in N, SW and SE directions and at least 50 m from the stand edge. I used non-toxic propylene glycol in the traps and later transferred the beetles to 70% alcohol solution for preservation.

2.2.2 Window traps for within scale variation (Paper III)

During the summer of 2015, I placed window traps in the selectively felled stands to measure the variation in beetle richness, abundances and assemblage

structure within a stand. Traps were placed on harvest trails and in adjacent retention strips in a randomly chosen location within each experimental stand. The paired traps had the same alignment.

2.2.3 Beetle sampling using experimental logs (Paper IV)

Experimental logs (bolts) were cut from healthy living spruce trees of approximately 70 years that all came from a single location. All logs were distributed to experimental stands in May 2014. In each stand, I placed five pieces, approximately 40 cm long with a diameter ranging from 20-30 cm. In late august 2015, I removed the bark and extracted the beetles through sieving and light extraction. For a more detailed method description, see paper IV.

2.3 Stand characteristics

I measured deadwood volume in three randomly distributed 1000 m² plots per stand. All deadwood including coarse woody material with a diameter ≥ 0.1 m and length ≥ 1.3 meters were assigned a decay class (McCullough, 1948; Jonsson, 2000), tree species and substrate type (snags or logs). Diameters of individual trees were measured in a 500 m² plot, using the same centroid as for deadwood. I calculated basal area and tree species composition using the diameter data. From the owners' forest management databases I extracted information about stand size, average stand age and altitude.

2.3.1 Microclimate assessment (Paper III)

I measured three microclimatic variables within the selectively felled stands: canopy openness, air temperature, and relative humidity at each trapping location. For a more comprehensive description see Paper III.

2.4 Statistical analysis

2.4.1 Paper I, II, IV

Treatment effect on beetle species richness and abundance was tested using generalized linear models (GLM) in the R package 'lme4' (Bates *et al.*, 2016). To evaluate the effect of treatment on the structure of the beetle assemblage, we used the manyGLM function from R package 'mvabund' (Wang *et al.*, 2016). ManyGLM uses the sum of log-likelihoods from many individual GLMs to create a test statistic verified through randomization. In this test, statistical significance was evaluated using 999 resampling iterations via 'Probability Integral Transform residual bootstrap' (PIT-trap) resampling (Wang *et al.*, 2012) and all individual univariate GLM models were fitted

using negative binomial link functions. For all the analyses, I pooled the catches from the three traps in each stand. I repeated the analyses separately for saproxylic beetles, non-saproxylic beetles and for each feeding guild. Stand size and altitude were included as covariates in the model. If the overall test was significant, I conducted pairwise comparisons. To visualize the species assemblage data I created Non-Metric Multidimensional Scaling (NMDS) plots based on Bray-Curtis distances on square-root transformed data, with 20 random starts to find a stable final solution (R package 'vegan' (Oksanen *et al.*, 2007)). I also tested for associations between treatment and average tree age, tree species composition, basal area and deadwood volume using GLM.

To study how stand characteristics influenced beetle communities in Paper IV, I fitted stand variables to the NMDS plots using function envfit from the R package 'vegan'. I used the stand variables presented in Table 1, with the exception of the number of years since treatment. The significance test was based on 999 random permutations of the data. I excluded clearcuts and repeated the analyses in order to explore which variables had the highest influence on the beetle assemblage in selective-felling, thinning, reference and old growth stands.

2.4.2 Paper III

The effect of openings of harvest trails in uneven-aged stands were studied using both beetle and microclimate data. Canopy openness, temperature and relative humidity were analysed separately to quantify the microclimatic differences between harvest trails and retention strips. I fitted linear mixed-effects models with Gaussian error distribution where treatment effect on canopy openness, daily maximum and minimum temperature and humidity were included as a fixed and stand-identity as random factor. Temporal autocorrelation was accounted for by using 'corAR1' function in the model. Due to high daily fluctuations in both temperature and humidity, I used a generalized additive mixed models (GAMM) with Gaussian error distribution to test for average differences in temperature and humidity between retention strips and harvest trails. Treatment and time were used as fixed factors, and stand-identify was a random factor. The analyses were conducted in R packages "nlme" (Pinheiro *et al.*, 2014) and "mgcv" (Wood & Wood, 2016).

Treatment effect on beetle abundance and richness was tested using generalized linear mixed models (GLMM) with negative binomial error distribution with stand as random factor in packages "nlme" (Pinheiro et al., 2014). In addition, I created rarefied species richness rarefaction curves, using 100 randomizations (Colwell, 2006) to compare species richness while accounting for differences in abundance. Treatment effect on species

assemblage was tested using permutational multivariate analysis of variance (PERMANOVA) (Anderson et al., 2008). To test for associations between species and treatment, I performed an indicator species analysis (Dufrêne & Legendre, 1997). This analysis considers both relative abundance and relative frequency, and provides indicator-value based only on within-species abundance and occurrence comparisons, without any comparison among species. I performed the analysis in the R package "indicspecies" (De Caceres *et al.*, 2015).

3 Results

3.1 Uneven-aged silviculture as a management option (Paper I)

I selected stands to minimize differences in stand size, tree species composition and altitude between included stand types. Basal area and deadwood volume did however differ due to the different management regimes. Reference stands had the highest basal area followed by selective-felled, thinned and clear-cut stands. Deadwood volume was greatest in reference and selectively felled stands, followed by clear-cut and finally thinned stands (Table 1).

Table 1. *Overview of the 30 experimental stands. Mean ± SE is provided for stand variables. The results from the GLM of stand variables are presented on the right. Bold numbers highlight significant differences at p < 0.05. SF= selective felling. CC= clearcut, T= thinning. R= reference. BA= basal area*

Stand type	CC	T	SF	R	P (Chi^2)
Original state	Uneven	Even	Uneven	Uneven	
Current state	Even	Even	Uneven	Uneven	
Number of stands	8	5	9	8	
Size (ha)	5.7 ± 1.3	7.7 ± 3.0	8.0 ± 0.7	7.2 ±1.6	0.41
Altitude (m)	376 ± 18	366 ± 34	391 ± 9	364 ± 25	0.75
Years since treatment	6.7 ± 1.8	6.2 ± 2.2	7.4 ± 1.7	NA	0.85
Mean tree age	2.6 ± 1.4	51 ± 3.1	120 ± 6.3	132 ± 7.1	**<0.01[1]**
Basal area (m^2)	0.3 ± 0.12	18.5 ±2.3	17.9 ± 1.0	24.5 ± 1.0	**<0.01[2]**
Deadwood (m^3)	8.5 ± 3.2	4.6 ± 1.0	13.0 ±3.5	16.9 ± 5.5	**0.03[3]**
Spruce % of BA	NA	83.2 ± 7.1	80.0 ± 4.1	80.2 ± 3.7	0.90
Pine % of BA	NA	6.3 ± 5.1	6.3 ± 3.8	4.5 ± 2.9	0.92
Birch % of BA	NA	8.0 ± 3.0	13.4 ± 2.1	14.1 ± 3.4	0.34

1: CC < T < SF = R, **2:** CC < T =SF < R, **3:** CC, T < R; T < SF; SF=R

I collected 15,147 beetles representing 461 species using window traps in the 30 stands included in Paper I. Uneven-aged silviculture had limited impacts on beetle composition; selective felling did not differ from unmanaged reference stands ($p=0.12$), except from cambium consumers ($p=0.04$). Only 15 species, or 8% of all species, captured in reference stands were absent from selective fellings, indicating relatively minor impacts from selective felling on the existing beetles community. However, selective fellings harboured 65 additional species absent from reference stands. The majority of those species were common in clear-cut and thinned stands.

