Retention Forestry as a Conservation Measure for Boreal Forest Ground Vegetation

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Cover: The orchid species *Goodyera repens* (L.)
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Abstract

The boreal forest is prone to natural disturbances, especially fire. Despite this, the disturbance caused by forest management is shown to have a severe effect on the system's biodiversity. Besides threatening rare species especially sensitive to clearfelling, forestry in Sweden and Finland is reported to negatively affect also common and functionally important plant species. A strategy that is proposed to halt these negative effects is the implementation of retention forestry. This measure is based on retaining dead and living structures during clearfelling and is meant to increase the heterogeneity of both managed stands and landscapes. Retained structures such as standing trees and forest patches are hypothesized to affect the restructuring process of the stand both by acting as lifeboats for and by promoting recolonization of forest species. In this thesis I examine the effects of retained forest patches on the dynamics of boreal forest ground vegetation in Sweden and Finland. As study systems I use an experimental set-up in East Finland as well as a normally managed landscape in Central Sweden containing both harvested stands and mature forest stands of different age. I show that retaining patches constituting as much as 17% of the stand area does not affect vegetation dynamics over a whole stand. However, if the aim of the retention patches is that they should function as lifeboats that can secure that species survive in situ over the clearcut phase, also patches as small as 0.1 ha can be effective. Such patches favour functionally important species like the dwarf-shrub *Vaccinium myrtillus* and the moss *Hylocomium splendens*. To effectively lifeboat more sensitive species however, the canopy openness and patch size is important. I.e. the red-listed orchid *Goodyera repens* does generally not survive in 0.1 ha patches, probably due to poor microclimatic conditions. I also show that *G. repens* is, probably as a consequence of dispersal limitation, strongly associated with forest older than 120 years. The normal rotation time in Swedish forestry of about 100 years is thus problematic for this species. Finally I show that retention forestry in combination with prescribed burning can promote the production of bilberries (*V. myrtillus*) and cowberries (*V. vitis-idaea*). My results demonstrate that the application of retention forestry promotes both biodiversity and provisioning of non-timber products. However, in order to be effective, both level and type of retention need to match the specific goal of the measure.

Keywords: retention patch, lifeboating, prescribed burning, clearcut, forest age, vascular plant, bryophyte, orchid, berry production

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Effekterna av naturhänsyn i skogsbruk på markvegetationen i boreal skog.

Sammanfattning

Den boreala skogen är anpassad till återkommande störningar, främst brand. Trots detta har den störning som orsakas av skogsbruk visat sig vara ett hot mot den biologiska mångfalden i dessa skogar. Förutom att många sällsynta arter är utrotningshotade i det brukade skogslandskapet i både Sverige och Finland har även vanligare och funktionellt viktiga växtarter visat sig minska på grund av modernt skogsbruk i denna region. Naturhänsyn vid avverkning har föreslagits som en åtgärd som kan minska dessa negativa effekter. Metoden bygger på att spara döda och levande strukturer vid slutavverkning vilket leder till att brukade bestånd och landskap blir mer heterogena. Kvarlämnade strukturer som död ved, stående träd och trädgrupper föreslås främja återuppbyggnadet av systemet genom att ”livbåta” och påskynda återkolonisation av skogsarter i avverkade bestånd. I den här avhandlingen har jag undersökt vilken effekt naturhänsyn i form av sparade trädgrupper har på markvegetationen i boreala skogar i Sverige och Finland. Som studiesystem har jag använt ett storskaligt experiment i östra Finland och ett normalt brukat landskap i norra Hälsingland med både avverkade och uppvuxna bestånd i olika åldrar. Mina resultat visar att en hänsynsnivå med ca 17 % sparade träd i grupper inte räcker för att påverka vegetationen på den avverkade ytan av ett hygge. Om man däremot vill skydda markvegetation inne i sparade trädgrupper, räcker det att spara grupper så små som 0.1 ha. Grupper av den storleken gynnar, jämfört med kalhyggen, funktionellt viktiga arter som blåbär (*Vaccinium myrtillus*) och husmossa (*Hylocomium splendens*), även 20 år efter avverkning. För att skydda mer känsliga arter är dock både gruppernas krontäckning och storlek viktig. Som exempel överlever den rödlistade orkidén knärot (*Goodyera repens*) generellt inte i grupper så små som 0.1 ha, förmodligen på grund av ogynnsamt mikroklimat. Arten är även starkt knuten, troligen på grund av långsam spridning, till skogsbestånd som är äldre än 120 år. Då den normala avverkningsåldern i Sverige är ca 100 år leder skogsbruk till minskade populationstätheter. Slutligen kan jag visa att naturhänsyn i kombination med naturvårdsbränning har en positiv påverkan på bärproduktionen av blåbär och lingon. Naturhänsyn vid avverkning kan gynna både biologisk mångfald och viktiga funktioner som bärproduktion. För att vara verkligt effektiv, krävs det dock att hänsynen anpassas efter åtgärdens specifika mål, både i hur mycket som sparas och på vilket sätt det görs.

Nyckelord: hänsynsyta, naturvårdsbränning, kalhygge, skogsålder, kärlväxter, mossor, knärot, blåbär, lingon, bärproduktion.

Dedication

Till Kirsi.

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 Johnson, S., Strengbom, J. & Kouki, J. (2014). Low levels of tree retention do not mitigate the effects of clearcutting on ground vegetation dynamics. *Forest Ecology and Management* 330: 67-74.

II Johnson, S., Gustafsson, L., Öckinger, E. & Strengbom, J. Tree retention alleviates logging effects on functionally important ground vegetation (manuscript).

III Johnson, S., Gustafsson, L., Öckinger, E. & Strengbom, J. Prolonged rotation times may halt the decline of an orchid species threatened by intensive forest management (manuscript).

IV Strengbom, J. Johnson, S. & Kouki, J. Deliveries of non-timber forest products in relation to conservational measures (manuscript).

The contribution of Samuel Johnson to the papers included in this thesis was as follows:

I Main author and analysis. Developed research questions and wrote the paper together with JS and JK.

II Main author, field work and analysis. Developed research questions, design and wrote paper with JS, LG and EÖ.

III Main author, field work and analysis. Developed research questions, design and wrote paper with JS, LG and EÖ.

IV Second author, field work and part of the analysis. Developed research questions and wrote the paper together with JS and JK.

1 Introduction

1.1 Boreal forests

The boreal forest is one of the largest biomes in the world, comprising about 27% of the global forest area (Hansen et al. 2010). The type of forest found in this zone is typically dominated by coniferous trees with a smaller amount of deciduous species intermixed. In Fennoscandia Norway spruce, *Picea abies* (L.), and Scots pine, *Pinus sylvestris* (L.), are the dominating tree species, while birch *Betula spp.* (L.), Aspen (L.), *Populus tremula*, and grey alder, *Alnus incana* (L.), are the most common deciduous trees (Hytteborn et al. 2005). A typical feature of boreal forests is the prominent role of natural disturbances including i.e. fire, flooding and pest outbreaks (Johnson 1992; Esseen et al. 1997; Bergeron et al. 1998).

Like in other disturbance prone systems community composition and diversity in boreal forest are largely dictated by large- and small-scale disturbance events as well as the recovery process that follows (Conell & Slatyer 1977; Angelstam & Kuuluvainen 2004). The reassembly of an ecosystem after a disturbance is not a random process but depends on a number of factors that collectively can be called ecological memory (Bengtsson et al. 2003). External memory is the recolonization of the disturbed areas by dispersal from the surrounding landscape. Thus, external memory is largely determined by the landscape configuration. The other component of the ecological memory depends on structures or remnant vegetation that survived within the perimeter of the disturbed area, i.e. internal memory. Besides that remnant vegetation may function as internal dispersal sources, remnant structures, such as woody debris and standing dead trees, can also facilitate the colonization of new species and provide habitat and resources otherwise rare in the early successional stages of forest development (Del Moral et al 1995; Franklin et al. 2000). The remnant part of the post-disturbance community state is often referred to as biological legacies (Franklin et al. 2000). Legacy effects are likely very important drivers of the dynamics of reassembling systems, i.e. the composition of species that are first present in a disturbed area can determine the direction the system will change through so called priority effects (Connell & Slatyer 1977; Chase 2003).

