Dissertationes Forestales 259

Impacts of fire in active and passive restorations on boreal forest soils and vegetation

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Academic dissertation

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ABSTRACT

Passive recovery or active restoration approaches may be used in the repair of degraded ecosystems. The effects of such measures on ecosystem patterns and processes, including boreal forest soils and vegetation, are poorly understood. This thesis examines the impacts of both active and passive restoration approaches on soil organic matter (SOM) and vegetation in the boreal forests of eastern Finland.

The study sites were located in managed and protected boreal forests in the same region in Finnish North Karelia. In the study sites, I measured soil and vegetation patterns, and the environmental controls on SOM decomposition in relation to the proximity of decaying logs.

In actively restored sites, the burned, partly harvested site had lower humus SOM stocks and displayed vegetation biomass and cover patterns that suggested stronger disturbance than the other sites. Burning decreased and homogenized vegetation diversity through spatially-uniform extinctions and limited colonization 10 years after fire. Green tree retention partially alleviated the impacts of disturbance on vegetation biodiversity. Proximity of dead wood (but only of non-charred logs) enhanced conditions for SOM decomposition. Charred logs did not exhibit this effect, which suggests a previously unknown linking of forest fires to soil processes via charred wood.

In the passive recovery sites, legacies of slash-and-burn regimes have persisted in the forests for more than a century. The disturbed forests had a higher volume of large birch trees and lower SOM stocks. In boreal conditions, passive restoration may take more than a century before ecosystem properties return to their pre-disturbance state. Soil properties may be more challenging to restore than above-ground tree structures.

My results indicate that active and passive restoration approaches may produce quite different pathways and outcomes. In general, the active restoration approach with low severity fires that is currently applied appeared to not harm forest soils; in particular it left the deeper mineral layers intact, and may provide a more rapid way to restore ecosystem properties. However, there is an urgent need to cover a longer successional time series to reveal the exact differences between active and passive restoration trajectories. The inherent differences between the focus of the passive restoration approach (to recover ecosystem naturalness in a more holistic sense) and the active restoration approach (targeting specific species, habitats, structures and processes in the ecosystem) should be duly acknowledged.

Keywords: Decomposition, historical legacies, passive recovery, prescribed burning, slash-and-burn, soil organic matter.

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"*Nature is ever at work building and pulling down, creating and destroying, keeping everything whirling and flowing, allowing no rest but in rhythmical motion, chasing everything in endless song out of one beautiful form into another.*" – John Muir (1901)

LIST OF ORIGINAL ARTICLES

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

I Čugunovs M., Tuittila E.-S., Mehtätalo L., Pekkola L., Sara-Aho I., Kouki J. (2017). Variability and patterns in forest soil and vegetation characteristics after prescribed burning in clear-cuts and restoration burnings. Silva Fennica 51(1) article id 1718. https://doi.org/10.14214/sf.1718

II Tatsumi S., Strengbom J., Čugunovs M., Kouki J. Disturbance alters beta diversity via colonization-extinction dynamics. Manuscript.

III Čugunovs M., Tuittila E.-S., Kouki J. Proximity to non-charred logs in burned forests affects decomposition processes in soil. Manuscript.

IV Čugunovs M., Tuittila E.-S., Sara-Aho I., Pekkola L., Kouki J. (2017). Recovery of boreal forest soil and tree stand characteristics a century after intensive slash-and-burn cultivation. Silva Fennica 51(5) article id 7723. https://doi.org/10.14214/sf.7723

Author's contribution in the co-authored articles and manuscripts:

Mihails Čugunovs (MČ) actively participated in the different phases of all four manuscripts. He participated in the development of the original ideas in papers **I**, **III** and **IV**. In papers **I** and **IV**, MČ participated in sampling design as well as in the development and implementation of field procedures. In paper **III**, MČ led the sampling design and development of field procedures and led the data collection in the field. In papers **I** and **IV**, MČ participated in data collection, and in papers **I** and **III** in the extensive laboratory work. MČ carried out data analyses in papers **I**, **III** and **IV**. In papers **I**, **III** and **IV**, MČ wrote the first version and the main text as lead author, and he contributed to the writing and editing of manuscript **II**.

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1 INTRODUCTION

1.1 Current challenges and background concepts in boreal forest ecosystem management

Since the beginning of the industrial revolution in the 18th century, human activities have increasingly transformed the land surface, species composition and biogeochemical cycles on Earth. These changes are so profound that the period beginning from the industrial revolution is now considered as a new and current geological epoch – the Anthropocene (Crutzen 2002). The time since the mid-20th century has seen an even more dramatic and unprecedented increase in human exploitation of Earth's ecosystems, and it is called the great acceleration (Steffen et al. 2004). In addition, many scientists argue that our planet is now undergoing a sixth major species extinction event that has mostly been caused by anthropogenic impacts (Chivian and Bernstein 2008; Wake and Vredenburg 2008).

Boreal forests form a major and globally significant biome, stretching in a band across the northern circumpolar areas of our planet. With ongoing human technological development and increasing resource use, even these far reaches of nature are increasingly subjected to impacts and transformation, such as long-range pollution, the effects of mining and logging, urbanization, road construction. There are, however, large regional differences within the boreal zone, as boreal forests in North America (Canada and Alaska) and Siberia are still much less impacted than the boreal forests of northwestern Europe.

In the European boreal forests of Fennoscandia, many forest-dwelling species linked to habitats, structures and processes typical of natural landscapes are threatened due to modern large-scale and intensive forestry (Berg et al. 1994; Tikkanen et al. 2006; Kuuluvainen 2009). The modern forestry operations result in radically different boreal forest structures and processes as compared to the ones created by natural disturbance regimes (Kuuluvainen 2009). The landscape is becoming fragmented (Kouki et al. 2001), forest tree species composition homogenized and changed (van der Plas et al. 2016), and structural variation, along with natural microhabitats, such as large dead wood pieces and large old deciduous trees, is lost (Kuuluvainen 2009). There are growing concerns that ecosystem functioning could be disrupted, thus endangering the biosphere life-support systems crucial for the wellbeing of our societies (Barnosky et al. 2014).

