Dissertationes Forestales 218

Retention forestry and intensified biomass harvest: epiphytic lichen assemblages under opposing ecological effects in pine-dominated boreal forests

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Academic dissertation

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ABSTRACT

Intensive forestry has led to changes in the structure and function of boreal forests and to the endangerment of forest-dwelling species. Different management methods, such as retention forestry, have been developed to counter the negative biodiversity impacts, although forest use has intensified at the same time: for example, stumps and logging residues are commonly harvested for biofuel. This thesis examines the potential impacts of biofuel harvest, retention forestry and prescribed burning on epiphytic lichen assemblages in pine-dominated boreal forests. In addition, post-harvest dynamics of retention trees were studied to assess their capacity to support species diversity in the early successional forests. The study is based on a large, empirical dataset collected in eastern Finland from 24 study sites that were treated experimentally with a combination of retention harvest and prescribed burning, and, additionally, from 13 sites that represent different stages of forest succession.

The results show that retention forestry has the potential to maintain pre-harvest legacies and support high lichen diversity on harvested sites: 85 lichen species, including Red-Listed species and dead wood specialists, were recorded on retained Scots pines (*Pinus sylvestris* L.) or their dead wood legacies 11 years post-harvest. However, the outcome of retention forestry is affected by post-harvest mortality rates and the fall patterns of the retained trees, which in turn differ depending on the retention tree volume, possible application of prescribed burning, and tree-level factors.

Prescribed burning of harvested sites increased retention tree mortality rates and decreased epiphytic lichen richness 11–12 years post-fire. However, in combination with high retention volumes, burning created more diverse dead wood habitats than retention forestry alone. Thus, despite the initial negative effect, the application of prescribed burning on part of the harvested sites could eventually increase lichen diversity at the landscape scale.

Scots pine stumps on harvested sites hosted 83 lichen species, and may be a valuable habitat resource for wood-dwelling lichens if dead wood volumes in the landscape are otherwise low. Therefore, large-scale stump harvest may decrease lichen diversity. Instead, fine woody debris was found to be a less valuable substrate for epiphytic lichens and could be harvested for biofuel without notable effects on lichen populations.

This study shows that retention forestry can be used to enhance lichen species richness in managed forests, while stump harvest has the opposite effect by reducing lichens' habitats. Prescribed burning decreases lichen species richness at the stand scale but may enhance it at the landscape scale, provided that burning is avoided on the most valuable, lichen-rich stands.

Keywords: Prescribed burning, Tree dynamics, Dead wood, Stump harvest, Logging residues

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LIST OF ORIGINAL ARTICLES

This thesis is based on the following articles, referred to in the text by the Roman numerals I–IV. The articles are reprinted here with the kind permission of the publishers.

I Heikkala O., Suominen M., Junninen K., Hämäläinen A., Kouki J. (2014). Effects of retention level and fire on retention tree dynamics in boreal forests. Forest Ecology and Management 328: 193–201.
http://dx.doi.org/10.1016/j.foreco.2014.05.022

II Hämäläinen A., Hujo M., Heikkala O., Junninen K., Kouki J. (2016). Retention tree characteristics have major influence on the post-harvest tree mortality and availability of coarse woody debris in clear-cut areas. Forest Ecology and Management 369: 66–73.
http://dx.doi.org/10.1016/j.foreco.2016.03.037

III Hämäläinen A., Kouki J., Lõhmus P. (2014). The value of retained Scots pines and their dead wood legacies for lichen diversity in clear-cut forests: The effects of retention level and prescribed burning. Forest Ecology and Management 324: 89–100.
http://dx.doi.org/10.1016/j.foreco.2014.04.016

IV Hämäläinen A., Kouki J., Lõhmus P. (2015). Potential biodiversity impacts of forest biofuel harvest: lichen assemblages on stumps and slash of Scots pine. Canadian Journal of Forest Research 45: 1239–1247.
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Species identification	-	-	AH, PL	AH, PL
Data analyses	OH	AH, MH	AH, PL	AH, PL
Writing of the manuscript, revisions	OH, MS, KJ, AH, JK	AH, OH, KJ, JK	AH, JK, PL	AH, JK, PL

OH, Osmo Heikkala; MH, Mika Hujo; AH, Aino Hämäläinen; KJ, Kaisa Junninen; JK, Jari Kouki; PL, Piret Lõhmus; MS, Mai Suominen

TABLE OF CONTENTS

1 INTRODUCTION

Northern boreal forests have changed markedly in the past century due to intensive forest management, which has created structurally simple, even-aged forest stands that have, to a large extent, replaced structurally diverse late-successional forests (e.g. Esseen et al., 1997; Siitonen, 2001; Cyr et al., 2009). Furthermore, forest dynamics have changed as clear-cutting has largely replaced natural disturbances, such as windstorms or wildfires (Esseen et al., 1997). Young forest stands that originate from clear-cuttings are markedly different from those that develop after natural disturbances, since clear-cut stands lack the structural legacies, such as dead wood, that are generally left by natural disturbances (Franklin et al., 2000; Kouki et al., 2001; Swanson et al., 2010). These changes in the structure and dynamics of boreal forests have led to the endangerment of many forest-dwelling species (Rassi et al., 2010). Recently, forest use has intensified even further as the rising demand for renewable energy has resulted in an increase in the harvest of forest biomass, such as stumps and logging residues, for energy production (Helmisaari et al., 2014). On the other hand, the negative impacts of intensive forestry on biodiversity have received increasing attention over the past two decades, and various methods have been developed for more ecologically sustainable forest use that aims to halt the loss of diversity in the managed forests (Gustafsson et al., 2012; Lindenmayer et al., 2012); for example, development of sustainable forest management is currently supported by various international forest policies and regulations (MacDicken et al., 2015). Enhancing species diversity in managed forests is necessary as the area of protected forest throughout the boreal region is low (Schmitt et al., 2009; Morales-Hidalgo et al., 2015) and not sufficient to sustain viable populations of forest-dwelling species (Lõhmus et al., 2004).

1.1 Retention forestry and prescribed burning

Retention forestry was first introduced in the Pacific Northwest in the 1990s and has since become a widely applied practice, particularly in northern Europe and North America (Gustafsson et al., 2012). It refers to the retention of part of the living trees or dead wood on the harvested site (Gustafsson et al., 2012) in order to provide structural legacies similar to those that occur after natural forest disturbances. These legacies increase the structural variability of the sites (Gustafsson et al., 2010; Kruys et al., 2013; Lõhmus et al., 2013) and enhance habitat connectivity at a landscape scale (Franklin et al., 1997). The retained trees can also "life-boat" populations of species on the harvested site through the early successional phases (Rosenvald and Lõhmus, 2008; Baker et al., 2015) to function as dispersal sources in the regenerating forest stand (Sillett and Goslin, 1999; Hedenås and Hedström, 2007). Sites with retention trees have been shown to have higher levels of species richness and abundance of forest-dwelling species than clear-cut sites (Fedrowitz et al., 2014).

While retention forestry adds structural variability on harvested sites, it lacks an important feature of natural forest dynamics: forest fires. In the past, fire has been one of the most important disturbances in the boreal forest (Zackrisson, 1977) and, consequently, several forest-dwelling species have specialized in fire-related habitats, such as dead and charred wood or young successional stands that originated from fires (Esseen et al., 1997). During the last century, fire frequency has decreased notably in many areas of the boreal region, for example in Fennoscandia (Zackrisson, 1977; Linder and Östlund, 1998; Granström, 2001), as well as in large parts of North America (Wallenius, 2011). This has led to a loss of fire-related habitats and, consequently, a decline in species dependent on them. To compensate for the decrease in wildfires, prescribed burning of mature stands, as well as retention cuts is currently practiced in Finland (Similä and Junninen, 2012) and Sweden (Olsson and Jonsson, 2010). Prescribed burning has been found to be beneficial for certain species groups, such as beetles (Hyvärinen et al., 2005; Hjältén et al., 2010a) and also for polypore fungi over longer timescales (Olsson and Jonsson, 2010; Penttilä et al., 2013; Suominen et al., 2015).

To evaluate the benefits of retention forestry – also when applied in combination with prescribed burning – it is necessary to understand the post-harvest dynamics of the retention trees, as this determines their role and effectiveness as legacy structures. In general, tree mortality increases after harvest in comparison to uncut stands (Bladon et al., 2008; Lavoie et al., 2012). It can be affected by both stand- and tree-level factors: tree mortality is usually lower when the retention level is high (Scott and Mitchell, 2005; Busby et al., 2006; Solarik et al., 2012) or when the trees are retained in groups rather than dispersed (Scott and Mitchell, 2005). Tree-level factors, such as tree species, diameter or height may also affect mortality rates (e.g. Bladon et al., 2008; Rosenvald et al., 2008; Lavoie et al., 2012); for example, trees with larger height-diameter ratios tend to be more susceptible to windthrow (Scott and Mitchell, 2005). However, a majority of the studies that have addressed the mortality and dynamics of retention trees have been conducted in North American boreal and temperate forests (e.g. Busby et al., 2006; Bladon et al., 2008; Lavoie et al., 2012), and the results may not be applicable elsewhere due to differences, for example, in tree species composition and climatic conditions (Lavoie et al., 2012) or in the applied harvesting methods, such as the volume of retained trees (Gustafsson et al., 2012). Furthermore, tree mortality following fire has been assessed only in closed forests (e.g. Hely et al., 2003; Sidoroff et al., 2007): the effect of prescribed burning on retention tree mortality has not been examined so far, even though it would be critical to know in order to properly evaluate the effectiveness of this combined practice as a part of sustainable forest management.

1.2 Forest biofuel harvest

Despite the wide application of sustainable forest management methods, such as retention forestry, there is also pressure to intensify forest use in the boreal region by harvesting biomass for renewable energy production. Currently, retention forestry and intensive biomass harvest can be applied on the same harvested site despite their apparently opposing aims, and the combined effect of these measures on the stand-level biodiversity is not clear. One source of forest biomass are stumps and logging residues (i.e. slash) collected from clear-cut sites. During the last decade, the volume of slash and stumps harvested for energy has increased markedly in the boreal and northern temperate forests (Directive 2009/28/EC… 2009; Bradley, 2010), particularly in Fennoscandia. For example, slash was harvested from 30% and stumps from 10% of all clear-cut sites in 2012 in Finland (Asikainen et al., 2013).