In the vast boreal biome both diversity and function are largely dictated by disturbance (Esseen et al. 1997: Nilsson & Wardle 2005), and disturbance generated by fire is considered as the most important disturbance agent

(Zackrisson 1977; Johnson 1992; Bergeron et al. 1998; Gromtsev 2002). Fire can influence structure and functioning on spatial scales ranging from continents to regions as well as to the scale within the perimeter of a single fire event (Schimmel & Granström 1996; Bergeron et al. 2002; Heyerdahl et al. 2001; Hylander & Johnson 2010). In Fennoscandia, it is believed that natural fires were prominent and important for creating heterogeneity at multiple scales, but not as large and stand replacing as for an example in Central Canada (Zackrisson et al 1977; Niklasson & Granström 2000; Kuuluvainen 2002). Ever since the first settlements humans have had a major influence on the fire regime of the region. It is believed that the presence of humans increased the frequency but decreased the average size of fires (Niklasson & Granström 2000). In the modern forest landscape of Fennoscandia however, effective fire prevention since the early 1900's has almost eliminated forest fires (Östlund et al. 1997).

1.2 Effects of forestry

Forestry has become a prominent influence on boreal forests in many parts of the Northern Hemisphere (Hansen et al. 2010). In Fennoscandia a big change occurred after ca. 1950 when forestry methods became more efficient and clear-cutting forestry was introduced (Esseen et al. 1997). Sweden and Finland are among the countries with the most intensive forestry operations in Europe and few regions in the boreal zone are as affected by forestry (Levers et al. 2014). It is estimated that around 1% of the forest area in Sweden is harvested annually and the rotation time is between 80 and 120 years (Anonymous 2013; Jansson 2011). The vast majority of Swedish managed stands are subjected to clearcutting which is usually followed by soil scarification and planting of new trees. Tree species used by forestry are almost exclusively Norway spruce, Scots pine and the introduced pine species *Pinus contorta*. Today only a fraction of the Swedish forests remains untouched by clearcutting forestry (Esseen et al 1997).

Unlike forests structured by natural dynamics, managed forest often consist of even-aged monocultures that lack richness of structures including coarse woody debris, snags and ancient trees (Bengtsson et al. 2000; Löfman & Kouki 2001). This homogeneity at multiple scales has severe effects on the biodiversity of the forest landscape. Studies have showed negative influences of managed forests on a wide range of organisms including, among others, fungi, birds and arthropods (Penttilä et al. 2000; Drapeu et al. 2000; Niemilä 1997). This is also reflected in national red lists, e.g. in the Swedish red-list over 50% of the species are associated with forest habitats (Gärdenfors et al. 2010).

1.3 Retention forestry

Conservation of boreal forests, in both Fennoscandia and other regions, was for a long time mostly in the form of land-sparing measures, i.e. setting aside protected areas such as reserves and national parks. It has been argued however, that protected areas are too few and too small to incorporate the long-term and large-scale dynamics of the ecosystem (Bengtsson et al. 2003). An alternative way, which arguably would promote biodiversity and ecosystem functions on a wider scale, would be to also focus on conservation measures in the managed parts of the landscape, a strategy known as land-sharing, (Green et al. 2005). Such measures have been proposed as appropriate in boreal forests as these are adapted to reoccurring disturbances that somewhat resemble the effect that clearcut forestry may have (Angelstam 1998). The idea that boreal forests, even in areas with very frequent fires, can tolerate modern clearcutting forestry without changing state, is however criticized (Bergeron et al. 2002). Instead it is suggested that forestry practices could modify its operation and by changing from clearcutting forestry to creating stands that more resembles natural stands regenerating after disturbance (Franklin 1997). This kind of forestry is often termed retention forestry (Gustafsson et al. 2012).

Retention forestry is the practice to retain living or dead structures for conservation purposes during final harvesting. The implementation of retention forestry can vary both in level (e.g. how much is retained) and the spatial arrangement of retained structures. The latter is often divided into either aggregated or dispersed retention. The main focus of the practice is biodiversity conservation but other functions such as enhancing eco-system services and improving the aesthetics of harvested stands have been suggested (Gustafsson et al. 2012; Millennium Ecosystem Assessment 2005; Shelby et al. 2005). The idea behind retention forestry as tool for conservation, is that retained structures act as biological legacies so that they can play a similar role in managed forests has they have been shown to do after natural disturbance. Franklin (1997) summarizes three different objectives of tree retention that can be said to reflect the different functions of biological legacies in the recovery process of the harvested stand. These objectives are: (1) “Lifeboating species and processes immediately after logging and before forest cover is re-established.” (2) “Enriching re-established forest stands with structural features that would otherwise be absent. (3) “Enhancing connectivity” in the managed landscape.

Retention forestry was first introduced in North-western North America in the 1980’s (Franklin 1989) and is today implemented in the forestry on several continents (Gustafsson et al. 2012). Level and type of retention varies considerably both between and within regions of the world. In Fennoscandia it has been implemented at a large scale since the mid 1990’s and regulations for retention forestry are included in the legislation of Sweden, Norway and Finland (Gustafson et al. 2010). The type of retention used in the region is mainly in the form of aggregated retention and retaining trees along riparian buffer zones. The levels applied are between 1-5% which is low in an international perspective (Gustafsson et al. 2012).

Since its implementation a great number of studies have evaluated the effects of retention forestry on biodiversity of managed forests. They generally conclude that it has a positive effect compared to clearcutting if the level is high enough. Species that generally respond positively to retention includes ectomycorhizal fungi, epiphytic lichens, and small mammals while i.e. bryophytes are often not favoured (Rosenvald & Lõhmus 2007; Fedrowitz et al. 2014).

1.4 Prescribed burning

Prescribed burning has long been used by forestry to prepare clear-cuts before planting of trees (Esseen et al. 1997) but more recently the use of fire as a conservation measure has received an increased interest (Granström 2001). There are several reasons to use prescribed burning as a conservation tool in managed forests. Fire has a long history as a disturbance agent in boreal forests and is therefore a way to create natural structures and small scale heterogeneity important for many forest organisms (Kuuluvainen 2002). It has also been suggested that burning in combination with retention forestry is an effective strategy to mimic effects of natural fire in managed forest (Jalonen & Vanha-Majamaa 2001). There are furthermore many species depending explicitly on burned substrates (Risberg & Granström 2009; Ranius et al. 2014) and such species cannot, under the current low fire frequency, solely be conserved in reserves or with retention forestry.

1.5 Ground vegetation of boreal forest

The vegetation of boreal forests can be characterized as rather species poor and compared to other forest systems dominated by dwarf shrubs and bryophytes. In Fennoscandia dwarf shrubs of the genus *Vaccinium*, especially *V. myrtillus* (L.) and *V. vitis-idaea* (L.) and the so called feathermosses *Hylocomium splendens* (Hedw.) and *Pleaurozium schreberi* (Brid.) often form a very dominant part of the vegetation. Although these species may not contribute much to the overall species richness, they are nevertheless functionally important (Nilsson & Wardle 2005). Species of the genus *Vaccinium* also provide a food resource for both arthropod larvae and game birds (Baines et al 1994; Altegrim & Sjöberg 1996: Lakka & Kouki 2009). Although these species are still dominating the vegetation of managed forests in Fennoscandia, surveys in Finland have shown that *V. myrtillus* and *H. splendens* have decreased since the introduction of clearcutting forestry in the 1950's (Reinikainen 2001).

1.5.1 Effects of disturbance on ground vegetation

In Fennoscandian boreal forest the vegetation following logging is often characterized by more species of grass and herbs and a different set of bryophyte species compared to in intact forest (Bergstedt & Milberg 2001; Strengbom & Nordin 2008, 2012). The grass species *Deschampsia flexuosa* (L.) is often very dominating in clearcuts but is not that prominent in areas regenerating after fire (Uotila & Kouki 2005). Fire has a different effect compared to logging as it generally promotes species with deep rhizomes, and depth of burn is reported as the most important factor explaining the response of the vegetation to fire in this system (Granström & Schimmel 1996). The combination of efficient fire suppression and the large scale introduction of clearcut forestry is aso suggested as the main explanation behind the described changes in vegetation in Fennoscandian forests (Reinikainen 2001; Uotila & Kouki 2005).

