

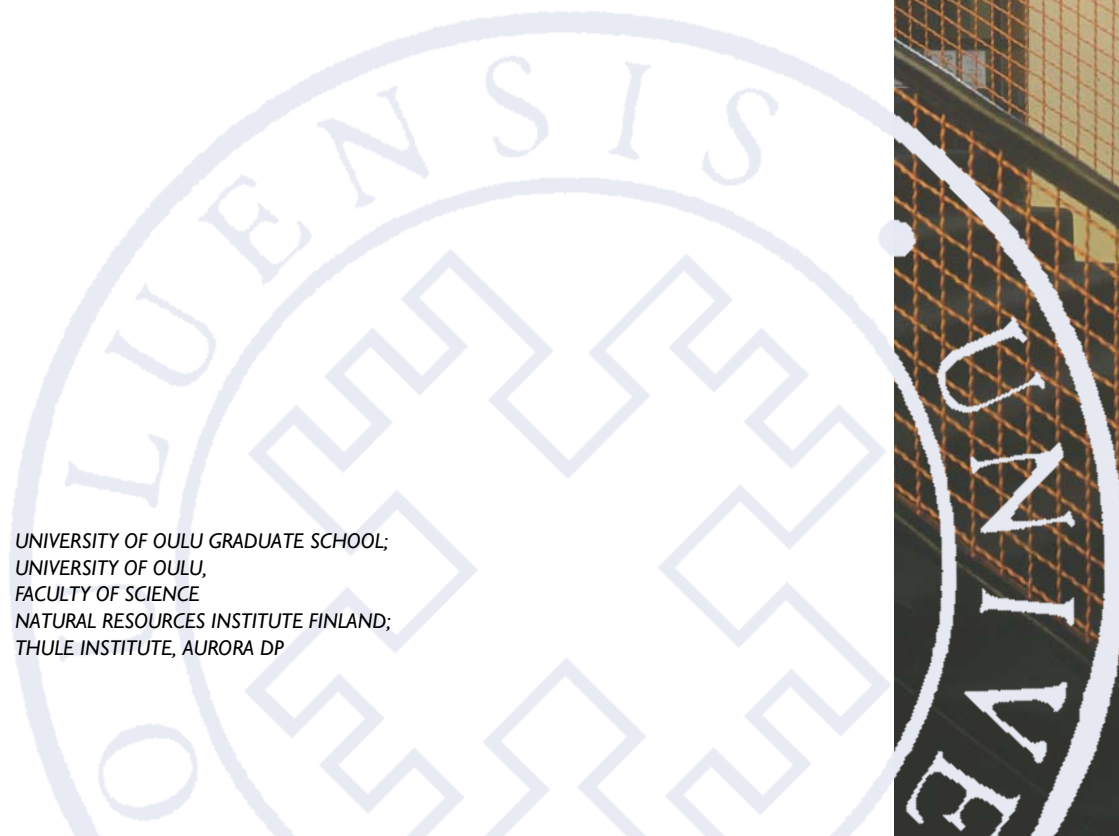
Anne-Maarit Hekkala

RESTORATION OF THE NATURALNESS OF BOREAL FORESTS

UNIVERSITY OF OULU GRADUATE SCHOOL;
UNIVERSITY OF OULU,
FACULTY OF SCIENCE
NATURAL RESOURCES INSTITUTE FINLAND;
THULE INSTITUTE, AURORA DP

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ANNE-MAARIT HEKKALA

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THE NATURALNESS OF BOREAL
FORESTS**

Academic dissertation to be presented with the assent of the Doctoral Training Committee of Technology and Natural Sciences of the University of Oulu for public defence in Keckmaninsali (HU106), Linnanmaa, on 9 October 2015, at 12 noon

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Abstract

Restoration is considered to be a crucial action in order to maintain and enhance ecosystem functioning and halt the decline of biodiversity. Within forested ecosystems, heavily exploited forests have lost a great part of their biodiversity values, and even nature conservation is insufficient to prevent the loss of habitats and the endangerment of species. The aim of this thesis was to provide new information on the impacts of forest restoration methods on boreal forest naturalness, including forest structure, forest-dwelling species and ecosystem processes and functions. This information is needed to develop the restoration methods and their cost-efficiency and to support decision-making concerning restoration and nature conservation. The restoration methods studied were felling with a chainsaw either without or with subsequent burning, and storm treatment, in which the trees were uprooted with an excavator. The variables measured were vegetation assemblages, deadwood dynamics, and deadwood-dependent insect assemblages. In addition to field measurements, a simulation approach was used so as to predict deadwood continuity after different restoration methods. The main finding of this thesis is that the aspects of naturalness studied were most enhanced by burning, whereas felling had the least effect. Restoration burning increased deadwood volume and diversity, enabled the establishment of pioneer plants, increased the relative cover of the forest keystone species *Vaccinium myrtillus*, enhanced the regeneration of the keystone tree *Populus tremula*, and provided habitat for red-listed, especially pyrophilous beetles (Coleoptera) and flat bugs (Heteroptera: Aradidae). Felling only increased the volume of deadwood. Storm treatment with tree uprooting was a more effective method than felling with a chainsaw, due to the additional disturbance it caused to ground, enhancing the regeneration of e.g. *Pinus sylvestris*. According to simulation models, compared to controls restored stands are predicted to have greater deadwood volumes at least for 40 years. The study shows that restoration can be used to accelerate the development of degraded forests towards a higher level of naturalness. The results can be used to choose appropriate restoration methods for forests, based on their initial stage and the goal set for the level of their naturalness.

Keywords: *Aradus*, Coleoptera, Controlled burning, Deadwood, Disturbance dynamics, Storm, Vegetation assemblages

Hekkala, Anne-Maarit, Boreaalisten metsien luonnontilan ennallistaminen

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Tiivistelmä

Ennallistamista pidetään tärkeänä keinona palauttaa ja ylläpitää luonnontilaisten ekosysteemien toimintaa. Metsien ennallistamista tarvitaan, koska tehokkaasti hoidettujen metsien monimuotoisuus on köyhtynyt niin pitkälle, ettei pelkkä suojele enää riitä pysäyttämään elinympäristöjen häviämistä ja lajien uhanalaistumista. Väitöskirjan tavoitteena oli tuottaa uutta tietoa siitä, miten erilaiset metsien ennallistamiskeinot vaikuttavat metsän luonnontilaisuuden elementteihin, kuten rakennepiirteisiin, lajistoon ja toiminnallisuuteen. Tietoa tarvitaan ennallistamismenetelmien ja niiden kustannustehokkuuden parantamiseksi sekä tukemaan ennallistamista ja luonnonsuojelua koskevaa päätöksentekoa. Tutkitut ennallistamismenetelmät olivat: lahoppuun lisäys sahaamalla joko ilman polttoa tai polton kanssa ja myrskytuhokäsittely, jossa puut kaadettiin juurineen. Metsän aluskasvillisuus, lahoppuusto ja lahoppuusta riippuvaisten hyönteisten lajiryhteisöt olivat mitattuja muuttujia. Maastoinventointien ohella tehtiin simulaatiomallinnuksia, joilla ennustettiin ennallistamisen jälkeistä lahoppuujatkumoa. Väitöskirjatyön keskeisin havainto on, että ennallistamispolto paransivat tutkittuja luonnontilaisuuden elementtejä eniten, kun taas lahoppuun lisäyksellä oli vähäisimmät vaikutukset. Ennallistamispolto lisäsi lahoppuun tilavuutta ja monimuotoisuutta, mahdollisti sukcession varhaisvaiheen kasvillisuuden kehittymisen, lisäsi mustikan (*Vaccinium myrtillus*) suhteellista peittävyttä, paransi monimuotoisuudelle tärkeän puulajin, haavan (*Populus tremula*), uudistumista sekä lisäsi lahoppuuriippuvaisten, erityisesti palanutta puuta suosivien kovakuoriaisten (Coleoptera) ja latikoiden (Heteroptera:Aradidae), laji- ja yksilömääriä. Myrskytuhon jäljittely oli tehokkaampi ennallistamiskeino kuin lahoppuun lisäys sahaamalla, sillä juurilaikku lisäsi maanpinnan häiriötä parantaen samalla mm. männyn (*Pinus sylvestris*) taimettumista. Simulaatiomallinnus osoitti, että verrattuna kontrollialueisiin ennallistetuilla alueilla lahoppuuta on runsaammin vähintään 40 vuoden ajan. Väitöskirja osoittaa, että kaikkia työssä tutkittuja ennallistamismenetelmiä voidaan käyttää nopeuttamaan metsän kehittymistä kohti luonnontilaa, mutta menetelmät eroavat toisistaan vaikutuksiltaan. Saatuja tuloksia voidaan käyttää, kun valitaan metsiin niihin parhaiten soveltuvaa ennallistamismenetelmää.

Asiasanat: Ennallistamispolto, Häiriödynamiikka, Kovakuoriaiset, Lahoppuut, Latikat, Metsäkasvillisuus, Myrskytuhot

To natural forests and their fascinating creatures

Preface

Conducting such a large-scale experimental project has demanded years of work on the part of many people. I have been privileged to work in such a coherent and interesting restoration experiment, from the very beginning in 2005. Later, personal funding allowed me to continue with this experiment, to struggle with huge amounts of interesting data, from which it was very difficult to decide what to use for this thesis. I have had a great opportunity to broaden my knowledge from saproxylic beetles to vegetation, trees, simulation models and flat bugs. I will never forget these restored forests in Oulanka, Pahamaailma, Elimyssalo and Lentua, and I will visit them regularly to see how they are developing.

Without guidance and support, this study could have not been made. First of all, I want to thank my closest supervisor, colleague and friend, Professor Anne Tolvanen, who with great enthusiasm and efficiency has been my role model of a researcher. Anne's comments always came during the same day or next day at latest, and she really taught me how to do science and how to see the forest for the trees. Anne, it has been a pleasure to work with you! My other supervisor, Jari Oksanen, has saved me many days of searching the internet for why my R-code doesn't work, and whether the tests are appropriate or not, and do I really understand my tests and models? Thank you, Jari, for all your help! Secondly, I thank the pre-examiners of the thesis, Professor Mikko Mönkkönen and Dr Asko Löhmus, for their constructive comments on the thesis.

In most cases, in order to be completed scientific research demands more than just one person. I have had a great group to work with. My deepest gratitude is expressed to Oili Tarvainen. Oili was always there when I needed someone to discuss with. Marja-Leena Päätaalo helped me with the huge tree datasets, explained things over and over, and made calculations for the data in many ways I needed. Anssi Ahtikoski shared my enthusiasm for simulation models and was such an efficient person the work with. Jouni Siipilehto was extraordinarily fast in helping me with some details of the data. Ruaridh Hägglund and Joakim Hjältén from SLU Umeå, working with you has been great! Thank you for sharing your project with me. Jouni Karhu and Irene Murtovaara, your help during the analysing and publishing part of my project was valuable. Many things would have taken me a lot longer than without your excellence in Excel and graphics. I am also grateful to the personnel of the former Metla Muhos. Especially, I thank Kari Kukko-oja, for hiring me in the first place and giving me the first glimpse of the exciting world of forest biodiversity, and for making me understand why

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Oulu, September 2015

Anne-Maarit Hekkala

List of original publications

This thesis is based on the following publications or manuscripts, which are referred to throughout the text by their Roman numerals:

- I Hekkala A-M, Tarvainen O & Tolvanen A (2014) Dynamics of understory vegetation after restoration of natural characteristics in the boreal forests in Finland. *Forest Ecol Manag* 330: 55–66.
- II Hekkala A-M, Ahtikoski A, Pääatalo M-L, Siipilehto J & Tolvanen A Volume and diversity of deadwood after restoration of boreal forests – short-term results and long-term predictions. Manuscript.
- III Hekkala A-M, Pääatalo M-L, Tarvainen O & Tolvanen A (2014) Restoration of young forests in eastern Finland: Benefits for saproxylic beetles (Coleoptera). *Restor Ecol* 22: 151–159.
- IV Häggglund R, Hekkala A-M, Hjältén J & Tolvanen A Positive effects of forest restoration on a rare and threatened insect genus – Flat bugs (Aradidae). Manuscript.

Contributions

The following table shows the major contributions of authors to the original articles or manuscripts.

	I	II	III	IV
Idea for the paper	A-MH , AT	A-MH , AT	A-MH , AT	RH, A-MH , JH, AT
Sampling design	AT	AT, M-LP	A-MH , AT	JH, A-MH , AT
Responsible of data collecting	AT	AT, M-LP	AT, A-MH , M-LP	JH, A-MH
Data analyses and interpretation	A-MH	A-MH , AA*, JS*	A-MH	RH, A-MH
Responsible for writing	A-MH	A-MH	A-MH	RH

*AA conducted the MOTTI-simulations, JS conducted the height models.

AA: Anssi Ahtikoski, AT: Anne Tolvanen, JH: Joakim Hjältén, JS: Jouni Siipilehto, M-LP: Marja-Leena Pääatalo, OT: Oili Tarvainen, RH: Ruairidh Häggglund

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1 Introduction

1.1 The changes in the boreal forest disturbance regime in Fennoscandia

Disturbances and subsequent successional processes are the fundamental driving forces of forest dynamics (Pickett & White 1985, Attiwill 1994, Peterken 1996, Angelstam & Kuuluvainen 2004). In the past, the structure of boreal forests was shaped by unpredictable natural disturbances varying in extent, frequency and severity, from large stand-replacing fires to single windblown trees that created a complex forest landscape through a continuity of different successional stages (Angelstam & Kuuluvainen 2004). In the boreal region, fire has for thousands of years been the most powerful large-scale disturbance, but in Fennoscandia, changes in climate, land use, decline in human ignitions and efficient fire suppression have caused a nearly total termination of wildfires (Zackrisson 1977, Niklasson & Granström 2000, Wallenius 2011).

Today, fire plays only a minor role in Fennoscandian boreal forest dynamics. Since the late 19th century, the average annually burned land area has in Sweden been reduced to less than 0.01% of the forested land cover (Granström 2001). In Norway, the shift in fire frequency to “unnaturally low” occurred in the late 17th century (Blanck 2015). In Finland, during the period 1980–2010 the average annually burned land area has been only approximately 500 ha (Finnish Forest Research Institute 2013), including restorative burnings and prescribed burnings, while during the peak fire years in the 19th century, the annually burned land area was as high as 70,000 ha (Vanha-Majamaa & Reinikainen 2000).

Besides changes in fire disturbance, past forest utilization, including agriculture (grazing, the establishment of pastures, slash-and-burn cultivation), selective cuttings, firewood collection and tar burning had already altered the forest structure, leading to a loss of structural heterogeneity within forest stands and in a great decrease in the volume of dead wood (Esseen *et al.* 1997, Östlund *et al.* 1997, Linder & Östlund 1998, Siitonen 2001). Modern forest industry started in Fennoscandia at the beginning of 20th century, with a general idea of cleaning up the wild forests with dead and diseased trees and making them healthy, efficient and high-yielding domesticated forests (see Östlund *et al.* 1997 and references therein). Since World War II, the forest industry has played the most important role in boreal forest dynamics, and unpredictable disturbances

have been replaced with well-organized even-age management with clearcutting, planting, regular thinnings and short rotation times (Esseen *et al.* 1997, Linder & Östlund 1998). According to the Finnish National Forest Inventories conducted from 1952, forest productivity has increased as the growing stock density and volume has increased due to efficient forestry, and because mires and bogs have been drained for forestry (Reinikainen *et al.* 2000, Tonteri *et al.* 2013, Finnish Forest Research Institute 2013). At the same time, forests have become younger (Finnish Forest Research Institute 2013) and the proportion of one-storeyed forest stands has greatly increased, while multi-storeyed stands are scarce (Östlund *et al.* 1997). In Finland, it has been estimated that the average volume of deadwood in the forest landscape has decreased by approximately 90–98% due to commercial forest management (Siitonen 2001). Today, natural forests without traces of human influence are virtually non-existent in Finland, as even the most remote forest stands have probably been utilized by man at some point in their existence. Also, most forest reserves, especially those in southern Finland, have been under commercial management, resulting in a current lack of structural characteristics of natural forests (Uotila *et al.* 2002, Lilja & Kuuluvainen 2005). Such negative changes have also occurred in large parts of Canadian boreal forests, where commercial forest management has driven the forests outside their natural variability (Bergeron *et al.* 2002, Cyr *et al.* 2009), has altered forest structure and changed the relative abundances of tree species as compared with natural fire-disturbance (Boucher *et al.* 2009, Bouchard & Pothier 2011).

1.2 Restoration of boreal forests

Recognizing and setting aside the last remnants of natural forests is of the utmost importance in species conservation, but these remnants cover only small fractions of the forest landscape in Fennoscandia and cannot support the threatened species (Hanski 2000, Rassi *et al.* 2001, 2010). Moreover, protected areas may not ensure habitat persistence and species survival, when major disturbance factors such as fire have been eradicated. The concept of mimicking natural disturbances so as to alleviate the negative effects of forestry was introduced in the 1990s (Attiwill 1994, Angelstam 1998). It was soon understood that active measures are needed to alleviate the changes that commercial forest management and fire suppression have caused to biodiversity and the structure of boreal forest (e.g. Angelstam 1998, Kouki *et al.* 2001, Kuuluvainen 2002, Cyr *et al.* 2009).

Restoration is broadly defined as “a process of contributing to the recovery of an ecosystem that has been degraded, damaged or destroyed” (Society for Ecological Restoration 2004). Worldwide, the term “forest restoration” includes rehabilitation or reclamation of e.g. old mining areas or afforestation of old fields or other open areas (Fischer & Fischer 2006, Burton & Macdonald 2011, Stanturf *et al.* 2014). Here, the term “forest restoration” is defined as an action to restore the natural characteristics of forests by increasing the quantity and diversity of deadwood and by diversifying the tree stand structure, including tree species composition, tree age and size structure and the spatial distribution of trees (Similä & Junninen 2012, Halme *et al.* 2013). The goal in boreal forest restoration is, hence, to speed up the re-development of the characteristic processes and structural features of natural forests. For that, the restoration actions aim to mimic natural disturbances, such as wildfire, tree stem breakage during windstorms or heavy loads of snow, and storm damage, in which the trees are uprooted (Similä & Junninen 2012, Halme *et al.* 2013). The intensity or severity of restoration fire is often controlled by fuel load, i.e. the number of trees felled on the ground prior to burning. In the conservation areas of Finland, restoration does not include the removal of timber from restored stands, in contrast to more broadly defined restoration actions carried out in forests under commercial management, aiming also for silvicultural profit (e.g. Vanha-Majamaa *et al.* 2007).