In response to these environmental challenges, there has been a discussion of the core values and targets for a **conceptual framework** to direct concerted ecosystem management, including that of boreal forests. One of these guiding principles is *ecosystem naturalness*, which in its strong theoretical sense (freedom from human impacts) can be considered non-attainable in our current age, as probably all ecosystems have now been directly or indirectly impacted by humans and, moreover, this impact is ongoing (Cole and Yung 2010). Nonetheless, some boreal forests in Fennoscandia feature markedly few (or negligible) legacies of direct human impacts (e.g. cut stumps) and thus can be called "near-natural" or "semi-natural" (Uotila et al. 2002; Rouvinen and Kouki 2008; Brūmelis et al. 2011). The ecological structures and processes in such forests have, arguably, an intrinsic value and positively affect the capacity of the ecosystem to meet society's needs for ecosystem services (Kuuluvainen 2009). Such ecosystems in a near-natural state and featuring natural dynamics can ideally be used as references in the management of boreal forests (Angelstam 1998; Bergeron et al. 2002). Another related guiding concept is *ecosystem integrity*, which is related to an ecosystem displaying a full, unimpaired set of biotic and abiotic components and functioning well and stably over time. *Resilience* is sometimes linked to this concept (Cole and Yung 2010). In its broadest sense, resilience is the capacity of a social-ecological system to absorb a spectrum of shocks or perturbations and to sustain and develop its fundamental function, structure, identity, and feedbacks through either recovery or reorganization in a new context (Chapin et al. 2009). Currently, resilience frameworks are widely used in the analysis and planning, for instance, of human production systems or ecosystem services (e.g. Liu et al. 2007). In this regard, however, it is imperative to define in each case two objects, i.e. resilience of *what,* and *to what*? Ultimately, the policy-guiding anthropocentric principle is to safeguard the capacity of ecosystems to meet human needs, both material and immaterial, i.e. ecosystem services (Chapin et al. 2011).

To achieve the sustainability of ecosystem services and repair the naturalness of communities and the function of Earth's ecosystems, either passive recovery (through set-aside practices) or active ecological restoration approaches have been increasingly carried out in degraded ecosystems (Jones et al. 2018). For example, Aichi targets under the Convention on Biological Diversity list ecological restoration as one of the main activities to reach global biodiversity management goals (UN environment 2017). Thus, ecological restoration has become increasingly topical worldwide. I further discuss and introduce the basics of ecological restoration in section 1.3 below.

1.2 The impacts of fire disturbance on boreal forest soils and vegetation

Boreal forests are naturally disturbance-driven ecosystems. Consequently, the disturbance ecology of boreal forests could provide an excellent template or model for planning and studying restoration activities (Pasanen 2017). Understanding the inherent disturbance dynamics of the boreal forest biome is also a prerequisite for its management as a complex adaptive system facing global directional change, such as increases in temperature (Gauthier et al. 2015). Previously, boreal forest disturbance dynamics have been studied for various reasons: to advance the general understanding within the field of ecology (Pickett and White 1985), to address global change issues such as changes in the carbon (C) cycle in relation to land use, climate change and forest fires (Turetsky et al. 2011), and to describe the natural variability and processes within the boreal biome in order to guide sustainable use of boreal forest resources (Kuuluvainen 2002).

Disturbances in boreal forests occur at different spatial and temporal scales, and the main disturbance agents are fire, wind, insects, browsing animals, fungal disease, competition and senecescence (Angelstam and Kuuluvainen 2004). Fire, windthrow, defoliating insects and bark beetle outbreaks can occur at the landscape scale and thus affect large forest areas. Browsing animals usually affect smaller areas at a time, occuring at a forest community scale, and inter-plant competition and senescence are considered small-scale disturbances, operating at the level of individual trees or other plants.

Fire disturbance has the most apparent impact on boreal landscapes and has been widely studied. In boreal forests, fire can proceed as surface fire, crown fire, smoldering ground fire or as a combination of all three. The impacts of fire on soil and vegetation are related to the depth and duration of heating and the temperatures reached in or above the soil (Schimmel and Granström 1996; Neary et al. 2005).

Boreal forest fires affect soil physical, chemical and biological properties in multiple ways, and some of the impacts can lead to permanent changes at the ecosystem scale (Certini 2005). Fire impacts forest soils by causing short- and longer-term changes in soil C, nitrogen

(N) and other nutrients, soil structure and porosity, increasing soil hydrophobicity possibly leading to erosion, and altering microbial and soil invertebrate communities (Certini 2005; Neary et al. 2005). Fire volatilizes and reduces N stored in soil and vegetation, and in boreal forests this has implications on C cycle, as N is often the limiting nutrient for tree growth (Palviainen et al. 2017). It is highly important to understand the changes in soil C stocks due to fire disturbance for two main reasons: (i) soil C as "the currency of life" largely determines soil fertility, functioning and resilience, and (ii) soils can act both as a source and sink of C on a global scale thereby affecting the global climate (Johnson and Curtis 2001; DeLuca and Boisvenue 2012). In the short term, soil C stocks usually decrease during and after a fire event in direct proportion to fire severity due to combustion of soil organic matter (SOM) (Neary et al. 2005). However, soil C stocks in sites ten years or more after fire have been found to exceed pre-fire levels, which may be due to: (i) the incorporation of unburnt residue into the soil that prevents biochemical decomposition, (ii) the transformation of labile organic materials into more recalcitrant forms, such as pyrogenic black C, and (iii) the effects of secondary succession, whereby naturally invading post-fire N-fixing vegetation species significantly increase soil C stocks (Johnson and Curtis 2001). The importance in soil C cycling of belowground litter production, principally via fine roots, has been increasingly recognized (Helmisaari et al. 2000; Makkonen and Helmisaari 2001; Finér et al. 2011). Fire can affect both these processes and soil C stocks through its impact on belowground fine root biomass turnover, either directly or via above-ground vegetation succession (Finér et al. 1997).

The study of forest fire effects on soils is complicated by large variation in fire characteristics between fires, small-scale variation in fire severity spatially within one forest stand, and also inherent small-scale spatial variation in soil properties. Thus, studies quantifying these elements of variation are crucial to adequately understand the impacts of fire (e.g. Liski 1995). In general, studying the impacts of fire disturbance on forest ecosystems to uncover meaningful trends is very laborious, and large sample sizes are necessary (Larjavaara et al. 2017).

Vegetation is affected by fires that consume, damage and kill the aboveground and belowground parts of plants (Schimmel and Granström 1996). Plant response to fire is affected by the fire severity and the characteristics of the affected plants, such as their inherent resistance to injury and their ability to recover afterwards (Brown and Smith 2000). The secondary succession of understory and canopy vegetation in boreal forests after a fire event can lead to altered species composition and plant coverage, although plants are usually quick to recolonize a burnt site (Certini 2005), and in the long-term after a single fire event, the vegetation community most often resembles the pre-fire community (Brown and Smith 2000). Changes in the fire return interval (i.e. fire regime), however, can lead to a shift in the vegetation stability domain, e.g. from conifer-dominated to deciduous-dominated tree canopies, as currently seen in boreal Alaska (Johnstone et al. 2010).

How fire and other disturbances can affect biodiversity (e.g. species richness) at a regional or local scale has received much attention (e.g. Eales et al. 2016). In addition, it is also important to understand the mechanisms and processes of community assembly, convergence and divergence (Vellend et al. 2007; Myers et al. 2015), as impacted by different and possibly interacting disturbance types, such as fire and logging. Such knowledge would both advance community ecology and inform best conservation and restoration practices.