Both even-aged silvicultural treatments had different beetle compositions (clearcut ($p<0.01$) and thinning ($p=0.05$)) compared to the reference stands, indicating that assemblages had yet to recover even 50 years into the rotation. Immediately following clearcutting, beetle composition differed from all other treatments for all groups of beetles. As even-aged stands regrew and were thinned, overall composition and composition of non-saproxylics and predators continued to differ from reference stands. However, beetle composition did not differ between selective fellings and thinned stands (Table 2).

Nearly 40% of the species occurred in all treatments, suggesting some degree of ecological resilience. Species richness and abundance did not differ significantly between any treatments with the exception of the subgroups cambivores (lower abundance on clear-cut than in thinning and selective-felling) and non-saproxylic beetles (lower species richness in reference than in clear-cut and thinning).

Table 2. ManyGLM analyses testing differences in beetle assemblage structure among stand types for all species and for functional groups. The overall results from manyGLM are presented, followed by the treatment effect from the pairwise comparisons. SF= selective felling. CF= clear-felling T= thinning. R= reference. Bold numbers highlight significant differences

	Res DF	DF	All species deviance	p	Saproxylic deviance	p	Non saproxylic deviance	p	Fungivore deviance	p	Predator deviance	p	Cambivore deviance	p
Treatment	26	3	2161	**<0.01**	1755	**<0.01**	407	**<0.01**	943	**<0.01**	787	**<0.01**	199	**<0.01**
Altitude	25	1	423	**0.018**	354	**0.017**	69	0.195	195	**0.011**	146	0.052	43	*0.058*
SF -R	15	1	457	0.115	301	0.125	50	0.361	188	*0.082·*	118	0.249	51	**0.038**
SF-T	12	1	307	0.287	305	0.252	59	0.252	112	0.520	120	0.214	37	0.150
R-T	11	1	416	**0.05**	328	*0.067·*	88	**0.02**	174	*0.087·*	148	**0.048**	42	*0.098·*
R-CF	14	1	1348	**<0.01**	871	**<0.01**	210	**<0.01**	498	**<0.01**	393	**<0.01**	99	**<0.01**
SF-CF	15	1	1338	**<0.01**	908	**<0.01**	205	**<0.01**	457	**<0.01**	409	**<0.01**	95	**<0.01**
T-CF	11	1	1057	**<0.01**	671	**<0.01**	179	**<0.01**	352	**<0.01**	324	**<0.01**	76	**<0.01**

3.2 Uneven-aged silviculture as a conservation tool (Paper II)

Selective felling reduced basal area, but had no additional effects on other stand variables compared to the reference. Basal area did not differ between reference and the old growth stands. However, old growth forest had lower volume of birch, higher volumes of aspen (*Populus tremula* L.) and goat willow (*Salix caprea* L.) compared to selective-felling and reference stands. Furthermore, tree density was marginally lower in old growth stands. Deadwood volume was highest in the old growth compared to selective felling and reference. (Table 3).

Table 3. *Structural characteristics of the experimental forest stands. Sample mean ± standard error. Note that all stand characteristics except, size, age and altitude were measured after selective felling were conducted. GLM analyses were used to test for differences between forest types. Letters after mean values denotes significant differences in the post-hoc test (P<0.05).*

	Selective felling	Uncut	Old Growth	GLM statistics
Size (ha)	7.99 (±0.76)	7.19 (±1.57)	19.53(±9.00)	P=0.072
Stand age (years)	120 (±6.33)	132 (±7.11)	136 (±8.24)	P=0.215
Altitude	391 (±8.65)	364 (±24.7)	418 (±22.8)	P=0.142
Pine Vol-%	6.31 (±3.75)	4.46 (±2.93)	7.76 (±5.07)	P=0.839
Spruce Vol-%	80.0 (±4.16)	80.2 (±3.76)	80.8 (±6.00)	P=0.985
Birch Vol-%	13.4 (±2.07) a	14.1 (±3.44) a	6.12 (±1.66) b	**P=0.025**
Aspen & Salix Vol-%	0.92 (±0.44) a	0.28 (±0.28) a	5.00 (±2.34) b	**P=0.024**
Dead wood (m^3ha^{-1})	13.0 (±3.52) a	16.9 (±4.21) a	64.7 (±10.2) b	**P<0.001**
Basal area (m^2ha^{-1})	17.9 (±1.00) a	24.5 (±0.98) b	25.7 (±2.92) b	**P=0.006**
Stem number (no/ha)	862 (±68.0)	902 (±68.0)	702 (±46.7)	P=0.063

In total we captured 14,199 beetles belonging to 360 species (of which 120 were singleton captures) in the three treatments included in Paper II. The GLM analysis of species richness revealed a tendency of higher species richness in selective felling and old growth than in reference stands, but the effects were not significant. I found that assemblages of obligate saproxylics and cambivores (ManyGLM: $p < 0.049$ and $p < 0.032$, respectively) were affected by treatment. Reference stands had a different assemblage composition compared to selective felling and old growth (marginally significant for obligate saproxylic) (Table 4).