Restoration actions to enhance structural diversity of boreal forests have been actively carried out in Finland and increasingly in other European countries (Similä & Junninen 2012, Halme *et al.* 2013). In the state-owned forests in Finland over 16,000 ha of forests have been treated with restorative actions between 2003 and 2011, and another 13,000 ha are planned to be treated by 2016 by the Natural Heritage Services of Metsähallitus (Similä & Junninen 2012). During a decade of active forest restoration in Finland, several methods have been used to create as ‘natural’ a deadwood as possible, including trials with the use of explosives, girdling in different ways in order to slow the death of the tree, inoculation of fungi, tree felling with chainsaw and excavator, and burning, mainly to restore the degraded parts of protection areas (Similä & Junninen 2012, Halme *et al.* 2013, Finnish Forest Research Institute 2013).

The ultimate goal of these actions is to restore the typical natural biota of the respective habitat type that is self-sustainable without further human interventions (Halme *et al.* 2013). The increased complexity of forest structure leads to an increased number of microhabitats which may benefit many red-listed forest-dwelling species. Furthermore, restoration can be seen as an important tool for

increasing the connectivity or quality of conservation areas (Hanski 2000, Kuuluvainen *et al.* 2002). Especially the formerly silviculturally managed protection areas that lack the structure and functions of natural forests can be helped towards a natural successional trajectory with restorative treatments that emulate natural disturbances and initiate succession (Kuuluvainen *et al.* 2002).

The need to restore ecosystems has been recognized worldwide. In the strategic plan of the Convention on Biological Diversity (CBD 2010), it was stated that continuing actions are needed in order to safeguard and restore biodiversity and ecosystems. In addition, the EU Biodiversity Strategy to 2020 (European Union 2011) demands maintenance and restoration of ecosystems, stating that “by 2020, ecosystems and their services are maintained and enhanced by establishing green infrastructure and restoring at least 15% of degraded ecosystems”.

The controversy in boreal forest restoration is that the stand structure of managed forests will eventually develop into natural forests, if enough time is given. However, considering the extinction debt (Tilman *et al.* 1994) in Fennoscandian boreal forests (Hanski 2000), the waiting time might be too long for the most threatened species to recover. In order to be effective, restoration should speed up the development towards natural forests so that the negative development in the number of rare and threatened species is impeded or even returned to positive.

1.3 The concept of naturalness

In general, forest naturalness and its potential degradation can be presented and measured using three co-dominant aspects: forest structure, species assemblages, and ecosystem processes and functions (Fig. 1) (Kuuluvainen 2002, Brūmelis *et al.* 2011). All aspects of naturalness are intermingled, as processes determine structures and vice versa, and structure consists of species, all forming a dynamic, functional ecosystem (Burton & Macdonald 2011). The aspects also vary in space and time; hence quantitative definitions for natural forests cannot explicitly be given, as old-growth stands and young naturally regenerated stands are equally important stages of the succession, supporting species of different habitat preferences (Peterken 1996, Rouvinen & Kouki 2008, Brūmelis *et al.* 2011, Halme *et al.* 2013).

Restoration aims to increase naturalness but, as was shown above, such quantitative measures of naturalness cannot precisely be defined. Hence, the

target of restoration is not, or at least should not be, a certain level of naturalness, but fluctuation in space and time, “a moving target” (Fig. 2, see also Burton & Macdonald 2011). The effectiveness of restoration treatment is measured by the rate at which it increases the naturalness of the forest, in terms of structures, species, and ecosystem processes and functions (Figs. 1 & 2). Similarly, restoration should not aim to improve only one of these aspects, but consider the whole picture, i.e. the multiple aspects of the forest ecosystem (Burton & Macdonald 2011, Thorpe & Stanley 2011, Halme *et al.* 2013, Stanturf *et al.* 2014). In this thesis, I concentrate on some of the components of naturalness and measure the success of restoration in terms of changes caused to the structural components (deadwood), species assemblages, and ecosystem processes, according to Figure 1.

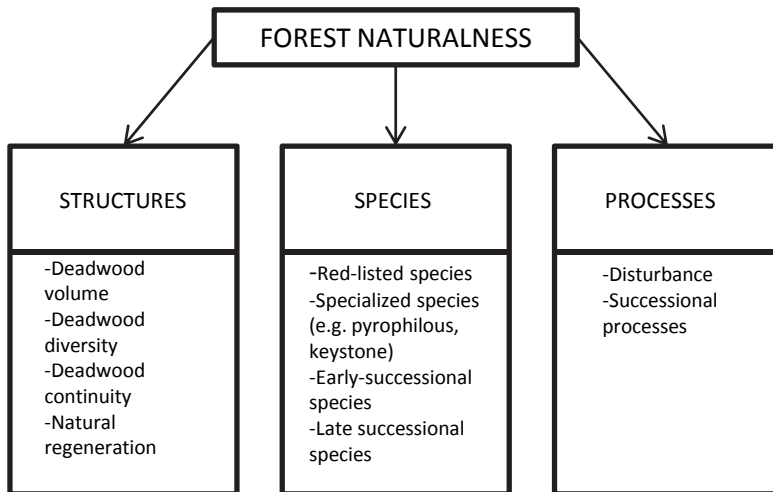


Fig. 1. The three aspects of forest naturalness and the variables used in this thesis to measure the effectiveness of restoration.

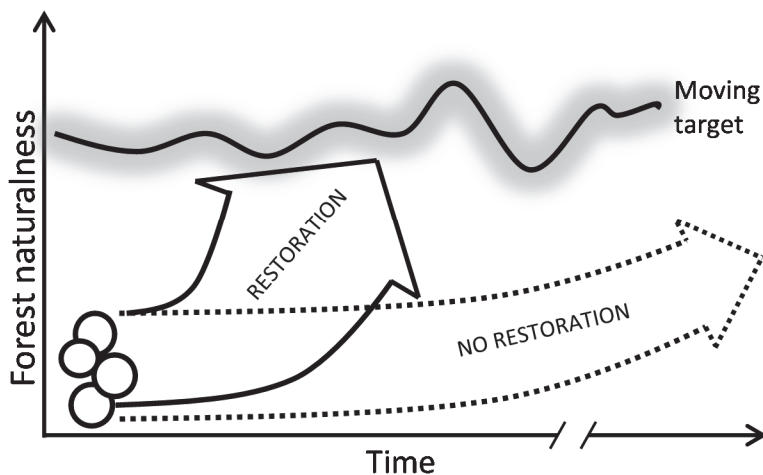


Fig. 2. An illustration of the conceptual framework of this study. The target of restoration is changing in space and time (moving target), towards which the structurally degraded forests (open circles) are assisted by restoration actions. Even without restoration, the naturalness is assumed to increase. The rate of recovery depends on the degree of degradation.

1.3.1 Structures

Together with the structural characteristics of living trees (i.e. diverse tree species composition, age/size structure, spatial distribution), deadwood characteristics (volume, diversity and continuity) comprise an essential part of forest naturalness (Franklin *et al.* 1987, Siitonen 2001, Stokland *et al.* 2012). The volume and diversity of deadwood in terms of tree species, size, position (snag, log) and mortality factor determine the richness of many deadwood-dependent species (Martikainen *et al.* 2000, Similä *et al.* 2003, Lonsdale *et al.* 2008). Deadwood contributes to e.g. nutrient cycling and soil formation (Harmon *et al.* 1986, Franklin *et al.* 1987, Janisch & Harmon 2002), and facilitates tree regeneration (Kuuluvainen & Kalmari 2003, Marzano *et al.* 2013). The continuity in deadwood supply is determined by tree mortality and decomposition process. Because deadwood produces a dynamic, ephemeral habitat, temporal and spatial continuity are crucial in preserving deadwood-dependent species (Siitonen & Saaristo 2000, Ranius *et al.* 2014).

Tree regeneration is vital for ecosystem functioning, and can hence be considered both as a structural (through the understorey component it forms) and a functional (through e.g. carbon sequestration and litter production) aspect of forest naturalness. Recurrent fires favour shade-intolerant species such as Scots pine (*Pinus sylvestris*) and deciduous trees (*Betula* spp., *Populus tremula*) while reducing fire frequency promotes the undergrowth of the shade-tolerant Norway spruce (*Picea abies*) (Östlund *et al.* 1997, Lilja & Kuuluvainen 2005, Uotila *et al.* 2002, Rouvinen *et al.* 2002). Following efficient fire suppression, dense spruce undergrowth has been observed in the formerly pine-dominated Finnish Karelian landscapes (Lilja & Kuuluvainen 2005, Wallenius 2007). Also, sexual reproduction of a keystone tree species, European aspen (*P. tremula*), is threatened even in nature conservation areas (Kouki *et al.* 2004). Aspen hosts a great diversity of species (Hammond 1997), with numerous red-listed species (Martikainen 2001, Sverdrup-Thygeson & Ims 2002, Tikkanen *et al.* 2006). Aspen recruitment is partially dependent on forest fires, because the seedlings cannot establish themselves easily in unburned soil (*P. tremuloides*, Turner *et al.* 2003, *P. tremula*, Latva-Karjanmaa *et al.* 2006). Thus, I am considering tree regeneration as an important variable of forest naturalness to be measured in this thesis.

1.3.2 Species

The degradation of structural naturalness and loss of habitat has caused hundreds of species, mainly deadwood-dependent insects and fungi, to become threatened in Fennoscandia (Siitonen 2001, Gärdenfors 2010, Rassi *et al.* 2001, 2010). The most significant threats to the species are the decrease in coarse woody debris (=deadwood larger than 10 cm in diameter; CWD), the decreasing number of large senescent trees and changes in tree species composition, especially the decline of large deciduous trees in the landscape (Jonsell *et al.* 1998, Rassi *et al.* 2010, Tikkanen *et al.* 2006). Reduced occurrence and intensity of natural processes such as wildfires poses a threat to many species; the decline in burned forests and other natural young successional forest stages threaten over 60 species in Finland alone (Rassi *et al.* 2010). In order to quantify the effectiveness of the restoration of structural characteristics, these threatened and specialized species that have suffered from anthropogenic changes offer a good sample to be measured. Among insects, beetles (Coleoptera) are the one of the most threatened forest-dwelling taxa (Rassi *et al.* 2010). The beetle assemblages have previously

been shown to benefit from retention cutting and burning (Hyvärinen *et al.* 2005, 2006) and restoration burning in mature forests (Toivanen & Kotiaho 2007a, Laarmann *et al.* 2013). Flat bugs (Heteroptera: Aradidae) consists a very poorly studied group of saproxylic insects, which includes several red-listed species that are threatened by commercial forest management (Rassi *et al.* 2010). Their responses to restoration actions have not previously been studied, even though they seem to benefit from prescribed fire (Johansson *et al.* 2010, Viiri & Eerikäinen 2012).

Changes in disturbance regime may affect even the common forest vegetation dynamics by changing the relative abundances of plants and/or functional groups of plants (see e.g. Mallik 2003, Wardle *et al.* 2003). This has also been observed in the long-term National Forest Inventories in Finland (NFI: Reinikainen *et al.* 2000) and in comparisons of vegetation composition between Finnish and Russian forests (Uotila *et al.* 2005). The possible reasons for these observed changes in boreal forest vegetation composition in Finland are the shift in disturbance regime, from natural disturbances to clearcutting and soil preparation that breaks the belowground stems and rhizomes, and the use of fertilizers (Reinikainen *et al.* 2000). In Finland, typical boreal forest species, i.e. dwarf shrubs, including keystone species bilberry (*Vaccinium myrtillus*) and evergreen cowberry (*Vaccinium vitis-idaea*) and heather (*Calluna vulgaris*) have decreased in cover since the 1950s, whereas the relative covers and thickness of some late successional forest floor mosses (e.g. *Pleurozium schreberi*, *Dicranum polysetum*) have increased (Reinikainen *et al.* 2000). Even though many dwarf shrubs are clonal, they may need natural disturbances so as to be able to rejuvenate and avoid the stage of degeneration (Barclay-Estrup 1970, Tolvanen 1994, Hautala *et al.* 2001). Instead, without fire fire-sensitive vegetation, such as crowberry (*Empetrum nigrum*, including *E. hermaphroditum*) may become dominant and interfere with the seedling establishment and growth of trees and other vegetation through the allelopathic compounds (Zackrisson *et al.* 1997, Nilsson *et al.* 2000, Nilsson & Wardle 2005). These changes in species composition may affect the nutrient cycle (Wardle *et al.* 2003, 2004, 2012; MacKenzie *et al.* 2006) and may hinder natural regeneration of e.g. trees (Zackrisson *et al.* 1997, Mallik 2003, Soudzilovskaia *et al.* 2011), and hence negatively affect the forest ecosystem functioning.

1.3.3 Processes and functions

The ecosystem processes, such as disturbance regime and primary or secondary succession, and functions, such as primary production, hydrologic and nutrient cycling, carbon sequestration and decomposition provided by natural forest are numerous (e.g. Burton & Macdonald 2011). In this thesis I concentrate only on ecosystem processes, i.e. disturbance simulated by restoration, and the secondary succession following disturbances (Fig. 3).

In natural boreal forests, the disturbance types vary from high intensity fire or severe storm causing stand-replacing disturbance, to the deaths of single trees, occurring over a wide range of spatial (from small to large) and temporal (from discrete to continuous) scales. In addition, the disturbances often operate simultaneously in a nested manner (Kuuluvainen 2002) (Fig. 3). Following natural disturbances, three broad types of forest dynamics (successional processes) have been described from unmanaged Fennoscandian forests, i.e. successional dynamics, cohort dynamics and gap-phase dynamics (Angelstam & Kuuluvainen 2004) (Fig. 3). According to McCarthy (2001), gap-phase dynamics can be further divided into small-scale ($>200\text{ m}^2$, $<1\text{ ha}$) patch dynamics, that produce canopy openings by affecting groups of trees, and fine scale gap dynamics that affect only single trees and small tree groups ($<200\text{ m}^2$) (dashed line in Fig. 3). In pine-dominated boreal forests, intermediate-scale cohort- or fine-scale gap-dynamics have dominated (Kuuluvainen & Aakala 2011). As a disturbance factor, fire has been mainly responsible for stand-replacing and cohort dynamics, whereas windstorms have mainly been responsible for gap dynamics (Kuuluvainen & Aakala 2011).

In this study, restoration burning aims to simulate stand-replacing disturbances such as a high-severity fire that initiates succession completely by killing all trees and most of the aboveground vegetation, or a low-severity fire that sustains old and large (pine) trees, thus resulting in multi-cohort dynamics. Felling by chainsaw aims to produce gaps of various intensity and extent. Felling is thus assumed to affect forest stands by reducing canopy closure and root competition, leading to small-scale patch dynamics or fine-scale gap dynamics (Angelstam 1998, Kuuluvainen 2002) (Fig. 3). Storm simulation additionally produces small uprooted patches, causing small and fine-scale disturbance and leading to gap- and patch dynamics.

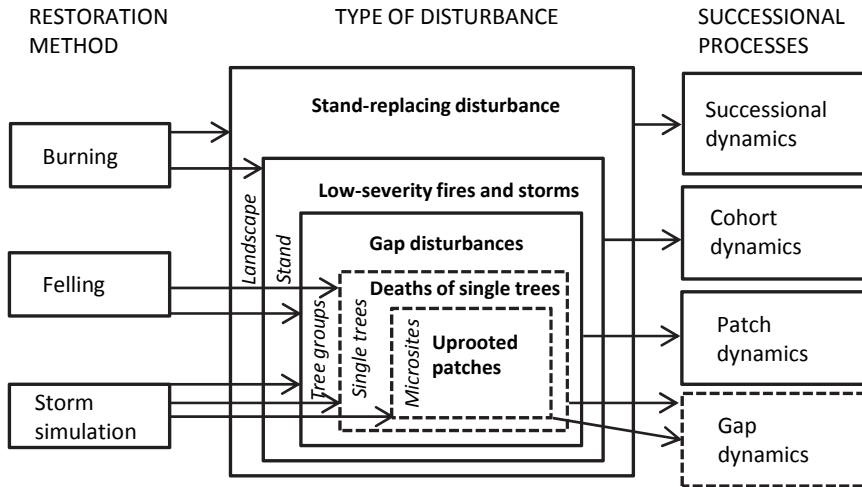


Fig. 3. An illustration of the relationship of the restoration methods used in this study, types of natural disturbances the restoration is emulating, and the successional processes that usually follow natural disturbances. The spatial scale within which the disturbances naturally operate is given in italics. According to McCarthy (2001), the gap dynamics are further divided into larger scale patch dynamics and finer scale gap dynamics (dashed line). The largest scale, geographical-scale global change is omitted from the figure. Figure modified from Kuuluvainen (2002).

1.4 Need for and significance of the current study

Because forest restoration is still a rather new branch of scientific research in Fennoscandia, no long-term quantitative results exist (but see Penttilä *et al.* 2013), and well-planned short-term studies are limited to a few examples even on a Northern European scale (for a summary of a large-scale Finnish experiment see Vanha-Majamaa *et al.* 2007, in Estonia Laarmann *et al.* 2013). Worldwide, most forest restoration studies are restricted to reporting the results of only a maximum of two years following restoration treatments, and boreal forests are among the least studied forest types (Burton & Macdonald 2011).

This study was initiated to fulfil several information gaps related to the impacts and effectiveness of boreal forest restoration, such as:

- Insufficient information on the responses of boreal vegetation to forest restoration. Forest vegetation is an important driver of ecosystem functions, such as primary production and nutrient cycling (Nilsson & Wardle 2005). By providing new information on the vegetation responses to different restoration methods, this study contributes to our understanding of the importance of types and severities of disturbances on typical boreal forest vegetation structure and composition.
- Short-term results of restoration, which make it difficult to evaluate the long-term benefits of forest restoration. Even though the time scale of the study in this thesis is ‘only’ seven years, it represents a considerably longer time frame than in most restoration studies. In addition, simulation modelling, which is a completely new approach in forest restoration studies, may provide important information on, for example, deadwood continuity after different restoration actions and intensities. Simulation models have previously been used to predict stand-scale deadwood volumes under biodiversity-oriented forest management operations (e.g. Ranius & Kindvall 2004, Tikkanen *et al.* 2012), or predict suitable habitat distribution for a set of forest-dwelling species (e.g. Mönkkönen *et al.* 2014), but they have not previously been used to combine the actual measurements of deadwood with predictions of deadwood decaying and formation.
- Difficulties in assessing restoration outcomes under high natural variability. With only a restricted number of studies, it is difficult to evaluate whether the recent forest restoration measures have truly increased or will increase biodiversity values in the future (Halme *et al.* 2013). By providing information from a well-designed and monitored field experiment, this thesis brings new high quality information, which is crucial in evaluating the effectiveness of restoration for example within different forest stand ages and types and in comparing the impacts of restoration on different taxa and between restoration methods.
- Missing information on saproxylic beetles in young forests. The beetle assemblages’ responses to restoration methods have been studied in mature spruce stands in southern Finland (Toivanen & Kotiaho 2007a) and in another stand in Estonia (Laarmann *et al.* 2013), but no studies have been conducted in young forest stands. Young forests (20–40 years) are today the dominant forest age class in Finland (Finnish Forest Research Institute 2013), and they are often very low in biodiversity. If these stands can be restored to be

suitable for red-listed and rare deadwood-dependent species, restoration can also be targeted on young stands.