Harvest of slash and stumps (hereafter “biofuel harvest”) increases the intensity of forest use in comparison to conventional stem-only-harvesting (Walmsley and Godbold, 2010) and may cause marked changes in the forest ecosystems, especially if practiced on a large scale. The most significant impacts on forest-dwelling species are related to reduction of dead wood: biofuel harvest can decrease the total volume of dead wood on a harvested site by 40% (Eräjää et al., 2010). This is problematic particularly in Fennoscandia where the amount of dead wood in managed forests is already very low in comparison to old-growth stands, and as such many dead wood-dependent species have consequently become threatened (Siitonen, 2001). Even though coarse woody debris (CWD) is usually regarded as the most important substrate for dead wood-dwelling species, stumps and slash (or fine woody debris (FWD) in general) can also host species-rich assemblages of basidio- and ascomycete fungi (Kruys and Jonsson, 1999; Nordén et al., 2004; Juutilainen et al., 2014), epiphytic lichens (Caruso et al., 2008; Svensson et al., 2013), bryophytes (Humphrey et al., 2002) and saproxylic beetles (Hjältén et al., 2010b). Large-scale biofuel harvest can be a threat to these species, as stumps and slash constitute a major part of the dead wood available on clear-cut sites (Eräjää et al., 2010; Lõhmus et al., 2013) and may thus currently be a significant resource for the species.

1.3 Epiphytic lichens and intensive forest management

The species group addressed in this thesis are epiphytic lichens, i.e. bark- and wood-dwelling species of lichenized fungi as well as lichenicolous fungi and saprotrophic calicioid fungi (traditionally treated by lichenologists in floristical and ecological research). Epiphytic lichens are an important component of forest ecosystems (Ellis, 2012): they participate in the water and nutrient cycles, as well as in the forest food webs, providing forage and habitats for several invertebrates, birds and small mammals. Epiphytic lichens tend to be sensitive to the impacts of forestry: forestry reduces the amount of lichen-rich substrates, such as old trees or CWD (Jääskeläinen et al., 2010) and leads to the fragmentation of forest landscapes with increased distances between suitable habitat patches, which restricts many epiphytic lichens to old-growth forests with sufficient habitat continuity (Sillett et al., 2000b; Hilmo and Såstad, 2001). In Finland (Jääskeläinen et al., 2010) and Sweden (Thor, 1998) commercial forestry has been proposed as the most important threat to lichen species. The current status of Finnish lichen species is alarming: in the latest Finnish Red List, 44% of the assessed lichen species are classified as threatened or near-threatened, and the main factors threatening lichens are related to forestry (Jääskeläinen et al., 2010). To halt this negative development, it is necessary to examine in detail the impacts of different forest management methods on epiphytic lichens.

Retention forestry has the potential to reduce the negative impacts of forest management on epiphytic lichens. Studies on lichen diversity and survival rates on retention trees show that despite an initial decline of species' abundance after harvest (Lõhmus and Lõhmus, 2010) and low survival rates due to high irradiation (Jairus et al., 2009), retained trees can provide habitats for various specialized lichen species (Lõhmus et al., 2006; Rosenvald and Lõhmus, 2008). Small lichen populations can persist on the living retained trees for over 10 years after harvest (Gustafsson et al., 2013; Lundström et al., 2013). However, studies in European boreal forests have concentrated mainly on retained aspen trees (*Populus tremula* L.), and since aspen has quite specific lichen assemblages (Kuusinen, 1996) the results may not be applicable to other tree species. In particular, the importance of retained Scots pines (*Pinus sylvestris* L.) for lichen diversity is poorly studied, even though pine-dominated forests are widespread throughout northern Europe. Dead, retained Scots pines can host high lichen diversity (Runnel et al., 2013), however lichen assemblages on living retained Scots pines have not been studied so far.

In comparison to retention forestry, the impact of prescribed burning and the significance of fire-related habitats for epiphytic lichen species are less studied. The immediate effect of burning on lichens is known to be negative (e.g. Vanha-Majamaa et al., 2007), but post-fire succession has so far been mainly assessed for ground-dwelling macrolichens (Johansson and Reich, 2005; Holt et al., 2008). Only a few studies have reported the response of epiphytic macrolichens after fire (Bartels and Chen, 2015) or colonization of charred wood by epiphytic species (Johansson et al., 2006; Lõhmus and Kruustük, 2010). In the short term, charred wood is colonized by common species with high dispersal capacity (Eversman and Horton, 2004; Johansson et al., 2006). Still, certain lichen species, such as *Carbonicola anthracophila* (Nyl.) Bendiksby & Timdal and *C. myrmecina* (Ach.) Bendiksby & Timdal as well as *Hertelidea botryosa* (Fr.) Printzen & Kantvilas seem to be specialized in burned substrates and have been found to occur predominantly on dead pine snags or stumps with charred wood (Grossmann, 2014; Källén, 2015).

While ecologically sustainable management measures may increase lichen diversity in managed forests, biofuel harvest can pose a threat especially for dead wood-dwelling lichens. The studies conducted so far suggest that the slash of Norway spruce (*Picea abies* (L.) Karst.) is not a significant substrate for lichens (Caruso et al., 2011), but spruce stumps on clear-cut sites can host species-rich assemblages (Caruso and Thor, 2007; Caruso and Rudolphi, 2009; Svensson et al., 2013). Diverse lichen assemblages are also known to occur on old stumps in mature forests (Kuusinen and Siitonen, 1998; Humphrey et al., 2002; Nascimbene et al., 2008b), but since both stand age (Bunnell et al., 2008) and decay stage (Nascimbene et al., 2008a) affect the composition of lichen assemblages on dead wood, further research is needed to determine the value of older stumps for epiphytic lichens (however, see Caruso and Rudolphi (2009) for lichens on spruce stumps). The impacts of retention forestry and prescribed burning on the species assemblages that occur on stumps and slash have not been studied either. For example, retention trees may function as a source of dispersal (Sillett and Goslin, 1999) or alter the microclimate of the harvested site (Hautala et al., 2011), and thus affect the species assemblages on stumps and slash. Therefore, retention forestry or prescribed burning on harvested sites can alter the habitat value of stumps and slash.

1.4 Thesis aims

This thesis focuses on the effectiveness of retention forestry and prescribed burning for sustaining species diversity in Scots pine-dominated boreal forests, and on the potential impacts of biofuel harvest on species diversity. The first objective was to study the post-harvest dynamics of retained trees in order to assess their capacity to maintain species diversity in early successional forests; the second objective was to examine the impact of retention forestry and prescribed burning on epiphytic lichen species richness and composition; the third objective was to estimate the potential impact of biofuel harvest on the epiphytic lichen assemblages that occur on stumps and FWD.

Specifically, the studied questions were:

1. Do retention level, prescribed burning after harvest and tree-level factors (e.g. tree species, diameter) impact the post-harvest mortality of retained trees that are the main substrate for epiphytic lichens in harvested stands? (Studies I, II)
2. Do the species richness and composition of epiphytic lichens on retained Scots pines and their dead wood legacies 11 years after harvest differ from those on old-growth stands, or between retention levels? (Study III)

3. What are the effects of prescribed burning on the species richness and composition of epiphytic lichens on retention trees and their dead wood legacies as well as on stumps and FWD 11–12 years after burning? Do the effects depend on the retention level? (Studies III, IV)
4. Which lichen species occur on stumps and FWD of Scots pine on recently harvested sites, on mature managed sites and on old-growth forests, and are they potentially threatened by biofuel harvest? (Study IV)
5. Do retention forestry and prescribed burning mitigate or deepen the potential impact of biofuel harvest on the epiphytic lichen assemblages? (Study IV)

2 METHODS

2.1 Study sites and experimental design

The data for all four studies were collected from the municipality of Lieksa, in eastern Finland (approximately 63° N, 30° E, with an elevation above sea level ranging between 150–200 m). The area is on the border of the southern and middle boreal zones (Ahti *et al.*, 1968). The study design included two parts: the experimental study system (Studies I–IV) and the successional study system (study IV).

The experimental study system (studies I–IV) was initiated in 2000 (e.g. Hyvärinen et al., 2005; Junninen et al., 2008; Kouki, 2013) and is comprised of 24 study sites, each 3–5 ha in size (Figure 1). Before the experimental treatments, the sites were approximately 150 year old, moderately dry forests dominated by Scots pine. Norway spruce and birch (*Betula pendula* Roth and *B. pubescens* Ehrh.) were also common on the sites, whereas aspen, grey alder (*Alnus incana* (L.) Moench), goat willow (*Salix caprea* L.) and rowan (*Sorbus aucuparia* L.) occurred in smaller numbers. The sites had not been intensively managed, though some selective, low-intensity harvesting had taken place during the late 1800s or early 1900s. Before the treatments, the volume of living trees or dead wood did not differ between the treatment groups (Hyvärinen et al., 2005). The distance between the different study sites varied, but with the exception of a few sites, it was always greater than one kilometer.

The experimental treatments consisted of two factors: retention level and burning. Eighteen of the sites were harvested in winter 2000–2001, at living retention tree levels of either 0, 10 or 50 m^3 ha^{-1}. The trees were retained mainly in small groups, but each retention harvested site also had several dispersed trees. In addition, six uncut sites were used as controls. After the harvests, half of the sites in each harvest category (including the controls) were burned in June 2001. This resulted in a total of eight different treatment combinations, each replicated in three sites (Figure 2). The treatments were randomly allocated to the sites, except for the uncut control sites, which had to be situated inside the nearby Patvinsuo National Park in order to guarantee that they would not be harvested in the future.