Boreal forest vegetation and soil compartments are linked by organic matter decomposition – an integrative process for ecosystem functioning. Decomposition of SOM regulates ecosystem nutrient cycles and soil fertility, thereby impacting on plants and other forest-dwelling organisms throughout the whole food web. As an integrative process, decomposition is often used to concisely capture and describe the ecosystem state in ecological studies on disturbance effects, including that of fire (Harmon et al. 1999). Coarse woody debris (CWD), which originates from fire and the mortality of retention trees, is known for its important functions as a microhabitat for several different organisms that include microbes, beetles and polypore species (Lassauce et al. 2011, Heikkala et al. 2016). Although in boreal Swedish island forests 50 to 70% of accumulated soil carbon has been found to be derived from roots and root-associated microorganisms (Clemmensen et al. 2013), in the forest floor and soil of northern coniferous forests more than half of accumulated organic matter can be derived from CWD (Laiho and Prescott 2004). Large CWD pieces, i.e., downed logs can also affect SOM decomposition at the ecosystem scale through different mechanisms that include fungal translocation of nutrients (Rinne et al. 2017).

1.3 Ecological restoration practices as a means to address environmental challenges in boreal forests

Ecological restoration actions have been increasingly applied to facilitate the recovery of the degraded processes, habitats, structures and populations caused by the aforementioned pervasive human-induced loss of ecosystem naturalness, biodiversity and services (Halme et al. 2013; McDonald et al. 2016; UN environment 2017).

Globally, forest restoration is more prominent in the tropical biome, where forests are replanted after deforestation, and treeless landscapes are restored back to forested ones. In boreal Fennoscandia, forest cover has been stable and increasing in recent years, although the restoration practices here instead address the degradation in the *quality* of forest ecosystems (Halme et al. 2013).

Boreal forest restoration actions can be subdivided into active and passive restoration approaches. In active restoration, the ecosystem is deliberately manipulated, for instance, by burning the forest or uprooting, felling or killing the trees. For active restoration, an understanding of the ecology of the target ecosystem, treatment effects and targets of the treatment actions are necessary prerequisites. In passive restoration, the ecosystem is intentionally left outside direct human influence so that it can regain its natural structures or processes by itself with time, i.e. the “hands off” approach (Bernes et al. 2015). Recently, Jones et al. (2018) argued in their systematic review for the use of passive recovery as an efficient and cost-effective option whenever possible. In some cases it may be not possible to restore an ecosystem back to its historical state, historical trajectory or natural reference, e.g. due to global directional changes such as climate warming, or simply because the ecosystem may have crossed an irreversible tipping point and is beyond restoration (Hobbs et al. 2009). In repair of such “novel ecosystems” it has been suggested that possible future-directed active interventions are termed “ecosystem renewal” rather than “restoration” (Chapin et al. 2011). However, the importance of this conceptualization of novel ecosystems, and the abundance of such ecosystems, is currently hotly debated.

Both active and passive restoration can lead to more natural-like structures and processes in boreal forests and are potentially beneficial for biodiversity. By definition, only the passive restoration approach can possibly lead to a more natural ecosystem state in the sense of the absence of human impacts. However, it is argued that even then the “strict” version of naturalness is unattainable in passive ecosystem restoration for two reasons: (i) indirect human impacts are still exerted onto the ecosystem in question from dispersed, long-ranging factors like pollution, and (ii) if we exclude and isolate an ecosystem from the otherwise unnatural global landscape, it becomes "managed" to a certain extent and thus is no longer natural (Cole and Yung 2010). From a practical perspective, this means that ecosystem restoration is better justified when it is aimed at safeguarding and improving the important processes, structures and services in the ecosystem based on our scientific understanding (McDonald et al. 2016) and not when it attempts to actualize the philosophical idea of naturalness itself. However, in some cases the "hands off" approach is an efficient option (Jones et al. 2018) where near-natural ecosystems can be used as references in active restoration. Moreover, studies on passive ecosystem recovery after the cessation of anthropogenic disturbance regimes may be viewed as belonging to the currently growing discipline of land change science (Turner II et al. 2007). There are, thus, important intrinsic differences between the intentions typically elucidated in the active and passive restoration approaches; while passive restoration can be viewed more often as attempting to achieve the integrated natural self-regulation of the ecosystem, active restoration, at least initially, aims at the (re)-introduction, for instance, of specific species, habitats, structures, processes, patterns into the ecosystem in question. However, despite the potentially differing premises in active and passive restoration, it is possible that the outcomes may be similar and beneficial for the provision of ecosystem services to society in both cases. The pathways and outcomes of both approaches need to be carefully studied and compared along similar (long-term) timeframes to better understand these complexities.

The positive impacts of ecological restoration treatments on biodiversity, such as beetle (Hyvärinen et al. 2006) and polypore (Junninen et al. 2008; Suominen et al. 2015) species richness, have already been established. However, the effects of restoration burnings on boreal forest vegetation and soil properties and the C cycle in particular, are still largely unknown (Similä and Junninen 2012).

1.4 Aims of the dissertation

This thesis investigates the variability of boreal forest SOM and its relationship with vegetation as impacted by active and passive restoration approaches. The thesis objectives were as follows:

(a) to investigate the small-scale spatial variability of the soil, and ground- and field-layer vegetation parameters in relation to active restoration with fire, clearcutting and green tree retention treatments. These results were then used to plan prospective sampling efforts using a statistical simulation approach (**I**);

(b) to assess and disentangle how active restoration disturbance impacts the understory vegetation community assembly processes and diversity (**II**);

(c) to ascertain and compare the environmental controls on SOM decomposition near charred and non-charred CWD fragments that result from clearcutting, green tree retention and restoration burning (**III**);

(d) to assess how boreal forest soils and vegetation recover naturally ("passive restoration") after cessation of a historical disturbance regime of frequent burning for slash-and-burn agriculture (**IV**).

In relation to the thesis aims, I tested the following hypotheses:

(a) Variability in soil and vegetation parameters does not differ between sites that have undergone different active restoration disturbances, but vegetation variability is generally higher than that of the soil parameters (**I**);

(b) Fire reduces understory vegetation diversity and homogenizes vegetation composition, while green tree retention patches partially alleviate the impact of logging on vegetation diversity (**II**);

(c) Soil microsites adjacent to the CWD fragments have enhanced conditions for SOM decomposition, leading to increased decomposition rates. Slower decomposition rates are likely to occur nearer a piece of charred CWD than nearer a non-charred CWD piece (**III**);

(d) After approximately a century of passive recovery from slash-and-burn disturbance regimes, mesic boreal spruce forests have partially recovered, but still feature disturbance legacies such as lower SOM stocks and more deciduous trees than the nearby undisturbed reference areas (**IV**).

2 MATERIAL AND METHODS

The forest study sites used in this thesis are located in Patvinsuo National Park and in the surrounding landscape in eastern Finland, North Karelia (Fig. 1).

The material gathered in the active restoration sites ("FIRE" experiment, see http://forest.uef.fi/jarikouki/project_fire.htm) concerns the short-to-medium term (2-16 years since disturbance) impacts of prescribed restoration burning on SOM and ground- and field-layer vegetation in sub-xeric boreal pine forests. The material gathered in the passively recovering forest area concerns long-term (~130 years) recovery of SOM and tree layer vegetation in boreal mesic spruce forests after the cessation of slash-and-burn cultivation.