1.5.2 Effects of retention forestry on ground vegetation

During the last decade several studies on the effect of retention forestry on ground vegetation have been published, the majority of them from North America and Europe (Jalonen & Vanha-Majamaa 2001; Halpern et al. 2012; Fedrowitz et al. 2014) but there are also a few studies from South America and

Australia (Lancinas et al. 2011; Baker et al. 2013). The studies generally confirm that retention cutting alleviates the negative effects of logging, and that a higher retention level will have less impact on both the composition and the abundance of plant species (Beese & Bryant 1999; de Graaf & Roberts 2005; Halpern et al. 2012). Most studies, however, only report effects a few years after harvest, but see Halpern et al. (2012) and Craig & Macdonald. (2011) that reports effects up to ten years after logging. The majority of the studies have used retention levels exceeding 20% of the standing volume or area and, for aggregated retention, patches around 1 ha in size (e.g. Beese & Bryant 1999; de Graaf & Roberts 2005; Lencinas et al 2011; Halpern et al. 2012). Such studies may not be representative for Fennoscandia, where levels as low as 5% and patch sizes as small as 0.1 ha are common practice (Gustafsson et al. 2012). The specific effect of retention patch size is generally little studied, but a few studies from Sweden and Finland have considered patches smaller than 0.1 ha and they conclude that this size is not enough to lifeboat more sensitive species such as bryophytes (Jalonen & Vanha-Majamaa 2001; Perhans et al. 2009). Perhans et al. (2009) also found that the bryophyte species *Hylcomiastrum umbratum* responded to patch shape indicating that it is sensitive to the edge effects of small retention patches. Studies that have focused on larger retention patches, however, have concluded that a size between a half and one ha is enough to preserve the species of interior forest such as sensitive bryophyte and lichens species (Halpern et al. 2012; Rudolphi et al. 2014). Several studies support that bryophytes, and especially liverworts, are sensitive to altered microclimate and depend on high retention levels to survive logging (Dovčiak et al 2006; Hylander et al. 2005).

2 Thesis aims

The general aim of this thesis was to gain knowledge on the effects of the conservation measure retention forestry on ground vegetation of boreal forests. Although the retaining of forest patches is the main factor that is investigated, the thesis also covers the use of prescribed burning. The more specific questions of the papers in the thesis are:

- What are the effects of retaining forest patches during clearfelling, with or without prescribed burning, on the ground vegetation dynamics on the stand scale? (Paper I)

- How are time after clearfelling, retention patch size, and canopy openness affecting the ground vegetation dynamics in retained forest patches? (Paper II)

- How is a declining late successional forest species affected by clearfelling and retention of forest patches? (Paper III)

- How is the delivery of a non-timber forest product, berries of the species *Vaccinium myrtillus* and *V.vitis-idaea*, affected by the conservation measures of retaining forest patches and prescribed burning? (Paper IV)

3 Methods

3.1 Study areas

The studies in this thesis were conducted in two areas, one in South-eastern Finland and one in Gävleborg county in central Sweden (Fig. 1). Both areas are situated in the middle boreal zone (Ahti et al. 1968). Papers I and IV were both conducted in an experimental set up in Finland, while studies II and III were conducted using a time for space design in actual managed forests.

Fig. 1. Map over Fennoscandia and the locations of the studies in this thesis. Area 1 marks the location of the study landscape in Gävleborg county that was used in papers II and III. Area 2 marks the location of the FIRE experiment near Lieksa in Eeast Finland, that was used in papers I and IV.

3.2 Experimental design papers I and IV

FIRE is a large scale experiment focused on effects of forest management and fire. The experiment was set up in year 2000 and consists of 24 different sites scattered in an area of approximately 500 km^2. All experimental sites were placed in approximately 150 years old pine forests that had not previously been subjected to clearcutting, although low levels of selective harvesting might have occurred in the early 1900's. The sites were subjected to four different levels of harvesting and prescribed burning in a factorial manner with burning as the first factor and harvesting intensity as the other (Fig. 2). The types of harvesting used were clearcutting (no retention), low level of retention (10m^3 of retained wood per ha), elevated level of retention (50m^3 of retained wood per ha) and no harvesting (full retention). All retention treatments used aggregated retention with circular patches. The burning was conducted during two consecutive days with similar weather conditions in June 2001. The fire intensity was generally higher in harvested treatments compared to intact forest and also level of retention had an affect with higher levels leading to a less severe burning (Hyvärinen et al 2005).

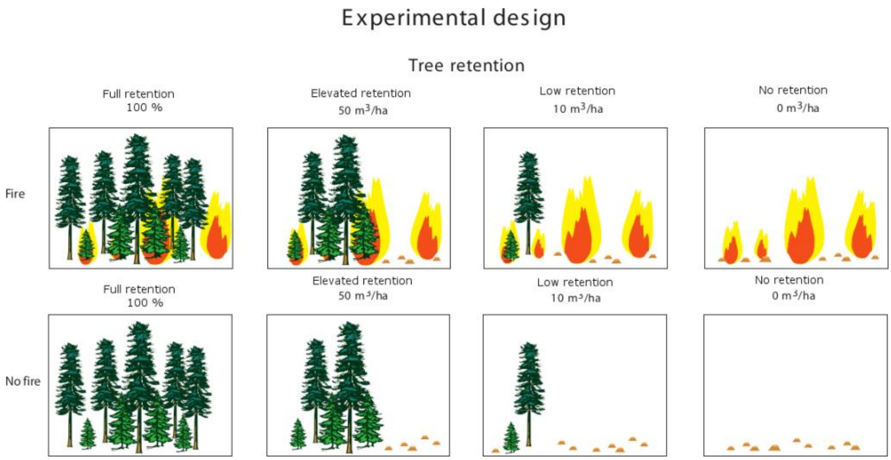

Figure.2 The eight treatment combinations with and without prescribed burning and four levels of harvest intensity used in FIRE experiment. This experimental set-up was used in papers I and IV.

3.3 Study landscape papers II and III

A study landscape situated in the municipalities of Ljusdal and Ovanåker in the north-western parts of Gävleborg county was chosen. The area has a long history of forestry but clearcut forestry was introduced in the 1950's. Today only 7.6% of the forests in the county are 120 years or older while 43.9% are younger than 40 years (Anonymous 2014).

3.3.1 Selection of stands

Harvested stands with retention that were used in the papers II and III were chosen in several steps. First stand data obtained from forest companies Sveaskog and Bergvik was used to pick out stands that had been harvested between 1990 and 2009. Other variables used as criteria for inclusion were dominating tree species (Norway spruce), vegetation (*Vaccinium* type) and ground moisture (mesic). In a second step, aerial photography was used to find stands that had retained tree patches at least 20 m separated from the stand edge or any other patch. About 100 stands were chosen using these steps and they were visited in the summer of 2011 to make a final selection. In this step I chose stands with retention groups that were representative of the entire stand. Around 50 % of the stands had to be omitted because they were placed in a wet area with peat soil and had clearly deviant vegetation compared to the rest of the stand. Finally a selection of appropriate stands was made to get a balanced distribution of patch size and stand age, ending up with 43 stands (Fig.3).

For each harvested stand, I also chose a mature stand (visually estimated to be over 70 years old) as a reference. In order to make sure that the stands were as similar as possible I chose, when possible, a stand that was adjacent to the harvested stand. In a few cases I was forced to choose stands up to two km away however. In three cases no suitable mature forest stand could be found meaning that 40 mature forest stands were used in total. In paper III I also needed mature forest stands of different age in the same landscape. These stands were obtained using stand data provided by forest company Bergvik.

Figure 3. To the left: a stand, 22 years after harvest. To the right: a stand five years after harvest with a retained tree patch to the far right. Both stands were included in papers II and III. (Photo S. Johnson).

3.4 Time for space design vs. experimental design

The use of differently aged samples to extract a temporal trend, often referred to as time for space design, is a common technique in ecological research (Pickett 1989). This strategy is often used as substitute for expensive and time consuming experimental set ups but it is often noticed that it has certain shortcomings and that conclusions drawn from such studies should sometimes be made cautiously (Walker et al. 2010). A major part of the research on retention forestry has so far been concentrated to a handful of large-scale experiments (Gustafsson et al. 2012). These experiments, however, are still quite young and cannot yet supply data on long term dynamics. Studies that also incorporate older natural study systems have therefore been called for (Vanha-Majamaa & Jalonen 2001). The experimental set-ups in the retention experiments are moreover often poorly designed to study lifeboating effect more specifically. In many cases, the sampling of vegetation has been designed to detect effects on the stand level which makes it hard to draw direct conclusions concerning lifeboating (Halpern et al. 2005; Johnson et al. 2014). Moreover, even though both patch size and shape are suggested as important for the functionality of patches as lifeboats (Perhans et al. 2009), no studies from retention experiments have, to our knowledge, been able to incorporate these factors (Halpern et al. 2012; Graaf & Roberts 2005; Jalonen & Vanha-

Majamaa). Studies on the effects of retention forestry incorporating over 20 years old stands can thus provide novel insights into both long term effects and small scale dynamics of retention patches that previous studies have not been able to provide.

3.5 Vegetation surveys

In paper II vegetation composition including vascular plants, bryophytes (mosses and liverworts) and macrolichens was surveyed in 15 permanent plots evenly spaced in three rows measuring 2 x 2 m at each experiment site. The first survey was conducted in the summer of 2000 prior to the harvest and burning treatments, the second survey was conducted in 2003, i.e. two years after the treatments and the third survey was conducted in 2011 ten years after the treatments. All species were, if possible, noted down to species level in the field or otherwise collected and determined in the lab. The percent cover of each species was visually estimated.