The successional study system (study IV) consisted of 13 sites (Figure 1), including five old-growth sites (over 150 years old), four mature managed sites (50–80 years old), and four sites harvested with living retention trees (10–15 m^3 ha^{-1}) 5–6 years ago. All sites were dry, Scots pine -dominated stands of at least 2 ha in size. The selection of the sites was based on a cluster design: four old-growth forests were selected from the forest database of Metsähallitus, and one mature managed and one harvested stand were visually selected from the surroundings of each old-growth site. This resulted in four clusters with one old-growth, one mature managed and one harvested site in each; a fifth old-growth site was added later to increase the sample size.

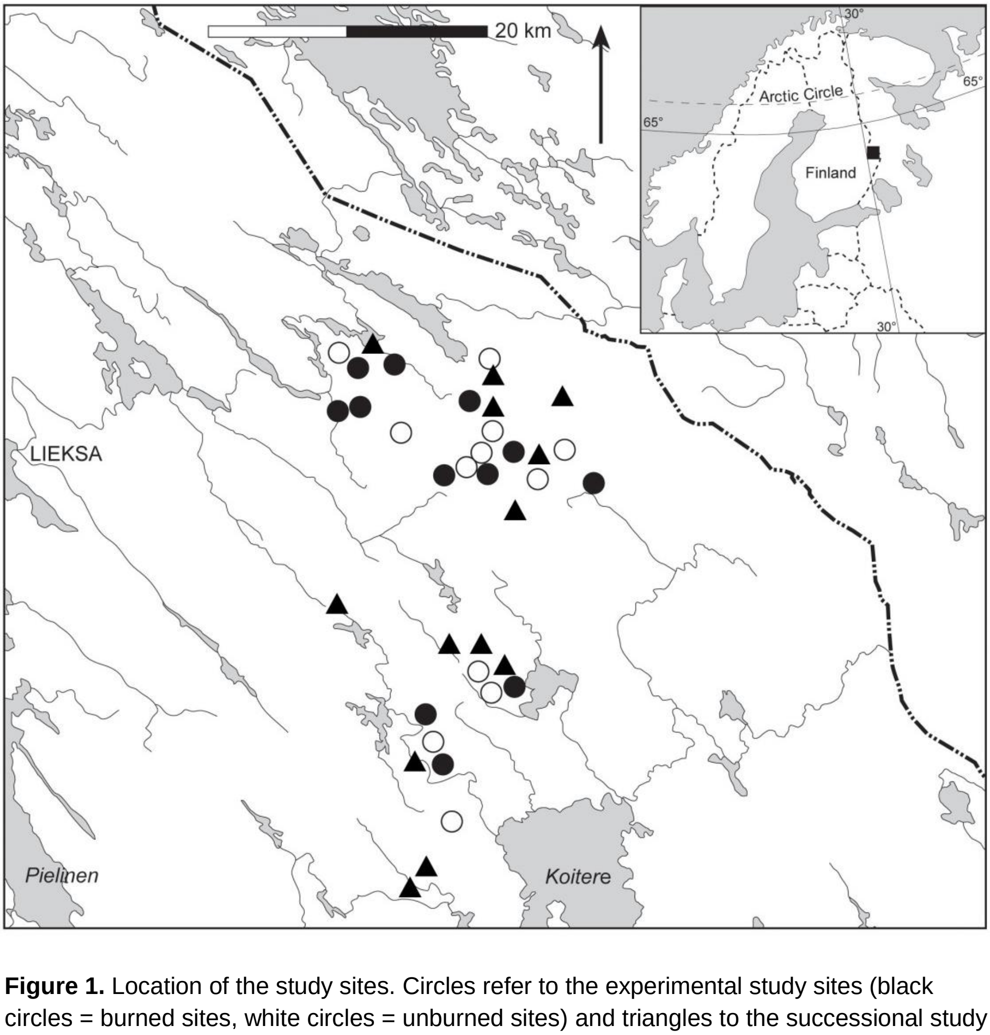

Figure 1. Location of the study sites. Circles refer to the experimental study sites (black circles = burned sites, white circles = unburned sites) and triangles to the successional study sites.

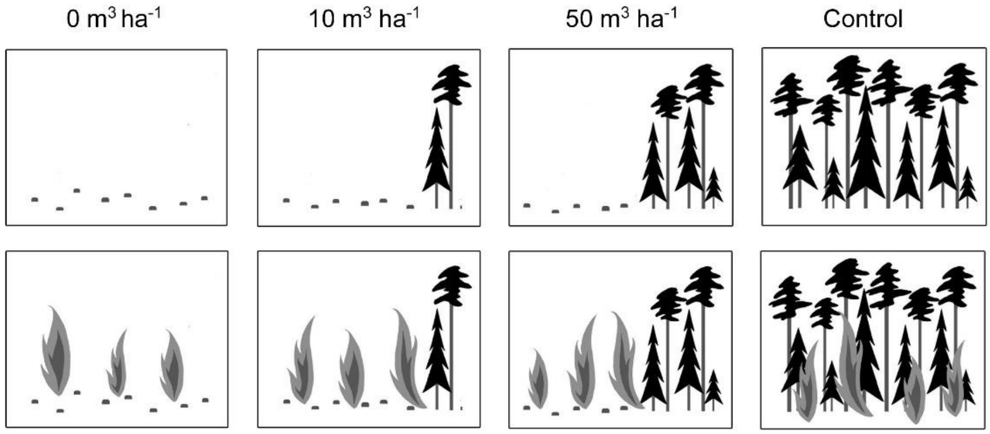

Figure 2. The experimental study design. Each of the eight treatments (combinations of prescribed burning and harvest) was replicated on three study sites.

2.2 Inventory of retention tree dynamics

Retention tree dynamics were studied on the 12 experimentally treated study sites at the 10 or 50 m^3 ha^{-1} retention levels (studies I–II). Before the treatments, all trees that were to be retained were numbered individually and mapped, and the species, diameter at breast height (1.30 m) and height of each tree were recorded. The trees were re-inventoried in summer 2001 (one month after the treatments) and again in 2005, 2008 and 2011. During each of these inventories, the condition of each tree was assessed, and the trees were marked either as living, standing dead or fallen.

2.3 Lichen inventories

Lichen species were inventoried from Scots pines on 18 sites of the experimental study system (including the harvested sites with retained trees and control sites, excluding sites where the retention level was 0 m^3 ha^{-1}) during summer 2012 (study III). On each site, the aim was to randomly select and inventory 15 Scots pines (including 5 living trees, 5 standing dead trees and 5 fallen trees), however the actual number of selected trees per site varied since it was not always possible to find five trees of each type on some of the sites. All retained trees had been alive at the time of the harvest and the selected dead trees were legacies of retention trees that had died after the harvest. All lichen species were inventoried from the trunks of standing trees below a height of 2 m, and along 2 m from the base for fallen trees.

Lichens were inventoried from stumps and FWD on all 24 study sites of the experimental study system (study IV). Four 2 x 8 m study plots were established on each site; on the sites with retention trees, two plots were situated close to the tree groups and two further away. The volume of FWD (all dead wood objects with a diameter of 1–10 cm) and stumps was measured from these plots in 2012 and lichen inventories were carried out in the same plots in 2013. The FWD of Scots pine was examined for 30 minutes on each plot with the aim of finding as many lichen species as possible. In addition, lichen species were inventoried from eight Scots pine stumps situated closest to the center of the plot. Five of these stumps were created during the harvest in 2000 and three were older specimens; either natural or stumps cut before 2000. On the control sites, only these older stumps were inventoried. The total number of inventoried stumps was 32 on each harvested site and 12 on each control site.

On the successional study sites (study IV), lichen species were inventoried at a stand scale in 2010 and 2011. A 2 ha plot was delineated on each site without prior knowledge of the lichen biota, and all substrates were examined over a 4 hour period within this plot with the aim of finding as many lichen species as possible. For each species, all inhabited substrate types (e.g. trunk or branches of living trees, standing or downed CWD, stumps, FWD) were recorded. These data were used to evaluate whether lichen species inhabit the stumps and slash of Scots pine and other dead wood substrates, which may be destroyed during the biofuel harvest, and whether they can be found on other substrate types and tree species as well.

If a lichen species could not be identified immediately in the field during the inventories, samples of unidentified specimens were collected for later laboratory examination that included microscopy and standard thin-layer chromatography (TLC) to detect lichen compounds. Some species were treated collectively due to taxonomic difficulties. The nomenclature of lichen species follows Jääskeläinen et al. (2015).

2.4 Data analyses

The impacts of burning, retention level and monitoring year on the stand-level mortality of retention trees were examined with a factorial repeated measures analysis of variance (study I). The analyses were performed separately for different tree species (pine, spruce and deciduous trees). In study II, the effects of tree-level factors on the dynamics of individual trees were modelled using Cox proportional hazards regression (Cox, 1972). Two separate models were fitted: the first described the survival of the trees after harvest (time from harvest until tree death) and the second described the fall rate of the dead trees (time from tree death until tree fall). The factors considered were tree species (pine, spruce or deciduous), diameter, height/diameter ratio and location of the tree (in group or dispersed).

A two-way analysis of variance was used to study the impacts of burning and retention level on the mean species richness of epiphytic lichens on the retained trees (study III). Separate analyses were performed for macrolichens (species with foliose or fruticose thallus) and microlichens (species with crustose thallus), since species morphology can affect their response to forestry (e.g. Ellis and Coppins, 2006; Johansson et al., 2006; Hedenås and Hedström, 2007). In addition, the analyses were done separately for living trees, standing dead trees (i.e. snags) and fallen trees (i.e. logs). Non-metric multidimensional scaling (NMS) and multi-response permutation procedure (MRPP) were used to study the differences in lichen species composition between the experimental treatments. The MRPP was also performed separately for living trees, snags and logs. In addition, a set covering approach was used to assess the value of the three tree types (i.e. living trees, snags and logs) for lichen diversity. In this analysis, the smallest possible combinations of living trees, snags and logs required to maintain all observed lichen species were calculated.