2.1 The experimental setup related to the sites of active restoration treatments ("FIRE" experiment)

The "FIRE" experiment ("Fire and retention trees in facilitating biodiversity in boreal forests") is a large-scale field experiment in ecological restoration and forest management located in the Lieksa and Ilomantsi municipalities, eastern Finland (approximately 63° N, 30° E), near the southern edge of the middle boreal zone (Ahti et al. 1968). The aim of the experiment is to examine the impacts of fire and tree retention on species occurrence patterns and biodiversity.

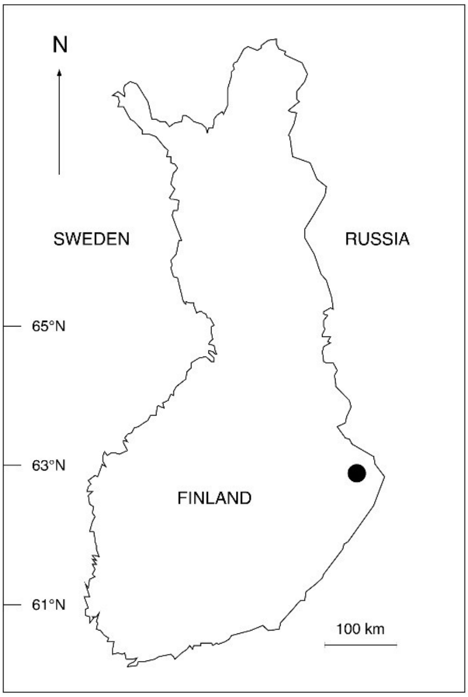

Figure **1**. The location of study sites in eastern Finland.

The experiment features eight different treatment combinations of the two applied factors - fire and tree retention/cuttings (fire: yes/no, and tree retention: full (100%) – uncut forests, 50 m^3 ha^{-1} retention, 10 m^3 ha^{-1} retention and 0 m^3 ha^{-1} retention – complete clearcut, Fig. 2). Each treatment is replicated three times, i.e. there are a total of 24 forest sites, each 3-5 ha in size, where the treatments have been carried out in 2001. All the sites were ecologically similar sub-xeric Scots pine (*Pinus sylvestris* L.) dominated heath forests (sensu Hotanen et al. 2008) with some interspersion of Norway spruce (*Picea abies* (L.) Karst.) and birch (*Betula* spp.) trees. Before the start of the treatments, the sites were all old-growth forest (dominant canopy age ~150 years) with an average living tree volume of 288 m^3 ha^{-1} (S.D. 67.8) and an average dead wood volume of 40 m^3 ha^{-1} (S.D. 16.9 [Heikkala et al. 2014]). The sites that were left unharvested are located in the Patvinsuo National Park (protected areas), and the harvested sites are located in managed forests owned by Metsähallitus. The harvested experimental sites, however, were left untouched since the start of experimental treatments in 2001.There were high mortality and fall-down rates in the retention trees after the treatments, especially on burned sites (see Heikkala et al. 2014 for details on retention tree dynamics). More detailed descriptions of the experiment and the sites are available in Hyvärinen et al. (2005), Heikkala et al. (2014), and Kouki (2017).

2.2 Sampling of soil and ground- and field- layer vegetation in active restoration sites (I, II)

I intensively sampled four sites of the “FIRE” experiment to quantify the small-scale, location-dependent spatial variation in soil and vegetation parameters. The four sites that were sampled to address the parameter variability belonged to four distinct treatments: unburnt/no cuttings - control (UBNC, Fig. 2a), burned/no cuttings – restoration burn (BNC, Fig. 2b), burned/50 m^3 ha^{-1} retention - silvicultural burn (B50, Fig. 2e), and unburnt/0 m^3 ha^{-1} retention – complete clearcut (UBCC, Fig. 2d). In each of the four sites, I established approximately 80 sample plots at a spacing of approximately 10 m between the plots, and recorded the sample plot locations with a survey-grade GPS receiver with an accuracy of about 1 m. In each of the plots, I took samples of the organic hemic and sapric (Oe/Oa) soil layers (hereafter humus layer) and the uppermost mineral soil to a depth of 10 cm with a cylindrical corer (diameter 5.7 cm). At 10 % of the sampling locations in each study site, an additional soil sample for pH analysis was taken 30 cm away from the main sample.

I also estimated ground- and field- layer vegetation cover (%) within a 15 cm radius of the sample plot centre and collected the plant material for biomass estimation from the same circle. The vegetation cover was estimated for the dominant species or species groups (*Vaccinium myrtillus* L., *Vaccinium vitis-idaea* L., *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) Schimp., *Polytrichum spp.*, *Dicranum spp.*, *Calluna vulgaris* (L.) Hull, *Epilobium angustifolium* L., *Calamagrostis spp.*, *Deschampsia flexuosa* (L.) Trin., and *Cladonia spp.*). Plant biomass was collected for the following species and groups: *Vaccinium myrtillus*, dead parts of *Vaccinium myrtillus*, other dwarf shrubs (principally *Vaccinium vitis-idaea*), litter, moss, lichen, forb, graminoid and seedling (**I**). The four sites were sampled over a time period of approximately 9 weeks from early June to early August 2014, and each week the samples were collected from all four sites.

To study the vegetation dynamics using diversity indices, the ground and field layer vegetation presence/absence data by species was collected from the full set of “FIRE” experiment sites (total of 24 sites). In the summer of 2000, 15 (2 x 2 m) plots were established in each stand before the start of the experimental treatments. The plots were evenly spaced in three rows approximately 40 m apart from each other. The vegetation data was collected from the plots in 2000 (before treatments), 2003 (two years after treatments) and 2011 (10 years after treatments).

2.3 Sampling for spatial patterns of SOM decomposition in relation to coarse woody debris in active restoration sites (III)

To investigate the spatial patterns of environmental controls on SOM decomposition in relation to large pieces of CWD, namely lying dead wood, I sampled three sites, or replicates, of the B50 (burned/50 m^3 ha^{-1} retention - silvicultural burn) treatment within the “FIRE” experiment (Fig. 2e).

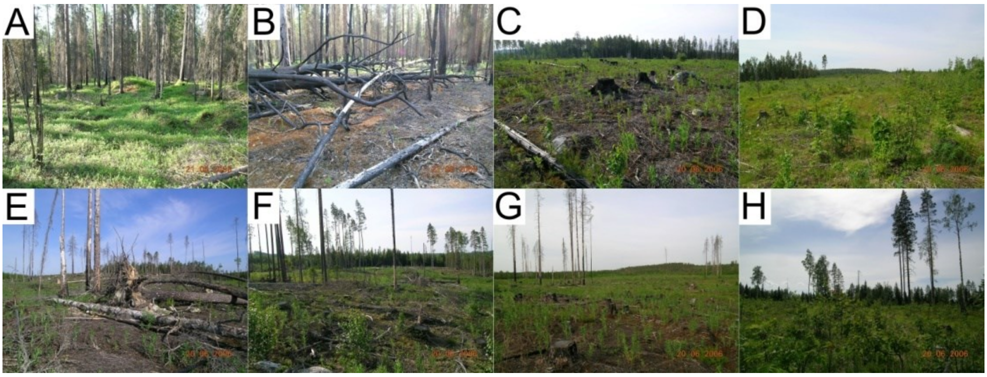

Figure **2**. Forests subjected to different treatment types within the "FIRE" experiment. A: - unburnt/no cuttings - control (UBNC), B: burned/no cuttings – restoration burn (BNC), C: burned 0 m^3 ha^{-1} retention – burned complete clearcut (BCC), D: unburnt/0 m^3 ha^{-1} retention – unburnt complete clearcut (UBCC), E: burned/50 m^3 ha^{-1} retention - silvicultural burn (B50), F: unburnt 50 m^3 ha^{-1} green tree retention, G: burned 10 m^3 ha^{-1} green tree retention, H: unburnt 10 m^3 ha^{-1} green tree retention. Photos taken by Jari Kouki.