Table 4. *Results of the manyGLM analyses exploring the effect of forest type, altitude and stand size on species composition of beetles. DF = Residual degrees of freedom, Dev = deviance. Significant differences are marked in bold to highlight the results. The p-values from the pairwise comparison follows. SF=selective-felling, R =reference, OG=old growth*

		Overall comparison			SF vs R	SF vs OG	OG vs R
		DF	Dev	p	p	p	p
All beetles	Forest type	22	2739	*0.089*	0.123	0.228	0.123
	Altitude	21	1479	**0.005**	**0.016**	**0.016**	**0.007**
	Size	20	1364	0.096	0.284	0.055	0.048
Obligate saproxylic	Forest type	22	393.7	**0.049**	*0.094*	0.184	*0.085*
	Altitude	21	243.9	**0.005**	**0.015**	**0.040**	**0.015**
	Size	20	210.6	**0.017**	0.296	**0.018**	**0.034**
Non saproxylic	Forest type	22	72.8	0.474			
	Altitude	21	55.5	*0.061*			
	Size	20	31.1	0.742			
Cambivores	Forest type	22	100.6	**0.032**	**0.038**	0.183	**0.036**
	Altitude	21	48.4	**0.040**	**0.005**	0.167	0.136
	Size	20	60.9	**0.010**	0.113	**0.024**	**0.013**
Fungivores	Forest type	22	339.6	*0.091*	*0.071*	0.270	0.190
	Altitude	21	202.9	**0.016**	0.069	0.173	**0.009**
	Size	20	148.4	0.291	0.303	0.145	0.199
Predators	Forest type	22	277.2	0.090	0.254	0.110	0.128
	Altitude	21	196.3	**0.003**	**0.028**	**0.008**	**0.021**
	Size	20	124.3	0.214	0.649	0.154	0.064

Differences between reference, selective felling and old-growth forest were largely explained by a higher abundance of saproxylic species presumably associated with old growth conditions and large volumes of deadwood. The difference between reference and old growth stands were mainly explained by higher abundances of the cambivores *Crypturgus cinereus*, *Pissodes harcyniae*, *Pityogenes chalcographus* and *Polygraphus punctifrons* in old growth stand. *Crypturgus hispidulus* and *C. cinereus* had higher abundance in selective fellings than in reference while *Phloeotribus spinulosus* had higher abundance in reference (Figure 3).
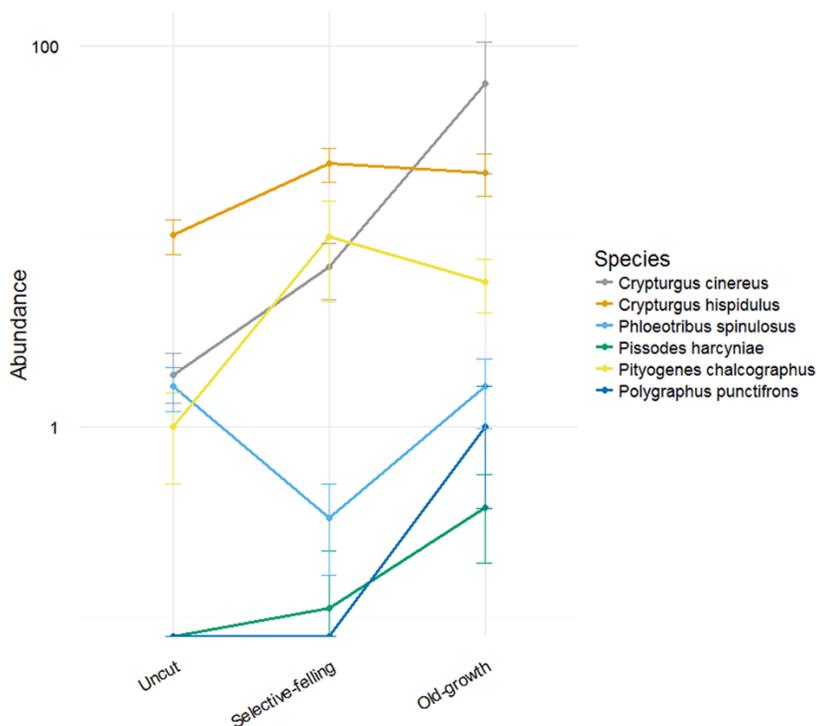
Figure 3. Mean ± CI abundance per species and stand type for the cambivore species that differed significantly (p < 0.05) in abundance between uncut stands and selective felling as well as between uncut and old growth stands in the manyGLM analysis. The y-axis is log-transformed.

3.3 Stand scale heterogeneity within selectively felled stands (Paper III)

Harvest trails and retention strips generated different climatic conditions; the nearly doubled canopy openness resulted in temperature increase by 0.5°C (p=0.02) and a humidity decrease of 0.7 % RH units (p<0.01) compared to the retention strips. Daily variation suggested even greater differences; harvest trail had daily maximum temperature of 1.9° higher and daily minimum 0.3° lower compared to the retention strips. The daily minimum humidity was on average 4.5 %-units lower in harvest trails, whereas daily maximum humidity was 0.9 %-units higher.

Traps in harvest trails and retention strips collected different beetle assemblages. Species richness and abundance were higher in the harvest trails than in the retention strips and the species composition differed (PERMANOVA: p<0.01, Figure 4).
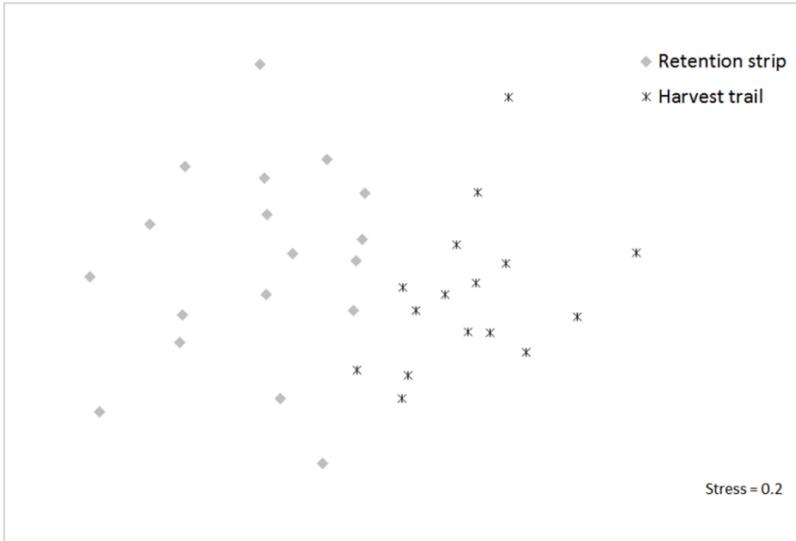
Figure 4. NMDS plot visualizing the differences in species assemblage structure between treatments. The axes are without scale but points close together represent site with similar assemblages. The sites' assemblage structures become increasingly dissimilar from one another as the distance increases. Stress value is 0.2

We captured a total of 10,291 beetles belonging to 278 species. One-hundred fifty-one species were found in both habitats. Ninety-three of these species were unique to the harvest trails and 34 were unique to the retention strips (Figure 5). Without singletons, those numbers decreased to 43 and 8 respectively. We observed 25 species with significant associations with harvest trails in the indicator species analyses. Half of the indicator species were fungivores. Six fungivore species occurred exclusively on harvest trails, one of them the red-listed species *Agathidium discoideum*, which known to be strongly associated with old-growth forest and declining due to intense forest management (Westling, 2015). By contrast, retention strips only had one species with significant indicator value, the cambivore species *Xylechinus pilosus.* This species has been identified as a forest interior specialist and is often found in forest
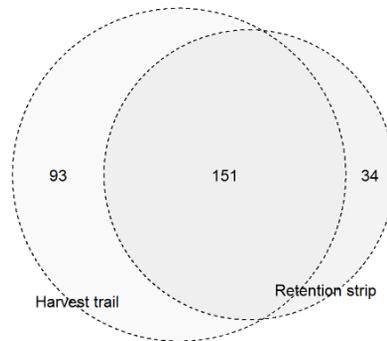

Figure 5. Venn-diagram displaying the number of unique and shared species for the two treatments. The size of the circles represents total number of species per treatment

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reserves. . *X. pilosus* is known to avoids forest edges (Peltonen & Heliövaara, 1998; Hjältén *et al.*, 2012).