General linear models were used to study the effects of burning, retention level and substrate volume on lichen species richness on FWD and stumps (study IV). The models were run separately for different substrates: FWD, new stumps and old stumps. Two models were run for both new and old stumps: the first described the total number of species per site ("stand scale"), and the second the average number of species per stump on each site to assess the abundance of lichens ("stump scale"). The composition of lichen assemblages on FWD and stumps was studied with NMS and MRPP. These analyses were performed both with the data collected from the experimental study sites as well as with the data from the successional study sites.

The statistical analyses were performed with IBM SPSS Statistics 19.0 (Studies I, III and IV; IBM Corp., Armonk, New York, USA), package *survival* of R (Study II; Therneau, 2015) and PC-ORD 5.0 (Studies III–IV; McCune and Mefford, 1999).

3 RESULTS AND DISCUSSION

3.1 Retention tree dynamics

The post-harvest mortality of the retention trees was high: 55% of the inventoried trees or 59% of their total volume died during the 10-year survey period (I, II). Prescribed burning significantly increased mortality rates: on the unburned sites 32% of the trees or 34% of the total volume died, while on the burned sites the proportion of dead trees was notably higher; 95% of the trees or 84% of the total volume (I, II). Tree mortality on the unburned sites was fairly constant between years and between retention levels, whereas on the burned sites mortality rates were highest during the first post-fire years (I). Burning is known to result in a similar peak in mortality rates in mature forests, where fire-injured trees generally die within 2–3 years (DeBano et al., 1998).

On the burned sites, mortality rates also differed between retention levels. At the lower retention level, virtually all trees died within four years; on the sites with the high retention level, mortality was high immediately after burning, with 75% of the retention tree volume dying during the first four years, but after this mortality rates decreased so that the sites still had approximately 10 m^3 ha^{-1} of living trees ten years after fire (I). The difference may be due to a higher fire intensity at the lower retention level, caused by a larger amount of dry, easily flammable logging residues (Sidoroff, 2001). Furthermore, the retention tree groups were slightly larger at the higher retention level, which possibly resulted in lower fire intensity and thus lower mortality rates within the groups. In study II, the risk of mortality was found to be lower for grouped than dispersed trees on both burned and unburned sites. Previous studies have explained this by a lower risk of windthrow in the groups (e.g. Lavoie et al., 2012), however the tree groups studied here were apparently too small to offer any protection against wind, since the proportion of fallen trees was actually higher within the groups than among dispersed trees (II).

At the tree level, the risk of mortality decreased with increasing tree diameter on the burned sites (II). This result could be expected, since larger trees tend to have thicker bark that provides protection against the flames; in addition, the risk of crown scorch is generally smaller for large trees due to a higher crown baseline (Harmon, 1984; Hely et al., 2003). On the unburned sites, diameter still had a positive effect on the survival of pines and deciduous trees, while in contrast spruces with larger diameters had higher mortality rates (II). This can be explained by an increased risk of windthrow, since large trees are more exposed to wind than smaller ones (Solarik et al., 2012), and spruce is more susceptible to windthrow than pine or birch (Peltola et al., 2000). Thus, on both burned and unburned sites, spruce had the highest mortality rates when larger trees (diameter over 20 cm) were compared, while among smaller trees spruce appeared to survive as well or even better than the other tree species (II). However, the latter result is more likely to be due to the low number of small-diameter pines in the data rather than an actual difference in survival rates.

The majority (81%) of the retention trees that died after harvest also fell down during the 10-year survey period (II). Tree fall was common in the first post-treatment years, but declined with time (I), and this finding is consistent with previous observations (e.g. Busby et al., 2006; Urgenson et al., 2013). The proportions of fallen trees and snags did not differ between burned and unburned sites ten years post-harvest (II), although as a result of the significantly higher mortality rates the volume of snags was higher on the burned sites, especially during the first post-treatment years (I). At the unburned sites, the volume of snags remained lower and fairly constant throughout the survey period (I). On all sites, the risk of tree fall varied among tree species (II), as has also been observed in previous studies (e.g. Bladon et al., 2008; Rosenvald et al., 2008). Pines were most likely to remain as snags, while spruces were three times more likely and deciduous trees two times more likely to fall (II). As noted also by previous studies (e.g. Scott and Mitchell, 2005; Lavoie et al., 2012), the risk of tree fall increased with increasing diameter and height-diameter ratio for all tree species (II).

3.2 Epiphytic lichens' occurrence on harvested sites

Retained trees, their dead wood legacies (i.e. snags and logs), stumps and logging residues form the main substrates for epiphytic lichens in harvested boreal forest stands. In studies III and IV, the lichen assemblages were inventoried from all these substrates, and they were found to sustain high species richness on the harvested sites. When all the harvested study sites were combined, 85 species were found to occur on living retention trees, snags or logs, while 83 species were found on stumps and 59 species on FWD (III, IV). The majority of the lichens that inhabited the inventoried trees, stumps and FWD were common and mostly generalist species, but both retention trees and stumps also hosted Red-Listed lichen species. Although these were generally more common in closed forests, some species, such as *Hertelidea botryosa*, *Cladonia parasitica* (Hoffm.) Hoffm. and *Alectoria sarmentosa* (Ach.) Ach. were also found in the harvested sites (III, IV). In addition, several species regarded as specialists on dead wood substrates (Spribille et al., 2008) occurred on stumps, snags and logs (III, IV). Thus, living Scots pines, their dead wood legacies and stumps appear to be essential substrates for epiphytic lichens on harvested sites. The total species number on FWD was clearly lower than on stumps and, more importantly, FWD was inhabited mainly by common species with no particular conservation concern (IV). Therefore, FWD can be considered a less valuable habitat for epiphytic lichens, which is in accordance with previous studies from Sweden (Caruso et al., 2008; Svensson et al., 2014; 2016).

In addition to surviving on the retention trees, several lichen species had also colonized the newly exposed substrates on harvested sites within a decade. In particular, several species were found on the exposed wood of dead retention trees or on the cut surfaces of stumps: these substrates were colonized after the harvest. Colonization had also occurred on logging residues, which hosted various dead wood- and ground-dwelling species, such as *Placynthiella icmalea* (Ach.) Coppins & P. James and *Trapeliopsis granulosa* (Hoffm.) Lumbsch. Epiphytic lichens have been also previously found to colonize living retention trees

(Lõhmus and Lõhmus, 2010; Lundström et al., 2013), snags (Runnel et al., 2013), as well as stumps and logs (Caruso et al., 2010) on harvested sites 5–18 years post-harvest.

3.2.1 Retention trees

When lichen species richness was compared between the harvested and old-growth control sites, the retained Scots pines, snags and logs displayed a species richness comparable to the trees on the old-growth sites (III). In addition, species richness was similar between the two studied retention levels; 10 and 50 m^3 ha^{-1} (III). Previous studies have also shown that live retained aspens (Hedenås and Hedström, 2007; Lundström et al., 2013) and birch (Lõhmus and Lõhmus, 2010) on harvested sites sustain as rich lichen assemblages as do living trees in mature forests. Similarly, lichen species richness has been found to be comparable between old and young forest stands on dead wood substrates (Bunnell et al., 2008).

However, even though lichen species richness was similar between harvested and control sites the species composition on the living retention trees differed considerably (III), which would indicate that the ability to colonize and persist on harvested sites varied between lichen species. Specifically, microlichens were found to be more vulnerable to the impact of harvest than macrolichens: the mean species richness of microlichens was lower on harvested than old-growth control sites, even though the actual difference in species number was fairly low (III). Indeed, lichen morphology is regarded as important in determining their ability to survive in open sites (Jairus et al., 2009). High light levels can be harmful for microlichens, especially those that lack a protective cortex (Hedenås and Hedström, 2007; Jairus et al., 2009), while certain foliose macrolichens may, on the contrary, benefit from the increased light (Sillett et al., 2000a; Gauslaa et al., 2006) or from higher precipitation at ground level after harvest (Boudreault et al., 2013).

To date, studies on the significance of retention forestry for epiphytic lichens have concentrated on living trees, even though dead wood is also an important substrate for lichens (e.g. Lõhmus and Lõhmus, 2001; Spribille et al., 2008). Snags and logs in particular are considered to be key habitats for epiphytic lichens in the boreal pine forests, especially for species with crustose thallus (Esseen et al., 1997). Recently, Runnel et al. (2013) showed that dead retention trees, especially Scots pine snags, also host diverse lichen assemblages. The high lichen richness found on dead Scots pines on both harvested and control sites in study III is in agreement with their results. In general, snags have been regarded as a more valuable lichen habitat than logs (Kuusinen and Siitonen, 1998; Humphrey et al., 2002; Runnel et al., 2013), which in turn are often more important for bryophytes. However, the results of the set-covering approach showed that logs in both harvested and old-growth control sites are also valuable habitats for epiphytic lichens, as broadly similar numbers of living pines, snags and logs were required to support all observed species, and each of these substrate types hosted unique species (III). The importance of downed CWD was further supported by the high species richness and number of Red-Listed species found on downed CWD and on root plates of pine on the successional study sites in study IV.

3.2.2 FWD and stumps

Lichen species richness on FWD was similar between all harvested and old-growth sites, after controlling for the substrate volume (IV). FWD was mainly occupied by generalist species, which were apparently able to tolerate the environmental changes that followed harvest. On new stumps, stand-scale species richness was slightly higher on the sites with the higher retention level than on the clear-cuts (IV). The retention trees possibly increased species numbers by functioning as dispersal sources to the stumps; this would explain why the effect of retention was apparent only on new stumps, but not on the old ones that were already occupied by lichens and probably offered less free surfaces for colonization (IV). Also microclimatic effects can affect the occurrence of lichens on cut sites (Caruso *et al.*, 2011), but these were not likely to be significant in study IV, as retention levels comparable to those on the experimental study sites should have had a minimal impact on the microclimate (Heithecker and Halpern, 2006).