In each of the sites, 20 large downed logs with a diameter not less than 15 cm were selected. Surface charring of the logs was visually estimated and recorded (Yes/No). At each of the logs, in a segment with complete uninterrupted contact between the log and the ground for at least 30 cm, bags of standard decomposing material were placed approximately 20-30 cm away from the log-ground contact area. Decomposition material was also placed at locations at least 10 m distance from the nearest large downed log. In one of the three sites, the minimum distance between the sample plots and the logs was reduced to 3 m due to the abundance of downed logs. The planted decomposition material included green and rooibos tea, based on standard method (Keuskamp et at. 2013), and three cellulose bags with differing mesh size (1 mm, 50 µm, 1 µm). The differing mesh size was used to compare decomposition rates based on the size of the various decomposing agents that could access the substrate; mesofauna, fungal hyphae, and bacteria only. All the decomposing material was buried at the interface of the organic and mineral soil horizons, in practice at depths ranging from 1 to ~10 cm. The tea bags were buried on August 1-2 2016, and retrieved on October 20 2016 (79-80 day period). Cellulose bags were buried on August 1-2 2016 and retrieved on September 28-29 2017 (14 month period).

2.4 Sampling of soil and tree parameters in protected old-growth forests of Autiovaara – passive restoration (IV)

I sampled in Autiovaara, a protected area located in eastern Finland, to assess the long-term recovery of boreal forest ecosystem naturalness after historical intensive, frequent and large-scale slash-and-burn disturbance regimes (Fig. 1, Fig. 3); an area that has been extensively studied in regard to its fire and slash-and-burn agricultural history (Lehtonen 1997). The Autiovaara area (~300 ha in size) belongs to the Patvinsuo National Park, North Karelia, eastern Finland (63°7'N, 30°40'E), located within the Lieksa and Ilomantsi municipalities.

The forests of Autiovaara belong to the mesic fresh heath group (Cajander 1949; Hotanen et al. 2008) and are dominated by Norway spruce.

Two types of areas were delineated based on old land-use maps (PKMMKA 1899): (1) areas that are known to have been used in slash-and-burn agriculture until about a century ago, and nearby (2) control areas known to have not been intentionally burned. Soils were sampled in two slash-and-burn and two control areas, and tree stand characteristics were sampled in three slash-and-burn and three control areas. Within each of the studied slash-and-burn and control areas, 7-11 sample plots were established for the sampling of soil and tree stand parameters. Each sample plot had a fixed radius of 10 m. For soil parameter characterization, composite soil samples consisting of eight subsamples per plot were taken with a soil corer (diameter 5.7 cm), separately for the humus layer and the uppermost 8-10 cm of mineral soil. For tree stand structure sampling, the diameter at breast height (DBH) of all live trees higher than 1.3 m and thicker than 5 cm was recorded. The dominant height of the canopy trees was measured. Seedlings and saplings were also quantified to describe current regeneration. Dead wood pieces that fell within the sample plot were measured to obtain dead wood volume values per hectare in the following categories: standing dead wood, lying dead wood, and stumps.

2.5 Laboratory procedures related to soil and vegetation samples

*2.5.1 Soil and biomass samples from actively restored "FIRE" sites **(I)** and soil samples from passively recovering protected old-growth forests in Autiovaara **(IV)***

Soil and plant biomass samples from the "FIRE" sites, and soil samples from Autiovaara were first air-dried in paper bags before delivery to the laboratory and then oven-dried at 60 ºC until a constant weight. All the samples were then weighed. Soil samples were analyzed for SOM content by mass loss on ignition (LOI) in an oven at 550º C for two hours. The pH level of the soil samples that were specifically taken for pH measurements was measured by a standard electrode in water solution.

*2.5.2 Decomposition bags from "FIRE" sites **(III)***

Green and rooibos tea bags were stored at 4 ºC before they were oven-dried at 60 ºC until a constant weight, then manually cleaned with a brush and weighed as per standard protocol (Keuskamp et al. 2013).

The cellulose decomposition bags were stored at -20 ºC before treatment. Then the bags were cut open and the cellulose material remaining inside was scraped off and put into small pre-weighed paper bags to dry at 60 ºC until a constant weight before being weighed to obtain the mass of cellulose remaining after decomposition.

Figure **3**. The old-growth Autiovaara mesic spruce forest. Photo taken by Varpu Heiskanen.

2.6 Data analysis

*2.6.1 Analysis of soil and vegetation data from active restoration sites (**I, II**)*

Sample mean, sample median and sample variance were calculated for the soil and vegetation parameters of the four "FIRE" sites used in study **I**. Variance equality between the four sites was tested by a Levene's rank sum test using IBM SPSS v.21 software (IBM corp. 2012). Data were checked for spatial autocorrelation using Global Moran's I parameter based on 999 permutations in GeoDa software (Anselin et al. 2006), and by visually estimating sample semivariograms and their confidence envelopes in the R program (R Core Team 2013).

A Monte-Carlo simulation approach based on the linear mixed-effects model theory was then used to estimate the amount of replication necessary in future studies to statistically capture the differences in means found in this study. In the simulations, the statistical power to detect between-treatment differences was assessed for different combinations of number of replicates (sites per treatment), number of soil and vegetation samples per site, and the proportion of within-site variance of the total sample variance. These simulations permitted an investigation (under a fixed total number of samples through constrained effort budget) of the optimal relationship between the number of sample plots per replicate and the number of replicates, so that the statistical power gained from the sampling is maximized. The simulations also addressed the question as to whether it would be feasible to confirm the differences observed between single sites in future studies that employ a suitably replicated setup. In the simulations, a dataset for the linear random-effects model based on the setup of study **I** was simulated. Then a model was fitted to the simulated dataset and the null hypothesis (i.e. the means were the same between the treatments) was tested. After 100 or 1000 iterations of this procedure, the proportion of cases where the null hypothesis was rejected, was calculated. A detailed description of the method is given in Supplementary file 1 of study **I**. These simulations were done with R software.

General multivariate patterns in the joint variation of soil and vegetation data were described using principal component analysis (PCA) in the Canoco 5 software (Šmilauer 2016).