3.4 Effects on early and late stage saproxylic beetles, using direct and indirect sampling (Paper IV)

Beetle assemblages differed with management history (p<0.01) and that result was consistent regardless of sampling method or decay-class preference. Even-aged silviculture altered beetles assemblage; clear-cutting differed from all other stand types and thinning differed from reference in both trap types and decay-preference classes. The window trap data showed a significant difference in species assemblage of early successional species between reference stands and old-growth forests. The same trend was visible for bolts (p=0.10). Species assemblages associated with later decay stages were marginally different in thinned stands compared to selective-felling and old growth forest (Table 5, Figure 6)

Table 5. *ManyGLM analyses tested a treatment effect in beetle assemblage structure among stand types for our four included subgroups/data sets. Presented at the top of the table are the overall results from manyGLMs, followed by the treatment effect from the pairwise comparisons. Dev= Deviance. SF = selective felling. CC = clearcut T = thinning. R = reference, OG= Old growth. Bold numbers highlight significant differences*

	Blots			Window trap comparison			Early species			Late species	
	Dev	p	DF	Dev	p	DF	Dev	p	DF	Dev	p
Treatment	178	**<0.01**	34	310	**<0.01**	33	575	**<0.01**	33	951	**<0.01**
Stand size	25	0.75	33	67	**<0.01**	32	127	**0.01**	32	133	0.2
Altitude	44	*0.09*	32	53	**0.03**	31	134	**0.01**	31	210	**<0.01**
Pairwise comparisons	Dev	p	DF	Dev	p	DF	Dev	p	DF	Dev	p
CC vs T	65.6	**<0.01**	11	136.9	**<0.01**	10	213.4	**0.02**	10	357.8	**<0.01**
CC vs SF	54.6	**<0.01**	15	147.3	**<0.01**	14	208.2	**<0.01**	14	387.4	**<0.01**
CC vs R	55.9	**<0.01**	13	142.5	**<0.01**	12	213.8	**<0.01**	12	340.1	**<0.01**
CC vs OG	70.5	**<0.01**	14	118.8	**<0.01**	13	220.8	**<0.01**	13	389.3	**<0.01**
T vs SF	41.0	0.14	10	66.0	*0.09*	10	98.2	0.30	10	193.7	*0.10*
T vs R	34.3	**0.05**	9	56.5	**0.03**	9	82.3	**0.05**	9	130.0	**0.05**
T vs OG	35.4	0.29	9	69.9	0.14	9	114.6	0.20	9	183.5	*0.10*
SF vs R	19.4	0.41	12	32.8	0.19	12	70.2	0.13	12	109.7	0.11
SF vs OG	29.4	0.13	13	12.0	0.9	13	61.7	0.32	13	117.0	0.12
R vs OG	31.2	*0.10*	11	33.2	0.17	11	89.0	**0.04**	11	85.1	0.22

Decay-class preference had only a minor influence on the response of beetle assemblages to different forest types and treatments. In addition, the ability to detect differences were not affected by sampling method, the window traps and bark sieving showed similar trends. We collected 14,811 individuals belonging to 220 obligate saproxylic species using window traps and 6,622 individuals belonging to 28 species sieving the bark from bolts. The corresponding abundance for the same species in window traps were 8,228 individuals. We could classify 80 % of species from window traps according to decay class preference; 75 species were associated with early and 103 species with late decay stages of deadwood. The representation feeding guilds differed between early and late successional species. Cambivores comprised 50% of the early successional species followed by predators (35%) and fungivores (12%). In contrast, fungivores dominated the late successional community representing 60% of the species. Predators comprised 26% of the late succession species and cambivores were represented by a single species (*Judolia sexmaculata*). Within experimental logs, most of the beetles collected (75 % of the species and 95% of the abundance) were early successional species. This assemblage was represented by 57 % cambivores, 25 % fungivores and 14 % predators.

Basal area correlated strongly with species assemblage. However, after removing clearcuts this correlation disappeared. Beetles assemblage in the bolts was correlated to the volume of early decay deadwood. Assemblage of early successional species collected in window traps was also correlated to volume of early decay deadwood. Late successional beetles showed no significant correlation to the measured stand characteristics (Figure 6).
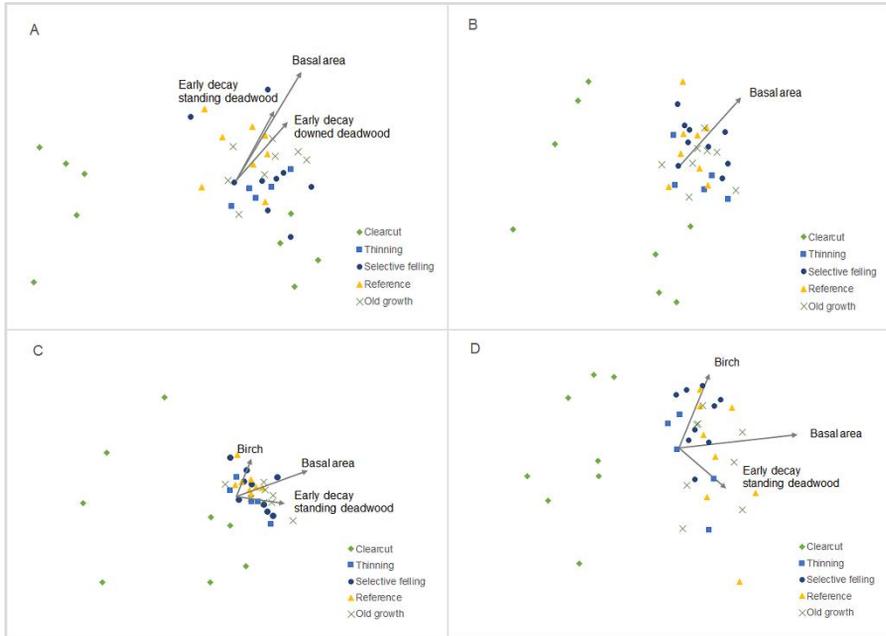
Figure 6. NMDS plots of four different data sets: A) bolts (stress = 0.15), B) species-by-species comparison with window traps (stress = 0.11), C) beetles associated with early decay stages of deadwood (stress = 0.12) and D) beetles associated with early decay stages of deadwood (stress = 0.15). The plots are based on square-root transformed data with Bray-Curtis distances and were run with 20 random starts to find a stable final solution. The axes are without scale but points close together represent site with similar assemblages. The sites' assemblage structures become increasingly dissimilar from one another as the distance increases. The fitted stand variables with a significant correlation (p ≤ 0.05) plotted as arrows. The length of the arrow indicates the strength of the correlation and the direction the positive correlation.