The age and decay stage of dead wood generally affect lichens species richness and composition (Nascimbene et al., 2008a; Botting and DeLong, 2009; Caruso and Rudolphi, 2009). The effect of substrate age was visible for stumps; while total species number remained fairly similar, a clear difference in assemblage composition was observed between the new (9 years old) and older (pre-harvest) stumps (IV). Notably, the older stumps hosted more dead wood specialists and Red-Listed species. A positive effect of stump age on the number of specialist lichen species has also been found by Svensson et al. (2013) who explained this by a longer colonization period to the older stumps; a longer colonization time may be important particularly for rare species with poorer dispersal capacities (Humphrey et al., 2002). In addition to stump age, the successional stage of the stand (i.e. retention cut, mature managed or old-growth) affected the species composition on both stumps and FWD.

3.3 Impact of prescribed burning on epiphytic lichens

Although approximately half of the species observed in studies III and IV were also found on charred wood or bark, the recovery of epiphytic lichens after fire appears to be fairly slow and the overall impact of fire on species richness was still negative 11–12 years after burning (III, IV). However, the impact of fire varied among stand and substrate types: the total species richness on both retention trees and old stumps (at the stand scale) was lower on burned than unburned harvested sites, whereas on the control sites the species richness increased slightly after burning (III, IV). This increase was mainly caused by a higher richness of common macrolichens, such as *Cladonia* spp. (III, IV), which may have benefited from the higher light levels that resulted from canopy openings (Boudreault et al., 2013). Furthermore, fire intensity was lower on the controls compared to the harvested sites, as the control sites lacked easily flammable logging residues. Lower fire intensity and higher structural variety on the control sites could enhance lichen survival rates by increasing the number of unburned refugia, which have previously been found to reduce the mortality of bryophytes (Hylander and Johnson, 2010) and lichens (Wolseley and Aguirre-Hudson, 1997) during a fire.

The response to fire also varied among lichen species, which can be seen by the very notable difference in species composition on both trees (III) and stumps (IV) between burned and unburned sites. As in the case of harvest, microlichens seemed to be more sensitive to burning than macrolichens: several microlichen species, such as *Calicium*, *Chaenotheca* and *Mycoblastus* spp. were less frequent on the burned sites (III, IV). A similar effect of morphology was observed by Johansson et al. (2006), who suggested that the vulnerability of epiphytic microlichens is due to their association with shady habitats, such as tree bases, which are greatly affected by fire. However, this does not explain why microlichens were found to suffer more from burning than macrolichens in studies III and IV, since in these cases fire intensity should not have varied notably within the studied substrates (e.g. within old stumps).

Even though the overall impact of fire on lichen richness was negative, certain species seemed to also benefit from the burning on the harvested sites. The species number on new stumps (at both the stand and stump scale) was slightly higher on burned sites due to efficient colonization by common pioneer species, such as *Parmeliopsis ambigua* (Hoffm.) Nyl. and *Trapeliopsis granulosa* (IV). Common lichen species have also shown efficient colonization on charred wood over similar timescales (i.e. 8–13 years) after a fire (Eversman and Horton, 2004; Johansson et al., 2006). However, the common species were the only ones that benefited from the fire. Of the eight Red-Listed species observed on the experimental study sites, only two (*Alectoria sarmentosa* and *Cladonia parasitica*) occurred on the burned sites (III, IV). Moreover, none of the lichen species previously regarded as preferring charred wood were found on the burned sites. However, these species may require a longer time for colonization after fire: for example, *Carbonicola* spp. and *Hertelidea botryosa* have been observed on old, charred stumps in mature forests (Grossmann, 2014; Källén, 2015) instead of fresh charred wood. In accordance with these previous observations, *H. botryosa* was found on unburned sites on old, charred stumps that originated from past fires on the sites (IV). However, *Carbonicola* spp. were not observed on any of the study sites (III, IV).

3.4 Implications for forest management

3.4.1 Retention forestry and prescribed burning

In comparison to clear-cuts, retention forestry appears to promote epiphytic lichen species richness on harvested sites in pine-dominated boreal forests. However, the outcome of retention forestry depends on the post-harvest dynamics of the retained trees, as a continuity of living trees and dead wood needs to be maintained to sustain lichen species richness. The “life-boating” function of retention forestry, which is very relevant for epiphytic lichens, is compromised by high tree mortality (Bladon et al., 2008). Furthermore, high mortality reduces the habitats of species associated with living trees and disrupts dead wood continuity. In addition to the mortality rate, the mode of tree death is important: snags and logs, which represent different habitats for deadwood-dwelling lichens, should be provided on the harvested sites. Given the high rate of tree fall observed in studies I and II, a scarcity of logs is not likely; instead, care should be taken to provide a sufficient number of snags, especially as epiphytic lichens may prefer snags over downed dead wood (e.g. Kuusinen and Siitonen, 1998; Humphrey et al., 2002).

The retention level is important for the continuity of living trees and dead wood, and for the survival of forest-dwelling species on the harvested site. The survival of species has been observed to be positively related with retention tree density (Rosenvald and Lõhmus, 2008), but the studied retention levels in this thesis; 10 and 50 m^3 ha^{-1}, were found to support a similar richness of epiphytic lichens. However, the higher retention level is more favorable from the point of habitat continuity, since it has the potential to maintain adequate levels of living trees and dead wood on the harvested site over a longer period: given the observed mortality patterns in study I, a shortage of these substrates is very likely at a retention level of 10 m^3 ha^{-1} or less. Therefore, even though the lower retention level was sufficient to sustain lichen richness on a 10-year timescale, a higher level is required to support this richness over an extended period. The establishment of a specific threshold for a sufficient retention level is difficult; however, it is clear that the current retention levels in Finland, approximately 4 m^3 ha^{-1} in privately-owned and 6 m^3 ha^{-1} in state-owned forests (Siitonen and Ollikainen, 2006), are far too low to sustain an adequate supply of living and dead trees on a stand scale over a longer time period.

Tree-level factors, such as tree species, diameter and location, were shown to affect post-harvest mortality and tree fall patterns, and could thus be a useful selection tool in determining appropriate trees to retain. The retention of large pines, which showed the lowest mortality rates, particularly on burned sites, seems to be a good strategy if the aim of retention is to maintain a continuity of living trees. Pines also provided a higher proportion of snags than deciduous trees or spruces, which had a higher risk of tree fall. However, the selection of retention trees should be based not only on the predicted tree dynamics, but also on the habitat value of the trees (e.g. Perhans et al., 2014). Ideally, all tree species should be included as retention trees to provide diverse habitats (Rosenvald and Lõhmus, 2008). Large trees, both living and dead, are considered more valuable for biodiversity, since they host specialized species that do not occur on smaller trees. Moreover, epiphytic lichen richness generally increases with host tree age and size (Lie et al., 2009). Still, the retention of only large-diameter trees may not be the best strategy. Rather, retention of a variety of different-sized trees may be a better approach to ensure that tree deaths are spread out over time, providing a continuous supply of fresh dead wood (Runnel et al., 2013) and living trees (Schei et al., 2013).

Even though retained Scots pines and their dead wood legacies have the potential to enhance epiphytic lichen diversity in managed forest landscapes, it is important to note that they were not able to maintain all the forest-dwelling lichen species on the harvested sites. Some of the observed species only occurred on the uncut control sites, and the same has been found to apply to other species groups as well (Fedrowitz et al., 2014). Therefore, in addition to the retention of trees and other structural legacies on clear-cuts, maintenance of larger intact forest areas is also required in order to maintain the diversity of the forest-dwelling species. From the viewpoint of maintaining diverse epiphytic lichen assemblages in boreal managed forests, retention measures can thus be seen as an important complementary tool that also requires additional measures to safeguard species.

Prescribed burning compromises the life-boating function of retention forestry by reducing the species richness of epiphytic lichens, and also drastically increases tree mortality rates. Therefore, burning should preferably be avoided on sites with high lichen richness. However, despite its initial negative effect on epiphytes, burning has otherwise positive effects on forest biodiversity: it is clearly beneficial for other species groups, for example saproxylic beetles and polypore fungi (e.g. Hjältén et al., 2010a; Penttilä et al., 2013), and in regions where wildfires are currently suppressed, prescribed burning is necessary for supporting populations of fire-related species. Furthermore, if applied in combination with a sufficiently high retention level, such as the 50 m^3 ha^{-1} level studied here, prescribed burning can result in low tree mortality and create more diverse dead wood habitats than retention forestry alone without disrupting the dead wood continuity. The application of prescribed burning to part of the harvested sites could thus increase habitat diversity and, consequently, also epiphytic lichen richness at the landscape scale.

3.4.2 Biofuel harvest

The importance of stumps for epiphytic lichens depends on the landscape-level availability of other dead wood habitats (Lamers et al., 2013). If the dead wood volume is as low as currently found in Fennoscandian managed forests, large-scale stump harvest might have a significant negative impact on dead wood-dwelling lichens. For example, in a recent evaluation in southern Sweden by Svensson et al. (2016) stumps were found to be the major substrate for approximately half of the observed dead wood-dependent lichens. In addition to the removal of stumps, biofuel harvest often leads to the destruction of old CWD, such as logs and windthrows as a side-effect (Rabinowitsch-Jokinen and Vanha-Majamaa, 2010); this intensifies the harmful impact on lichen populations, because these woody substrates can be even more valuable lichen habitats than stumps (IV). Thus, to mitigate the potential negative effects on epiphytic lichens, part of the clear-cut stands should be retained outside stump harvest. Preferably, these should also have a high tree retention level, as stumps on such stands were found to host higher lichen species richness. How large the proportion of stands outside the stump harvest should be, and how the stands should be located in order to guarantee habitat continuity for deadwood-dwelling species has yet to be estimated.

In contrast to stumps, the harvest of FWD could likely occur without significant effects on the lichen assemblages assuming that old dead wood is retained during the harvest. However, it is important to note that FWD may still be important for other species groups; for example, several polypore species are confined to small-diameter wood (e.g. Nordén et al., 2004) and would consequently suffer from a large-scale slash harvest.

4 CONCLUSIONS

Based on my results, harvested sites in pine-dominated boreal forests proved to be suitable habitats for a majority of the observed epiphytic lichen species 11–12 years after harvest, provided that suitable substrates, such as retention trees or their dead wood legacies were continuously available on the sites. Still, the succession of epiphytic lichen assemblages on retention trees or stumps over longer timescales after harvest has not been studied so far. Fairly high retention levels may be required in order to maintain a continuity of living trees and dead wood within a harvested stand, especially when retention forestry is applied in combination with prescribed burning.