In paper II the vegetation was surveyed in three types of sites: the centre of a retention group, a clearcut area at least 50 m from the stand edge or a retention group and in a mature forest (over 70 years old) at least 50 m from the nearest edge to an open area. Five inventory plots of 0.25 m^2 were placed in the centre of the retention patches one m apart. All species of vascular plants and bryophytes (mosses and liverworts) were determined, if possible, down to species level and otherwise collected and determined later. Percent cover was visually estimated for all species.

Figure. 4. Examples of stands of the three different age classes inventoried for *Goodyera repens* in paper III. Left: A over 120 years old stand. Top right: a 35-45 years old stand. Bottom left: a 70-80 years old stand. Photos: J. Strengbom.

3.6 Translocation experiment

In paper III I wanted to study the direct effects of different habitat conditions on a sensitive forest species, the orchid *Goodyera repens* (L.). *G. repens* is a perennial forest herb with creeping rhizomes that form mats on mossy forest floor (Fig.5). It is reported to be associated with old-growth forests (Økland 2000; Lõhmus & Kull 2011) and is declining in Sweden due to the effects of forestry (Gärdenfors 2010; Ståhl 2012). The growth form of the species allowed us to easily remove specimens and translocate them to different types of localities, including clearcut (n=5), retention patch (n=5) and three forest age classes (n=8). The translocations were conducted using a soil core drill with a 10 cm diameter (Fig. 5). At each translocation site three soil cores with intact layers of litter moss and containing at least three leaf rosettes of *G. repens* were dug down in a spot with a vegetation and ground layer similar to the source population. The translocations were conducted in late May 2013 and visited again in late September and early October that same year. In addition to the translocation, I also measured the temperature and air humidity using loggers making five measurements per day during the entire experiment.

Figure. 5. Translocation of *G.repens*. Left: The author removing rosettes of the study species using a soil core drill. Right: Close-up of translocated rosettes of *G. repens*. Photos: J. Strengbom.

3.7 Statistical analyses

3.7.1 Univariate models

Differences in occurrence of *G. repens* (paper III) as well as cover and berry densities (paper IV) among treatments and between types of habitat were statistically analysed by generalized linear models (GLM's) in the base package of R. Such models allow response variables from different distributions. Observations of *G. repens* were based on presence absence and were therefore fitted to a binomial distribution in the model, while number of berries and cover was count data and therefor fitted to a Poisson distribution. For certain cases I used generalized linear mixed models (GLMM's) in the R-package lme4 (Pinheiro et al. 2013). This is a class of models that allow the use of random effects to control for dependence structures of the data set (Bunnefeld and Fillemore 2012). In paper III I controlled for non-independent spatially structured obeservations of *G. repens* within landscapes and within stands using stand as a random factor. In paper IV I controlled for the hierarchical structure of the data set, which incorporated berry counts in different microhabitats within stands with different treatments, by using stand as a random factor.

3.7.2 Multivariate analysis

In papers I and II the focus of study is the structure of the plant communities rather than abundances of individual species. To explore species composition and how it changes between different treatments I used the ordination method non-metric multidimensional scaling (NMDS). Ordination methods, or multivariate analysis, visualize the level of similarity of individual cases of a dataset which makes it possible to explore how different species and treatments or sites relate to each other. NMDS is an ordination method that has no underlying assumptions of normal distribution or linear responses of the species to gradients. It is therefore generally considered as an appropriate tool to apply on most types of ecological data (Oksanen 2013). To run ordinations I used the metaMDS function of the vegan package in R (Oksanen 2013; R Foundation for Statistical Computing, Vienna, AT). This function uses a high number of random initial conditions to avoid the iteration getting trapped in a local optimum. Of the obtained solutions the one with the lowest stress value, i.e. the best representation in reduced dimensions, is chosen.

In both papers I and II I also used other methods to explore the species compositions further. The Adonis-function in the vegan package in R is a method to test for significant differences in species compositions among groups. Envfit is a function in the same package that fits environmental variables to an ordination and tests the strength of the fit (Oksanen 2013).

3.7.3 Indicator species analysis

In papers I and II Indicator species analysis (ISA) was used to test the affinity of different species do different treatments or habitats. ISA is a technique that combines data on species presences and tests if species are unique to certain groups (Dufrêne & Legendre, 1997). The tests were conducted in PC-ORD version 5.31(McCune & Mefford 2006).

4 Results and discussion

4.1 The effects of retention patches at the stand level.

- Neither low ($10m^3$/ha) nor elevated ($50m^3$/ha) retention had an effect on the vegetation dynamics relative to clearcut in the unburned treatment (Paper I).
- The berry production was slightly higher in the harvested area near retention patches (Paper IV).

The results in paper I show that in Fennoscandian pine forest, even a retention level of $50m^3$ per ha (equivalent to retaining 17% of the stand area) is not enough to influence the vegetation dynamics over 10 years at the stand level (Fig. 5). This means that the retention groups did not affect vegetation in the harvested area. It can be hypothesized that the retention patches could have had such an effect, either as propagule sources promoting colonization of forest species or through altering the microclimate of the adjacent area by i.e. shading. That the patches did not promote colonization of forest species concurs with a previous study which has shown that boreal forest bryophytes are not limited in their dispersal at this scale (Hylander 2009). However, in paper IV when considering the production of bilberries (*V. myrtillus*) there was a positive, although weak, effect of the retention patches even outside the patches themselves. This effect was probably not caused by shading, as there was no difference between the north and the south of the groups. Another explanation could be that the berry production is promoted by a higher density of pollinators that are drawn to the environment around retention groups.

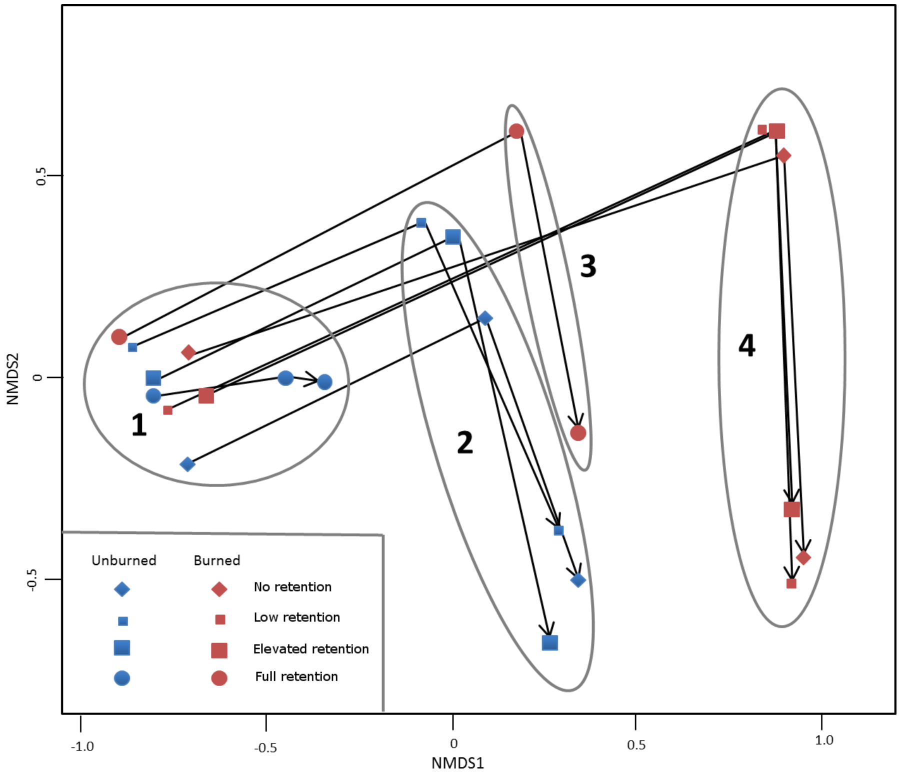

Figure 5. Ordination graph showing differences in species composition of all treatment combinations and years in paper I. The arrows indicate changes within the same treatments between 2000 and 2011. **1** denote pre-treatment composition and composition in sites with no treatment (full retention and no burning) in 2003 and 2011. **2** denote all unburned and harvested treatments after treatment in 2003 and 2011. **3** denote unharvested treatment with burning in 2003 and 2011. **4** denote harvested treatments with burning in 2003 and 2011.

4.2 The lifeboating effect of retention patches.

- Vegetational composition of even small retention patches was generally similar to that in mature forest even 20 years after clearcutting (Paper II).
- Common and functionally important species are lifeboated also in small (0.18 ha) retention patches (Paper II).