4 Discussion

With increased pressure on forests to produce both timber and biodiversity, management methods that can meet production and environmental goals are needed. Uneven-aged silviculture has been proposed as a means to better maintain biodiversity within the managed forest landscape. In my dissertation, I show that, uneven-aged silviculture mostly maintained the beetle assemblage of the unmanaged forest while even-aged silviculture resulted in drastic changes to the local beetle assemblages.

The rationale behind uneven-aged silviculture is that by mimicking small scale disturbances and processes, the associated biodiversity will be maintained (Kuuluvainen & Grenfell, 2012). The structure of selectively felled stands included in this study resembled unmanaged stands, with layered structure, trees of multiple ages and diversity of deadwood. In late successional forest, processes such as tree senescence, fungi or insect attacks would open small gaps, add deadwood and increase structural heterogeneity (Esseen *et al.*, 1997). The main disturbance in selectively felled forest was harvesting, as tree removal along the harvest trails creates openings in the canopy. Harvest trails altered both the microclimate and the beetle assemblage. The species benefitting from harvest trail included both clear-cut species and old growth specialists. Forest interior specials benefitted from the more intact forest in-between harvest trails.

Clear-cutting has more resemblance to stand-replacing disturbance, with an almost complete tree cover removal and consequently benefit species associated to open habitats or early successional forest. Thinning, on the other hand, takes place after renewal of tree cover and it does resemble selective felling in some aspects. In both cases, approximately 30 % of the standing volume is harvested and harvest trails open up gaps in the canopy, hence the disturbances as such is small-scale. However, the stand structure is very different, since the thinned stands have evenly distributed trees of similar sizes

and ages. The previous forest continuity break in the thinned stands also affects the deadwood availability and ecological legacies. The purpose of the two harvesting operations also differ from each other. Thinning aims to keep the even-aged structure whereas selective-felling aims to maintain an uneven-aged structure.

4.1 Uneven-aged silviculture could preserve biodiversity in the managed landscape

Selective felling maintained beetle abundance, richness and assemblage in levels comparable to the reference stands. Thus, I could confirmed the trend seen by others, that 70% retention appears sufficient to maintain the species assemblage of the unmanaged forest (Atlegrim & Sjöberg, 1996; Koivula, 2002; Siira-Pietikainen *et al.*, 2003; Siira-Pietikainen & Haimi, 2009; Work *et al.*, 2010). High levels of tree retention can preserve microclimate typical of unmanaged forest (Jacobs & Work, 2012; Lee *et al.*, 2015). Already at lower level, green tree retention increases structural diversity (Kruys *et al.*, 2013) and benefit biodiversity (Fedrowitz *et al.*, 2014), but around 50-70% tree retention might be needed to preserve old-growth associates (Work *et al.*, 2010; Boudreault *et al.*, 2013) Selective fellings harboured old-growth associated species, such as *Triplax scutellaris, Xylechinus pilosus* and *Eudectus giraudi* (Peltonen & Heliövaara, 1998; Gibb *et al.*, 2006b; Olsson *et al.*, 2012; Westling, 2015), which indicate that selective felling preserved old-growth habitat (Drever *et al.*, 2006; Boudreault *et al.*, 2013). Some saproxylic beetles prefer shaded condition and moist deadwood (Hjältén *et al.*, 2007; Stokland *et al.*, 2012) and might only persist in forests with relatively high tree retention.

High tree retention may also assure a more constant supply and diverse composition of deadwood (Kuuluvainen *et al.*, 2012). Diversity of deadwood is at least as important as the total volume, as many saproxylic species are habitat specific, for example to a certain tree species, substrate size and type or the surrounding microclimate (Gibb *et al.*, 2006b; Stokland *et al.*, 2012; Seibold *et al.*, 2016). Deadwood composition in selective felling stands were similar to reference stands and might explain the maintained beetle composition.

In contrast, even-aged silviculture disrupted species assemblage. Most of the species associated with clear-cuts had lower abundance or were absent from the other treatments with closed canopy forests, a trend that has been extensively documented in previous studies (Grove, 2002; McGeoch *et al.*, 2007; Stenbacka *et al.*, 2010; Hjältén *et al.*, 2012). Effects of clear-cutting decreased with time; beetle assemblages in thinned stands was more similar to reference stands than to clear-cuts. Nonetheless, species assemblages still

differed significantly from reference. In this study, a lack of mature even-aged stands (70-100 years) precluded the inclusion of older even-aged stands in my experiment. Thus, even though recovery appears to proceed, it remains untested whether, and in that case when, assemblages in the even-aged stands resemble reference stands immediately prior to cutting.

I did not find any significant difference for species richness, abundance or assemblage structure between selective felling and thinning. Even though selective felling and thinning differ in terms of both current structures and management history, it did not translate into different beetle communities. Nonetheless, after clear-cutting follows a period with altered habitat. I cannot conclude how long it takes before the beetle compositions are restored after clearcutting has taken place, but Stenbacka et al. (2010) found that the effect of even-aged silviculture remained in stands 30-50 years after clear-felling. Before the habitat is inhabitable again for the species found in selective-felling, which could take considerable time, species have to persist elsewhere.

A major benefit with selective felling is that species are less dependent on fast recolonization since a stand maintains species even after harvest. Selective fellings maintained at least some important microhabitats comparable to what can be found in reference stands, such as remaining old trees and undisturbed field vegetation (Kuuluvainen *et al.*, 2012) which could benefit species with limited dispersal capacity. Species that are slow dispersers are often connected to late successional forest where stand-replacing disturbances would rarely occur (Nordén & Appelqvist, 2001). Uneven-aged silviculture might create a feasible habitat for those species and could possibly act as an important biodiversity source.