It is also noteworthy that this thesis did not cover issues on landscape-level management. If retention volumes at the stand-level are very low, habitat continuity could still be maintained at a landscape level. Higher landscape-level retention, together with good connectivity between the retained patches could compensate for low retention levels on the individual stands. However, such landscape-level planning may be only relevant for species with relatively good dispersal capacities, while species with poor dispersing capacities may still require habitat continuity within one stand. As relatively little is still known about the dispersal distances of epiphytic lichens, further studies are needed to determine the relevance of such landscape-level planning for them. For a comprehensive evaluation of the outcome and biodiversity effects of measures such as retention forestry or biofuel harvest, it is necessary to assess the impacts both at the stand- and landscape-scale, including, for example, species' dispersal abilities. This study has provided data on the stand-level impacts and has shown how these could be accounted for in forest management.

In summary, an understanding of the biodiversity impacts of different forest management methods is essential for the evaluation of the ecological sustainability of forest use. The impacts of intensified forest use (in the form of biofuel harvest) as well as two methods that aim at more sustainable forest management were examined in this thesis. All activities were found to have potential impacts on the epiphytic lichen assemblages: harvest of stumps could threaten dead wood-dwelling lichens in particular, while retention forestry has the potential to increase the lichen species richness on harvested sites and possibly compensate for the negative effects of stump removal, by providing snags and logs for dead wood-dependent species. However, the retention tree dynamics and resulting structural patterns can vary depending on the retention level, application of prescribed burning and tree-level characteristics, which is important to consider when planning for retention harvest and estimating its potential benefits. Finally, prescribed burning of harvested sites decreases epiphytic lichen richness at the stand scale, especially when retention levels are low, but may increase it at the landscape scale, provided that the most valuable, lichen-rich stands are left outside the burning area.

REFERENCES

Asikainen, A., Ilvesniemi, H., Hynynen, J. (2013). Bioenergiaa metsistä kestävästi ja kilpailukykyisesti. In: Asikainen, A., Ilvesniemi, H., Muhonen, T. (Eds.), Bioenergiaa metsistä - Tutkimus- ja kehittämisohjelman keskeiset tulokset. Metlan työraportteja 289.

Baker, S.C., Halpern, C.B., Wardlaw, T.J., Crawford, R.L., Bigley, R.E., Edgar, G.J., Evans, S.A., Franklin, J.F., Jordan, G.J., Karpievitch, Y., Spies, T.A., Thomson, R.J. (2015). Short- and long-term benefits for forest biodiversity of retaining unlogged patches in harvested areas. Forest Ecology and Management 353, 187–195.
http://dx.doi.org/10.1016/j.foreco.2015.05.021

Bartels, S.F., Chen, H.Y.H. (2015). Epiphytic macrolichen cover, richness and composition in young successional boreal forest: A comparison of fire and logging disturbance. Forest Ecology and Management 347, 149–155.
http://dx.doi.org/10.1016/j.foreco.2015.03.025

Bladon, K.D., Lieffers, V.J., Silins, U., Landhäusser, S.M., Blenis, P.V. (2008). Elevated mortality of residual trees following structural retention harvesting in boreal mixedwoods. The Forestry Chronicle 84, 70–75.
http://dx.doi.org/10.5558/tfc84070-1

Botting, R.S., DeLong, C. (2009). Macrolichen and bryophyte responses to coarse woody debris characteristics in sub-boreal spruce forest. Forest Ecology and Management 258, Supplement, S85–S94.
http://dx.doi.org/10.1016/j.foreco.2009.08.036

Boudreault, C., Zouaoui, S., Drapeau, P., Bergeron, Y., Stevenson, S. (2013). Canopy openings created by partial cutting increase growth rates and maintain the cover of three *Cladonia* species in the Canadian boreal forest. Forest Ecology and Management 304, 473–481.
http://dx.doi.org/10.1016/j.foreco.2013.05.043

Bradley, D. (2010). Canada report on bioenergy 2010.
http://www.canbio.ca/upload/documents/canada-report-on-bioenergy-2010-sept-15-2010.pdf [Cited 9 Feb 2015].

Bunnell, F.L., Spribille, T., Houde, I., Goward, T., Björk, C. (2008). Lichens on down wood in logged and unlogged forest stands. Canadian Journal of Forest Research 38, 1033–1041.
http://dx.doi.org/10.1139/x07-206

Busby, P.E., Adler, P., Warren, T.L., Swanson, F.J. (2006). Fates of live trees retained in forest cutting units, western Cascade Range, Oregon. Canadian Journal of Forest Research 36, 2550–2560.
http://dx.doi.org/10.1139/x06-140

Caruso, A., Rudolphi, J. (2009). Influence of substrate age and quality on species diversity of lichens and bryophytes on stumps. The Bryologist 112, 520–531. http://dx.doi.org/10.1639/0007-2745-112.3.520

Caruso, A., Thor, G. (2007). Importance of different tree fractions for epiphytic lichen diversity on *Picea abies* and *Populus tremula* in mature managed boreonemoral Swedish forests. Scandinavian Journal of Forest Research 22, 219–230. http://dx.doi.org/10.1080/02827580701346031

Caruso, A., Rudolphi, J., Rydin, H. (2011). Positive edge effects on forest-interior cryptogams in clear-cuts. PLoS ONE 6, e27936. http://dx.doi.org/10.1371/journal.pone.0027936

Caruso, A., Rudolphi, J., Thor, G. (2008). Lichen species diversity and substrate amounts in young planted boreal forests: A comparison between slash and stumps of *Picea abies*. Biological Conservation 141, 47–55. http://dx.doi.org/10.1016/j.biocon.2007.08.021

Caruso, A., Thor, G., Snäll, T. (2010). Colonization-extinction dynamics of epixylic lichens along a decay gradient in a dynamic landscape. Oikos 119, 1947–1953. http://dx.doi.org/10.1111/j.1600-0706.2010.18713.x

Cox, D.R. (1972). Regression models and life-tables (with discussion). Journal of the Royal Statistical Society B 34, 187–220.

Cyr, D., Gauthier, S., Bergeron, Y., Carcaillet, C. (2009). Forest management is driving the eastern North American boreal forest outside its natural range of variability. Frontiers in Ecology and the Environment 7, 519–524. http://dx.doi.org/10.1890/080088

DeBano, L.F., Neary, D.G., Ffolliot, P.F. (1998). Fire's effects on ecosystems. John Wiley & Sons, New York, USA.

Directive 2009/28/EC of the European Parliament and of the Council of 23 April 2009 on the promotion of the use of energy from renewable sources and amending and subsequently repealing Directives 2001/77/EC and 2003/30/EC.

Ellis, C.J. (2012). Lichen epiphyte diversity: A species, community and trait-based review. Perspectives in Plant Ecology, Evolution and Systematics 14, 131–152. http://dx.doi.org/10.1016/j.ppees.2011.10.001

Ellis, C.J., Coppins, B.J. (2006). Contrasting functional traits maintain lichen epiphyte diversity in response to climate and autogenic succession. Journal of Biogeography 33, 1643–1656. http://dx.doi.org/10.1111/j.1365-2699.2006.01522.x

Eräjää, S., Halme, P., Kotiaho, J.S., Markkanen, A., Toivanen, T. (2010). The volume and composition of dead wood on traditional and forest fuel harvested clear-cuts. Silva Fennica 44, 203–211.

Esseen, P.-A., Ehnström, B., Ericson, L., Sjöberg, K. (1997). Boreal forests. Ecological Bulletins 46, 16–47.

Eversman, S., Horton, D. (2004). Recolonization of burned substrates by lichens and mosses in Yellowstone National Park. Northwest Science 78, 85–92.

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). Review: Can retention forestry help conserve biodiversity? A meta-analysis. Journal of Applied Ecology 51, 1669–1679.
http://dx.doi.org/10.1111/1365-2664.12289

Franklin, J.F., Berg, D.R., Thornburgh, D.A., Tappeiner., J.C. (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 D.C., p. 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.
http://dx.doi.org/10.1111/j.1526-4629.2000.tb00155.x

Gauslaa, Y., Lie, M., Solhaug, K., Ohlson, M. (2006). Growth and ecophysiological acclimation of the foliose lichen *Lobaria pulmonaria* in forests with contrasting light climates. Oecologia 147, 406–416.
http://dx.doi.org/10.1007/s00442-005-0283-1

Granström, A. (2001). Fire management for biodiversity in the European boreal forest. Scandinavian Journal of Forest Research 16, 62–69.
http://dx.doi.org/10.1080/028275801300090627

Grossmann, F. (2014). Environmental variables determining the occurrence of the Red-listed *Carbonicola anthracophila* and *C. myrmecina* in boreal forests. MSc thesis. Department of Ecology, Swedish University of Agricultural Sciences, Uppsala.

Gustafsson, L., Fedrowitz, K., Hazell, P. (2013). Survival and vitality of a macrolichen 14 years after transplantation on aspen trees retained at clearcutting. Forest Ecology and Management 291, 436–441.
http://dx.doi.org/10.1016/j.foreco.2012.12.005

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, 295–308.
http://dx.doi.org/10.1080/02827581.2010.497495

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D.B., Lõhmus, A., Pastur, G.M., Messier, C., Neyland, M., Palik, 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. http://dx.doi.org/10.1525/bio.2012.62.7.6

Harmon, M. (1984). Survival of trees after low-intensity surface fires in Great Smoky Mountains national park. Ecology 65, 796–802. http://dx.doi.org/10.2307/1938052

Hautala, H., Laaka-Lindberg, S., Vanha-Majamaa, I. (2011). Effects of retention felling on epixylic species in boreal spruce forests in southern Finland. Restoration Ecology 19, 418–429. http://dx.doi.org/10.1111/j.1526-100X.2009.00545.x

Hedenås, H., Hedström, P. (2007). Conservation of epiphytic lichens: Significance of remnant aspen (*Populus tremula*) trees in clear-cuts. Biological Conservation 135, 388–395. http://dx.doi.org/10.1016/j.biocon.2006.10.011

Heithecker, T.D., Halpern, C.B. (2006). Variation in microclimate associated with dispersed-retention harvests in coniferous forests of western Washington. Forest Ecology and Management 226, 60–71. http://dx.doi.org/10.1016/j.foreco.2006.01.024

Helmisaari, H.-S., Kaarakka, L., Olsson, B.A. (2014). Increased utilization of different tree parts for energy purposes in the Nordic countries. Scandinavian Journal of Forest Research 29, 312–322. http://dx.doi.org/10.1080/02827581.2014.926097

Hely, C., Flannigan, M., Bergeron, Y. (2003). Modeling tree mortality following wildfire in the southeastern Canadian mixed-wood boreal forest. Forest Science 49, 566–576.