To assess how plant biodiversity is impacted by active forest restoration (**II**), we first calculated alpha, gamma and beta diversity indices for plant assemblage data collected in the eight treatments; 24 stands of the "FIRE" experiment in 2000, 2003 and 2011 (in fifteen plots per stand). Alpha and gamma diversity were defined as the number of species in each plot and stand, respectively. For beta diversity definition and quantification, the Raup-Crick index of vegetation compositional dissimilarity within each stand was used (Raup and Crick 1979). Mean pairwise dissimilarities between the 15 plots in each stand were used for the calculation of the beta diversity Raup-Crick index, with randomization across those 15 plots within each stand. For each survey year, these biodiversity indices were then compared between treatments using two-way ANOVA (fire and harvesting, including their interaction, as factors).

To further disentangle the processes behind the snapshot observations of biodiversity, extinction and colonization beta diversity was examined for two periods – before disturbance to two years after disturbance, and from two to ten years after disturbance. Extinction and colonization beta diversity was calculated for species that went locally extinct from each plot between the pairs of survey years, and species that newly colonized each plot between the pairs of survey years, respectively. Similarly, extinction and colonization alpha and gamma diversity were recorded for the species at plot and stand level, respectively, for the two periods. Extinction and colonization beta, alpha and gamma diversity were compared between treatments using two-way ANOVA.

For all biodiversity analyses, the R 3.4.4 statistical software was used (R Core Team 2018).

2.6.2 Analysis of standardized substrate decomposition data from active restoration sites (III)

To assess the impact of fire and the proximity of fallen tree logs on the proxy of decomposition activity potential or microenviroment that controls the rates of decomposition, the 'S' and 'k' parameters were calculated from tea bag weights before and after the decomposition period, based on the standard method provided in Keuskamp et al. (2013). The 'S' parameter is the stabilization factor and 'k' is the decay rate constant. The 'S' and 'k' parameters were then compared between positions (at the log vs. away from the log) using a linear mixed-effects model with the three sampled forest sites as random groups in the 'nlme' package of the R program (R core team 2013; Pinheiro et al. 2017). Position at the log was further divided into *at a charred* and *at a non-charred log*, so that there were three classes in the random-effect analysis of variance (ANOVA): near charred log, near non-charred log, and away from log.

For the cellulose bags, the percent remaining mass was compared between the positions in relation to the logs in a similar manner to the tea bag parameters. In addition, the probability of some cellulose surviving in the bags at the end of field decomposition period was compared between treatments using a binomial model in the 'lme4' package of the R program (Bates et al. 2015).

*2.6.3 Analysis of soil and tree stand data from protected old-growth forests of Autiovaara – passive restoration (**IV**)*

Humus layer thickness, SOM content, soil pH and bulk density were compared between the slash-and-burn and control forests using a linear mixed-effect model with two separate sampling areas as random groups. Tree stand data was similarly compared, but with three sampled areas as random groups. In cases where the parametric assumption of normality based on residual checks was not met, the non-parametric unpaired Wilcoxon Signed-rank test, equivalent to the Mann-Whitney U-test (Hollander and Wolfe 1973), was used instead of the mixed-effects model. When the variance of response was unequal between groups (slash-and-burn and control), the unequal variance Welch t-test (Ruxton 2006) was used instead of the mixed-effects model.

Seedling count by species was compared between the slash-and-burn and control areas using a quasi-Poisson model with a categorical predictor (slash-and-burn vs. control) as the data showed overdispersion, and a zero-inflated negative binomial model was used for data that featured excess zeroes.

To compare the tree stand structure between the slash-and-burn and control plots, I fitted a two-parameter Weibull distribution to tree DBH data using a maximum likelihood estimator. Fitting a Weibull distribution to tree stand DBH data is considered a robust means to describe and compare stand structure between forest sites or treatments (Sarkkola 2006). The shape and scale parameters of the fitted Weibull plot-wise distributions were then extracted and compared between slash-and-burn and control treatments using a linear mixed-effects model, similarly to previous analyses.

Correlations between SOM stocks, tree stand volume and dead wood volume were evaluated using a linear mixed-effect model, including a power function for residual variance as required by residual structure. The random groups used were the two separate sampling areas in the terrain.

All the inferential data analysis and distribution fitting was performed in R (R Core Team 2013). PCA was performed in the Canoco 5 program (Šmilauer 2016) to explore the joint patterns of variability and interrelationships between soil and tree stand structure parameters.

3 MAIN RESULTS AND DISCUSSION

The main results of the thesis sub-studies (**I-IV**) are presented below, and include a brief discussion related to each finding.

3.1 Soil variability was similar after different active restoration treatments, while vegetation showed more complex patterns and heterogeneity (I).

The results based on spatially intensive sampling showed that the small-scale location-related spatial variability (represented by stand-level sample variance) for soil parameters was broadly similar with four different sites representing four different treatments (partly supporting hypothesis ‘a’). For most vegetation biomass and cover parameters, however, the variance was widely different between the sites with different treatments (partly rejecting hypothesis ‘a’). In general, vegetation variability in relation to mean values, as shown by the coefficient of variation (CV), was higher than the variability in soil parameters (supporting the second part of hypothesis ‘a’).

It is well established that vegetation is more strongly impacted than soil by forest fires (Brown and Smith 2000; Neary et al. 2005). While some properties of the soil may remain unchanged or are relatively mildly altered after a fire, vegetation is most often killed or completely consumed in the process (Brown and Smith 2000; Neary et al. 2005). Thus, it is to be expected that the differing magnitude of fire impacts on the soil vs. vegetation would be reflected in the location-related variability of the relevant parameters, i.e. vegetation parameters with higher CV values. However, the difference in the variability of vegetation biomass and cover between sites in the different treatments, as opposed to similar variances for soil parameters across sites, was somewhat unexpected. I initially assumed that only the central tendency of vegetation and soil parameters would be different between sites of different treatments. I expected that the total within-site variance, on the other hand, would be similar between sites, as they represented very similar background ecological conditions before the execution of the treatments. I expected that the site-level treatments would then affect all the local sampling plots in each site to generally the same extent.

The soil and vegetation parameter variability results are also valuable in the light of statistical testing procedures – equal variance makes comparisons between groups easier for soil parameters. Information on data variability is also a prerequisite for power analysis and planning of future studies. Our simulation approach, based on data variability and the central tendencies in study **I,** has shown, for instance, that for humus layer SOM analysis in comparable disturbance types, six replicates would be necessary to reveal the disturbance effects. For vegetation biomass, four to five replicates were found to be sufficient based on the simulation-based power analysis. More details on this issue are given in section 3.6. of this thesis.

3.2 Burned/50 m^3 ha^{-1} retention - silvicultural burn site (B50) had lower humus SOM stocks than the burned/no cuttings – restoration burn site (BNC) and two other studied sites (I).