On the other hand, even-aged forest supports species absent from uneven-aged forest. For example, species dependent on sun-exposed wood could be negatively affected by selective felling. Eight red-listed species were collected, whereof five exclusively, in clear-cuts. Thus, complete replacement of even-aged silviculture to uneven-aged silviculture would likely lower landscape biodiversity.

4.2   Added benefits with uneven-aged silviculture

Selective felling, to a certain extent, added conservation value to the forests compared to leaving the forest unmanaged. Both selective felling and old-growth forest had different assemblages of cambivores and obligate saproxylics (marginally) compared with reference stands, but did not differ from each other. The difference between selective felling and reference stands was explained by higher abundance of two and lower abundance of one

cambivore species in selective felled stands. Species that benefitted from selective felling are associated with early decay stages of deadwood, semi-open canopy cover and low stumps created by harvest. Both *Crypturgus hispidulus* and *C. cinereus* utilize wind-thrown areas and reach their highest population in reserves (Hjältén *et al.*, 2010) which may explain why they are attracted to selective fellings where semi-closed forest and fresh deadwood in the form of low-stumps and harvest debris is available. In contrast, *Phloeotribus spinulosus* that was negatively affected by selective felling has previously been link to closed stands and dense undergrowth (Similä *et al.*, 2003) and was possibly disadvantaged by the increased canopy openness in selective fellings.

Differences between the reference and old-growth forest was explained by higher abundance of some cambivore species in old growth forest. High levels of deadwood, in combination with lower tree density and potentially more light in old growth stands might explain the higher abundances. Interestingly, these species often occurred in high or intermediate abundances in selective fellings, indicating that they benefitted from selective felling as well.

Increased canopy openness and input of fresh deadwood appeared to drive the assemblage structure in selective felling closer to the one in old-growth forest. Thus, selective felling may add biodiversity value compared to the reference stand in a short-term perspective. Nonetheless, only a small proportion of the collected species benefitted from selective felling and the positive effects are therefore limited. At the same time, there were no substantial negative effects by the selective felling and could therefore be considered as an alternative to clear-felling in areas with production forest where it is especially important to mitigate negative effects of forestry on biodiversity.

4.3   Stand scale heterogeneity increases beetle diversity

Uneven-aged silviculture strives to mimic small-scale disturbances, with the intention to maintain natural processes and associated species (Kuuluvainen & Grenfell, 2012). Removal of canopy by cutting the harvest trail open might provide conditions that resembles the conditions in a natural gap in late successional old-growth forest, where small-scale dynamics alter light and temperature (Muscolo *et al.*, 2014). Uneven-aged silviculture enhanced within-stand scale heterogeneity, both in terms on beetle assemblage and microclimate. The microclimatic factors such as temperature and humidity differed between harvest trails and retention strips, which most likely influenced beetle activity and composition. Species adapted to old-growth forests could possible benefit from those openings and harvest trails did indeed

favoured some beetles commonly regraded as old-growth specialists (Hjältén *et al.*, 2007; Hjältén *et al.*, 2012; Bell, 2015; Seibold *et al.*, 2015b). Earlier studies (Paper II) indicates that stand assemblage in selective fellings and old growth forest is similar. However, since I did not compare beetle assemblage from harvest trails and retention strips with beetle assemblage on unmanaged old growth forest I lack knowledge about the extent that harvest trails resemble species and microclimatic responses to gap dynamics in natural forest.

Interestingly, both open-habitat specialists and forest species were represented among the beetles benefitted by the lighter conditions and warmer climate in the harvest trails. Increased sun exposure has been shown to increase both species richness and abundance of beetles (Lindhe *et al.*, 2005; Vodka & Cizek, 2013). Small gaps and linear structures can act both as corridors and habitat for species (Larrieu *et al.*, 2013; Berg *et al.*, 2016) and my data shows that the relatively small openings (approx. 4 meter wide) from harvest trails where enough to affect beetle richness, abundance and assemblage. The degree of sun exposure on deadwood has a strong effect on the colonizing saproxylic assemblage (Lindhe *et al.*, 2005; Hjältén *et al.*, 2012; Seibold *et al.*, 2016). However, sun exposure preference varies among species (Lindhe *et al.*, 2005; Seibold *et al.*, 2016). The fact that retention strips harboured unique species suggests that some of the more light intolerant forest specialists avoid the more open parts of the stand.

Approximately 50% of species associated to harvest trails were fungivores. Level of sun exposure is a strong determinant of which fungal species colonize the dead wood, and may alter both species composition and the fungal growth rate (Bouget & Duelli, 2004). While I did not directly assess fungal composition in my study, Jacobs and Work (2012) demonstrated a shift in fungal composition after uneven-aged silviculture, possibly as an effect of more days with beneficial growth temperatures for fungi. Both direct abiotic factors and indirect effects related to changes in fungal composition could influence beetle trap catches and are not mutually exclusive.

One forest interior specialist species *(Xylechinus pilosus)* was strongly associated to retention strips. This suggests that, for at least some species, retention strips are not necessarily edge-habitat but rather contain habitat and conditions consistent with closed canopy forest and might therefore further enhance the stand scale diversity.

4.4 Effect of decay-stage preferences

Decay stage preference played a minor role of how beetle assemblages responded to forest with different management history. Beetles living on early decay stages of deadwood depends on rapidly consumed phloem of recently killed trees and are generally considered capable of long and fast movement by flight (Gibb *et al.*, 2006a; Vanderwel *et al.*, 2006). They might therefore be more influenced by quality of the cambium than by quality of surrounding habitat (Gibb *et al.*, 2006a; Hjältén *et al.*, 2010; Lee *et al.*, 2014). Woody debris and low-stumps from harvest operations create an input of fresh deadwood in managed stands, which might explain why there was no detectable difference among old growth, selective-felling and thinning despite the difference in deadwood volumes. However, reference stands had the second highest level of early decay deadwood among the different stand type, but the assemblage of early successional beetles still differed from old-growth stands, which suggest that other factors may influence. Level of sun exposure can affect both the beetle activity and assemblage (Larrieu *et al.*, 2013). High basal area and number of stems in reference stand causes a dense canopy, which could possibly be an important influencer on the assemblage structure.

Late successional species showed a marginally non-significantly difference between thinning and selective felling, and between thinning and old growth forest. This tendency did not occur for the assemblage structure of early successional species. Late successional species are thought to be more dispersal restricted and often with more specific habitat demands (Gibb *et al.*, 2006a; Vanderwel *et al.*, 2006; Stokland *et al.*, 2012), and the higher proportion of maintained habitat structure in selective felling might explain this tendency. The volumes of deadwood in late decay stages were much lower in thinned stands than in the other stand types but there was no detectable correlation between deadwood and late successional species.