Hilmo, O., Såstad, S.M. (2001). Colonization of old-forest lichens in a young and an old boreal *Picea abies* forest: an experimental approach. Biological Conservation 102, 251–259. http://dx.doi.org/10.1016/s0006-3207(01)00100-8

Hjältén, J., Gibb, H., Ball, J.P. (2010a). How will low-intensity burning after clear-felling affect mid-boreal insect assemblages? Basic and Applied Ecology 11, 363–372. http://dx.doi.org/10.1016/j.baae.2009.12.012

Hjältén, J., Stenbacka, F., Andersson, J. (2010b). Saproxylic beetle assemblages on low stumps, high stumps and logs: Implications for environmental effects of stump harvesting. Forest Ecology and Management 260, 1149–1155. http://dx.doi.org/10.1016/j.foreco.2010.07.003

Holt, E.A., McCune, B., Neitlich, P. (2008). Grazing and fire impacts on macrolichen communities of the Seward Peninsula, Alaska, U.S.A. The Bryologist 111, 68–83. http://dx.doi.org/10.1639/0007-2745(2008)111[68:gafiom]2.0.co;2

Humphrey, J.W., Davey, S., Peace, A.J., Ferris, R., Harding, K. (2002). Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and deadwood. Biological Conservation 107, 165–180. http://dx.doi.org/10.1016/S0006-3207(02)00057-5

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. http://dx.doi.org/10.1111/j.1654-1103.2010.01220.x

Hyvärinen, E., Kouki, J., Martikainen, P., Lappalainen, H. (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. http://dx.doi.org/10.1016/j.foreco.2005.03.029

Jairus, K., Lõhmus, A., Lõhmus, P. (2009). Lichen acclimatization on retention trees: a conservation physiology lesson. Journal of Applied Ecology 46, 930–936. http://dx.doi.org/10.1111/j.1365-2664.2009.01672.x

Johansson, P., Reich, P.B. (2005). Population size and fire intensity determine post-fire abundance in grassland lichens. Applied Vegetation Science 8, 193–198. http://dx.doi.org/10.1658/1402-2001(2005)008[0193:psafid]2.0.co;2

Johansson, P., Wetmore, C.M., Carlson, D.J., Reich, P.B., Thor, G. (2006). Habitat preference, growth form, vegetative dispersal and population size of lichens along a wildfire severity gradient. Bryologist 109, 527–540. http://dx.doi.org/10.1639/0007-2745(2006)109[527:hpgfvd]2.0.co;2

Junninen, K., Kouki, J., Renvall, P. (2008). Restoration of natural legacies of fire in European boreal forests: an experimental approach to the effects on wood-decaying fungi. Canadian Journal of Forest Research 38, 202–215. http://dx.doi.org/10.1139/x07-145

Juutilainen, K., Mönkkönen, M., Kotiranta, H., Halme, P. (2014). The effects of forest management on wood-inhabiting fungi occupying dead wood of different diameter fractions. Forest Ecology and Management 313, 283–291. http://dx.doi.org/10.1016/j.foreco.2013.11.019

Jääskeläinen, K., Pykälä, J., Vitikainen, O., Ahti, T. (2015). Suomen jäkälien luettelo. In: Stenroos, S., Velmala, S., Pykälä, J., Ahti, T. (Eds.), Suomen rupijäkälät. Norrlinia 28: 1–454.

Jääskeläinen, K., Pykälä, J., Rämä, H., Vitikainen, O., Haikonen, V., Högnabba, F., Lommi, S., Puolasmaa, A. (2010). Lichens. In: Rassi, P., Hyvärinen, E., Juslén, A., Mannerkoski, I. (Eds.), The 2010 Red List of Finnish Species. Ympäristöministeriö & Suomen ympäristökeskus, Helsinki. p. 278–310.

Kouki, J. (2013). Nuoret luonnonmetsät metsien hoidon ja suojelun mallina - Uusia mahdollisuuksia metsäluonnon suojeluun talousmetsissä. Luonnon Tutkija 117, 4–19.

Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S., Uotila, A. (2001). Forest fragmentation in Fennoscandia: Linking habitat requirements of wood-associated threatened species to landscape and habitat changes. Scandinavian Journal of Forest Research, 27–37.
http://dx.doi.org/10.1080/028275801300090564

Kruys, N., Jonsson, B.G. (1999). Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. Canadian Journal of Forest Research 29, 1295–1299.
http://dx.doi.org/10.1139/x99-106

Kruys, N., Fridman, J., Götmark, F., Simonsson, P., Gustafsson, L. (2013). Retaining trees for conservation at clearcutting has increased structural diversity in young Swedish production forests. Forest Ecology and Management 304, 312–321.
http://dx.doi.org/10.1016/j.foreco.2013.05.018

Kuusinen, M. (1996). Cyanobacterial macrolichens on *Populus tremula* as indicators of forest continuity in Finland. Biological Conservation 75, 43–49.
http://dx.doi.org/10.1016/0006-3207(95)00039-9

Kuusinen, M., Siitonen, J. (1998). Epiphytic lichen diversity in old-growth and managed *Picea abies* stands in southern Finland. Journal of Vegetation Science 9, 283–292.
http://dx.doi.org/10.2307/3237127

Källén, I. (2015). Environmental variables determining the occurrence of *Cladonia parasitica* and *Hertelidea botryosa*, two boreal lichens confined to wood. MSc thesis. Department of Ecology, Swedish University of Agricultural Sciences, Uppsala.

Lamers, P., Thiffault, E., Paré, D., Junginger, M. (2013). Feedstock specific environmental risk levels related to biomass extraction for energy from boreal and temperate forests. Biomass and Bioenergy 55, 212–226.
http://dx.doi.org/10.1016/j.biombioe.2013.02.002

Lavoie, S., Ruel, J.-C., Bergeron, Y., Harvey, B.D. (2012). Windthrow after group and dispersed tree retention in eastern Canada. Forest Ecology and Management 269, 158–167.
http://dx.doi.org/10.1016/j.foreco.2011.12.018

Lie, M., Arup, U., Grytnes, J.-A., Ohlson, M. (2009). The importance of host tree age, size and growth rate as determinants of epiphytic lichen diversity in boreal spruce forests. Biodiversity and Conservation 18, 3579–3596.
http://dx.doi.org/10.1007/s10531-009-9661-z

Lindenmayer, D.B., Franklin, J.F., Lõhmus, A., Baker, S.C., Bauhus, J., Beese, W., Brodie, A., Kiehl, B., Kouki, J., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., Wayne, A., Gustafsson, L. (2012). A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. Conservation Letters 5, 421–431.
http://dx.doi.org/10.1111/j.1755-263X.2012.00257.x

Linder, P., Östlund, L. (1998). Structural changes in three mid-boreal Swedish forest landscapes, 1885–1996. Biological Conservation 85, 9–19.
http://dx.doi.org/10.1016/S0006-3207(97)00168-7

Lõhmus, A., Lõhmus, P. (2010). Epiphyte communities on the trunks of retention trees stabilise in 5 years after timber harvesting, but remain threatened due to tree loss. Biological Conservation 143, 891–898.
http://dx.doi.org/10.1016/j.biocon.2009.12.036

Lõhmus, A., Kraut, A., Rosenvald, R. (2013). Dead wood in clearcuts of semi-natural forests in Estonia: Site-type variation, degradation, and the influences of tree retention and slash harvest. European Journal of Forest Research 132, 335–349.
http://dx.doi.org/10.1007/s10342-012-0678-6

Lõhmus, A., Kohv, K., Palo, A., Viilma, K. (2004). Loss of old-growth, and the minimum need for strictly protected forests in Estonia. Ecological Bulletins 51, 401–411.

Lõhmus, P., Kruustük, K. (2010). Lichens on burnt wood in Estonia: a preliminary assessment. Folia Cryptogamica Estonica 47, 37–41.

Lõhmus, P., Lõhmus, A. (2001). Snags, and their lichen flora in old Estonian peatland forests. Annales Botanici Fennici 38, 265–280.

Lõhmus, P., Rosenvald, R., Lõhmus, A. (2006). Effectiveness of solitary retention trees for conserving epiphytes: differential short-term responses of bryophytes and lichens. Canadian Journal of Forest Research 36, 1319–1330.
http://dx.doi.org/10.1139/x06-032

Lundström, J., Jonsson, F., Perhans, K., Gustafsson, L. (2013). Lichen species richness on retained aspens increases with time since clear-cutting. Forest Ecology and Management 293, 49–56.
http://dx.doi.org/10.1016/j.foreco.2012.12.027

MacDicken, K.G., Sola, P., Hall, J.E., Sabogal, C., Tadoum, M., de Wasseige, C. (2015). Global progress toward sustainable forest management. Forest Ecology and Management 352, 47–56.
http://dx.doi.org/10.1016/j.foreco.2015.02.005

McCune, B., Mefford, M. (1999). PC-ORD. Multivariate analysis of ecological data, version 4. MjM Software Design, Gleneden Beach, Oregon.