- Virtually missing information on restoration impacts on extremely rare taxa, such as flat bugs (Heteroptera: Aradidae). So far, there has been only one study on the responses of flat bugs to clear-cutting and fire (Johansson *et al.* 2010). By providing information on flat bugs, this thesis contributes to the knowledge of the benefits of restoration efforts on rarely studied taxa, and increases our understanding of the causes of endangerment of these species.

2 Study questions and aims of the study

This thesis summarizes the information on the effectiveness of three commonly used restoration methods to restore the naturalness of boreal forests, including structural variables, species assemblages and ecosystem processes (Fig. 1). The aim of this thesis was to provide new information on the impacts of forest restoration methods on boreal forest naturalness, including forest structure, forest-dwelling species and ecosystem processes.

The studied restoration methods are those typically used in Finnish restoration proceedings; felling with a chainsaw to produce deadwood (F), felling combined with burning (FB), and storm simulation (S), in which the trees are felled with an excavator. In addition, two levels of felling were applied, 1: 20% and 2: 40% of initial volume of living trees. The forest structure is measured in terms of the volume, diversity and long-term availability of deadwood (II), and in terms of tree regeneration (I, II). Species assemblages include deadwood-dependent beetles (III), flat bugs (IV) and boreal forest vegetation (I). Processes are discussed in terms of disturbances and succession caused by restoration in relation to natural disturbance dynamics (this thesis).

I used seven-year before-after data collected from a large-scale controlled restoration experiment in Finland (EU-LIFE project 2005-2011) to accomplish this thesis. In sub-study IV, data from a large-scale restoration experiment in Sweden was also used. In each of the four sub-studies, we concentrated on one (taxonomic) group. The specific questions and their hypotheses were as follows:

1. How do restoration felling, storm simulation and burning affect the dynamics of boreal forest vegetation within five years after restoration? Does the method and intensity of restoration lead to different stages in the successional pathway? (I)
 - 1.1. We hypothesized that 1) restoration felling will result in only slight changes in vegetation cover and composition, because the ground is not mechanically disturbed. F1 causes lesser effects than F2. 2) Soil disturbance caused by storm simulation (S1) and burning (FB1, FB2) will increase species richness on a stand scale, 3) burning will shift species composition towards early successional stages more efficiently than less intensive restoration treatments by reducing the cover of late-successional species while increasing the cover of early-successional species.

2. How do restoration felling, storm simulation and burning affect deadwood volume and diversity in the short term (i.e. one and five years after restoration)? Do the restored forest stands still differ in deadwood volume 20, 40 and 60 years after restoration? (II)
 - 2.1. We hypothesized that 1) in the short-term, burning causes the greatest increase in deadwood volume and produces the highest deadwood diversity due to higher tree mortality as compared with felling or storm simulation, 2) in the long term (60 years), the decomposition process and natural mortality will level off the differences in deadwood volume between controls and treatments.
3. How do saproxylic (deadwood-dependent) beetles (Coleoptera) respond to two restoration burning treatments in the short term? How do the beetle assemblages change in the five years after restoration? (III)
 - 3.1. We hypothesized that 1) restoration burning with a higher fuel load (FB2) increases the number of species more than FB1 due to higher deadwood volume, 2) the species richness declines in the five years after restoration due to succession (see e.g. Siitonen 2001).
4. How does restoration burning affect the richness and abundance of flat bug (Heteroptera: Aradidae) species in two Fennoscandian countries? Do the species respond similarly to restorative gap-cutting and burning in Sweden? (IV)
 - 4.1. We hypothesized that 1) in Finland, restoration burning increases the number of flat bugs, because some species are defined as pyrophilous and they are assumed to benefit from restoration burning. 2) In Sweden, burning and gap-cutting treatments result in greater richness and abundance of flat bug species compared to the control.
5. What is the most effective restoration method in Finland's boreal forests to restore forest naturalness in terms of structures, species and ecosystem processes? (This thesis).
 - 5.1. Based on the measured and simulated data, I hypothesized that 1) burning is the most effective method to increase forest naturalness, as it creates more variability in the deadwood variables and vegetation composition than the other methods, and 2) storm simulation is more effective than felling treatment, as it promotes the small-scale gap dynamics succession from the exposed soil patches.

3 Material and methods

3.1 Study areas

The study areas are located in two countries, Finland (I, II, III IV) and Sweden (IV), in the northern and middle boreal vegetation zones (Ahti *et al.* 1968, Figs 4 & 5, Table 1). In Finland, the experimental stands were established in four Natura 2000 protection areas (hereafter study areas), and in Sweden in 18 voluntarily set-aside forest stands. Prior to the treatments, the forests were dominated by Scots pine (*Pinus sylvestris* L.) and/or Norway spruce (*Picea abies* L.), with scattered birches (*Betula pubescens* Ehrh. and *B. pendula* Roth.), European aspens (*Populus tremula* L.), Goat willows (*Salix caprea* L.) and rowans (*Sorbus aucuparia* L.). The understorey vegetation was dominated by the ericaceous dwarf shrubs cowberry *Vaccinium vitis-idaea* (L.), bilberry *V. myrtillus* (L.) and moss *Pleurozium shreberi* (Brid.)Mitt.. The forests had been silviculturally managed previously, and they lacked or had reduced levels of characteristics typical of natural forests, for example deadwood, diverse tree size and tree species composition and/or random spatial distribution of trees. The fire history of the forests was not known, but in general, the dryer Scots pine-dominated forest types (EVT, EMT, see Table 2) have burned more frequently as compared with moister Norway spruce-dominated forest types (HMT) (Zackrisson 1977, Wallenius *et al.* 2004). In Vienansalo, Russia, close to our study areas (64°58'N, 30°11'E) fire frequency was measured at 1.9±0.3 fires/300 years (1669-1969) in mesic forests and 3.2±0.3 fires/300 years in dryer forests (Wallenius *et al.* 2004).

Table 1. The environmental and structural characteristics of the study areas.

Name of the study area	Finland: Oulanka	Finland: Pahamaailma	Finland: Elimyssalo	Finland: Lentua	Sweden: Västernorrland, Västerbotten
Natura number	2000 FI 1101645	FI 1200744	FI 1200220	FI 1200251	-
Size of 2000 area (ha)	Natura 29 390	2072	8293	6591	-
Environmental characteristics on experimental stands					
Latitude, longitude (degrees)	66°23' N, 29° 33' E	65°28' N, 29°37' E	64°14' N, 30° 22' E	64°12' N, 29° 36' E	63°23' - 64°30' N 17°37' - 21°20' E
Elevation (metres above sea level)	260	260	230	180	210-408
Temperature (mean July)	14.7 °C	15.1 °C	15.7 °C	15.7 °C	10.8-14.4 °C
Precipitation (average mm/a)	568	627	606	606	490-641
Temperature sum	819	853	945	945	699-879
Vegetation type ¹	HMT	EVT	EVT	EMT	HMT
Structural characteristics on experimental stands prior to the treatments, mean±s.e.					
Volume of growing stock (m ³ ha ⁻¹)	63.6±2.8	155.9±7.4	88.1±10.3	141.4±8.1	209±10.8
<i>Pinus sylvestris</i> Vol-%	7.7±2.4	94.4±1.0	93.0±1.7	99.2±0.5	57±3.7
<i>Picea abies</i> Vol-%	45.0±3.9	1.1±0.3	1.2±0.4	0±0	31.8±3.8
<i>Betula pubescens/pendula</i> Vol-%	42.3±5.2	4.6±0.7	5.6±1.4	0.8±0.5	10.5±1.6 ²
<i>Populus tremula</i> Vol-%	5.1±4.1	0±0	0±0	0±0	Not Available
Volume of deadwood (m ³ ha ⁻¹)	1.8±0.6	32.5±3.2	1.3±0.4	2.4±1.1	Not Available
Age of forest stands	26-50	70-100	27-40	60-70	82-172

¹Vegetation type=EVT: *Empetrum nigrum-Vaccinium vitis-idaea* -dominated sub-xeric shrub heath, EMT=*Empetrum nigrum-Vaccinium myrtillus* -dominated dry heath, HMT=*Hylocomium splendens-Vaccinium myrtillus* -dominated moist heath (Cajander 1926).

²All deciduous trees, including *Betula pendula*, *B. pubescens*, *Populus tremula*, *Salix caprea*, *Sorbus aucuparia*, and *Alnus incana*.

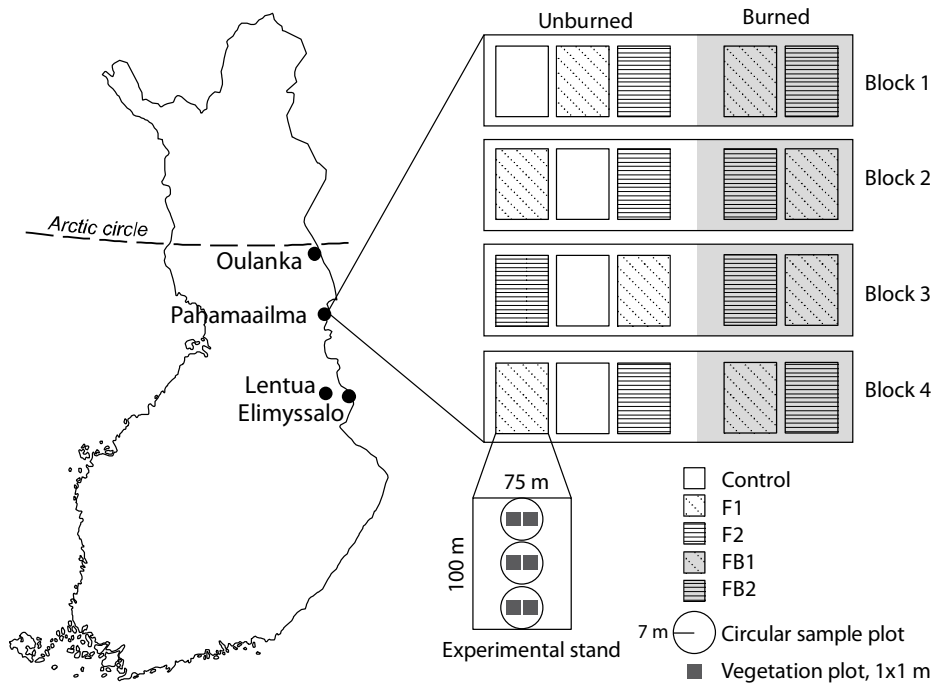


Fig. 4. The locations of study areas and conceptual figure of the study design in Finland (I,II). The example is from Pahamaailma. See Table 2 for the full study design. Control=no treatments, F1=felling treatment with 20% of initial living tree volume felled with chainsaw and left on the stand, F2=felling treatment with 40% of initial living tree volume felled and left on the stand, FB1=F1 with subsequent burning, FB2=F2 with subsequent burning.

3.2 Restoration treatments and experimental design

3.2.1 Finland (I-IV)

The restoration treatments consisted of two thinning treatments (F1 and F2), one storm simulation treatment (S1), and two thinning treatments combined with subsequent burning (FB1 and FB2). All restoration treatments were carried out on reasonably large (6.7–29.2 ha) areas, and the experimental stands are random samples of the treatments. However, due to practical reasons arising from the management of the Natura 2000 areas, a fully factorial experiment could not be carried out across the restoration treatments and study areas (Table 2). In the

treatments F1, S1, and FB1, 20% of the initial volume of randomly selected living trees was felled. In the treatments F2 and FB2, the proportion of felled trees was 40%. Trees were cut down from the base of the trunk with a chainsaw, except for the storm simulation treatment S1, in which randomly selected trees were uprooted by an excavator. In the burning treatments, trees were felled in February–March 2006, and burnings took place from late June to early July 2006, which is a naturally high fire risk period. In the felling and storm simulation treatments, felling was conducted between October 2005 and May 2006. All felled trees were left in the study areas, and no further actions such as tree planting or sowing were carried out. All regeneration was, therefore, natural.

The burning treatments with two different proportions of felled trees (20% and 40% of initial living volume) aimed to cause fire damage of varying severity, and felling treatments (F1 and F2) aimed to mimic a windstorm of heavy snow or ice load that breaks tree stems. The storm simulation treatment, in which the trees were pushed down by excavator, was taken in this study as a case, because the first field observations after restoration treatments suggested that the early successional fungal assemblages are dominated by a common polyporus fungus (*Trichamptum abietinum*). Such dominance was suggested to differ from naturally fallen logs (Similä & Junninen 2012). Today, tree felling with a chainsaw has largely been replaced with felling with an excavator (Similä & Junninen 2012).

In each study area, three to four replication blocks were established, each containing randomly placed experimental stands of size 75 m x 100 m (Fig. 4, Table 2). Each experimental stand included three circular sample plots in which the tree measurements and insect and vegetation sampling were conducted (radius 7 m=153.9 m²). The three circular sample plots were pooled for the calculations of stand characteristics, the sampling unit for the tree stand characteristics hence being 462 m².

3.2.2 Sweden (IV)

In Sweden, the restoration treatments consisted of gap-cutting (Gap) and burning (Burn) treatments, besides untreated control (Fig. 5). The treatments and controls were replicated in six separate areas (Table 2). Prior to burning in 2011, 5%–30% of trees were cut and removed from the experimental stands, and approximately 5 m³/ha was felled to serve as fire fuel. The burning was conducted between June 10 and August 3, 2011. The gap-cutting was conducted in the spring of 2011 by cutting six small gaps (diameter 20 m) per hectare. From half of the gap area, all

the trees were cut and removed and from the other half the trees were felled and left on the site, cut as high stumps or girdled and left on the site.

Table 2. The restoration treatments conducted during the study, number of replication blocks (“*replicates*”), and number of study areas (“*areas*”) in each original study (I-IV). Control=no treatments, F1=felling treatment with 20% of initial living tree volume felled with chainsaw and left on the stand, S1=similar to F1, but the trees were uprooted by pushing with an excavator, F2=felling treatment with 40% of initial living tree volume felled and left on the stand, FB1=F1 with subsequent burning, FB2=F2 with subsequent burning. In Sweden burning (Burn) and Gap-cutting (Gap) were used besides untreated controls, see text 3.2.2. for description of the methods.

Country	Treatment	Vegetation (I)		Deadwood (II)		Beetles (III)		Flat bugs (IV)	
		replicates	areas	replicates	areas	replicates	areas	replicates	areas
FIN	Control	15	4	15	4	3	1	6	2
FIN	F1	12	3	12	3	-	-	-	-
FIN	S1	4	1	4	1	-	-	-	-
FIN	F2	8	2	8	2	-	-	-	-
FIN	FB1	8	2	8	2	3	1	6	2
FIN	FB2	11	3	11	3	3	1	6	2
SWE	Control	-	-	-	-	-	-	6	6
SWE	Burn	-	-	-	-	-	-	6	6
SWE	Gap	-	-	-	-	-	-	6	6

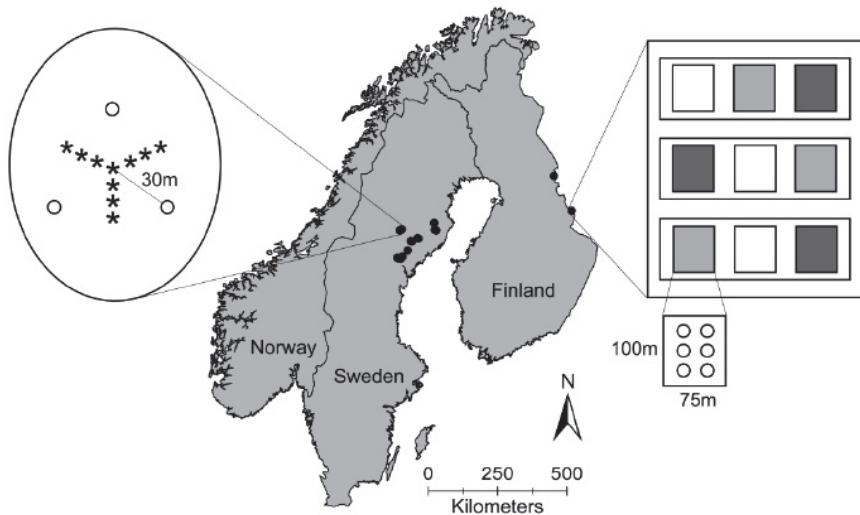


Fig. 5. Study design of the flat bug study conducted in Finland and Sweden (IV). Black circles represent the study areas, open circles represent flight-intercept traps, and stars represent pitfall traps. White square=control, light grey=FB1, Dark grey=FB2 (Figure copyright Ruaridh Hägglund)

3.3 Sampling design

The detailed sampling designs are explained in original articles, and here I only briefly elucidate the main points of the sampling procedures.

3.3.1 Vegetation sampling (I)

The understory vegetation was sampled in all the study areas of the Finnish restoration experiment. Three surveys were carried out: before the restoration in 2005, one year after the restoration in 2007, and five years after the restoration in 2011. The sampling was conducted in six permanent 1 m x 1m vegetation sampling plots per experimental stand (Fig. 4). On storm simulation treatment (S1) in Lentua, six extra sampling squares were established in 2006 on the soil exposed by tree uprooting.

Vascular plants, bryophytes and lichens were identified to species, and their cover was estimated at the scale from 0–100%. All species were divided into two

subgroups: field layer vegetation and ground layer vegetation. Ground layer consisted of bryophytes and lichens, and field layer of other species <50 cm in height. Furthermore, vegetation was classified into eight plant functional types (PFTs), according to their growth form and life-history traits: 1) deciduous dwarf shrubs; 2) evergreen dwarf shrubs, including Lycopodiaceae; 3) forbs and graminoids; 4) deciduous tree saplings; 5) coniferous tree seedlings (*Pinus sylvestris*, *Picea abies*); 6) forest mosses; 7) pioneer mosses, and 8) lichens (for typing, see Appendix A in I). The dominant dwarf shrub species were also analysed by species (*Vaccinium myrtillus* L., *V. vitis-idaea* L., *Calluna vulgaris* (L.) Hull., *Empetrum nigrum* L.), and species difficult to identify in the field were pooled by genus or group. The proportion of burned ground was measured from each vegetation sampling plot.