- Canopy openness is the most important factor influencing the species composition of vegetation in retention patches followed by patch size (Paper II).
- More sensitive forest species are not lifeboated in retention patches ranging from 0.05 to 0.5 ha (Papers II & III).
- Small retention patches (0.05 to 0.2 ha) experience fluctuating daily temperature and humidity more resembling clearcuts than intact forest (Paper III).

In study II I show that the species composition in retention patches is very similar to that in mature forests (Fig. 6). Also, even though the stands with patches ranged in age from 3 to 22 years old, the species composition was unaffected by time since logging. This suggests that even small patches of the type used in the study (mean 0.18 ha ±0.06) are functional lifeboats for typical forest ground vegetation for at least 20 years. In paper III I also show that forests as young as 35-45 years are a suitable habitat for typical forest species. Hence, the period that forest species need to be lifeboated does not have to be very much longer than 20 years, suggesting that the forest vegetation within the patches likely will persist long enough to enrich the regenerating forest stand.

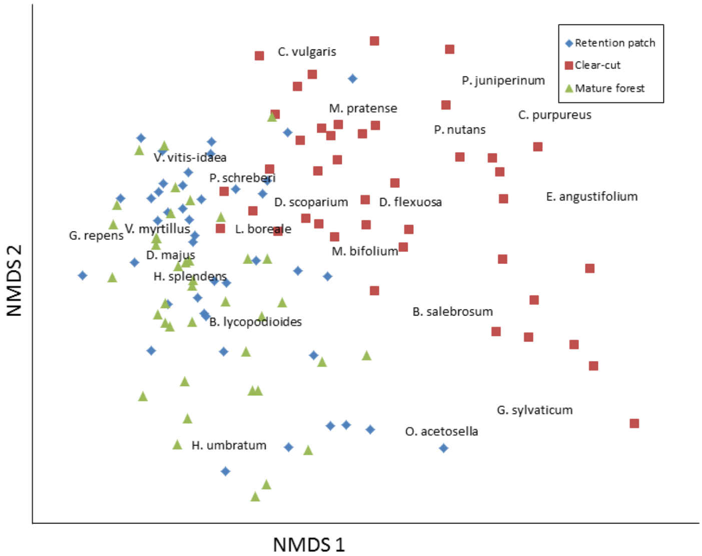

Figure 6. Non-metric multi-dimensional (NMDS) ordination of the species composition (vascular plants and bryophytes) of all sites in paper II including retention patches, clearcuts and mature forests.

Indicator species analysis revealed that species typical of forests, including the dwarf shrub *Vaccinium myrtillus* and mosses *Hylocomium splendens* and *Ptilium crista-castrensis*, were more common in retention patches compared to clearcuts, i.e. they were lifeboated in retention patches. These species are functionally important members of the typical boreal forest ground vegetation community (Esseen et al. 1997) and are also reportedly disfavoured by clearcutting forestry (Reinikainen 2001). I also found that typical clearcut species such as the grass *Deschampsia flexuosa* and the herb *Epilobium angustifolium* were less common in retention patches compared to logged areas. Hence it can be argued that retention patches, by promoting vegetation more similar to mature forest compared to harvested areas, create a vegetation mosaic in the harvested stand that, compared to clearcutting, more resembles the effects of natural disturbance dynamics.

Vegetation composition in retention patches was best explained by canopy openness and patch size. Of these two variables, canopy openness was the most important factor. Results from an ordination fitted with the variables indicate that they have opposing effects on the vegetation, with larger patch area favouring typical forest species, i.e. *V. myrtillus* and several species of liverworts, while higher canopy openness disfavoured the same species. It can be argued that both these factors influence the vegetation by altering the microclimate of the patches. Several studies conclude that edge effects in retained forest patches can have detrimental effects on sensitive forest species such as bryophytes (Hylander 2005; Löbel et al. 2012), and fluctuating temperature and humidity are known to affect many forest plant species negatively (Chen et al. 1993). In study III I measured both temperature and humidity in forests that had reached the stage of a closed canopy cover, small retention patches (mean 0.13 ha ±0.06 S.E.) and in clearcuts. The results showed that both the patches and clearcuts had much more fluctuating daily temperature and humidity, as well as many more extreme temperature events throughout the growing season, compared to grown up forests.

Some of the forest indicator species in study II, including several species of liverworts and the red-listed orchid *Goodyera repens*, were very rare in retention patches. Based on my results concerning which environmental factors that influence the species composition, it can be argued that if these species are to be lifeboated in retention patches, they need to be larger than what is currently practiced in Fennoscandia, and perhaps even more important, have a dense tree canopy. In study III I also show that translocated specimens of *G.repens* survives well in mature forests at least 50 m from the nearest edge to an open area. Moreover, measures of temperature and humidity show that such distances from an open area is far enough to offer a microclimate that is more stable compared to what present in retention patches of around 0.1 ha. This means that the very centre of a circular patch with radius 50 m (equals a size of 0.78 ha) should offer conditions similar to interior forest and would perhaps be a suitable habitat for *G. repens* and similar species. Previous studies from both North America and Sweden have also concluded that patches between 0.5 and one ha are sufficient for preserving interior forest vegetation as well as sensitive lichens and bryophytes (de Graaf & Roberts 2009; Halpern et al. 2012; Rudolphi et al. 2014).

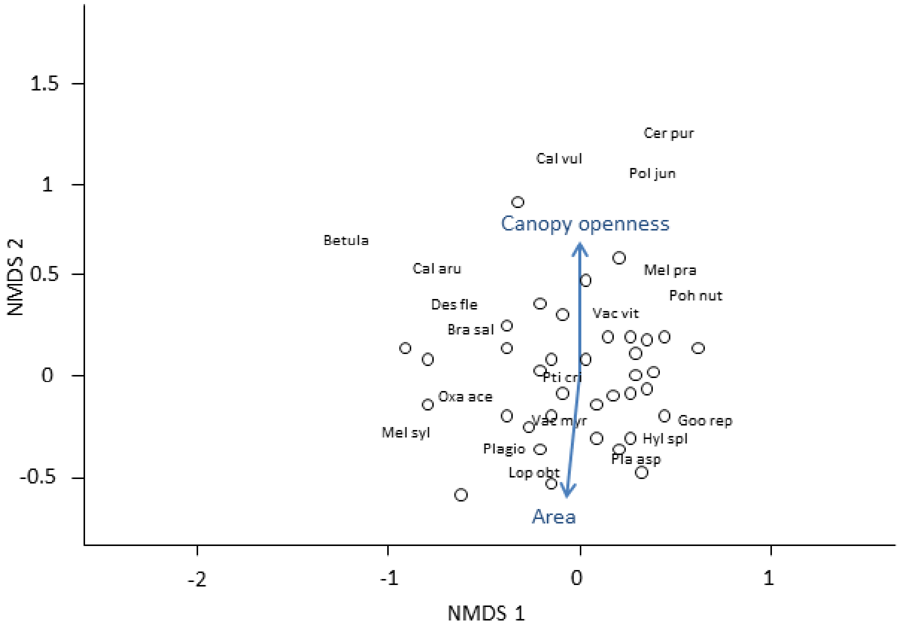

Figure.7. NMDS ordination showing the species composition of all retention patches and the position of some indicative or common species. Arrows are showing environmental variables with a significant fit to the gradient. Length of the arrow is proportional to the strength of the fit. Species are abbreviated as follows: Betula: *Betula pendula/pubescens*, Bra sal: *Brachythecium salebrosum*, Cal aru: *Calamagrostis arundinacea*, Cal vul: *Calluna vulgaris*, Cer pur: *Ceratodon purpureus*, Des fle: *Deschampsia flexuosa*, Goo rep: *Goodyera repens*, Hyl spl: *Hylocomium splendens*, Lop obt: *Lophozia obtusa*, Mai bif: *Maianthemum bifolium*, Mel pra: *Melampyrum pretense*, Mel syl: *Melampyrum sylvaticum*, Oxa ace: *Oxalis acetosella*, Pla asp: Plagiochila asplenioides, Plagio: *Plagiothecium curvifolium/laetum*, Ple sch: *Pleurozium schreberi*, Poh nut: *Pohlia nutans*, Pol com: *Polytrichum commune*, Pol jun: *Polytrichum juniperinum*, Pti cri: *Ptilium crista-castrensis*, Vac myr: *Vaccinium myrtillus* & Vac vit: *Vaccinium vitis-idaea.*

4.3 The effects of intensive forestry on a sensitive forest plant species.

- *G. repens* does not survive in-situ in clearcuts and is very rare in retention patches.
- It occurs in 90% of the stands older than 120 years, in 50% of the stands 70-80 years old, but in less than 10% of the stands 35-40 years old.
- It is four times more abundant in old than intermediate aged stands, and 40 times more abundant in old than in young stands.
- A translocation experiment showed that the mortality was equally low in 35-40 year old stands as in stands over 120 years old.