Morales-Hidalgo, D., Oswalt, S.N., Somanathan, E. (2015). Status and trends in global primary forest, protected areas, and areas designated for conservation of biodiversity from the Global Forest Resources Assessment 2015. Forest Ecology and Management 352, 68–77.
http://dx.doi.org/10.1016/j.foreco.2015.06.011

Nascimbene, J., Marini, L., Caniglia, G., Cester, D., Nimis, P. (2008a). Lichen diversity on stumps in relation to wood decay in subalpine forests of Northern Italy. Biodiversity and Conservation 17, 2661–2670.
http://dx.doi.org/10.1007/s10531-008-9344-1

Nascimbene, J., Marini, L., Motta, R., Nimis, P.L. (2008b). Lichen diversity of coarse woody habitats in a Pinus-Larix stand in the Italian Alps. Lichenologist 40, 153–163.
http://dx.doi.org/10.1017/S0024282908007585

Nordén, B., Ryberg, M., Götmark, F., Olausson, B. (2004). Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. Biological Conservation 117, 1–10.
http://dx.doi.org/10.1016/s0006-3207(03)00235-0

Olsson, J., Jonsson, B.G. (2010). Restoration fire and wood-inhabiting fungi in a Swedish Pinus sylvestris forest. Forest Ecology and Management 259, 1971–1980.
http://dx.doi.org/10.1016/j.foreco.2010.02.008

Peltola, H., Kellomäki, S., Hassinen, A., Granander, M. (2000). Mechanical stability of Scots pine, Norway spruce and birch: an analysis of tree-pulling experiments in Finland. Forest Ecology and Management 135, 143–153.
http://dx.doi.org/10.1016/S0378-1127(00)00306-6

Penttilä, R., Junninen, K., Punttila, P., Siitonen, J. (2013). Effects of forest restoration by fire on polypores depend strongly on time since disturbance – A case study from Finland based on a 23-year monitoring period. Forest Ecology and Management 310, 508–516.
http://dx.doi.org/10.1016/j.foreco.2013.08.061

Perhans, K., Haight, R.G., Gustafsson, L. (2014). The value of information in conservation planning: Selecting retention trees for lichen conservation. Forest Ecology and Management 318, 175–182.
http://dx.doi.org/10.1016/j.foreco.2014.01.020

Rabinowitsch-Jokinen, R., Vanha-Majamaa, I. (2010). Immediate effects of logging, mounding and removal of logging residues and stumps on coarse woody debris in managed boreal Norway spruce stands. Silva Fennica 44, 51–62.
http://dx.doi.org/10.1080/10549811.2011.582825

Rassi, P., Hyvärinen, E., Juslén, A., Mannerkoski, I. (2010). The 2010 Red List of Finnish Species. Ympäristöministeriö & Suomen ympäristökeskus, Helsinki.

Rosenvald, R., Lõhmus, 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.
http://dx.doi.org/10.1016/j.foreco.2007.09.016

Rosenvald, R., Lõhmus, A., Kiviste, A. (2008). Preadaptation and spatial effects on retention-tree survival in cut areas in Estonia. Canadian Journal of Forest Research 38, 2616–2625.
http://dx.doi.org/10.1139/x08-093

Runnel, K., Rosenvald, R., Lõhmus, A. (2013). The dying legacy of green-tree retention: Different habitat values for polypores and wood-inhabiting lichens. Biological Conservation 159, 187–196.
http://dx.doi.org/10.1016/j.biocon.2012.11.029

Schei, F.H., Blom, H.H., Gjerde, I., Grytnes, J.-A., Heegaard, E., Sætersdal, M. (2013). Conservation of epiphytes: Single large or several small host trees? Biological Conservation 168, 144–151.
http://dx.doi.org/10.1016/j.biocon.2013.10.001

Schmitt, C.B., Burgess, N.D., Coad, L., Belokurov, A., Besançon, C., Boisrobert, L., Campbell, A., Fish, L., Gliddon, D., Humphries, K., Kapos, V., Loucks, C., Lysenko, I., Miles, L., Mills, C., Minnemeyer, S., Pistorius, T., Ravilious, C., Steininger, M., Winkel, G. (2009). Global analysis of the protection status of the world's forests. Biological Conservation 142, 2122–2130.
http://dx.doi.org/10.1016/j.biocon.2009.04.012

Scott, R.E., Mitchell, S.J. (2005). Empirical modelling of windthrow risk in partially harvested stands using tree, neighbourhood, and stand attributes. Forest Ecology and Management 218, 193–209.
http://dx.doi.org/10.1016/j.foreco.2005.07.012

Sidoroff, K. (2001). Metsäpalon vaikutus puuston kuolleisuuteen ja lahopuun määrään: kokeellinen tutkimus Lieksassa. MSc thesis. Faculty of Forestry, University of Joensuu.

Sidoroff, K., Kuuluvainen, T., Tanskanen, H., Vanha-Majamaa, I. (2007). Tree mortality after low-intensity prescribed fires in managed Pinus sylvestris stands in southern Finland. Scandinavian Journal of Forest Research 22, 2–12.
http://dx.doi.org/10.1080/02827580500365935

Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49, 11–41.

Siitonen, J., Ollikainen, M. (2006). Talousmetsät. In: Horne, P., Koskela, T., Kuusinen, M., Otsamo, A., Syrjänen, K. (Eds.), Metson jäljillä. Etelä-Suomen metsien monimuotoisuusohjelman tutkimusraportti. Maa- ja metsätalousministeriö, ympäristöministeriö, Metsäntutkimuslaitos ja Suomen ympäristökeskus, Finland, p. 53–85.

Sillett, S.C., Goslin, M.N. (1999). Distribution of epiphytic macrolichens in relation to remnant trees in a multiple-age Douglas-fir forest. Canadian Journal of Forest Research 29, 1204–1215.
http://dx.doi.org/10.1139/x99-081

Sillett, S.C., McCune, B., Peck, J.E., Rambo, T.R. (2000a). Four years of epiphyte colonization in Douglas-fir forest canopies. Bryologist 103, 661–669.
http://dx.doi.org/10.1639/0007-2745(2000)103[0661:fyoeci]2.0.co;2

Sillett, S.C., McCune, B., Peck, J.E., Rambo, T.R., Ruchty, A. (2000b). Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. Ecological Applications 10, 789–799.
http://dx.doi.org/10.1890/1051-0761(2000)010[0789:dloelr]2.0.co;2

Similä, M., Junninen, K. (Eds.) (2012). Ecological restoration and management in boreal forests - best practices from Finland. Metsähallitus, Vantaa.

Solarik, K.A., Volney, W.J.A., Lieffers, V.J., Spence, J.R., Hamann, A. (2012). Factors affecting white spruce and aspen survival after partial harvest. Journal of Applied Ecology 49, 145–154.
http://dx.doi.org/10.1111/j.1365-2664.2011.02089.x

Spribille, T., Thor, G., Bunnell, F.L., Goward, T., Björk, C.R. (2008). Lichens on dead wood: species-substrate relationships in the epiphytic lichen floras of the Pacific Northwest and Fennoscandia. Ecography 31, 741–750.
http://dx.doi.org/10.1111/j.1600-0587.2008.05503.x

Suominen, M., Junninen, K., Heikkala, O., Kouki, J. (2015). Combined effects of retention forestry and prescribed burning on polypore fungi. Journal of Applied Ecology 52, 1001–1008.
http://dx.doi.org/10.1111/1365-2664.12447

Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B., Swanson, F.J. (2010). The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9, 117–125.
http://dx.doi.org/10.1890/090157

Svensson, M., Dahlberg, A., Ranius, T., Thor, G. (2013). Occurrence patterns of lichens on stumps in young managed forests. PLoS ONE 8.
http://dx.doi.org/10.1371/journal.pone.0062825

Svensson, M., Dahlberg, A., Ranius, T., Thor, G. (2014). Dead branches on living trees constitute a large part of the dead wood in managed boreal forests, but are not important for wood-dependent lichens. Journal of Vegetation Science 25, 819–828.
http://dx.doi.org/10.1111/jvs.12131

Svensson, M., Johansson, V., Dahlberg, A., Frisch, A., Thor, G., Ranius, T. (2016). The relative importance of stand and dead wood types for wood-dependent lichens in managed boreal forests. Fungal Ecology 20: 166–174.
http://dx.doi.org/10.1016/j.funeco.2015.12.010

Therneau, T. (2015). A Package for Survival Analysis in S. Version 2.38. http://CRAN.R-project.org/package=survival. [Cited 15 Feb 2016].

Thor, G. (1998). Red-listed lichens in Sweden: habitats, threats, protection, and indicator value in boreal coniferous forests. Biodiversity and Conservation 7, 59–72.
http://dx.doi.org/10.1023/a:1008807729048

Urgenson, L.S., Halpern, C.B., Anderson, P.D. (2013). Level and pattern of overstory retention influence rates and forms of tree mortality in mature, coniferous forests of the Pacific Northwest, USA. Forest Ecology and Management 308, 116–127.
http://dx.doi.org/10.1016/j.foreco.2013.07.021

Wallenius, T. (2011). Major decline in fires in coniferous forests – reconstructing the phenomenon and seeking for the cause. Silva Fennica 45, 139–155.

Walmsley, J.D., Godbold, D.L. (2010). Stump harvesting for bioenergy – A review of the environmental impacts. Forestry 83, 17–38.
http://dx.doi.org/10.1093/forestry/cpp028

Vanha-Majamaa, I., Lilja, S., Ryömä, R., Kotiaho, J.S., Laaka-Lindberg, S., Lindberg, H., Puttonen, P., Tamminen, P., Toivanen, T., Kuuluvainen, T. (2007). Rehabilitating boreal forest structure and species composition in Finland through logging, dead wood creation and fire: The EVO experiment. Forest Ecology and Management 250, 77–88.
http://dx.doi.org/10.1016/j.foreco.2007.03.012

Wolseley, P.A., Aguirre-Hudson, B. (1997). Fire in tropical dry forests: Corticolous lichens as indicators of recent ecological changes in Thailand. Journal of Biogeography 24, 345–362.
http://dx.doi.org/10.1046/j.1365-2699.1997.00125.x

Zackrisson, O. (1977). Influence of forest fires on North Swedish boreal forest. Oikos 29, 22–32.
http://dx.doi.org/10.2307/3543289