3.3.2 Tree stand measurements and simulations (II)

Measurements of living and dead trees

Tree stand measurements were conducted in all of the study areas in 2005 and 2006 or 2007. In 2011 the class (alive, dead, standing, fallen) of each individual tree was re-checked. The tree species were Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* L.), Downy birch (*Betula pubescens* Ehrh.), Silver birch (*Betula pendula* Roth.) and European aspen (*Populus tremula*, L.). The diameter of each tree with dbh (diameter at breast height) >45 mm was measured. The height was measured from minimum three sample trees of each tree species and diameter category (4.5–9.9 cm, 10–19.9 cm and over 20 cm) within each circular sampling plot.

The height, diameter, species and decay class (1–5, Renvall 1995) of all standing dead trees (‘snags’, including broken trees ≥ 1.3 m in height) from each circular sample plot were measured before restoration. After restoration in 2007, the proportion and height of the blackened part of the trunk was also measured.

All down deadwood (‘logs’) at least 10 cm in diameter were measured for their species, diameter, stem length and decay class (1–5 Renvall 1995, the most decayed trunks, decay stage 5, were omitted) in 2005 and 2006/2007 and re-checked in 2011. Whether the logs had been produced by chainsaw or excavator (‘artificial log’) during restoration or fallen naturally (‘natural log’) was also recorded.

The number of seedlings or saplings (>0.1 m and <1.3 m in height) and understorey trees (≥ 1.3 m in height and $\text{dbh} \leq 45$ mm) of each tree species was counted from the each circular sample plot in 2005, 2007 and 2011.

The hectare-based tree stand characteristics were calculated using KPL software developed at the Finnish Forest Research Institute (Heinonen 1994). After KPL calculations, deadwood was classified either by species or to coniferous and deciduous tree species. For calculations of deadwood diversity, eight types of deadwood were used: 1) ‘old coniferous logs’ and 2) ‘old deciduous logs’ that were present before restoration in 2005, 3) ‘coniferous snags’ and 4) ‘deciduous snags’ that were classified into their categories irrespective of their time of death, 5) ‘artificial coniferous logs’ and 6) ‘artificial deciduous logs’ that were felled during the restoration in 2006, 7) ‘new coniferous logs’ and 8) ‘new deciduous logs’ that fell naturally between 2007 and 2011.

To predict the decomposition process (loss of volume) of the deadwood measured in 2011 the wood decomposition models of Mäkinen *et al.* (2006) was applied. The model accounts for the tree diameter, time since tree death and species (pine, spruce and birch). The decomposition process of all deadwood types measured was separately predicted in five-year time intervals, starting from the volume measured in 2011, until 2066 (55 years period, i.e. 60 years from restoration). The predicted volumes were then summed for the total deadwood, and for the volume of pine, spruce and deciduous deadwood separately.

Simulations for future deadwood dynamics using MOTTI stand simulator

In order to predict the formation of deadwood in the future, and hence to ascertain whether the restoration treatments differ in deadwood supply, we used a simulation approach. The simulations of stand dynamics, particularly deadwood volumes, were conducted using the MOTTI stand simulator (Salminen *et al.* 2005, Hynynen *et al.* 2005, Hynynen *et al.* 2014). MOTTI comprises specific distance-independent tree-level models for predicting variables such as natural regeneration, tree growth, and mortality, as well as the effects of management on tree growth (Salminen *et al.* 2005). The models are based on extensive empirical data from permanent field sites and forest inventory plots (Hökkä, 1997, Hynynen *et al.* 2002, Matala *et al.* 2003, Hökkä & Salminen, 2006). With respect to regeneration and early growth, stand-level models by Siipilehto (2006) and Siipilehto *et al.* (2014) were applied. Natural mortality was predicted with a system of individual-tree survival models controlled by stand-level models for

self-thinning (see Hynynen 1993, Hynynen *et al.* 2002). After the simulated tree death, the decomposition models of Mäkinen *et al.* (2006) were used to predict the loss of volume in the decomposition process.

The last year of measurement (2011) was used as a baseline for the simulations. The species, height, age and diameter of each living tree within the sampling unit of the experimental plot (462 m²) in 2011 were given as input data for MOTTI. The counted number, estimated age, species and measured height of the understorey tree layer (trees with $d_{1.3} < 45$ mm) and seedlings 0.1–1.3 m in height were given similarly as input data. The simulations were run separately for each experimental stand until 60 years from restoration in five-year intervals without further management operations (e.g. thinning). This 60-year time window was selected to reduce the chance of natural disturbance occurring during the period of simulations.

3.3.3 Insect sampling (III, IV)

Saproxyllic beetles (Coleoptera) (III)

Saproxyllic beetles, i.e. beetle species that are dependent upon dead or dying wood during at least a part of their life cycle (Jonsson & Siitonen 2012), include several thousands of species worldwide. In Finland, there are approximately 2,000 forest-dwelling beetle species, of which approximately 800 are defined as obligatorily saproxyllic (Siitonen 2001). At the same time, the number of red-listed (IUCN categories CR=critically endangered, EN=endangered, VU=vulnerable, NT=nearly threatened and DD=data-deficient) beetle species is highest among forest-dwelling species (Rassi *et al.* 2001, 2010).

Beetles are well suitable for studying the effects of forest restoration, as they are easy to collect, they quickly respond to environmental changes, e.g. changes in microclimate, and due to a long tradition of entomology in Fennoscandia, their ecology and habitat requirements are relatively well known (Saalas 1917, 1923, Palm, 1951, 1959, Koch 1989a,b, Koch 1992, Ehnström & Axelsson 2002, Hyvärinen 2006). They also comprise interesting taxa in ecological studies due to the high number of red-listed species. The large number of species, however, makes the identification work laborious and costly. The number of specimens needed to make conclusions about the changes in species assemblages is very

high, preferably tens of thousands, especially when the target is to find the rare and red-listed species (Martikainen & Kouki 2003).

Due to the laboriousness of beetle sampling and identification, beetles were sampled only from three replicate blocks including controls and two burning treatments located in Elimyssalo (the treatment abbreviations differ in this summary from the original article III: BF1=FB1, BF2=FB2). The beetles were sampled with six large (40 x 60 cm) trunk-attached flight-intercept window traps placed on each experimental stand (54 traps in total) (Fig. 3, Table 2) in 2005, 2006, 2007 and 2011. In 2005–2007 the sampling period was from middle of May to middle of September and in 2011 from June 11th to July 10th. The catches of beetles within each experimental stand (six traps) were pooled into one sample, which was used for the analyses. To reveal the five year responses of beetles, we used a beetle sample collected during a 1-month period in 2011. A similar 1-month period was separated from the earlier years' (2005–2007) whole summer samples in order to obtain a comparable sample.

The beetles were identified mainly (98.6% of the total capture) to the species level and classified as non-saproxyllic, saproxyllic, and pyrophilous species. Non-saproxyllic species were omitted from this study. The saproxyllic species and pyrophilous species were then classified into two overlapping groups; all saproxyllic species and red-listed, rare and/or pyrophilous species (hereafter called RRLP species). The red-list category (CR, EN, VU, NT) of the species followed Rassi *et al.* (2001), because the data was used for the assessment of the 2010 IUCN status of the species. Species that have been found from a maximum of 25 separate 100 km² squares in Finland during 1960–1990 (Rassi 1993) were considered to be rare. The nomenclature follows Silfverberg (2010).

Flat bugs (Heteroptera: Aradidae) (IV)

Worldwide, the family of flat bugs is a small and poorly studied family of saproxyllic insects. There are only 23 species of flat bugs in Fennoscandia, with 19 species found in Finland (Rintala and Rinne 2010) and 21 species found in Sweden (Coulianos 1989). A high proportion of Fennoscandian flat bugs are classified as red-listed (six in Finland, Rassi *et al.* 2001, 2010, and seven in Sweden, Gärdenfors 2010) and all but one species (*A. cinnamomeus*) are considered saproxyllic. Previous studies have shown that some species are attracted by fire (Deyrup & Mosley 2004, Hjältén *et al.* 2006, Johansson *et al.* 2010, Schmitz *et al.* 2010, Klocke and Schmitz 2012, Viiri and Eerikäinen 2012),

and hence they comprise an attractive group for studying the effects of forest restoration on their assemblages. However, due to rarity and low abundance of flat bug species, the number of specimens collected is usually much lower as compared with beetles (see e.g. Hjalten *et al.* 2006, Johansson *et al.* 2010).

In Finland, the flat bugs were collected in 2005–2006 from the same samples as the beetles in Study III and from an identical sampling design in Pahamaailma (6 traps per experimental stand, 102 traps in total). All flat bugs were identified to species level. The treatment abbreviations differ in this summary from the original manuscript IV: BurnLow=FB1, BurnHigh=FB2.

In Sweden, the flat bugs were collected one year after restoration in 2012 with three flight intercept traps (IBL2, see Petterson *et al.* 2007) and 10 pitfall traps per experimental stand (Fig. 4). The sampling period for flight intercept traps was from June 1 to September 30 and for pitfall traps from June 1 to July 15. The catches of all 13 traps per experimental stand were pooled for analyses. The IUCN categories are according to Rassi *et al.* (2001) and Gärdenfors *et al.* (2010).

3.4 Statistical analyses

The responses of taxa studied to restoration treatments in datasets in I, II and III were analysed using either linear mixed effect models or generalised linear mixed effect models (LME's or GLMM's, *lme4*-package, Bates *et al.* 2011, 2012, or *lmerTest*-package, Kuznetsova *et al.* 2013, Bates *et al.* 2013, or *glmmPQL*, *mass*-package, Venables & Ripley 2002), depending on the error distribution of response variable. The proportional variables (i.e. percentage cover of vegetation, I) were arcsine square-root transformed prior to analyses to attain normal error distribution (Crawley 2007). The count variables (species richness, abundance, I, III) were analysed with poisson or quasi-poisson error distribution and the volume variables in II were log-transformed prior to analyses. The random structure in the mixed effect model procedure allowed for repeated measures, unbalanced study design and the hierarchical structure of the data. The fulfilment of the requirements for normal error distribution and heteroscedasticity were checked using diagnostic plots. Generalized additive mixed models (GAMMs, *mgcv*-package (Wood 2004, 2006)) were used in I to reveal the responses of plant functional types on the proportion of burned ground. GAMMs are semiparametric extensions of generalized linear models (Hastie & Tibshirani 1990) that permit both linear and complex additive response shapes. In Study IV, the Kruskal-

Wallis rank sum test and Mann-Whitney U test were used to test the abundances of flat bugs between the treatments.

In I and III, non-metric multidimensional scaling (NMDS, *vegan*-package, Oksanen *et al.* 2011) was used to reveal the differences in species composition between restoration treatments and time in relation to restoration. Indicator species were searched for in I and III with indicator species analysis (Dufrene and Legendre 1997, De Cáceres *et al.* 2010) using *indicspecies*-package (De Cáceres & Jansen 2012). The Shannon-Weiner diversity index (H') for the deadwood diversity (II) (see section 3.3.2) was calculated using a *vegan*-package (Oksanen *et al.* 2013). All statistical analyses were carried out using R statistical environment (versions 2.14-0 - 2.15-2, R Development Core Team 2011, 2012)

4 Results

4.1 The effects of restoration on vegetation dynamics (I)

The restoration treatments studied varied in their effects on vegetation species richness, cover and composition. The dwarf shrub species and plant functional types PFTs studied showed differing responses to restoration treatments, and the responses were partially dependent of the scale they were measured (i.e. experimental stand scale or vegetation plot scale). The levels of felling, i.e. F1 and F2 or FB1 and FB2 did not differ in effect in any measured variable.

Felling treatments (F1 and F2) had virtually no impact on the cover of PFTs or species, or species richness, during the seven-year study. The only effect of felling treatment was a decreased cover of lichens in treatment F1.

The storm simulation treatment S1 increased the stand scale cover of deciduous trees from 0% cover to 0.45% cover, but the dwarf shrub species and PFTs remained unaffected by the treatment. However, the stand-scale species richness significantly increased in S1 from 2005 to 2011, especially on the ground layer (I: Fig. 4, Table 3).

In a comparison between initial cover (2005) and the cover during the first post-treatment year (2007), restoration burning treatments FB1 and FB2 caused the greatest disturbance by reducing the total cover of field layer vegetation by $81.1\% \pm 6.8\%$ (mean \pm s.e.) in FB1 and $70.7\% \pm 8.2\%$ in FB2 and ground layer vegetation by $83.6\% \pm 6.5\%$ and $77.5\% \pm 5.9\%$, respectively. The dwarf shrub species, forest mosses and lichens decreased the most, while forbs and graminoids, deciduous seedlings and pioneer mosses increased (I: Figs. 2–3). Within five years after restoration, the latter three had multiplied their cover as compared with the initial situation, and *Calluna vulgaris*, *Vaccinium myrtillus* and *V. vitis-idaea* were recovering, while *Empetrum nigrum* and forest mosses (mainly *Pleurozium schreberi* and *Hylocomium splendens*) did not show signs of recovery. The mean number of species was not greatly affected on a stand scale during the time of the study, as the number first decreased, but then returned back to the initial level by five years after burning (I: Fig. 4).

In the plot scale, burning and soil exposure after tree uprooting (UR) caused the greatest changes in the composition of vegetation species, while felling treatments did not differ from control stands (I: Fig. 5). UR and burned plots in 2011 differed slightly in species composition, UR having a greater cover of

mosses and burned plots having a greater cover of dwarf shrubs. The exposed soil patches in UR were especially characterized by a great cover of *Pinus sylvestris* seedlings and the absence of dwarf shrubs. Also *Betula* spp. seedlings became well established on uprooted and burned soil patches.

In comparison between the initial cover and the 2011 cover, the PFTs showed different responses along an increasing proportion of burned ground (I: Fig. 6). Forbs and graminoids showed the greatest positive change in cover at intermediate proportions of burned ground; late successional forest mosses and evergreen dwarf shrubs linearly decreased with an increasing proportion of burned ground, while early successional mosses (such as *Pohlia nutans* and *Ceratodon purpureus*) linearly increased with an increasing proportion of burned ground (I: Fig. 6). Deciduous dwarf shrubs (mainly *V. myrtillus*) did not provide clear responses on the increasing proportion of burned ground.

4.2 The effects of restoration on deadwood (II)

4.2.1 Short-term effects on deadwood volume and diversity

Prior to restoration treatments, the experimental stands in Pahamaailma had relatively high volume of deadwood, on average 32.5 m³ha⁻¹ (range 11.5–69.3 m³ha⁻¹), while the other experimental stands contained on average less than 2.4 m³ha⁻¹ (II: Table 1). The direct effects of restoration on deadwood volume and diversity were dependent on initial tree stand structure, i.e. the age of the stand, tree species composition, and initial volume of living trees and deadwood. Consequently, the study areas provided highly varying volumes and types of deadwood regardless of the restoration treatment. Supporting our first hypothesis, burning treatments created the highest volume of deadwood in five years (Table 3, II: Table 2). In addition, the burned experimental stands had the highest deadwood diversity index values ($H' = 1.05 \pm 0.09$, 1.04 ± 0.06 , mean \pm s.e. in FB1 and FB2, respectively), whereas the other treatments were similar to the controls in H' values (II: Table 2). Between 2007 and 2011, deadwood volume increased only slightly in F1, S1 and F2 (7.9 \pm 3.7%, 7.2 \pm 6.0% and 4.1 \pm 2.4% increase, respectively), whereas in burned stands the increase was much greater (71.1% \pm 34.0% and 41.7% \pm 14.2% (mean \pm s.e., FB1 and FB2, respectively). On burned stands, the increase was caused by the delayed deaths of trees (increase of snags), whereas in other treatment the increase was caused by falls of living trees (new logs, II: Fig.1).

Table 3. The total deadwood volumes after restoration treatments in 2011 in study areas. Mean±standard errors are shown. Control=no treatments, F1=Felling treatment with 20% of initial living tree volume felled with chainsaw and left on the stand, S1=Similar to F1, but the trees are uprooted with an excavator, F2=felling treatment with 40% of initial living tree volume felled and left on the stand, FB1=F1 with subsequent burning, FB2=F2 with subsequent burning.

Treatment	Oulanka	Pahamaailma	Elimyssalo	Lentua
Control	0.7±0.6	36.3±9.3	1.5±0.5	4.0±1.3
F1		64.0±5.4	15.0±3.0	26.9±1.2
S1				31.4±2.1
F2		93.1±10.7	24.7±4.4	
FB1		146.5±36.8	26.5±5.8	
FB2	42.7±3.0	127.9±39.6	42.2±6.1	

4.2.2 Simulated long-term effects on deadwood volume and diversity

All the restoration treatments clearly accelerated the development of the forests towards a more natural state regarding the total volume of deadwood. In the mixed effect model, the difference in total deadwood volume between the control and all of the treatments was predicted to be distinctive in 40 years after restoration. In sixty years, the differences between controls and treatments had levelled off (II: Table 3), supporting our second hypothesis.

The future formation of deadwood depended on the remaining volume of growing stock. On average, the lower felling level F1 was predicted to safeguard a greater formation of deadwood during the simulation period, whereas FB2 caused a considerable loss in the remaining volume of living trees, and future formation of deadwood was predicted to be hampered.

The decomposition process of coniferous deadwood created by restoration treatments was predicted to take more than 60 years, supporting the deadwood availability in the landscape (Fig. 6). However, deciduous deadwood was predicted to decompose faster, and hence its continuous supply is more regeneration-dependent during the simulation period. The simulations including seedling counts in 2011 showed that only the originally mixed stands at Oulanka and Elimyssalo had sufficient regeneration to provide deciduous deadwood in the future. After burning treatments, the number of deciduous seedlings was greater than in the controls or after felling treatments. In originally highly pine-dominated stands at Pahamaailma and Lentua, the regeneration of deciduous trees was scarce and nearly all of the deadwood was predicted to be pine-originated in the future (Fig. 6.) (II: Appendix C).