In paper III I use the red-listed orchid *G. repens* as a model species to examine how species associated with late forest successional stages are affected by clearcut forestry. In the 43 clearcuts that I inventoried I never encountered a single individual of the study species, suggesting that the species does not survive in cleatcuts. This is in accordance with previous studies that report that it is sensitive also to wind felling and fire (Lõhmus and Kull 2011; Lypowy 2009). When the species was survey in mature forests however, it was recorded in 36 % of the stands.

The experimental translocations to forests of the three different age classes did not result in any differences in mortality of the translocated specimens. The measurement of fluctuations in temperature and humidity show that there are no important differences in microclimate among the age classes either. As habitat quality cannot explain the distribution pattern, I conclude that the distribution pattern is generated by dispersal limitation. Hence, it takes long time before stands become recolonized after disturbance, meaning that young stands are often not occupied even though they offer suitable habitat. The slow reestablishment of the species also imply that it take long time before it reach high abundance in a stand, i.e. stands must be allowed to grow old before *G. repens* will be abundant.

These results imply that the current rotation time of Swedish managed forests of around 100 years disfavour the species, and can together with its inability to survive clearcutting explain why it is declining. Prolonged rotation times may, however, be an effective measure to stop the decline of both this species and other forest species that depend on forest continuity. Moreover, if levels of retention could be increased, so that also sensitive species such as *G. repens*, would be lifeboated, the situation would arguably be even better.

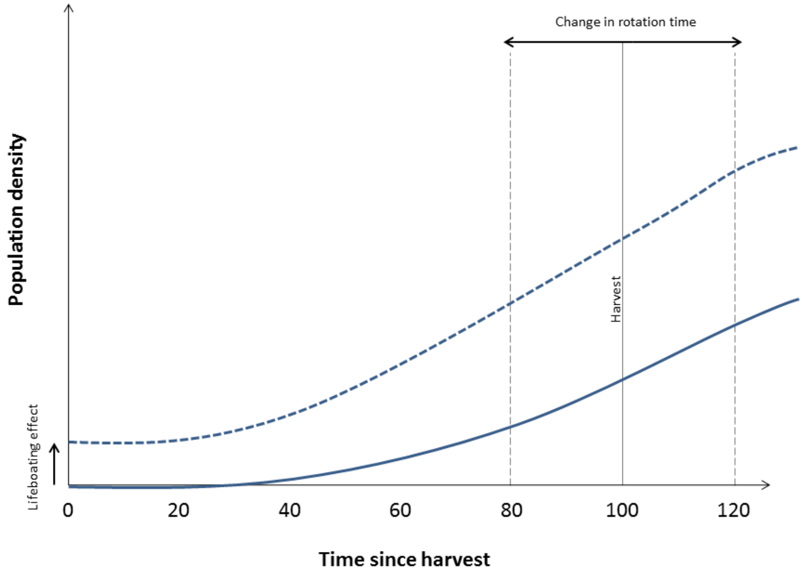

Figure 8. A conceptual model showing the stand level response of *G.repens,* and species with similar life history traits, to clearcutting. Different rotation times (stand age at the time of harvesting) are marked with grey bars. Dashed line show the hypothetical response when individuals are successfully lifeboated through the implementation of tree retention.

4.4 The effects of retention forestry in combination with prescribed burning

- Prescribed burning interacts with retention patches and affects the vegetation dynamics of the entire stand.
- The production of berries is positively affected when prescribed burning is combined with the implementation of aggregated retention.
- Prescribed burning in intact forest has effects on vegetation that resembles that of unburned clearcuts.

In combination with prescribed burning, the elevated retention treatment (50 m^3 or 17% of the standing area) had a slightly different effect on the vegetation composition compared to harvesting with no or low retention (Fig. 2). Indicator species analysis revealed that the dwarf-shrub cowberry, *Vaccinium vitis-idaea*, is more common in burned stands with elevated retention compared to burned clearcut and logged stands with low retention. Also in study IV I found an interaction between prescribed burning and tree retention. Cowberry production was promoted by prescribed burning, but only in combination with retention. Interestingly the highest production of cowberries that was measured in the study was scored in the vicinity of stumps, just outside retention patches in burned clearcuts. I argue that the retention patches alleviate the severity of the fire compared to clearcut, which allows both higher survival and faster recolonization of functionally important plants such as cowberry. The mechanism behind the interactive effects between retention and fire is likely that the amount of fuel on the ground, i.e. woody debris left from harvest, is higher in clearcut areas compared to in the area near retention patches. The same pattern of fire severity has previously been described from the same experiment by Hyvärinen et al. (2005).

The species composition of the vegetation in burned intact forest was most similar to unburned harvested treatments. This similarity is interesting but perhaps only superficial. I argue that the thinning caused by the low intensity fire applied in the forest stands is similar in magnitude to the stress caused by intensified radiation and climatic fluctuations (but without soil damage) in unburned clearcuts. The vegetation response in these two treatments is therefore both characterized by moderate survival of especially dwarf shrubs. The dwarf shrub *V. myrtillus* is previously shown to survive low intensive fire due to its rather deep rhizomes and is also reported to persist, although with lower abundance, in clearcuts (Schimmel & Granström 1996; Bergstedt & Milberg 2001).

4.5 The effects of retention forestry on the delivery of bilberries and cowberries

- Tree retention has a general positive influence on berry production.
- Production of bilberries (*V. myrtillus*) is promoted by low intensive burning in intact forest.
- Stumps are very important microhabitats for both survival and production of berries in clearcuts.

In study IV I show that the use of retention generally results in a positive effect on berry yields. Retention patches promote berry production of bilberry compared to clearcut and retention in combination with prescribed burning promote the production of cowberries (*V. vitis-idaea*) in the vicinity of retention patches.

For bilberry clearcutting with, or without, burning was detrimental. Even the interior conditions of retention patches had a slightly negative effect on berry production compared to intact forest, although positive compared to clearcut. The highest bilberry production in all treatments was, however, found in burned intact forest. As the total cover of the species was lower compared to intact forest it is evident that the burning had some sort of effect on the fertility. The fire severity of the burning in this treatment was low compared to the severity in clearcuts resulting in only low levels of tree mortality, which perhaps is comparable to the effect of thinning which is previously shown to have a positive effect on bilberry yields (Miina et al. 2010).

The vicinity of stumps had a strong positive effect on the production of berries for both species in the study. Only about 5% of the total amount of berries in clearcuts was found on flat grounds with no stump nearby. This can perhaps be explained by the fact that the habitat around stumps is generally less fertile compared to other parts of the harvested area, meaning that dwarf shrubs are not subjected to competitive exclusion by herbs and grasses there.

5 Conclusions and management implications

A general conclusion that can be drawn from this thesis is that the answer to questions concerning retention forestry such as "does it work?" or "how much is enough?" depends on context. In other words: to evaluate the effects of retention measures the aim needs to be very clear. If the aim is to affect the dynamics of the vegetation at the stand level, much higher levels are needed compared to if the goal is to lifeboat plant species typical for mature forests within retention patches. Similarly, if the aim is to lifeboat common, but functionally important species, the size of the retention patch does not need to be as large as if the aim is to protect sensitive species such as rare liverworts.

I end this summary with a list of the most important conclusions for managers that can be made from the studies in this thesis.

- **Low levels of tree retention have no effect on the stand level**

In paper I, I found that aggregated retention at a level of around 17% of the stand area had no effect on the ground vegetation dynamics at the stand level. I therefore argue that if the objective of applying tree retention in Fennoscandian forests is to mitigate the negative effects of harvesting of entire stands, retention level needs to be higher than 17% of the stand area.

- **Small retention patches can lifeboat functionally important species and increase stand heterogeneity**

Retention patches of size typically used in Swedish forestry, i.e. ranging between 0.05 and 0.6 ha, do lifeboat a ground vegetation composition resembling that of mature forests even 20 years after harvesting. Functionally important species such as bilberry and the feathermosses *H. splendens* and *P. crista-castrensis* were more frequent in retention groups compared to clearcuts. By promoting the preservation of patches of vegetation typical of the pre-harvest forests, retention forestry results in an increased heterogeneity at the stand level. Hence, retention patches create successional mosaics typically found following natural disturbances such as fires.

- **Sensitive forest species need large patches to be lifeboated**

Study III shows that retention patches smaller than 0.5 ha do not lifeboat the sensitive forest herb *G. repen*s, a species that depend on stable microclimatic conditions typical for intact forest stands. *G. repens* is a typical and widespread forest species and the results presented are probably relevant for other species with similar habitat preferences. In study II I show that low canopy openness has a positive effect on typical forest species in retention patches. I recommend that managers should implement the use of patches larger than 0.5 ha, as larger patches appear to be both more functional as lifeboats, and are less sensitive to wind throw, meaning that they are more likely to withhold a dense canopy and retain a size that makes them functional over the clearcut phase.