The results showed that the burned/50 m^3 ha^{-1} retention - silvicultural burn site (B50), which was both harvested and burned, had a lower humus layer SOM stock compared to the three other sites in the study (restoration burn – BNC, unburnt/no cuttings – control – UBNC, and unburnt/0 m^3 ha^{-1} retention – unburnt complete clearcut – UBCC, Fig. 2a, 2c in study **I**). Site B50 also had a lower total sum of litter mass and ground- and field-layer biomass than the other three sites (Fig. 2i in study **I**). Importantly, the SOM stock of the site that was burned but unharvested (burned/no cuttings – restoration burn - BNC) was similar to that of the control site (UBNC, Fig. 2c in study **I**). PCA ordination of the soil and vegetation parameters with four sites as environmental variables showed similar relationships. A gradient of disturbance severity could be delineated, where the unburnt/no cuttings - control site (UBNC) was the least disturbed, followed by the burned/no cuttings – restoration burn site(BNC), the unburnt/0 m^3 ha^{-1} retention – complete clearcut (UBCC) site and finally the burned/50 m^3 ha^{-1} retention - silvicultural burn site (B50) as the most disturbed. Burning the forest after harvesting is analogous to silvicultural prescribed burning that is used to improve the seedbed conditions for tree regeneration. Prescribed burning of a fully stocked site (such as BNC), on the other hand, is considered as analogous to a restoration burn for biodiversity protection and the creation of disturbance legacies in the forest.

These findings suggest that while silvicultural burning may have a detrimental effect on soil stocks 14 years after a disturbance event, restoration burning possibly does not impact the soil system to the same extent, and 14 years after restoration burning SOM levels are approximately at the same level as in the control forest. These findings, however, need to be replicated to be considered indicative of the treatment effects. The issue of replication is further discussed and addressed in chapter 3.6. of this thesis. In addition, even in the more aggressive silvicultural burn site (burned/50 m^3 ha^{-1} retention), the mineral SOM stock was at a similar level as in the other sites with typically lower disturbance severity (Fig. 2e of study **I**). This indicates a possibility that mineral soil layers were not severely affected by the treatments, but also this finding would need replicated verification.

3.3 Disturbance by burning and clearcutting decreased vegetation beta-diversity and homogenized forest vegetation via colonization-extinction dynamics (II).

Vegetation beta-diversity was impacted by time since disturbance, and disturbance type and severity. Plant beta-diversity differed between stands of differing treatments initially before the disturbance treatments were applied. Two years after disturbance, this variation became undetectable, and ten years after disturbance the vegetation beta-diversity became significantly lower in the burned than in the unburnt stands, demonstrating the homogenizing effect of fire (supporting first part of hypothesis ‘b’).

In addition, the tree retention patches seemed to act as refugia for plant species, as was shown by slightly higher extinction and colonization beta-diversity rates in the stands with a high level of green tree retention (50 m^3 ha^{-1}) than in the lower retention (10 m^3 ha^{-1}) and clearcut sites (supporting second part of hypothesis ‘b’).

The lower vegetation beta-diversity levels in the burned stands ten years after disturbance were most likely caused by low colonization rates after the spatially-uniform fire-driven extinctions.

Detailed examination of vegetation biodiversity patterns permits a better understanding of the processes that drive community assembly and species turnovers, as affected by disturbance and active restoration treatments. The results of the vegetation diversity study (**II**) reinforced the perception that vegetation is highly dynamic and volatile in response to disturbance (**I**), and also highlighted the importance of green tree retention in mitigating the impacts of disturbance on boreal forest vegetation.

3.4 The environment was more favorable for SOM decomposition in the vicinity of non-charred logs as compared to positions further away from the logs, but there was no such difference for charred logs (III).

In study **III**, I analyzed the decomposition rates of standard substrate (tea bags and cellulose) placed at the interface of the organic and mineral soil layers, as an indicator for environmental controls on SOM decomposition in the corresponding microsites. In the further discussion, environmental controls on SOM decomposition are also considered to include the community of decomposer organisms.

In the burned/50 m^3 ha^{-1} retention - silvicultural burn (B50) site, the effect of proximity to large downed non-charred logs on microenvironmental controls of SOM decomposition was observed. The decomposition of the standard substrate was faster close to the non-charred logs; the decomposition rate constant 'k' obtained using the tea bag method was 8.4 % higher in the sample plots at the non-charred logs than in the sample plots located further away from logs (supporting hypothesis 'c'). Interestingly, the sample plots at the charred logs exhibited a similar decomposition rate as the sample plots located further away from the logs, i.e. lower than at the non-charred logs (supporting second part of hypothesis 'c'). Further, I analyzed the decomposition of cellulose in bags of three mesh sizes: 1 mm, 50 μm, and 1 μm, to assess the differential effects of decomposer organisms based on their size. The decomposition of cellulose proceeded quite quickly, and only ~40% of decomposition bags had some cellulose left within them after 14 months in the field. In particular, only 14% of the 1 mm bags had any substrate left at the end of the experiment. Thus, a shorter incubation time would have been more appropriate in these conditions. There was no difference in mass of the remaining cellulose between locations with respect to logs or the different mesh sizes of the bags. However, for the smallest mesh size (1 μm) bags, the survival rate of cellulose material was lower in the sample plots at the non-charred logs than in the sample plots at the charred logs or those located further away from the downed logs (supporting hypothesis 'c'). This could mean that bacterial community was different at the non-charred logs, thereby leading to higher decomposition rates. Alternatively, this result could point to different moisture conditions and more pronounced leaching adjacent to non-charred logs.

The ecological effects of burning on CWD and SOM decomposition are complex. Pyrogenic carbon is very resistant to decomposition, but it also increases the substrate temperature via sunlight absorption (possibly enhancing decomposition), and simultaneously can decrease substrate moisture (possibly slowing down the decomposition, [Shorohova et al. 2008]). Overall, Shorohova et al. (2008) found a significant negative impact of burning on the decomposition rates of pine stumps. In study **III**, most of the downed logs sampled were Scots pine. Burning also changes the decomposer communities on CWD and increases the biodiversity of stump polypores (Suominen et al. 2018). In addition, changes due to burning occur in the soil, where the microclimate and decomposer communities can be altered, leading to changes in decomposition (Köster et al. 2015). Location depth of the decomposing material in the soil has an impact on the decomposition rates as well, and these impacts vary depending on soil temperature and moisture conditions (Finér et al. 2016). Furthermore, the dynamics of N in the soil and CWD fragments may also affect the decomposition rates (Finér et al. 2016; Rinne et al. 2017). It is also obvious that CWD and SOM are tightly linked in complex ways through physico-chemical interactions between the CWD fragments and the soil, and via decomposer organisms living both on dead wood and in the soil, which adds further complexity to OM turnover in this system. It is also possible that highly recalcitrant pyrogenic carbon compounds (Preston and Schmidt 2006; Knicker

2007) from the CWD can eventually be transported into the adjacent soil, altering decomposition dynamics therein. A small fraction of the pyrogenic carbon on CWD can be soluble and transported by leaching (Abiven et al. 2011), and physical fragmentation and transport of pyrogenic carbon from CWD surface into the soil is a further possibility.