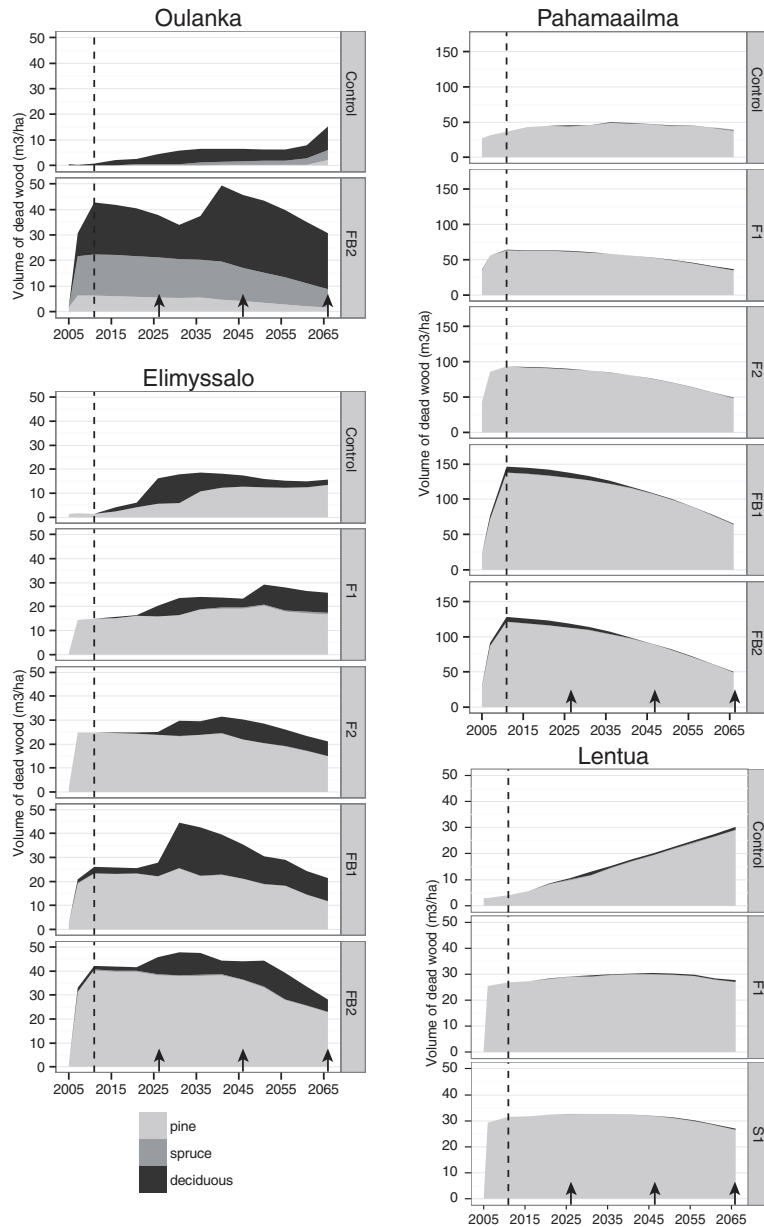


Fig. 6. The measured and simulated mean volume of deadwood before and after restoration treatments in study areas. The mean volumes of Scots pine, Norway spruce and deciduous trees (silver birch, downy birch and European aspen) are shown separately. Arrows show the time points of statistical testing of deadwood volumes (see Table 3 in II). The vertical dashed line indicates the starting point of

simulation (2011); on the left-hand side the volumes are based on measurements, and on the right-hand side on predictions and simulations. Control=untreated, F1=felling with chainsaw, 20% felling level, S1=F1, with the exception that trees were felled with root clumps by an excavator, F2=felling with a chainsaw, 40% felling level, FB1=felling 20% + subsequent burning, FB2=felling 40% + subsequent burning. See Appendix A in II for the total mean volumes and the standard errors of the means.

4.3 The responses of deadwood-dependent beetle assemblages on restoration burning (III)

The total number of beetles captured during the seven-year study was 33,338, of which 22,700 were classified as saproxylic, including 246 species, and 675 as red-listed, rare or pyrophilous (RRLP), including 48 species (species shown in Appendix A in III). Before the restoration in 2005, the experimental stands were similar in number of species, number of individuals and in the composition of the assemblage.

Immediately after restoration in 2006, the number of saproxylic species more than doubled from on average 35 species prior to restoration to 71 in FB1 and 77 in FB2. More importantly, the number of RRLP beetle species and their abundance significantly increased on burned stands (from 1.6 to 9.3 in FB1 and 2.6 to 9.3 in FB2), while the controls retained a similar abundance, number and composition of beetle species. In 2006, according to indicator species analysis (III: Fig. 4), the species assemblage on burned experimental stands was characterized by early successional beetles, such as bark beetles (Scolytinae: *Polygraphus poligraphus*, *Pityogenes chalcographus*), longhorn beetles (Cerambycidae: *Asemum striatum*, *Pachyta lamed* and *Acmaeops septentrionis* (VU)) and pyrophilous species such as *Stenotrachelus aeneus*, *Clypastrea pusilla* (VU) and *Sphaeriestes stockmanni* (NT).

A year after burning in 2007 the species richness and abundance further increased on restored stands. The average number of saproxylic species was 95 in FB1 and 90 in FB2. The ongoing species succession slightly altered the species composition in comparison to the previous year, and the first post-treatment year was characterized by secondary bark beetles such as *Hylastes opacus*, *Hylurgops palliatus* and *Orthotomicus suturalis* and the predator beetles (III: Fig. 4). Also the number of RRLP species further increased (on average 16.3 and 12.6 in FB1 and FB2, respectively), while in the controls the number of RRLP remained low, 2.6 on average.

In five years, the number of species declined back to the original level, although five RRLP species remained on the burned experimental stands, among them *Boros schneideri* (VU). The species composition changed from the previous years, and was still distinct from the control stands (III: Fig. 3).

The treatments FB1 and FB2 did not differ in the number or abundance of species or in species composition in any of the years. The volume of logs and total deadwood volume were significantly higher in 2006 on FB2 as compared with FB1; in 2007 and 2011 the treatments did not differ in deadwood volume (III: Table 2). When only burned experimental stands were included in analyses, there were no significant correlations between deadwood volume and the number of saproxylic species in any of the years.

4.4 The responses of flat bugs on restoration burning and gap-cutting in two countries (IV)

The total number of flat bugs sampled during the study was 81, of which 23 were collected from the Finnish study areas at Elimyssalo and Pahamaailma, and 58 from Swedish study areas. In Finland, where the study design included sampling before the treatments, no flat bugs were found prior to restoration treatments. Only one flat bug specimen was found from a control stand across the study areas in Finland and Sweden.

During the year of burning in Finland, a total of 22 specimens consisting of three species; *Aradus lugubris* (11 specimens), *A. laeviusculus* (EN, 9 specimens) and *A. angularis* (EN, 2 specimens), were found from the burned experimental stands. *A. angularis* was found only from Elimyssalo, whereas the other species were found from both study areas, in equal abundances from FB1 and FB2.

A year after burning in Sweden, 42 specimens consisting of seven species were found from burned experimental stands, *A. betulae* being the most abundant species, significantly more abundant on burned stands as compared with gap-cutting or control stands. *A. lugubris* was the only shared species in Finland and Sweden, but in Sweden the species was found as immature nymphs, whereas Finnish specimens were adults. In Sweden, its abundance was significantly higher on burned stands as compared with both Gap-cutting and Control. The other species that were found in significantly greater abundances from burned as compared with gap-cutting or control stands were *A. betulinus* and *A. crenaticollis*.

In Sweden, the gap-cutting treatment did not significantly affect the flat bug species richness or abundance.

4.5 Disturbance caused by restoration treatments

Restoration burning caused very variable disturbance on the ground on a small scale independent of burn load or study area, the proportion of burned vegetation sample plots (1m x 1m) varied between 0 to 100% (I). According to unpublished data and personal field observations, restoration burning caused greatly varying disturbance on an experimental stand scale, too. In three of the experimental stands in Pahamaailma, all the trees died due to a very severe fire, thus emulating stand-replacing disturbance (II) (Table 4). In Elimyssalo, a large proportion of small trees (4.5–9 cm in dbh) died following restoration burning, switching the diameter distribution towards a higher percentage of larger pine trees (>15cm) and emulating an intermediate severity fire (II and unpublished results) (Table 4). In Elimyssalo, this resulted in a great increase of deciduous trees, especially aspen, undergrowth and number of seedlings (II: Appendix C), whereas in Pahamaailma such a great number of seedling was not observed in five years. In four experimental stands in Pahamaailma and two stands in Oulanka, the fire was low in intensity and patchy in spatial distribution, emulating gap-disturbance and also causing the deaths of single trees (Table 4). In Oulanka, fire changed the composition of tree species from the dominance of spruce to the dominance of deciduous trees with only a minority of spruce (II: Appendix B).

Felling treatments F1 and F2 and Storm simulation treatment (S1) emulated a natural low- or medium-intensity windstorm by uprooting 20% or 40% of the initial volume and producing gaps in the canopy layer, thus causing small scale gap-disturbance and leading to patch- and gap dynamics (I,II). In addition, storm simulation created uprooted patches important for regeneration and successional processes. Storm simulation enhanced regeneration of pioneer plant species and deciduous trees, thereby increasing stand-scale richness of forest vegetation and tree stand structure.

4.6 Restoration methods in relation to their effectiveness in restoring forest naturalness

The aspects of naturalness considered in this study, i.e. structures and species assemblages were most affected by burning treatments, and the felling and gap-cutting treatments clearly had the least effects (Table 4). Restoration burning increased deadwood volume and diversity in the short-term and long-term (II), enabled pioneer plant, tree and insect species to establish (I, II, III, IV), increased

the relative cover of keystone species *V. myrtillus* (I) and enhanced aspen (*P. tremula*) regeneration (I,II), and provided habitat for red-listed, especially pyrophilous beetle and flat bug species (III, IV).

Table 4. The summary table of the results of restoring the naturalness of boreal forests (See Fig. 7). A +-sign indicates that the restoration method had a positive impact on measured variable on and a - -sign indicates a negative impact. 'No effect' means that no clear effect was detected. The article where the original result is shown is given in parenthesis. Blank cells mean that the combination was not studied in this thesis.

Measured variable	Burning (FB1, FB2, Burn)	Felling (F1, F2)	Storm- simulation (S1)	Gap-cutting (Gap)
Structures				
Deadwood volume	+ (II)	+ (II)	+ (II)	
Deadwood diversity	+ (II)	no effect (II)	no effect (II)	
Deadwood continuity	+ (II)	+ (II)	+ (II)	
Tree regeneration	+ (I, II)	no effect (I, II)	+ (I)	
Species				
Early successional plants	+(I)	no effect (I)	+ (I)	
Late successional plants	- (I)	no effect (I)	no effect (I)	
Keystone species (<i>Vaccinium myrtillus</i> , <i>Populus tremula</i>)	+ (I)	no effect (I)	no effect (I)	
Red-listed and pyrophilous insects	+ (III, IV)			no effect (IV)
Early successional beetles and flat bugs	+ (III, IV)			no effect (IV)
Processes simulated by restoration				
Stand-replacing disturbance (successional dynamics)	+ (I, II, this thesis)	no effect	no effect	
Low-severity disturbance (cohort dynamics)	+ (I,II, this thesis)	no effect	no effect	
Gap disturbance (patch dynamics)	+ (I,II, this thesis)	+ (II, this thesis)	+ (II, this thesis)	
Gap disturbance (gap dynamics)	+ (I,II, this thesis)	+ (II, this thesis)	+ (I, II, this thesis)	

According to the results of this thesis, the conceptual figure (Fig. 2) can be updated based on five years measurements and 60 years simulations (Fig. 7). Because the burning treatment brought back structural and functional aspects of

natural forest (Table 4), naturalness of burned stands increased immediately after restoration (Fig. 7). Instead, in felling and storm simulation treatments, the naturalness increased only slightly during the five-year measurements, as the volume of deadwood was increased, whereas the deadwood diversity was still low and vegetation was not affected. However, because the storm simulation treatment formed patches of highly disturbed ground and hence increased richness of plant species and forest floor heterogeneity, the increase in naturalness is greater as compared with felling with a chainsaw. Within the five year study period, the controls remained similar to their initial situation in measured variables; thus the level of naturalness remain similar to the pre-restoration situation in Fig. 7.

After 2011, the illustration of the development of naturalness (Fig. 7) is based on simulation modelling, i.e. on deadwood volumes only, and hence includes great uncertainty. In 60 years, the deadwood volumes were predicted to be rather similar on restored stands as compared with controls within each study area (II). However, as restoration treatments increased the volume of deadwood in 2006, some of the deadwood produced is predicted to remain on experimental stands as advanced decay deadwood (unpublished results). Hence, I suggest that naturalness of restored forest is higher after felling as compared with no restoration. Because storm simulation increases forest floor heterogeneity (I), I suggest this will produce greater naturalness as compared with felling treatment. According to simulation models (II), the control stands will slowly develop towards natural forests, and the time it takes depends on the initial degree of degradation (Fig. 7).

However, the surrounding forest matrix may affect the species assemblages. If the most demanding species cannot disperse to restored forests, the curve may level off before reaching a very high level of naturalness. The same is true of other treatments, even though these are not drawn in the figure (Fig. 7).

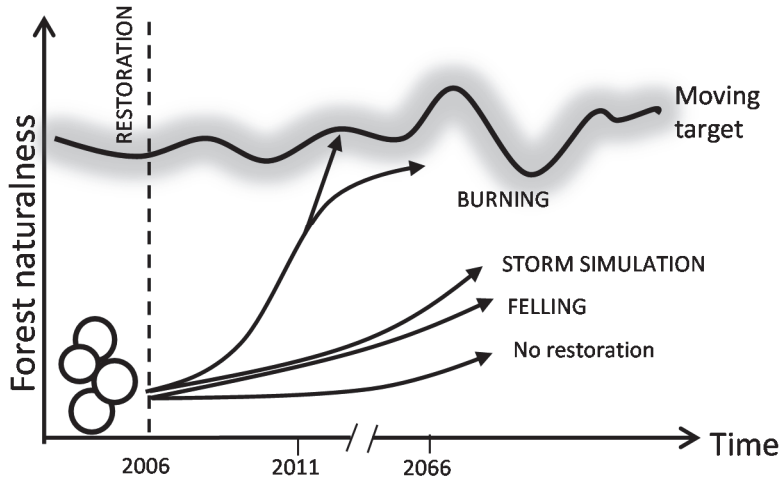


Fig. 7. The schematic figure of results of the thesis illustrated as in Fig. 2 (see section 1.3). The burning treatments were the fastest and greatest in effect in increasing the naturalness. Storm simulation was a slightly more effective method than felling. The control stands, i.e. the stands without restoration actions, will slowly develop toward natural forests.

5 Discussion

5.1 Vegetation dynamics following restoration treatments (I)

The forest understorey vegetation forms an essential part of forest naturalness, and it is one of the most important drivers of ecosystem functioning (Nilsson & Wardle 2005). Brūmelis *et al.* (2011) proposed that the assessment of forest naturalness could be measured using the occurrences of “typical”, “common”, “untypical” and “invasive” species populations. Considering the boreal forest vegetation studied in this thesis, all species are “typical” and “common”, which classification would not have made any clear differences between the treatments. Hence, in this thesis I concentrate on two keystone species, bilberry (*V. myrtillus*) and aspen (*P. tremula*, see section 5.2), both of which have suffered from commercial forest management practices, and changes in disturbance regime (Reinikainen *et al.* 2000). Because the late-successional species (here forest mosses, mainly *Pleurozium schreberi* and *Hylocomium splendens* and dwarf shrub *Empetrum nigrum*) declined in cover and were not able to recover within five years after restoration, and, in turn, bilberry showed a good ability to recover after even severe fire, its relative cover was increased by restoration burning (see also Schimmel & Granström 1996). The belowground stems of bilberry are located relatively deep in the soil, which protects them from the fire. This may be an adaptation to fire-disturbance. Bilberry was not able to reach a similar cover in five years as before the burning, and it may take decades to reach it (Schimmel & Granström 1996). However, previously highly dominant PFT, forest mosses, were replaced after restoration burning by a dominance of dwarf shrubs or pioneer mosses. In a comparison between semi-natural and managed forests, Uotila *et al.* (2002) noticed moss cover to be lower on semi-natural stands as compared with silviculturally managed stands of similar successional stage.

In previous studies, restoration burning has been also shown to increase the richness of plant species (Rees & Juday 2002, Marozas *et al.* 2007, Laarmann *et al.* 2013), possibly due to the intermediate disturbance caused by patchy burning on the vegetation, following intermediate disturbance hypothesis (Connell 1978). In our study, the rates of species loss and colonization were, however, rather equal after five years since the fire, and the species richness was generally low. Species richness declined immediately after burning, but reached its initial level in five years, although with a different composition.

Restoration with tree felling (F1 and F2) was assumed to affect vegetation principally through reduced shading and possibly also through reduced competition with tree roots that may affect the relative covers of understorey species and functional groups (Thomas *et al.* 1999). The felling level F2 was also supposed to affect vegetation more than F1, due to a greater abundance of felled trees. The observed lack of effect suggests that restoration felling 20% or 40% of trees can be considered as a light disturbance type, against which the boreal forest vegetation has been shown to be well buffered (Rydgren *et al.* 2004, Macdonald & Fenniak 2007, Hautala *et al.* 2008). However, because the felled logs and stumps increase the number of microhabitats by e.g. providing shade and later serving as seeding beds for tree seedlings and a habitat for epixylic lichens and mosses (Kuuluvainen & Juntunen 1998, Humphrey *et al.* 2002, Kuuluvainen & Kalmari 2003), the plant species richness is assumed to increase and composition to change in the long term.

Considering the vegetation, the most prominent difference between the felling and storm simulation treatments was the exposed soil that served as an important ‘window of opportunity’ for pioneer species, especially pines and deciduous trees (see also Eriksson & Fröberg 1996, Dahlberg *et al.* 1997, Kuuluvainen & Juntunen 1998). Exposure of mineral soil has previously been shown to enhance sexual reproduction and colonization by weaker competitors (e.g. Grime 1979, Hautala *et al.* 2001, 2008). The exposure of mineral soil is a severe small-scale disturbance, as it breaks the roots and below-ground stems of e.g. dwarf shrubs and may suppress their growth for decades (Jonsson & Esseen 1998, Rydgren *et al.* 2004). At the same time, species with efficient seed dispersal or horizontal vegetative growth (e.g. pleurocarpous mosses) may quickly inhabit the exposed patches (Rydgren *et al.* 2004), which was also seen in our study.

All of the species found in our study are native to Finnish forests, and because the typical boreal forest vegetation does not include many threatened species, no targets regarding the vegetation species composition have previously been set for restoration. However, by understanding the importance of species or functional group diversity for the various ecosystem services e.g. biomass production (Wardle & Zackrisson 2005) and ecosystem resilience in changing disturbance regime and changing climate (e.g. Thompson *et al.* 2009), great diversity in functional type and species composition should be targeted. The restoration treatments in this study maintained all functional groups, and burning and storm simulation treatments increased the diversity of functional groups.