- **Prolonged rotation times can halt the decline of threatened forest species**

Many threatened forest species are unable to survive the clearcut phase, and recolonize young forests at a slow rate. In study III I show that the typical forest specialist *G. repens* is largely missing from 35-40 years old forests despite that the habitat quality would allow it to grow there. This indicates dispersal limitations, implying that it will take long time before this species regains high densities following a stand replacing disturbance. However, if managed stands were allowed to become at least 120 years old, the probability that *G. repens*, and arguably many other forest species, had the time to recolonize and become abundant before cutting would increase significantly. Because this would increase population densities at both stand and landscape levels it would improve the probability of a favourable conservation status also in managed forest landscapes.

- **Tree retention alters the effect of prescribed burning**

In both study I and IV I show that the use of prescribed burning in clearcuts without or with low levels of retention has a severe effect on the vegetation. However, when 17% of the standing volume was retained the effect of fire was somewhat less intense, and increased the survival of functionally important dwarf shrubs such as cowberry. I argue that when prescribed burning is implemented in a harvested area it should be combined with tree retention as this will result in increased heterogeneity with subsequent improved legacy effects.

- **There is no conflict between biodiversity conservation and promoting berry production when implementing retention forestry**

The berry production of dwarf-shrubs bilberry *V. myrtillus* and cowberry *V. vitis-idaea* is in Fennoscandia valued for both its economical and recreational importance as well as being an important food source for wild animals. In study IV I show that the use of retention patches in combination with prescribed burning has a positive influence on berry production compared to clearcutting without retention. This effect was evident both within and around patches. Hence, apart from being a measure to conserve biodiversity, retention forestry can promote an important ecological, provisioning and cultural service of the boreal forest.

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References

Ahti, T., Hämet-Ahti, L., & Jalas, J. (1968). Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici, 5, 169-211.*

Angelstam, P. K. (1998). Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *Journal of Vegetation Science*, *9*, 593-602.

Angelstam, P., & Kuuluvainen, T. (2004). Boreal forest disturbance regimes, successional dynamics and landscape structures, a European perspective. *Ecological Bulletins*, 51, 117-136.

Atlegrim, O., and K. Sjöberg. (1996). Response of bilberry (*Vaccinium myrtillus*) to clear-cutting and single-tree selection harvest in uneven-aged boreal *Picea abies* forests. *Forest Ecology and Management* 86,39-50.

Baines, D. & Sage, R.B. (1994). The implications of deer grazing to ground vegetation and invertebrate communities of Scottish native pinewoods. Journal of Applied Ecology 31, 776-783.

Baker, S. C., Garandel, M., Deltombe, M., & Neyland, M. G. (2013). Factors influencing initial vascular plant seedling composition following either aggregated retention harvesting and regeneration burning or burning of unharvested forest. *Forest Ecology and Management, 306*, 192-201.

Beese, W. J., & Bryant, A. A. (1999). Effect of alternative silvicultural systems on vegetation and bird communities in coastal montane forests of British Columbia, Canada. *Forest Ecology and Management*, *115*, 231-242.

Bengtsson, J., Nilsson, S. G., Franc, A., & Menozzi, P. (2000). Biodiversity, disturbances, ecosystem function and management of European forests. *Forest Ecology and Management*, *132*, 39-50.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F. & Nyström, M. (2003). Reserves, resilience and dynamic landscapes. *AMBIO, A Journal of the Human Environment*, *32*, 389-396.

Bergeron Y, Engelmark O, Harvey B, et al 1998. Key issues in disturbance dynamics in boreal forests, Introduction. J Veg Sci 9,463-468.

Bergeron, Y., Leduc, A., Harvey, B. D., & Gauthier, S. (2002). Natural fire regime, a guide for sustainable management of the Canadian boreal forest. *Silva Fennica*, *36*, 81-95.

Bergstedt, J. & Milberg, P. (2001). The impact of logging intensity on field-layer vegetation in Swedish boreal forests. *Forest Ecology and Management* 154, 105–115.

Bunnefeld, N., & Phillimore, A. B. (2012). Island, archipelago and taxon effects, mixed models as a means of dealing with the imperfect design of nature's experiments. *Ecography*, 35, 15-22.

Chase, J.M. (2003). Community assembly, When should history matter? *Oecologia* 136, 489-498.

Chen, J., Franklin, J. F., & Spies, T. A. (1993). Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and forest meteorology*, *63*, 219-237.

Connell, J. H., & Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, 1119-1144.

Craig, A. & Macdonald, S. E. (2009). Threshold effects of variable retention harvesting on understory plant communities in the boreal mixedwood forest. *Forest Ecology and Management*, *258*, 2619-2627.

Del Moral, R., Titus, J. H., & Cook, A. M. (1995). Early primary succession on Mount St. Helens, Washington, USA. *Journal of Vegetation Science*, 6, 107-120.

Dovčiak, M., Halpern, C. B., Saracco, J. F., Evans, S. A., & Liguori, D. A. (2006). Persistence of ground-layer bryophytes in a structural retention experiment, initial effects of level and pattern of overstory retention. *Canadian Journal of Forest Research*, *36*, 3039-3052.

Drapeau, P., Leduc, A., Giroux, J. F., Savard, J. P. L., Bergeron, Y., & Vickery, W. L. (2000). Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. *Ecological Monographs*, *70*(3), 423-444.

Dufrêne, M. & Legendre, P. (1997). Species assemblages and indicator species, the need for a flexible asymmetrical approach. Ecological Monographs 67, 345–366.

Esseen, P. A., Ehnström, B., Ericson, L., & Sjöberg, K. (1997). Boreal forests. *Ecological Bulletins* 52, 16-47.

Fedrowitz, K., Koricheva, J., Baker, S. C., Lindenmayer, D. B., Palik, B., Rosenvald, R., Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A. & Gustafsson, L. (2014). Can retention forestry help conserve biodiversity? A meta-analysis. *Journal of Applied Ecology*, doi, 10.1111/1365-2664.12289.

Franklin, J. F. (1989). Toward a new forestry. *American Forests*, *95*, 37-44.

Franklin, J. F. (1990). Biological legacies, A critical management concept from Mount St. Helens. In *Trans. North American Wildlands Natural Resource Conference*, 55, 216-219.

Franklin, J.F. (1997) Alternative silvicultural approaches to timber harvesting, variable retention harvest systems.In, Kohm, K.A. & Franklin, J.F. (eds.) *Creating a forestry for the 21st century, the science of ecosystem management.* Island Press, Washington, DC, 111-139.

Franklin J.F., Lindenmayer D.B., MacMahon J.A., McKee A., Magnusson J., Perry D.A., Waide R. & Foster D.R. (2000) *Threads of continuity, Ecosystem disturbances, biological legacies and ecosystem recovery. Conservation Biology in Practice 1, 8–16.*

de Graaf M & Roberts M.R. (2009). Short-term response of the herbaceous layer within leave patches after harvest. *Forest Ecology and Management* 257, 1014-1025.

Granström, A. (2001), Fire management for biodiversity in the European boreal forest. *Scandinavian Journal of Forest Research* 16, 62-69.

Green, R. E., Cornell, S. J., Scharlemann, J. P., & Balmford, A. (2005). Farming and the fate of wild nature. *Science*, *307*, 550-555.

Gromtsev A. (2002). Natural disturbance dynamics in the boreal forest of Europeran Russia, a review. Silva Fennica 36,41-55.

Gustafsson, L., Kouki, J., & Sverdrup-Thygeson, A. (2010). Tree retention as a conservation measure in clear-cut forests of northern Europe, a review of ecological consequences. *Scandinavian Journal of Forest Research*, *25*(4), 295-308.

Gustafsson, L., Baker, S. C., Bauhus, J., Beese, W. J., Brodie, A., Kouki, J., Lindenmayer, D.B., Lõhmus, A., Martínez Pastur, G., Messier, C., Neyland, M., Pali, B., Sverdrup-Thygeson, A., Volney, W.J.A., Wayne, A. & Franklin, J. F. (2012). Retention forestry to maintain multifunctional forests, a world perspective. *BioScience, 62*, 633-645.

Halpern, C. B., McKenzie, D., Evans, S. A., & Maguire, D. A. (2005). Initial responses of forest understories to varying levels and patterns of green-tree retention. *Ecological Applications*, *15*, 175-195.

Halpern, C. B., Halaj, J., Evans, S. A., & Dovciak, M. (2012). Level and pattern of overstory retention interact to shape long-term responses of understories to timber harvest. *Ecological Applications*, *22*, 2049-2064.