The main difference between the early and late successional species was the shift in the proportion of feeding guilds represented. Diversity of decay stages of deadwood is a key source to saproxylic beetle diversity (Grove, 2002). Cambium consumers dominated the early successional community while fungivores dominated the late decay community, which is consistent with observed successional patterns in saproxylic assemblages (Vanderwel *et al.*, 2006; Stokland *et al.*, 2012). Both early and late decayed deadwood need to exist concurrently to maintain a diverse community of saproxylic beetles, or there is a risk of excluding most species of a specific feeding guild. Since it can take considerable time for late or advanced decay stages of deadwood to form, it is crucial to consider deadwood recruitment during all stages of forest management (Ranius *et al.*, 2003) especially for dispersal limited species

(Siitonen & Saaristo, 2000). Thus selective felling might, on a local scale, benefit saproxylic beetles since mature trees and potential supply of fresh deadwood are always present much like a late successional forest (Kuuluvainen, 2002; Jonsson *et al.*, 2016).

4.5   Consistency between different trapping types

Choice of trapping method only appeared to a have minor influence on our results. I saw the similar differences between treatments for both the bolts and the window traps. Thus, I found support for the assumption that general trapping methods (window trapping) shows consistency with a substrate specific trapping method. Beetle assemblage captured in window traps are influenced by the closest surroundings (Sverdrup-Thygeson & Birkemoe, 2008; Müller *et al.*, 2015), even though breeding in the focal stand is not guaranteed (Wikars *et al.*, 2005).

However, even though both trapping methods showed a similar treatment response, the treatment response were explain by different species depending on trapping method. In fact, even though I used the same sub-set of species to compare the two sampling methods, none of the species that fell out as significantly affected by treatment was shared. Preferred breeding substrate is likely a major determinant of species abundances from different trap types, and species captured in bolts were solely produced in spruce-deadwood of early decay. The individuals captured in window traps don´t have that restriction, and might occur in different abundances depending on availability of other substrates.

Nonetheless, even though the species explaining the difference between stand types, both trapping methods pick up the same between-stand differences. Thus, in coherence with the results from Sverdrup-Thygeson and Birkemoe (2008) and Müller *et al.* (2015) the two trapping methods appears to reflect environmental responses in similar ways.

5 Conclusions

I recommend that uneven-aged silviculture should be considered as an alternative to even-aged silviculture in areas with forest assigned to production where it remains highly important to mitigate negative effects on biodiversity.

The greater temporal continuity in selectively felled stands is likely to benefit species that rely on mature or old growth forest since some of the habitat qualities needed will be present throughout the rotation. This is in contrast with the abrupt habitat change caused by clear-cut in even aged silviculture. Even-aged silviculture alters the species assemblage dramatically in the short-term, but assemblages converge on those of uneven-aged silviculture as forests regrow. Fifty years after clear-cutting, the species assemblages still differ from reference stands, which could be viewed as 'pre harvest' condition, and the potential of those stands to act as a biodiversity source are likely limited. The proportion of clear-cut area and the speed with which beetles recolonize forest as they regrow define the limits for the sustainability of even-aged silviculture in a longer time perspective. The area with 'pre-harvest' species assemblage needs to be kept high enough to produce beetles that can recolonize as new stands develop sufficient tree ages or structures. However, that put high demands on both spatial and temporal planning, and much better knowledge in how species assemblage recovery in even-aged forests.

Within natural forest landscapes, I would anticipate heterogenic forests where differently sized canopy gaps occurred. Ongoing even-aged silviculture promote younger, healthy trees with rapid growth rates often resulting in dense forests without gaps. Since many species are evolutionary adapted to gap dynamic conditions, selectively felling is likely to positively affect these species by creating small openings in the closed forest. Species richness increased in harvest trails compared to retentions strips, indicating that the openings might actually add conservation value to the selective felled forest.

Comparing beetle assemblage in selective felling with old-growth forests and reference stand showed minor indications of conservation benefits compared to reference forests, suggesting that selective felling foremost should be viewed as a means to maintain rather than to restore biodiversity.

One aspect to consider is that a large part of the captured species were present in most stands. The lack of rarer species or differences between stand types may an effect of the long history of forest management in this area. The landscape may not support that many rare, demanding species after so many decades of intensive management (Kouki *et al.*, 2012), which would result in impoverished species pool and thus reduced variation in assemblage composition between stand types. Targeted sampling and comparison with a more pristine landscape might have reveal further differences or helped answering the question about the available species pool.

The primary goal of uneven-aged silviculture is still wood production, thus it should be viewed as an alternative to even-aged silviculture, rather than a conservation strategy such as protected forests and smaller set-asides. Although, implementing selective felling on some proportion of the landscape could suffice as a *de facto* conservation measure to benefit biodiversity at the same time as it allows continued timber extraction. However, repeated harvesting in uneven-aged managed stands may lower deadwood availability and therefore affect the saproxylic beetles. The positive results of uneven-aged silviculture seen here must be confirmed over longer periods of active management. Nonetheless, uneven-aged silviculture could be an important tool for landscape planning to benefit biodiversity and thus help fulfil environmental commitments.

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Popular science summary

Forest is one of the world's largest biomes and home to a vast number of animals and plants. Before large-scale forest management started, the forests were formed by natural disturbances such as fire, wind, natural forest succession, and insect outbreaks. The natural disturbance regime created a heterogenic landscape with large volumes of deadwood, forests of different ages and variation in forest continuity.

During the last century, humans has extensively modified most of the world's forests. The most common forest management practice is even-aged silviculture, i.e. clear-cutting. Even-aged silviculture breaks continuity and creates uniform forests were all trees are of similar size and age with low amounts of deadwood and few old trees. Even-aged silviculture has caused problems for many of the forest dwelling species and despite nature conservation measures in form of leaving trees and deadwood on the clear-cuts, many forest species have a hard time surviving in the new habitat. As a response, the interest for alternative management methods has increased.

One alternative to the current practice is uneven-aged silviculture. In uneven-aged silviculture is a large part of the tree cover left after harvest, and the harvesting are instead reoccurring more frequently, which makes maintaining a stratified forest with continuous cover and a stable microclimate possible. Due to preserved forest structures and retained habitat heterogeneity, uneven-aged silviculture may maintain species associated with old growth forest better than current forest management practices.

In my dissertation, I evaluated how uneven-aged silviculture affects beetles, a group of species negatively affected by even-aged silvicutural practice. I studied the species richness, abundance and community structure of beetles in an experimental system comprising of five different spruce forest types: clear-cutting, thinning (both representing even-aged silviculture), selective felling

(representing uneven-aged silviculture), reference, and old growth forest (both representing unmanaged controls).