5.2 Tree regeneration on restored forest stands (I, II)

Tree seedlings and saplings form structural component of forest understorey, but regeneration also affects forest functioning through e.g. carbon sequestration and changes that especially deciduous leaf litter causes to soil characteristics, litter- and soil-dwelling species assemblages, and the productivity of the forest stands (Koivula *et al.* 1999, Suominen *et al.* 2003). Natural regeneration is crucially important for restoration stands in Finland, because no planting or sowing is applied. However, in many other countries the restoration of forests includes planting of trees (e.g. Fischer & Fischer 2006). Burning has often been shown to accelerate the establishment especially of deciduous and pine seedlings (e.g. Johnstone *et al.* 2004, Laarmann *et al.* 2013), but our study showed great variation in seedling establishment after burning, even if it generally increased it (I) (see also de Chantal *et al.* 2009). Aspen (*Populus tremula*) was a weak indicator (in indicator species analysis, I) of burning treatment on vegetation sampling plots while *Betula* spp. were more generalists, appearing on disturbed ground, i.e. burned and uprooted ground, and *Pinus sylvestris* clearly increased in cover on uprooted soil patches, showing the importance of mineral soil in its successful establishment (see also e.g. Hille & den Ouden 2004). Even though the number of seedlings was low after storm simulation on a stand scale (II), the plot-scale measurements revealed the importance of small uprooted patches (I). The uprooted soil patches contributed only 1% of the area of experimental stands, and the increase in the number of seedlings could not be detected in the stand-level seedling inventory. The difference in the plot-scale seedling establishment may, however, lead to a difference in the future tree stand structure between felling and storm simulation treatments, even though our stand simulation models could not show this (II).

5.3 Deadwood volume and diversity following restoration treatments (II)

Deadwood is one of the most important structural characteristics of natural boreal forest, due to its importance for a multitude of species and ecosystem functions (Stokland *et al.* 2012 and references therein). The study showed the positive short-term and long-term impact of all restoration methods on deadwood volume, due to the experimental setup ensured that high deadwood volumes to be created. Even the lowest volume of deadwood created in experimental stands was higher

than the average volume in managed forests in Fennoscandia (Fridman & Walheim 2000, Finnish Forest Research Institute 2013). The highest restoration-created volume of deadwood, reaching above $200 \text{ m}^3\text{ha}^{-1}$, was fully comparable with those after stand replacing disturbances in boreal forests (e.g. Siitonen 2001, Wallenius *et al.* 2010). Furthermore, our study included only logs larger than 10 cm in diameter and snags >4.5 cm in dbh, hence the total deadwood volume including stumps and fine woody debris in restored stands was probably much higher (see also Eräjää *et al.* 2010).

The diversity of deadwood was not increased equally by all restoration methods. The restoration felling (F1 and F2) and storm simulation (S1) resulted in a rather high amount of deadwood of low diversity. The low diversity was caused by the initial stand structure, which was highly pine-dominated, and because the trees died immediately following restoration treatment, without the same delay in deaths as after burning treatments. It has been questioned whether chainsaw-felled logs comprise a natural habitat for species (Similä & Junninen 2012). Indeed, a recent study indicates, that sawn spruce logs may not support a similar polypore species assemblage as naturally fallen logs (Komonen *et al.* 2014a). Consequently, it may be assumed that the deadwood produced by storm simulation comprises a more natural habitat for some more demanding species, e.g. old-growth forest indicator species *Phellinus ferrugineofuscus* (Komonen *et al.* 2014a).

Burning treatments enhanced both the volume and diversity of deadwood. In fact, after burning, the diversity of deadwood is probably much higher than what was measured in our study, because we did not consider the degree of charring or scorching of wood or the diameter of produced deadwood (see Stokland 2001, Eriksson *et al.* 2013). The observed delayed deaths of weakened trees was an important aspect that affects the continuity of deadwood in the future, as not all the trees died immediately after burning and hence were more susceptible to various mortality factors. The varying mortality factors will result in diverging pathways in decay succession and thereafter result in different species assemblages of deadwood-dependent species (Stokland & Siitonen 2012). The burned snags and logs provide a habitat for different saproxylic insect species assemblages, depending on factors such as shadiness, fungal assemblage and stand type (e.g. Hilszczański *et al.* 2005, Johansson *et al.* 2007, Toivanen & Kotiaho 2007b), hence the more diverse the deadwood produced, the more species it can be assumed to support.

The MOTTI-simulations for future deadwood formation combined with predictions of the decaying process of the deadwood measured in 2011 showed how the deadwood volumes will fluctuate in time, depending on the rate of formation and decay. In the northern boreal and northern parts of middle boreal forest the decomposition rate is rather low, and the restoration-produced deadwood was predicted to last for more than sixty years, supporting the deadwood availability in the landscape. The selection of trees that are killed during the restoration comprises the starting point for future deadwood dynamics, but what and how much remains alive is important as well. The remaining volume of living trees and number of seedlings set the scheme regarding stand development. The simulations showed that, after the most intense treatment FB2, the remaining volume was too low to provide deadwood in the future, resulting in a gradual decline in deadwood supply. However, natural stand-replacing disturbance may cause a sudden great input of deadwood (e.g. Siitonen 2001, Wallenius *et al.* 2010). Therefore, in the situation as it is today in Finland where stand-replacing fires are extremely rare, such a restoration treatment provides a unique habitat for numerous deadwood-dependent species. However, as compared with natural stand-replacing fires, our study areas are very small, only a few hectares each. Hence, it is important to ensure the fire-continuum in the landscape in order to safeguard the persistence of pyrophilous deadwood-dependent species (see also Ranius *et al.* 2014).

Our results suggest that it may be sufficient to set mature forest stands aside i.e. do nothing, if the stand contains high volumes of deadwood, as the volume of deadwood, for example, in the controls of Pahamaailma was constant over the following 60-year period. Instead, young managed stands often contain very low volumes of deadwood, and their development into a stand with more natural deadwood volumes may take decades, if restoration is not applied (see also Ranius *et al.* 2003, Brassard & Chen 2008, Tikkanen *et al.* 2012).

5.4 Effects of restoration burning on saproxylic beetles (III)

The short-term studies of Hyvärinen *et al.* (2005, 2006) and Toivanen & Kotiaho (2007a,b) have pointed out the benefits of prescribed fire and retention trees on rare and red-listed saproxylic beetles in mature forests. Our results added to this knowledge by showing that young burned forest stands can also provide a habitat for a large number of saproxylic rare and red-listed species, at least when the areas are located near to possible species source areas (see e.g. Kouki *et al.* 2012).

We also showed how the beetle diversity declines as the species succession proceeds, supporting previous studies (Saint-Germain *et al.* 2004a, Boulanger & Sirois 2007, Toivanen & Kotiaho 2007b).

As was also shown in the previous section (5.3), fire creates a large amount of unique resources for saproxylic species, many of which are especially attracted to sun-exposed deadwood that is found in burned or clear-cut areas (Saint-Germain *et al.* 2004b, Lindhe *et al.* 2005). However, without a suitable breeding habitat the species will not survive in the area, and their populations will decline. Therefore, it was important to find several red-listed species, e.g. *Stephanopachys linearis* and *Boros schneideri* present in burned study areas during several years after restoration, indicating that the species were possibly able to reproduce in the burned areas. Thus, restored stands could act as a source population for surrounding areas. Ranius *et al.* (2014) found that e.g. the red-listed pyrophilous species *Stephanopachys linearis* may persist on the burned stand for several years, until the substrate, i.e. the inner bark, has been completely consumed. The decline in species diversity and abundance noticed is a natural consequence resulting in species turnover during the succession (Esseen *et al.* 1997, Saint-Germain *et al.* 2004b, Boulanger & Sirois 2007). Hence, a continuum in burned areas within a landscape is needed to sustain a high diversity of pyrophilous species, even though some of the pyrophilous species may persist on clear-cuts with sufficient volumes of retention trees (e.g. Hyvärinen *et al.* 2006, Toivanen & Kotiaho 2007b).

A greater volume of deadwood has often resulted in a greater diversity of beetles (e.g. Økland *et al.* 1996, Martikainen *et al.* 2000, Similä *et al.* 2003, McGeoch *et al.* 2007, Stenbacka *et al.* 2010), but we did not detect such a relationship in our experiment (see also Toivanen & Kotiaho 2007a). The reason might be the volatiles released by large numbers of dying trees and the warm microclimate that attracts beetles in their search for mating sites (Brattli *et al.* 1998), which may have masked the effect of deadwood volumes within the experimental stand. Furthermore, previous studies have shown that a local deadwood pool may not be as important for saproxylic species as a landscape deadwood pool, especially for red-listed species (Götmark *et al.* 2011, Gibb *et al.* 2006).

While studying the effects of restoration on beetle communities, we did not distinguish the effect of fire from the effect of felling. Indeed, in Finland, restoration burning usually includes tree felling for fuel (Similä & Junninen 2012). In a recent study, Komonen *et al.* (2014b) showed in a wide restoration

experiment including only deadwood addition that the number of species increases after the treatments, but the number of rare and red-listed species was rather low compared to ours, thus emphasizing the importance of either fire or good source areas for the rare and red-listed species (see also Toivanen & Kotiaho 2007a, 2010, Hyvärinen *et al.* 2005, 2006, Kouki *et al.* 2012).

Today, young forests stands (20–40 years old) cover most of the managed forest area in Finland (Finnish Forest Research Institute 2013). These stands are usually very low in biodiversity (III, IV) as they contain very low amounts of deadwood due to previous silvicultural management (II), and hence they are often distinctly different from natural young stands (see e.g. Uotila *et al.* 2002 for a comparison between young managed and young semi-natural stands in vegetation composition). We showed that these low-biodiversity stands can be restored effectively to become a suitable habitat for a large number of saproxylic species, without risking the assemblages of the species dependent of advanced decay logs, as there are no large logs. Such low-quality stands may be abundant near to protection areas, and their restoration would increase the effective size of protection areas. Previous studies have shown that fine woody debris (i.e. deadwood smaller than 10 cm in diameter) can support many deadwood-dependent species (e.g. Kruys & Jonsson 1999, Nordén *et al.* 2004). However, as some species are strictly dependent on large deadwood (e.g. Brin *et al.* 2011), the restoration actions should not be targeted only on young stands with small diameter trees.

5.5 Effects of restoration burning and gap-cutting on flat bugs (IV)

Even though the number of flat bug specimens and species was low in our study, we showed that flat bug abundance was greater after restoration burning both in Finland and Sweden as compared with controls or gap-cut stands. Even though the statistical testing was not conducted in Finland and only for some species in Sweden, the result showing that only one specimen was caught from the controls and none prior to restoration is rather clear evidence of the benefits of restoration burning on flat bug species. Instead, in contrast to the second hypothesis, the number of flat bugs was not increased by gap-cutting treatment, thus further underlining the importance of fire for these species.

The species caught in Finland were different to those caught in Sweden. The observed difference may be caused by the difference in sampling methods (freely hanging vs. trunk-attached window trap, the size of the traps), but a more likely

reason is the difference in sampling schedule after restoration, as in Finland the sampling was conducted immediately after restoration, and in Sweden a year after treatments. The species caught in Finland (*Aradus angularis* (EN), *A. laeviusculus* (EN) and *A. lugubris*) may be restricted to fresh burned areas (see also Viiri & Eerikäinen 2012, Moretti *et al.* 2004). In fact, the IR-sensing organ of *A. lugubris* (Schmitz *et al.* 2010) suggests that the species probably demands burned areas. Because in Sweden only immature nymphs of *A. lugubris* were found a year after burning, this may indicate that the species has reproduced on burned study areas. The other reason for red-listed species being missing in Sweden may be their very low densities and paucity of good-quality source areas close to restored stands, whereas in Finland the source areas are very close to study areas (see also Viiri & Eerikäinen 2012).

Also *A. betulae*, *A. betulinus* and *A. crenaticollis* showed a great attraction for burned stands in Sweden, which supports a previous study by Johansson *et al.* (2010) (see also Rinne & Rintala 2010). However, the reason behind the fire-attraction may not be the fire *per se*, but e.g. fungi inhabiting the burned wood, or a warmer microclimate. However, our study suggests that restoration burning is more beneficial for these flat bugs as compared with gap-cutting, and that restoration burning enhances the populations of deadwood-dependent flat bugs, including the red-listed flat bugs.

5.6 Effectiveness of restoration in mimicking natural disturbances

In this thesis, restoration simulated natural disturbances which initiate the successional development of forests. Restoration burning aimed to emulate wildfire of various severities, as the fuel load proportions used, 20% in FB1 and 40% in FB2, were intended to cause a difference in fire severity. However, regardless of the treatment and study area, fire burned a highly varying proportion of ground in the vegetation sampling plots and experimental stands. Hence the disturbance caused by restoration burning varied between patchy, low-severity surface fire that leads to i) gap dynamics by killing some of the vegetation and a few trees, to ii) cohort dynamics caused by low-intensity fire that killed the young cohort and most of the vegetation, or to iii) successional dynamics, caused by stand-replacing disturbance, in which all the trees in a forest stand are killed by fire. Thus, the restoration burning exhibited all types of main disturbance dynamics (Angelstam 1998, Angelstam & Kuuluvainen 2004, Kuuluvainen & Aakala 2011). However, natural wildfires are usually much larger compared to the

experimental burnings of a few hectares each, and the fire severity may vary greatly within the burned landscape, depending on site factors, stand composition and fire behaviour (Angelstam 1998, Kafka *et al.* 2001). Landscape level analyses were not conducted in this study, but in each of the study areas restoration included one to three separately burned stands, thus increasing the landscape-level heterogeneity.

The storm simulation treatment caused small and fine scale gap-disturbance by killing groups of trees and single trees by uprooting them, which is similar to the impacts after natural windfalls. Instead, felling with a chainsaw does not properly mimic disturbance events other than perhaps stem breakages, which occur due to e.g. high snow loads, and may cause significant impact on forest stands in especially at higher altitudes, >250 m a.s.l. (Jalkanen & Konopka 1998). Even under these situations, trees fallen or broken during a windstorm may have been weakened by e.g. decaying fungi, whereas trees felled in restoration are healthy. Despite its small short-term benefits on forest naturalness, felling may nevertheless be an efficient method to produce deadwood especially in areas where heavy machinery cannot be used.

6 Conclusions

According to the variables explored in this thesis, all of the restoration methods studied increased the naturalness of the forests in terms of structure, and hence they accelerated the development towards natural forests. However, throughout the study, burning caused the fastest and greatest changes on the structure and species assemblages, and caused the most variable disturbances as compared with felling or storm simulation treatments. Hence, we conclude that all restoration methods enhance the naturalness of the boreal forest stands studied, but burning is the most effective of them.

Rouvinen & Kouki (2008) have suggested a definition of “natural forest” as follows:

“a forest that has evolved and reproduced itself naturally from organisms previously established, and that has not been significantly altered by human activity, i.e. it is forest whose structure and dynamics have not significantly been affected by humans.”

By this definition, I can hardly claim that the restoration actions used in this study have produced natural forest. However, because the conservation areas in Finland are rather small and natural lightning-induced fires are rare, the chance of a natural lightning-induced fire within a conservation area is extremely low. Thus, I claim that human interference by restoration burning is needed to restore fire-disturbance, especially of intermediate or high severity, in Fennoscandian conservation areas. Restoration burning enhances naturalness of the forest stands by initiating natural post-fire succession. Restoration burning can also be used to mimic the impacts of small-scale disturbances, whereas tree felling and storm simulation caused only smaller patches and gaps. Burning is very unpredictable in its effects, thereby also mimicking natural disturbances, whereas felling and storm simulation produce predictable types of deadwood and remaining living tree structure. The surrounding landscape matrix should, however, determine the restoration method used, by acknowledging the missing components of naturalness in the ecosystem, and selecting the methods according to the needs.

6.1 Implications to practical forest restoration

According to the results of this thesis, I present some remarks for selecting where and when to restore and what methods to use, and I recommend improvements in the current restoration methods.

- Stand-replacing fire may hamper local deadwood formation in the future. To ensure landscape-level deadwood continuity over the following decades, I suggest that many different restoration methods could be used simultaneously, also to produce different types of deadwood.
- The burned stands seemed not to support high species richness of beetles for a long time, as after five years the species richness was similar to pre-restoration situation. Thus, the spatial and temporal continuum of fire needs to be maintained so as to benefit pyrophilous species populations most.
- Burning was the most efficient method to enhance deciduous and especially aspen regeneration, but it did not increase deciduous seedlings in all study areas. If the aim is to increase deciduous tree establishment (e.g. aspen), restoration should be targeted to sites where such trees occur initially to ensure their efficient regeneration.
- Low-biodiversity young stands (in the vicinity of good-quality source areas) were efficiently restored by burning to become suitable habitats for a large number of red-listed saproxylic species. If young stands without initial deadwood are located within a dispersal distance, they can be restored by burning without risking the assemblages of the species dependent of advanced decay logs. Such stands can serve as stepping stones between conservation areas or increase the size of conservation areas.
- The signs of human intervention will show for decades in the form of man-made sawn stumps produced in tree felling. Hence, the use of an excavator to push down the trees represents a more natural way of felling. I suggest that whenever possible the use of an excavator to fell trees should replace felling with a chainsaw, for greater and faster effects on the vegetation structure of the forest floor and seedling establishment and because it is not guaranteed that sawn logs comprise a suitable habitat for the most demanding deadwood-dependent species.

6.2 Future prospects

In this experimental study, restoration was conducted within a good-quality forest landscape, in a close proximity to the Russian border, where silvicultural forestry is not as intensive as in most of Finland, and forest fires (natural or human-induced) still occur in a rather regular manner. As a result, a high number of red-listed deadwood-dependent and pyrophilous species were able to disperse, possibly from the Russian side, or from the surrounding nature conservation areas, to restoratively burned stands in Finland that were originally poor in biodiversity. It remains to be studied whether restoration could improve the species pool sufficiently that the restored areas could act as source populations or stepping stones for red-listed species dispersal in the future.

Restoration burning is very expensive; the hectare-based cost in our study exceeded €2000. At the same time, firefighters extinguish natural wildfires that rather regularly occur during the high fire risk period, but which are not allowed to spread. One option to reduce the costs of burning at some sites and suppress wildfires at other sites would be to buy suitable burned forests for protection, or rent them for temporary protection. Suitable areas could be those in close connection with previously burned stands to enhance the fire continuum, or close to conservation areas, to increase the effective conservation area. The same approach could be applied to naturally storm- or snow-damaged forest stands, in which fallen trees increase structural naturalness, whereas economic loss is caused through lost net harvest revenues. Under present legislation, however, the dead and damaged trees need to be removed from the stand to prevent insect outbreaks (Laki metsätuhojen torjunnasta 1087/2013), which are risky especially for spruce forests in Southern Finland.