Hansen, M. C., Stehman, S. V., & Potapov, P. V. (2010). Quantification of global gross forest cover loss. *Proceedings of the National Academy of Sciences*, *107*, 8650-8655.

Heyerdahl E K, Brubaker LB, Agee JK. (2001). Spatial controls of historical fire regimes, a multiscale example from the interior west, USA. *Ecology* 82,660-678.

Hylander, K. (2005). Aspect modifies the magnitude of edge effects on bryophyte growth in boreal forests. *Journal of Applied Ecology*, *42*, 518-525.

Hylander, K. (2009). No increase in colonization rate of boreal bryophytes close to propagule sources. *Ecology*, *90*(1), 160-169.

Hylander, K., & Johnson, S. (2010). In situ survival of forest bryophytes in small-scale refugia after an intense forest fire. *Journal of Vegetation Science*, 21, 1099-1109.

Hytteborn, H., Maslov, A. A., Nazimova, D. I., & Rysin, L. P. (2005). Boreal forests of Eurasia. *Ecosystems of the World*, *6*, 23-99.

Hyvärinen, E., J. Kouki, P. Martikainen, and H. Lappalainen. (2005). Short-term effects of controlled burning and green-tree retention on beetle (Coleoptera) assemblages in managed boreal forests. *Forest Ecology and Management*, 212,315–332.

Jalonen, J. & Vanha-Majamaa, I. (2001). Immediate effects of four different felling methods on mature boreal spruce forest understorey vegetation in southern Finland. *Forest Ecology and Management*, *146*, 25-34.

Jansson, U., (2011). The National Atlas of Sweden. Agriculture and Forestry in Sweden since 1900 - a carthographic description. The Royal Swedish Academy of Agriculture and Forestry. Norstedts Förlagsgrupp, Stockholm.

Johnson EA. (1992). Fire and vegetation dynamics – studies from the North American boreal forest. Cambridge University Press, Cambridge, U.K.

Johnson, S., Strengbom, J., & Kouki, J. (2014). Low levels of tree retention do not mitigate the effects of clearcutting on ground vegetation dynamics. *Forest Ecology and Management*, *330*, 67-74.

Kuuluvainen, T. (2002). Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fennica*, 36, 97-125.

Lakka, J. & Kouki, J. (2009). Patterns of field layer invertebrates in successional stages of managed boreal forest, Implications for the declining Capercaillie Tetrao urogallus L. population. *Forest ecology and management*. 257, 600-607.

Lencinas, M. V., Pastur, G. M., Gallo, E., & Cellini, J. M. (2011). Alternative silvicultural practices with variable retention to improve understory plant diversity conservation in southern Patagonian forests. *Forest Ecology and Management*, *262*, 1236-1250.

Levers, C., Verkerk, P. J., Müller, D., Verburg, P. H., Butsic, V., Leitão, P. J. & Kuemmerle, T. (2014). Drivers of forest harvesting intensity patterns in Europe. *Forest Ecology and Management*, *315*, 160-172.

Löbel, S., Snäll, T., & Rydin, H. (2012). Epiphytic bryophytes near forest edges and on retention trees, reduced growth and reproduction especially in old-growth-forest indicator species. *Journal of Applied Ecology*, *49*, 1334-1343.

Löfman, S., & Kouki, J. (2001). Fifty years of landscape transformation in managed forests of southern Finland. *Scandinavian Journal of Forest Research*, *16*, 44-53.

Lõhmus, A., & Kull, T. (2011). Orchid abundance in hemiboreal forests, stand-scale effects of clearcutting, green-tree retention, and artificial drainage. *Canadian Journal of Forest Research*, *41*, 1352-1358.

Lypowy, J. N. (2009). The effect of forest fire on understory plant community development, A comparison of pre- and post-fire vegetation in the boreal mixedwood forest. In *Masters Abstracts International*, 48.

McCune, B. & Mefford, MJ. (2006). PC-ORD, Multivariate Analysis of Ecological Data. MjM Software Design. Gleneden Beach, Oregon

Miina, J., T. Pukkala, J-P. Hotanen, and K. Salo.(2010). Optimizing the joint production of timber and bilberries. *Forest Ecology and Management* 259,2065-2071.

Millennium Ecosystem Assessment (2005). Ecosystems and human well-being, current state and trends.

Niemelä, J. (1997). Invertebrates and boreal forest management. *Conservation biology*, *11*, 601-610.

Niklasson, M., & Granström, A. (2000). Numbers and sizes of fires, long-term spatially explicit fire history in a Swedish boreal landscape. *Ecology*, *81*, 1484-1499.

Nilsson MC, Wardle DA. (2005). Understory vegetation as a forest ecosystem driver, evidence from the northern Swedish boreal forest. Front Ecol Environ 3, 421-428.

Økland, R. H. (2000). Understorey vegetation development in North Finnish Picea forests after disturbance, re-analysis of Sirén's data. *Journal of Vegetation Science*, *11*, 533-546.

Oksanen, J. (2013). Multivariate Analysis of Ecological Communities in R, vegan tutorial. http,//cc.oulu.fi/~jarioksa/opetus/metodi/vegantutor.pdf University of Oulu.

Östlund, L., Zackrisson, O., & Axelsson, A. L. (1997). The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian journal of forest research*, *27*, 1198-1206.

Penttilä, R., Siitonen, J., & Kuusinen, M. (2004). Polypore diversity in managed and old-growth boreal Picea abies forests in southern Finland. *Biological Conservation*, *117*, 271-283.

Perhans, K., Appelgren, L., Jonsson, F., Nordin, U., Söderström, B., & Gustafsson, L. (2009). Retention patches as potential refugia for bryophytes and lichens in managed forest landscapes. *Biological Conservation*, 142, 1125-1133.

Pickett, S. T. (1989). Space-for-time substitution as an alternative to long-term studies. In *Long-term studies in ecology* , Springer, New York, 110-135.

Pinheiro J, Bates D, DebRoy S, Sarkar D and R Core Team (2014). *nlme, Linear and Nonlinear Mixed Effects Models*. R package version 3.1-118

Ranius, T., Bohman, P., Hedgren, O., Wikars, L. O., & Caruso, A. (2014). Metapopulation dynamics of a beetle species confined to burned forest sites in a managed forest region. *Ecography*. 37, 797–80

Reinikainen, A., Mäkipää, R., Vanha-Majamaa, I., & Hotanen, J. P. (2001). Kasvit muuttuvassa metsäluonnossa (Changes in the frequency and abundance of forest and mire plants in Finland since 1950). *Tammi, Helsinki*.

Rosenvald, R., & Lohmus, A. (2008). For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. *Forest Ecology and Management*. 255, 1-15.

Risberg, L., & Granström, A. (2009). The effect of timing of forest fire on phenology and seed production in the fire-dependent herbs Geranium bohemicum and G. lanuginosum in Sweden. *Forest ecology and management*, *257*, 1725-1731.

Rudolphi, J., Jönsson, M. T., & Gustafsson, L. (2014). Biological legacies buffer local species extinction after logging. *Journal of Applied Ecology*. 51, 53-62.

Schimmel, J., & Granström, A. (1996). Fire severity and vegetation response in the boreal Swedish forest. *Ecology*, 1436-1450.

Shelby, B., Thompson, J. R., Brunson, M., & Johnson, R. (2005). A decade of recreation ratings for six silviculture treatments in Western Oregon. *Journal of environmental management, 75*, 239-246.

Ståhl, P (2012). Knärot beroende av gammal skog. *Svensk Botanisk Tidskrift 106, 249-257.*

Strengbom, J., & Nordin, A. (2008). Commercial forest fertilization causes long-term residual effects in ground vegetation of boreal forests. *Forest Ecology and Management*, *256*, 2175-2181.

Strengbom, J & Nordin, A. (2012). Physical Disturbance Determines Effects from Nitrogen Addition on Ground Vegetation in Boreal Coniferous Forests. Journal of Vegetation Science 23, 361–371.

Swedish Forest Agency. (2014) Statistical yearbook of forestry 2014. Skogsstyrelsen, Jönköping.

Uotila, A. & Kouki, J. (2005). Understorey vegetation in spruce-dominated forests in eastern Finland and Russian Karelia, Successional patterns after anthropogenic and natural

Vanha-Majamaa, I., & Jalonen, J. (2001). Green tree retention in Fennoscandian forestry. *Scandinavian Journal of Forest Research*, *16*, 79-90.

Walker, L. R., Wardle, D. A., Bardgett, R. D., & Clarkson, B. D. (2010). The use of chronosequences in studies of ecological succession and soil development. *Journal of Ecology*, *98*, 725-736.

Zackrisson, O. (1977). Influence of forest fires on the North Swedish boreal forest. *Oikos*,29, 22-32.

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