The results showed that selective felling maintained a beetle community similar to the one in reference stands, while both young and old clearcuts differed from reference stands. Clear-cuts differed from all other stand types, while thinning had beetle assemblages closer to the uneven-aged stands, indicating that some beetles return after clear-cut as forest regrows. Beetle composition in selective felling became to some extent more similar to old-growth forest, which might suggest that selective felling could increase the conservation value. One possible explanation could be the increased sun exposure on trails created by harvesting in selective-fellings. Even the relative small gaps from the harvester led to increased temperature and decreased humidity. The beetle community of those harvest trails also differed from the one in the adjacent forest. Both species preferring open habitat and old-growth forest were found on the harvest trails.

The results from my dissertation provides support for the hypothesis that uneven-aged silviculture better maintains beetles assemblages associated with semi-natural mature forest than even-aged silviculture. Uneven-aged silviculture might therefore be a better management option when biodiversity conservation is of concern. The high continuity in selectively felled stands could benefit species dependent on mature or old growth forest since some of the needed habitat qualities persist. In addition, under uneven-aged silviculture, key structures such as old trees and deadwood can be recruited continuous, which is especially important for species that are slow movers.

However goal of uneven-aged silviculture is still timber production, thus it should be viewed as an alternative to even-aged silviculture, rather than a conservation strategy such as protected forests and smaller set-asides. Although, implementing uneven-aged silviculture in part the landscape could benefit biodiversity at the same time as it allows continued timber extraction. Uneven-aged silviculture could therefore be an important management tool for fulfilling environmental commitments.

Populärvetenskaplig sammanfattning

Människans brukande av skogen har förändrat skogsekosystemet. Före den storskaliga skogsskötsel började, formades skogslandskapet av naturliga störningar, som hög och lågintensiva bränder, storm, insekt-och svampangrepp. Den naturliga störningsdynamiken skapade ett heterogent landskap med höga volymer död ved, skogar i olika successionsstadier och av varierande kontinuitet. Idag sköts den största delen av skogen med trakthyggesbruk, det vill säga kalavverkning följd av plantering, gallring innan det är dags för slutavverkning igen. Trakthyggesbruket bryter skogskontinuiteten och skapar homogena, en-skiktade skogsbestånd med få gamla träd och låg dödvedsvolym, och bidrar till att landskapet blir allt mer fragmenterat. Trakthyggesbruket har skapat problem för många av våra skogslevande arter, och trots åtgärder som ökat hyggeshänsyn i form av kvarlämnade träd och skapade av död ved är det många arter som har svårt att överleva i de nya skogarna. Allteftersom medvetenheten kring problematiken har ökat, så har också intresset för alternativa skötselmetoder ökat.

Hyggesfritt skogsbruk, eller blädning, är ett alternativ till dagens trakthyggesbruk. Vid hyggesfritt skogsbruk/blädning lämnas en stor del av träden kvar vid avverkning, och istället sker avverkningarna mer frekvent. Vart 15-30 avverkas ca 30% av den stående volymen beroende på tillväxthastighet och en flerskiktad, olikåldrig skog bevaras. Ett syfte med blädning är att bevara naturliga strukturer och processer från sen successionsskog präglad av småskalig störningsdynamik. Genom att bevara skogskontinuiteten är förhoppningen att de arter som är knuta till sen successionsskog ska kunna fortleva i livskraftiga populationer i blädningsskogen.

I min avhandling utvärderade jag hur hyggesfritt skogsbruk påverkar mångfalden av skalbaggar, en artgrupp som påverkats negativt av trakthyggesbruk, både jämfört med trakthyggesbruk och obrukat, skiktad skog med och utan dokumenterade naturvärden. Totalt inkluderade jag fem olika

beståndtyper; blädad skog, nyligen kalavverkad skog, nyligen gallrad skog (kalavverkad för ca 50 år sedan), olikåldrig obrukad skog samt nyckelbiotoper (obrukad skog och skog med dokumenterat höga naturvärden). Alla beståndstyper var grandominerade. Skalbaggarna fångades med två olika metoder, fönsterfällor och sållning av barken från fångstved. Jag inventerade död ved samt diameter-, höjd- och träslagsfördelningen av den stående skogen.

Studierna visade att skalbaggssamhället i blädningsskogen och den obrukade skogen inte skiljde sig åt, medan både nya och äldre kalhyggen hyste en annan artsammansättning än den obrukade skogen. De nya kalhyggena skiljde sig från alla andra beståndstyper, inklusive gallringsskogen. Gallringsskogen var mer lik den obrukade skogen än nyligt kalavverkad skog, vilket tyder på viss återhämtning allteftersom skogen växer upp igen. Artsammansättningen skiljde sig inte signifikant åt mellan blädning och gallring. En jämförelse mellan blädning, obrukad skog och nyckelbiotoper indikerade att vissa arter potentiellt gynnades av blädning. De skalbaggar som konsumerar den döda vedens innerbark hade liknande artsammansättning i blädad skog som i nyckelbiotoper, medan båda skiljde sig från den obrukade skogen. En förklaring till förändringarna kan vara variationer i ljusinsläppet. Tidigare studier har kopplat ihop ökat ljusinsläpp med en ökad artrikedom. Luckor kan öka skogen heterogenitet. Trots att körvägarna skapar relativt små luckor, är dessa tillräckliga för att påverka både mikroklimatet och skalbaggssamhället. Det ökade ljusinsläppet på körvägarna bidrog till ett varmare och torrare habitat. Artrikedomen och abundansen av skalbaggar var högre och artsammansättningen skiljde sig åt från körvägarna jämfört med den mellanliggande skogen. Bland de arter som gynnades av körvägarna fanns både typiska hyggesarter och arter som vanligtvis är knutna till äldre skogar med längre kontinuitet.

Resultatet från min avhandling stöder prediktionen att hyggesfritt skogsbruk kan bevara arterna som finns i obrukade, semi-naturliga skogar. I sammanhang där bevarande av artmångfald är av extra vikt kan hyggesfritt skogsbruk därför vara ett bra alternativ. Hög kontinuitet i hyggesfria system är gynnsamt för arter som är beroende av äldre skog och har låg spridningsförmåga. Vid hyggesfritt skogsbruk bevaras den stabilt mikroklimatet och viktiga habitat som död ved och gamla träd skapas kontinuerligt eftersom äldre träd hela tiden finns kvar i bestånden. Fortsatt virkesproduktion är ett av huvudmålen med hyggesfritt skogsbruk, och det bör därför i första hand ses som ett alternativ till trakthyggesbruket, snarare är till avsättningar för miljöändamål. Likafullt kan implementering av hyggesfritt skogsbruk i delar av landskapet gynna biologiska mångfalden samtidigt som fortsatt utvinning av träråvara möjliggörs och kan därför vara ett viktigt verktyg för att uppnå miljömålen.

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