The increasing efficiency in management and salvage logging after fire or other natural disturbance (e.g. storm, insect outbreak) pose a threat to deadwood-dependent species and the functioning of the boreal forest ecosystem (Lindenmayer *et al.* 2004, Lindenmayer & Noss 2006, Cyr *et al.* 2009). Deadwood that is not salvaged after natural disturbances has also been recognized as a promising resource for bioenergy by the Intergovernmental Panel on Climate Change (IPCC) (see Barrette *et al.* 2015). Hence, the goals established in the Convention on Biological Diversity (CBD 2010) to halt the decline of biodiversity (through, for example, an increase of deadwood) and by the IPCC to increase bioenergy production (which removes the deadwood) are very controversial. It seems that the importance of deadwood on the biodiversity and

functioning of ecosystems is not fully understood globally and this stresses the need for further attention from researchers, especially in transferring the scientific knowledge into political decision-making.

References

- Ahti T, Hämet-Ahti L & Jalas J (1968) Vegetation zones and their sections in northwestern Europe. *Ann Bot Fenn* 5: 169–211.
- Angelstam PK & Kuuluvainen T (2004) Boreal forest disturbance regimes, successional dynamics and landscape structures – a European perspective. *Ecol Bull* 51: 117–136.
- Angelstam PK (1998) Maintaining and restoring biodiversity in European forests by developing natural disturbance regimes. *J Veg Sci* 9: 593–602.
- Attiwill PM (1994) The disturbance dynamics of forest ecosystems: the ecological basis for conservative managements. *Forest Ecol Manag* 63: 247–300.
- Barcley-Estrup P (1970) The description and interpretation of cyclical processes in a heath community: II. Changes in biomass and shoot production during the *Calluna* cycle. *J Ecol* 58: 243–249.
- Barrette J, Thiffault E, Saint-Pierre F, Wetzal S, Duchesne I & Krigstin S (2015) Dynamics of dead tree degradation and shelf-life following natural disturbances: can salvaged trees from boreal forests ‘fuel’ the forestry and bioenergy sectors? *Forestry* 88: 275–290.
- Bates D, Maechler M & Bolker B (2011) *lme4*: Linear mixed-effect models using S4 classes. R package version 0.999375-42. URL: <http://lme4.r-forge.r-project.org/>. Accessed 02/2012.
- Bates D, Maechler M & Bolker B (2012) Package *lme4*. Linear mixed effects models using S4 classes. Version 0.99999-0. URL: <http://lme4.r-forge.r-project.org/>. Accessed 08/2012.
- Bates D, Maechler M, Bolker B & Walker S (2013) Package *lme4*. Linear mixed effects models using Eigen and S4. Version 1.0-4. URL: <http://CRAN.R-project.org/package=lme4>. Accessed 05/2015.
- Bergeron Y, Leduc H, Harvey BD & Gauthier S (2002) Natural fire regime: a guide for sustainable managements of the Canadian boreal forests. *Silva Fenn* 36: 81–95.
- Blanck Y-I (2015) Historic range of variability in the fire regime of a Fennoscandian boreal forest – the Trillemarka-Rollagsfjell Nature reserve. PhD Thesis. Department of Ecology and Resource Management, Faculty of Environmental Science and Technology, Norwegian University of Life Sciences.
- Bouchard M & Pothier D (2011) Long-term influence of fire and harvesting on boreal forest age structure and forest composition in eastern Québec. *Forest Ecol Manag* 261: 811–820.
- Boucher Y, Arseneault D, Sirois L & Blais L (2009) Logging pattern and landscape changes over the last century at the boreal and deciduous forest transition in eastern Canada. *Landscape Ecol* 24: 171–184.
- Boulanger Y & Sirois L (2007) Postfire succession of saproxylic Arthropods, with emphasis on Coleoptera, in the North Boreal Forest of Quebec. *Environ Entomol* 36: 128–141.
- Brassard BW & Chen HY (2008) Effects of forest type and disturbance on diversity of coarse woody debris in boreal forests. *Ecosystems* 11: 1078–1090.

- Brattli JG, Andersen J & Nilssen AC (1998) Primary attraction and host tree selection in deciduous and conifer living Coleoptera: Scolytidae, Curculionidae, Cerambycidae and Lymexylidae. *J Appl Entomol* 122: 345–352.
- Brin A, Bouget C, Brustel H & Jactel H (2011) Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. *J Insect Conserv* 15: 653–669.
- Brümelis G, Jonsson BG, Kouki J, Kuuluvainen T & Shorohova E (2011) Forest naturalness in Northern Europe: Perspectives on processes, structures and species diversity. *Silva Fenn* 45: 807–821.
- Burton PJ & Macdonald SE (2011) The restorative imperative: challenges, objectives and approaches to restoring naturalness in forests. *Silva Fenn* 45: 843–863.
- Cajander AK (1926) The theory of forest types. *Acta Forest Fenn* 29: 1–108.
- CBD (Convention on Biological Diversity) (2010) COP 10 DecisionX/2: Strategic Plan for biodiversity 2011–2020. <http://www.cbd.int/decision/cop/?id=12268>. Accessed 05/2015.
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310.
- Coulianos CC (1989) New provincial records of bark stinkbugs (Hem.-Het., Aradidae) together with *Aradus truncatus*, new for Sweden. *Ent Tidskr* 110: 53–57.
- Crawley MJ (2007) *The R book*. West Sussex, John Wiley & Sons Ltd.
- 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. *Front Ecol Environ* 7: 519–524. doi:10.1890/080088.
- Dahlberg A, Zackrisson O, Nilsson MC & Jaderlund A (1997) Interference mechanisms in conifer – Ericaceae – feathermoss communities. *Oikos* 78: 209–220.
- de Cáceres M & Jansen F (2012) Indicspecies-package. Functions to assess the strength and significance of relationships of species site group associations. Version 1.6.5. <http://www.inside-r.org/packages/indicspecies/versions/1-6-5>. Accessed 12/2012.
- de Cáceres M, Legendre P & Moretti M (2010) Improving indicator species analysis by combining groups of sites. *Oikos* 119: 1674–1684.
- de Chantal M, Lilja-Rothsten S, Peterson C, Kuuluvainen T, Vanha-Majamaa I & Puttonen P (2009) Tree regeneration before and after restoration treatments in managed boreal *Picea abies* stands. *Appl Veg Sci* 12: 131–143.
- Deyrup M & Mosley JG (2004) Natural history of the flat bug *Aradus gracilicornis* in fire-killed pines (Heteroptera: Aradidae). *Florida Entomol* 87: 79–81.
- Dufrene M & Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol Monogr* 67: 345–366.
- Ehnström B & Axelsson R (2002) *Insektgnag i bark och ved*. Uppsala, ArtDatabanken.
- Eriksson O & Fröborg H (1996) ‘Windows of opportunity’ for recruitment in long-lived clonal plants: experimental studies of seedling establishment in *Vaccinium* shrubs. *Can J Bot* 74: 1369–1374.

- Eriksson A-M, Olsson J, Jonsson BG, Toivanen S & Edman M (2013) Effects of restoration fire on dead wood heterogeneity and availability in three *Pinus sylvestris* forests in Sweden. *Silva Fenn* 47: 954.
- Eräjää S, Halme P, Kotiaho JS, Markkanen A & Toivanen T (2010) The volume and composition of dead wood on traditional and forest fuel harvested clear-cuts. *Silva Fenn* 44: 203–211.
- Esseen P-A, Ehnström B, Ericson L & Sjöberg K (1997) Boreal forests. *Ecol Bull* 46: 16–47.
- European Union (2011) EU Biodiversity strategy to 2020. <http://ec.europa.eu/environment/nature/info/pubs/docs/factsheets/Biod%20Strategy%20FS.pdf>. Accessed 04/2015
- Finnish Forest Research Institute (2013) Finnish statistical yearbook of forestry 2013. Sastamala. ISBN 978-951-40-2450-4 (PDF). Available at <http://www.metla.fi/julkaisut/metsatilastollinenusk/>
- Fischer A & Fischer H (2006) Restoration of forests. In: van Andel J & Aronson J (eds.) (2006) *Restoration ecology: The new frontier*. Oxford, Blackwell Publishing: 124–140.
- Franklin JF, Shugart HH & Harmon ME (1987) Tree death as an ecological process. *Bioscience* 37: 550–556.
- Fridman J & Walheim M (2000) Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *Forest Ecol Manag* 131: 23–36.
- Gibb H, Hjältén J, Ball JP, Atlegrim O, Pettersson RB, Hilszczański J, Johansson T & Danell K (2006) Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: a study using experimental logs for monitoring assemblages. *Ecography* 29: 191–204.
- Granström A (2001) Fire management for biodiversity in the European boreal forest. *Scand J For Res Suppl* 3: 62–69.
- Grime JP (1979) *Plant strategies and vegetation processes*. New York, Wiley.
- Gärdenfors U (2010) The 2010 Red List of Swedish species. Uppsala, Artdatabanken.
- Götmark F, Asegard E & Franc N (2011) How we improved a landscape study of species richness of beetles in woodland key habitats, and how model output can be improved. *Forest Ecol Manag* 262: 2297–2305.
- Halme P, Allen KA, Auniņš A, Bradshaw RHW, Brūmelis G, Čada V, Clear JL, Eriksson A, Hannon G, Hyvärinen E, Ikauniece S, Iršėnaitė R, Jonsson BG, Junninen K, Kareksela S, Komonen A, Kotiaho JS, Kouki J, Kuuluvainen T, Mazziotta A, Mönkkönen M, Nyholm K, Oldén A, Shorohova E, Strange N, Toivanen T, Vanha-Majamaa I, Wallenius T, Ylisirniö A & Zin E (2013) Challenges of ecological restoration: Lessons from forests in northern Europe. *Biol Cons* 167: 248–256.
- Hammond HEJ (1997) Arthropod diversity from *Populus* coarse woody material in north-central Alberta: a review of taxa and collection methods. *Can Entomol* 129: 1009–1033.
- Hanski I (2000) Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. *Ann Zool Fenn* 37: 271–280.

- Harmon ME, Franklin JF, Swansson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkamper GW, Cromack KJ & Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15:133–302.
- Hastie TJ & Tibshirani RJ (1990) *Generalized Additive Models*. Boca Raton, Chapman and Hall/CRC.
- Hautala H, Tolvanen A & Nuortila C (2001) Regeneration strategies of dominant boreal forest dwarf shrubs in response to selective removal of understory layers. *J Veg Sci* 12: 503–510.
- Hautala H, Tolvanen A & Nuortila C (2008) Recovery of pristine boreal forest floor community after selective removal of understorey, ground and humus layers. *Plant Ecol* 194: 273–282.
- Heinonen J (1994) Koealojen puustotunnusten laskentaohjelma KPL. Käyttöohje. Metsäntutkimuslaitoksen tiedonantoja 504. 80 pp. In Finnish.
- Hille M & den Ouden J (2004) Improved recruitment and early growth of Scots pine (*Pinus sylvestris* L.) seedlings after fire and soil scarification. *Eur J For Res* 123: 213–218
- Hilszczański J, Gibb H, Hjältén J, Atlegrim O, Johansson T, Pettersson RB, Ball JP & Danell K (2005) Parasitoids (Hymenoptera, Ichneumonoidea) of Saproxylic beetles are affected by forest successional stage and dead wood characteristics in boreal spruce forest. *Biol Cons.* 126: 456–464.
- Hjältén J, Atlegrim O, Sandstöm F, Pettersson R & Rexstad EA (2006) Occurrence of flat bugs (Heteroptera: Aradidae) in burned and unburned forests. *Entomol Fenn* 17: 130–135
- Humphrey J, Davey S, Peace A, 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. *Biol Cons* 107: 165–180.
- Hynynen J (1993) Self-thinning models for even-aged stands of *Pinus sylvestris*, *Picea abies* and *Betula pendula*. *Scand J For Res* 8: 326–336.
- Hynynen J, Ahtikoski A, Siitonen J, Sievänen R & Liski J (2005) Applying the MOTTI simulator to analyse the effects of alternative management schedules on timber and non-timber production. *Forest Ecol Manag* 207: 5–18.
- Hynynen J, Ojansuu R, Hökkä H, Siipilehto J, Salminen H & Haapala P (2002) Models for predicting stand development in MELA system. In: Finnish Forest Research Institute, Research Papers 835, pp. 1–116.
- Hynynen J, Salminen H, Ahtikoski A, Huuskonen S, Ojansuu R, Siipilehto J, Lehtonen M & Eerikäinen K (2014) Long-term impacts of forest management on biomass supply and forest resource development: a scenario analysis for Finland. *Eur J For Res* 134: 415–431.
- Hyvärinen E (2006) Green-tree retention and controlled burning in restoration and conservation of beetle diversity in boreal forests. Academic dissertation. *Dissertationes Forestales* 21. University of Joensuu, Finland. 29 pp.

- Hyvärinen E, Kouki J & Martikainen P (2006) Fire and green-tree retention in conservation of red-listed and rare deadwood-dependent beetles in Finnish boreal forest. *Cons Biol* 20: 1711–1719.
- 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 Ecol Manag* 212: 315–332.
- Hökkä H (1997) Models for predicting growth and yield in drained peatland stands in Finland. In: Finnish Forest Research Institute Research Papers 651, pp. 45–53.
- Hökkä H & Salminen H (2006) Utilizing information on site hydrology in growth and yield modeling: peatland models in MOTTI stand simulator. In: Proc. Conf. Hydrology and Management of Forested Wetlands, New Bern, pp. 302–308.
- Jalkanen R & Konopka B (2001) Snow-packing as a potential harmful factor on *Picea abies*, *Pinus sylvestris*, and *Betula pubescens* at high altitude in Northern Finland. *Eur J For Pat* 28: 373–382.
- Janisch JE & Harmon ME (2002) Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. *Tree Phys* 22: 77–89.
- Johansson T, Hjältén J, Stenbacka F & Dysenius M (2010) Responses of eight boreal flat bug (Heteroptera: Aradidae) species to clear-cutting and forest fire. *J Insect Cons* 14: 3–9.
- Johansson T, Hjältén T, Gibb H, Hilszczanski, J Stenlid, J, Ball J, Alinvi O & Danell K (2007) Variable response of different functional groups of saproxylic beetles to substrate manipulation and forest management: Implications for conservation strategies. *Forest Ecol Manag* 242: 496–510.
- Johnstone JF, Chapin III FS, Foote S, Kemmett S, Price K & Viereck L (2004) Decadal observations of tree regeneration following fire in boreal forests. *Can J For Res* 34: 267–273. DOI: 10.1139/x03-183.
- Jonsell M, Weslien J & Ehnström B (1998) Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodivers Cons* 7: 749–764.
- Jonsson BG & Esseen PE (1998) Plant colonization in small forest-floor patches: importance of plant group and disturbance traits. *Ecography* 21: 518–526.
- Jonsson BG & Siitonen J (2012) Introduction. In: Stokland J, Siitonen J & Jonsson BG (2012) Biodiversity in dead wood. Cambridge University Press. Pp. 1–9.
- Kafka V, Gauthier S & Bergeron Y (2001) Fire impacts and crowning in boreal forests: a study of a large wildfire in Western Quebec. *Int J Wildland Fire* 10: 119–127.
- Klocke D, Schmitz H (2012) Material properties of photomechanical infrared receptors in pyrophilous *Melanophila* beetles and *Aradus* bugs. *Acta biomaterialia* 8: 3392–3399
- Koch K (1989a) Die Käfer Mitteleuropas: Ökologie. Band 1. Krefeld, Goecke & Evers Verlag.
- Koch K (1989b) Die Käfer Mitteleuropas: Ökologie. Band 2. Krefeld, Goecke & Evers Verlag.
- Koch K (1992) Die Käfer Mitteleuropas: Ökologie. Band 3. Krefeld, Goecke & Evers Verlag.

- Koivula M, Punttila P, Haila Y & Niemelä J (1999) Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) on the boreal forest. *Ecography* 22: 424–435.
- Komonen A, Halme P, Jäntti M, Koskela T, Kotiaho JS & Toivanen T (2014a) Created substrates do not fully mimic natural substrates in restoration: the occurrence of polypores on spruce logs. *Silva Fenn* 48 (1).
- Komonen A, Kuntsi S, Toivanen T & Kotiaho JS (2014b) Fast but ephemeral effects of ecological restoration on forest beetle community. *Biodivers Conserv* 23: 1485–1507.
- Kouki J, Arnold K & Martikainen P (2004) Long-term persistence of aspen – a key host for many threatened species – is endangered in old-growth conservation areas in Finland. *J Nat Conserv* 12: 41–52.
- 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. *Scand J For Res* 16: 27–37.
- Kouki J, Hyvärinen E, Lappalainen H, Martikainen P & Similä M (2012) Landscape context affects the success of habitat restoration: large-scale colonization patterns of saproxylic and fire-associated species in boreal forests. *Divers Distrib* 18: 348–355.
- Kruys N & Jonsson BG (1999) Fine woody debris is important for species richness on logs in managed boreal spruce forests of Northern Sweden. *Can J For Res* 29: 178–186.
- Kuuluvainen T (2002) Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fenn* 36: 97–125.
- Kuuluvainen T & Juntunen P (1998) Seedling establishment in relation to microhabitat variation in a windthrow gap in a boreal *Pinus sylvestris* forest. *J Veg Sci* 9: 551–462.
- Kuuluvainen T & Kalmari R (2003) Regeneration microsites of *Picea abies* seedlings in a windthrow area of a boreal old-growth forest in southern Finland. *Ann Bot Fenn* 40: 401–413.
- Kuuluvainen T & Aakala T (2011) Natural forest dynamics in boreal Fennoscandia: a review and classification. *Silva Fenn* 45: 823–841.
- Kuuluvainen T, Aapala K, Ahlroth P, Kuusinen M, Lindholm T, Sallantausta T, Siitonen J & Tukia H (2002) Principles of ecological restoration of boreal forested ecosystems: Finland as an example. *Silva Fenn* 36: 409–422.
- Kuznetsova A, Brockhoff PB & Christensen RH (2013) lmerTest: Tests for random and fixed effects for linear mixed models (lmer objects of lme4 package). R package version 2.0-0. URL: [http://CRAN.R-project.org/package=lmerTest].
- Laarmann D, Korjus H, Sims A, Kangur A & Stanturf JA (2013) Initial effects of restoring natural forest structures in Estonia. *Forest Ecol Manag* 304: 303–311.
- Laki metsätuhojen torjunnasta 1087/2013. Lag om bekämpning av skogskador 1087/2013. <https://www.finlex.fi/fi/laki/alkup/2013/20131087>. In Finnish and Swedish. Accessed 5/2015
- Latva-Karjanmaa T, Suvanto L, Leinonen K & Rita H (2006) Sexual reproduction of European Aspen (*Populus tremula* L.) at prescribed burned site: the effects of moisture conditions. *New Forests* 31: 545–558.

- Lilja S & Kuuluvainen T (2005) Structure of old *Pinus sylvestris* dominated forest stands along a geographic and human impact gradient in mid-boreal Fennoscandia. *Silva Fenn* 39: 407–428.
- Lindhe A, Lindelöw Å & Åsenblad N (2005) Saproxylic beetles in standing dead wood density in relation to substrate sun-exposure and diameter. *Biodivers Cons* 14: 3033–3053.
- Lindenmayer DB & Noss RE (2006) Salvage logging, ecosystem processes and biodiversity conservation. *Cons Biol* 20: 949–958.
- Lindenmayer DB, Foster DR, Franklin JF, Hunter ML, Noss RF, Schmiegelow FA & Perry D (2004) Salvage harvesting policies after natural disturbance. *Science* 303: 1303.
- Linder P & Östlund L (1998) Structural changes in three mid-boreal Swedish forest landscapes, 1885–1996. *Biol Cons* 85: 9–19.
- Lonsdale D, Pautasso M & Holdenrieder O (2008) Wood-decaying fungi in the forest: conservation needs and management options. *Eur J For Res* 127: 1–22.
- Macdonald SE & Fenniak T (2007) Understory plant communities of boreal mixedwood forests in western Canada: natural patterns and response to variable-retention harvesting. *Forest Ecol Manag* 242: 34–48.
- MacKenzie MD, DeLuca TH & Sala A (2006) Fire exclusion and nitrogen mineralization in low elevation forests of western Montana. *Soil Biol Bioc* 38: 952–961.
- Mallik AU (2003) Conifer regeneration problems in boreal and temperate forests with ericaceous understory: Role of disturbance, seedbed limitation and keystone species change. *Crit Rev Plant Sci* 22: 341–366.
- Marozas V, Racinskas J & Bartkevicius E (2007) Dynamics of ground vegetation after surface fires in hemiboreal *Pinus sylvestris* forests. *Forest Ecol Manag* 250: 47–55.
- Martikainen P (2001) Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. *Ecol Bull* 49: 205–218.
- Martikainen P & Kouki J (2003) Sampling the rarest: threatened beetles in boreal forest biodiversity inventories. *Biodivers Cons* 12: 1815–1831.
- Martikainen P, Siitonen J, Punttila P, Kaila L & Rauh J (2000) Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biol Cons* 94: 199–209.
- Marzano R, Garbarino M, Marcolin E, Pividori M & Lingua E (2013) Deadwood anisotropic facilitation on seedling establishment after a stand-replacing wildfire in Aosta Valley (NW Italy). *Ecol Eng* 51: 117–122.
- Matala J, Hynynen J, Miina J, Ojansuu R, Peltola H, Sievänen R, Väisänen H & Kellomäki S (2003) Comparison of a physiological model and a statistical model for prediction of growth and yield in boreal forests. *Ecol Model* 161: 95–116.
- McCarthy J (2001) Gap dynamics of forest trees: a review with particular attention to boreal forests. *Environ Rev* 9: 1–59.
- McGeoch M, Schroeder M, Ekbohm B & Larson S (2007) Saproxylic beetle diversity in a managed boreal forest: importance of stand characteristics and forestry conservation measures. *Divers Distrib* 13: 418–429.

- Moretti M, Obrist MK & Duelli P (2004) Arthropod biodiversity after forest fires: winners and losers in the winter fire regime of the southern Alps. *Ecography* 27: 173–186.
- Mäkinen H, Hynynen J, Siitonen J & Sievänen R (2006) Predicting the decomposition of Scots pine, Norway spruce and birch stems in Finland. *Ecol Appl* 16: 1865–1879.
- Mönkkönen M, Juutinen A, Mazziano A, Miettinen K, Podkopaev D, Reunanen P, Salminen H & Tikkanen O-P (2014). Spatially dynamic forest management to sustain biodiversity and economic returns. *J Environ Man* 134: 80–89.
- 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 M-C & Wardle D (2005) Understorey vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Front Ecol Environ* 3: 421–428.
- Nilsson M-C, Zackrisson O, Sterner O & Wallstedt A (2000) Characterisation of the differential interference effects of two boreal dwarf shrub species. *Oecologia* 123: 122–127.
- 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. *Biol Cons* 117: 1–10.
- Økland B, Bakke A, Hågvar S & Kvamme T (1996) What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodivers Cons* 5: 75–100.
- Oksanen J, Blanchet G, Kindt R, Legendre P, Minchin P, O'Hara B, Simpson GL, Solymos P, Stevens MHH & Wagner H (2011) *Vegan: Community ecology package*. R package version 2.0-8. URL: <http://cran.r-project.org/package=vegan>. Accessed 04/2012.
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHM & Wagner H (2013) *Vegan. Community Ecology Package*, version 2.0-6. URL: <http://vegan.r-forge.r-project.org/>. Accessed 05/2015.
- Olsson J & Jonsson BG (2010) Restoration fire and wood-inhabiting fungi in a Swedish *Pinus sylvestris* forest. *Forest Ecol Manag* 259: 1971–1980.
- Palm T (1951) Die Holz- und Rindenkäfer der nordschwedischen Laubbäume. Meddelanden från Statens Skogsforskningsinstitut, No. 40. 242 pp.
- Palm T (1959) Die Holz- und Rindenkäfer der Süd- und Mittelschwedischen Laubbäume. *Opuscula Entomol Suppl.* 16. 374 pp.
- 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 23-years monitoring period. *Forest Ecol Manag* 310: 508–516.
- Peterken GF (1996) *Natural woodland: ecology and conservation in northern temperate regions*. Cambridge, Cambridge University Press.
- Pettersson RB, Stenbacka F., Hjältén J & Hilzczański J (2007) Återfynd av rödhalsad brunbagge (*Phryganophilus ruficollis* Fabr.) och Huggerts plattbrackstekel (*Chartobracon huggerti* C.van Achterberg). *Ent Tidskr* 128: 101–105.
- Pickett STA & White PS (eds.) (1985) *The ecology of natural disturbance and patch dynamics*. New York, Academic Press.

- R Development Core Team (2011) R. A language and environment for statistical computing. R foundation for statistical computing, Vienna. URL: <http://www.R-project.org/>. Accessed 05/2013.
- R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Version 2.15-2 ISBN 3-900051-07-0, URL: <http://www.R-project.org/>. Accessed 05/2015.
- Ranius T & Kindvall O (2004) Modelling the amount of coarse woody debris produced by the new biodiversity-oriented silvicultural practices in Sweden. *Biol Cons* 119: 51–59.
- 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: 797–804
- Rassi P (ed.) (1993) Suomen kovakuoriaisten (Coleoptera) frekvenssipisteet 1.1.1960-1.1.1990. WWF:n Suomen rahaston raportteja 6. 136 pp. In Finnish.
- Rassi P, Alanen A, Kanerva T, Mannerkoski I. (eds.) (2001) The 2000 Red List of Finnish Species. Ympäristöministeriö & Suomen ympäristökeskus. Helsinki. 432 pp.
- Rassi P, Hyvärinen E, Juslén A & Mannerkoski I (eds.) (2010) The 2010 Red List of Finnish Species. Ympäristöministeriö & Suomen ympäristökeskus, Helsinki. 685 p.
- Rees D & Juday G (2002) Plant species diversity on logged versus burned sites in central Alaska. *Forest Ecol Manag* 155: 291–302.
- Reinikainen A Mäkipää R, Vanha-Majamaa I & Hotanen J-P (eds.) (2000) Kasvit muuttuvassa metsäluonnossa. Summary: Changes in the frequency and abundance of forest and mire plants in Finland since 1950. Kustannusosakeyhtiö Tammi, Jyväskylä.
- Renvall P (1995) Community structure and dynamics of wood-rotting basidiomycetes on decomposing conifer trunks in northern Finland. *Karstenia* 35: 1–51.
- Rintala T & Rinne V (2010) Suomen Luteet [Finnish Bugs]. Hyönteistarvike Tibiale, Helsinki.
- Rouvinen S & Kouki J (2008) The natural northern European boreal forests: unifying the concepts, terminologies, and their application. *Silva Fenn* 42:135.
- Rouvinen S, Kuuluvainen T & Karjalainen L (2002) Coarse woody debris in old *Pinus sylvestris* dominated forests along a geographic and human impact gradient in boreal Fennoscandia. *Can J For Res* 32: 2184–2200.
- Rydgren K, Økland R & Hestmark G (2004) Disturbance severity and community resilience in a boreal forest. *Ecology* 85: 1906–1915.
- Saalas U (1917) Die Fichtenkäfer Finnlands I. *Ann Acad Sci Fenn A* 8: 1–547.
- Saalas U (1923) Die Fichtenkäfer Finnlands II. *Ann Acad Sci Fenn A* 22: 1–746.
- Saint-Germain M, Drapeau P & Hebert C (2004a) Xylophagous insect species composition and patterns of substratum use on fire-killed black spruce in central Quebec. *Can J For Res* 34: 677–685.
- Saint-Germain M, Drapeau P & Hebert C (2004b) Comparison of Coleoptera assemblages from a recently burned and unburned black spruce forests of northeastern North America. *Biol Cons* 118: 583–592.
- Salminen H, Lehtonen M & Hynynen J (2005) Reusing legacy FORTRAN in the MOTTI growth and yield simulator. *Comp Electr Agric* 49: 103–113.

- Schimmel J & Granström A (1996) Fire severity and vegetation response in the boreal Swedish forest. *Ecology* 77: 1436–1450.
- Schmitz A, Schatzel H & Schmitz H (2010) Distribution and functional morphology of photomechanic infrared sensilla in flat bugs of the genus *Aradus* (Heteroptera, Aradidae). *Arth Struct & Dev* 39: 17–25.
- Siipilehto J (2006) Linear prediction application for modelling the relationships between a large number of stand characteristics of Norway spruce stands. *Silva Fenn* 40: 517–530.
- Siipilehto J, Ojansuu R, Miina J, Hynynen J, Valkonen S & Saksa T (2014) Metsikön varhaiskehityksen kuvaus MOTTI-ohjelmistossa. Metlan työraportteja 286. <http://www.metla.fi/julkaisut/workingpapers/2014/mwp286.pdf> (in Finnish). Accessed 06/2015.
- Siitonen J (2001) Forest management, coarse woody debris and saproxylic organisms: Fennoscandian forests as an example. *Ecol Bull* 49: 11–41.
- Siitonen J & Saaristo L (2000) Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forests. *Biol Cons* 94: 211–220.
- Silfverberg H (2010) *Enumeratio renovata Coleopterorum Fennoscandiae, Daniae et Baltiae*. *Sahlbergia* 16: 1–144.
- Similä M & Junninen K (eds.) (2012) Ecological restoration and management in boreal forests – best practices from Finland. Metsähallitus, Natural Heritage Services, Vantaa. 50 p.
- Similä M, Martikainen P & Kouki J (2003) Saproxylic beetles in managed and seminatural forests – quality of dead wood matters. *Forest Ecol Manag* 174: 365–381.
- Society for Ecological Restoration International Science & Policy Working group 2004. The SER International Primer on ecological restoration. Tucson, Society for ecological restoration International.
- Soudzilovskaia N, Graae B, Douma JB, Grau O, Milbau A, Wolters L & Cornelissen J (2011) How do bryophytes govern generative recruitment of vascular plants? *New Phytol* 190: 1469–8137 doi: 10.1111/j.1469-8137.2011.03644.x
- Stanturf JA, Palik BJ & Dumroese K (2014) Contemporary forest restoration: A review emphasizing function. *Forest Ecol Manag* 331: 292–323.
- Stenbacka F, Hjältén J, Hilszczański, J & Dynesius M (2010) Saproxylic and non-saproxylic beetle assemblages in boreal spruce forests of different age and forestry intensity. *Ecol Appl* 20: 2310–2321.
- Stokland J (2001) The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. *Ecol Bull* 49: 71–83.
- Stokland J, Siitonen J & Jonsson BG (2012) *Biodiversity in dead wood*. Cambridge, Cambridge University Press.
- Suominen O, Edenius L, Ericsson G & Resco de Dios V (2003) Gastropod diversity in aspen stands in coastal northern Sweden. *Forest Ecol Manag* 175: 403–412.
- Sverdrup-Thygeson A & Ims RA (2002) The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. *Biol Cons* 106: 347–357.

- Thomas S, Halpern C, Falk D, Liguori D & Austin K (1999) Plant diversity in managed forests: understory responses to thinning and fertilization. *Ecol Appl* 9: 864–879.
- Thompson I, Mackey B, McNulty S & Mosseler A (2009) Forest resilience, biodiversity, and climate change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems. Secretariat of the Convention on Biological Diversity, Montreal. Technical Series no. 43. 67 pp.
- Thorpe AS & Stanley AG (2011) Determining appropriate goals for restoration of imperilled communities and species. *J Appl Ecol* 48:275–279.
- Tikkanen O-P, Martikainen P, Hyvärinen E, Junninen K & Kouki J (2006) Red-listed boreal forest species of Finland: associations with forest structure, tree species and decaying wood. *Ann Zool Fenn* 43: 373–383.
- Tikkanen O-P, Matero J, Mönkkönen M, Juutinen A & Kouki J (2012) To thin or not to thin: bio-economic analysis of two alternative practices to increase amount of coarse woody debris in managed forests. *Eur J For Res* 131: 1411–1422.
- Tilman D, May RM, Lehman CL & Nowak MA (1994) Habitat destruction and the extinction debt. *Nature* 371: 65–66.
- Toivanen T & Kotiaho J (2007a) Mimicking natural disturbances of boreal forests: the effects of controlled burning and creating dead wood on beetle diversity. *Biodivers Cons* 16: 3193–3211.
- Toivanen T & Kotiaho J (2007b) Burning of logged sites to protect beetles in managed boreal forests. *Cons Biol* 21: 1562–1572.
- Toivanen T & Kotiaho JS (2010) The preferences of saproxylic beetle species for different dead wood types created in forest restoration treatments. *Can J For Res* 40: 445–464.
- Tolvanen A (1994) Aboveground growth habits of two *Vaccinium* species in relation to habitat. *Can J Bot* 73: 465–473.
- Tonteri T, Salemaa M & Rautio P (2013) Changes of understorey vegetation in Finland in 1985–2006. In: Merilä P & Jortikka S (eds.) (2013) Forest Condition Monitoring in Finland – National report. The Finnish Forest Research Institute. Available at <http://urn.fi/URN:NBN:fi:metla-201305087583>. Accessed 04/2015.
- Turner MG, Romme WH, Reed RA & Tuskan GA (2003) Post-fire aspen seedling recruitment across the Yellowstone (USA) landscape. *Landscape Ecol* 18: 127–140.
- Uotila A, Kouki J, Kontkanen H & Pulkkinen P (2002) Assessing the naturalness of boreal forests in eastern Fennoscandia. *Forest Ecol Manag* 161: 257–277.
- Uotila A, Hotanen J-P & Kouki J (2005) Succession of understory vegetation in managed and seminatural Scots pine forests in eastern Finland and Russian Karelia. *Can J For Res* 35: 1422–1441.
- Vanha-Majamaa I & Reinikainen A (2000) Muuttuvan maankäytön vaikutus kasvillisuuteen. In: Reinikainen A, Mäkipää R, Vanha-Majamaa I & Hotanen J-P (eds.) (2000) Kasvit muuttuvassa metsäluonnossa. Helsinki, Tammi. 304–306.
- Vanha-Majamaa I, Lilja S, Ryömä R, Kotiaho J, 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 Ecol Manag* 250: 77–88.

- Venables W & Ripley B (2002) *Modern Applied statistics with S*. 4th edition. New York, Springer.
- Viiri H & Eerikäinen K (2012) Red-listed *Aradus laeviusculus* (Hemiptera: Aradidae) inhabits burnt restoration sites in the Koli National Park, North Karelia, Finland. *Entomol Fenn* 23: 63–68.
- Wallenius T (2007) Menneet metsäpalot Kalevalan kankailla. Metsähallituksen luonnon-suojelujulkaisuja. Series A 176. 46 pp. In Finnish.
- Wallenius T (2011) Major decline in fires in coniferous forests – Reconstructing the phenomenon and seeking for the cause. *Silva Fenn* 45: 139–155.
- Wallenius T, Kuuluvainen T & Vanha-Majamaa I (2004) Fire history in relation to site type and vegetation in Vienansalo Wilderness in eastern Fennoscandia, Russia. *Can J For Res* 34: 1400–1409.
- Wallenius T, Niskanen L, Virtanen T, Hottola J, Brümelis G, Angervuori A, Julkunen J & Pihlström M (2010) Loss of habitats, naturalness and species diversity in Eurasian forest landscapes. *Ecol Ind* 10: 1093–1101.
- Wardle DA & Zackrisson O (2005) Effects of species and functional group loss on island ecosystem properties. *Nature* 435: 806–810.
- Wardle DA, Walker LR & Bardgett RD (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science* 305: 509–513.
- Wardle DA, Hörnberg G, Zackrisson O, Kalela-Brundin M & Coomes D (2003) Long-term effects of wildfire on ecosystem properties across an island area gradient. *Science* 300: 972–975.
- Wardle DA, Jonsson M, Bansal S, Bardgett RD, Gundale MJ & Metcalfe DB (2012) Linking vegetation change, carbon sequestration and biodiversity: insights from island ecosystems in a long-term natural experiment. *Journal of Ecology*. 100:16–30. Doi: 10.1111/j.1365-2745.2011.01907.x
- Wood SN (2004) Stable and efficient multiple smoothing parameter estimation for generalized additive models. *J Am Statist Assoc* 99: 673–686.
- Wood SN (2006) *Generalized Additive Models. An introduction with R*. Boca Raton, Chapman & Hall/CRC.
- Zackrisson O (1977) Influence of forest fire on the north Swedish boreal forest. *Oikos* 29: 22–32.
- Zackrisson O, Nilsson MC, Dahlberg A & Jäderlund A (1997) Interference mechanisms in conifer-Ericaceae-feathermoss communities. *Oikos* 78: 209–220.
- Östlund L, Zackrisson O & Axelsson A-L (1997) The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Can J For Res* 27: 1198 – 1206.

Original papers

- I Hekkala A-M, Tarvainen O & Tolvanen A (2014) Dynamics of understory vegetation after restoration of natural characteristics in the boreal forests in Finland. *Forest Ecol Manag* 330: 55–66.
- II Hekkala A-M, Ahtikoski A, Päätaalo M-L, Siipilehto J & Tolvanen A Volume and diversity of deadwood after restoration of boreal forests – short-term results and long-term predictions. Manuscript.
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