Some logs analyzed in study **III** were on the ground before the treatments, while some have originated from falling retention trees after the burning. Thus, the effects of forest floor burning interacting with CWD already present on the soil surface, as well as separate fire impacts on the soils (more severe burning), after which the retention trees died and fell down, may have been possible. In this context, it is very likely that both soil temperature and moisture conditions, and microbial biomass and community structure were different adjacent to the charred and non-charred logs, and farther away from logs. These differences possibly determined the spatial patterns of decomposition in relation to the logs.

In general and not necessarily related to burning, other studies have also shown that downed logs have important proximity effects on soil functioning in forest ecosystems (Gonzalez-Polo et al. 2013), and the term "pedogenic hotspot" has been proposed to capture the important impacts of downed logs on forest soils (Stutz and Lang 2017).

In summary, due to the immense complexities in SOM and CWD decomposition dynamics described above, extensive and highly detailed studies are necessary in the future to disentangle the mechanisms driving the patterns observed in study **III**. For that, I recommend the use of a combination of a distance gradient from downed logs and molecular tracing methods. The tea bag index can be used in such systematic studies as a robust and cost-effective method to obtain data on environmental controls on forest SOM decomposition. My results, however, point to a pattern of spatial variation of conditions for SOM decomposition that is related to the non-charred and charred logs in the context of burning.

3.5 Boreal forests recover slowly from historical slash-and-burn disturbance regimes, and a century later there were still legacies of past disturbance in the soil and tree stand structure (IV).

The data from the sites with historical frequent anthropogenic burnings showed that while affected forests have partially recovered, there were still clear legacies of slash-and-burn regimes more than a century after the cessation of this management practice in the boreal forests of eastern Finland. Specifically, the humus layer was 14 % thinner, and humus layer SOM stocks were 25 % lower in the slash-and-burn stands than in the control stands (supporting hypothesis 'd'). The volume of deciduous trees, specifically birch, also showed a historical legacy of slash-and-burn. The volume of birch was 48.2 m^3 ha^{-1} (or 158 %) higher in the historical slash-and-burn areas than in the control areas (supporting hypothesis 'd'). Similarly, the amount of standing dead wood was 11.6 m^3 ha^{-1} (or 75 %) higher in the slash-and-burn areas as compared to the controls. Interestingly, there were very few birch seedlings in either the slash-and-burn or the control areas at the time of data collection. There was also an observed correlation between birch volume and humus layer thickness and SOM stocks.

Under the slash-and-burn regime in our study area, forests were burned as often as every 11 years (Lehtonen et al. 1996). This very short interval between successive disturbance events most probably has prevented SOM from recovering through litterfall from secondary plant succession (Johnson and Curtis 2001). Silver and pubescent birch are known as pioneer species that colonize burnt forest areas with a thinned humus layer or even exposed mineral soil that are favorable to birch seedling germination. It is also known that spruce is very sensitive to fire and is usually killed by it, thereby opening gaps for birch recruitment (Pennanen and Kuuluvainen 2002; Johnstone et al. 2010). This is in agreement with our knowledge of post-fire succession in mesic spruce stands; increased amounts of deciduous trees, such as birch and aspen, are a transient phenomenon before spruce reestablishes again as a dominant tree species (Kouki et al. 2004; Lankia et al. 2012).

In summary, it takes more than a century for mesic spruce forests to recover their natural characteristics in above- and belowground components after the cessation of prolonged frequent and intensive disturbance regime related to slash-and-burn cultivation.

3.6 Methodological aspects

The critical methodological aspects of the studies included in this thesis are related mainly to the issue of replication in capturing the ecological effects of different disturbances and restoration treatments. An additional related issue is that of possible autocorrelation of field data and its effects on sampling and inference.

Autocorrelation occurs when data from locations closer to one another are either more or less similar than the data from a randomly picked set of locations from the study system. It has generally been found that the forest soil and the understory vegetation parameters are autocorrelated at distances of up to 10 m (Liski 1995; Smithwick et al. 2005; Lavoie and Mack 2012). Thus, the sampling setup in the first study (**I**) was based on these previous findings, and autocorrelation analyses demonstrated the spatial independence of the data that was collected at a ~10 m spacing between sample plots. In cases where the spatial autocorrelation existing in the data is not accounted for in statistical testing, a form of pseudoreplication takes place and false rejections of the null hypothesis (type I error) can occur (Hurlbert 1984; Beale et al. 2010).

The issue of replication is highly relevant for the four studies examined in this thesis. Study **I** explicitly addressed the basic level of replication required in future research on active restoration of boreal forests under conditions similar to those observed here. The observations of differences in soil and vegetation parameters between sites in study **I**, while featuring spatially intensive sampling, were not replicated by the treatments – each of the four treatments (UBNC, BNC, UBCC, B50) was represented by only one site. This precluded employing the statistical between-group tests to test for differences in the soil and vegetation parameters' means. With an unreplicated design, it is impossible to know if the observed differences originate from the treatment effect or random variation between sites. The aim of the spatially intensive sampling, however, was to ascertain the means and variances of the parameters, and then use these to plan future replicated sampling. In this regard, an important question is how to balance the number of samples per site vs. the number of sites per treatment (replicates) to maximize the statistical power within the constraints of a given time and effort budget. To do this, I employed a Monte-Carlo analysis of power (**I**), generating artificial datasets based on the means and variances found in this intensive sampling, and running a one-way random-effects ANOVA on the generated datasets multiple times to see how many times the null hypothesis (i.e. that the means are the same between treatments) is rejected. The simulation also included an assumption on the share of the within-site variance out of the total variance. For instance, Puhlick et al. (2016) have reported such distribution of variance from the forests of North-Eastern USA. Thus, with these simulations I explored the statistical power of testing under a differing number of replicates and samples per replicate, and differing variance distribution into between-site and within-site variance (**I**). In general, I found that for humus layer SOM stock data, six replicates with 30 samples per replicate provided the highest and sufficient statistical power to capture the differences within the range of values for the number of samples per replicate and the number of replicates used in the simulations. Mineral SOM stocks were so marginally different between sites, that according to simulations, statistically capturing such differences would be not feasible within the assumed effort budget. For vegetation ground- and field-layer biomass data inference under conditions found in this study **(I)**, generally four to five replicates per treatment with 30 samples per site would suffice. This simulation-based power analysis approach can further guide the design of experiments or assist in the compilation of existing data for meta-analyses. It answers an important question as to how many replicates are truly needed for successful statistical inference.

Thus, the amount of replication in sampling soil variables would benefit from preliminary data that can be used to guide the level of sampling per site and replication per treatment. Too small or unbalanced sampling and replication design may not always be sufficient for between-treatment comparisons of soils and vegetation or may not perform in the most efficient way. Nonetheless, using two or three replicates per treatment is still better than having only one site per treatment for observations because it still can provide estimates of within-treatment variability (studies **II**, **III**, **IV**).

4 CONCLUSIONS

In this doctoral study, I have attempted to explore the variation, interrelationships and differences in boreal forest soil and vegetation parameters with respect to different disturbance treatments and regimes.

My results from the active restoration study (**I**) showed that variability in soil parameters was generally similar across sites of different disturbance types, while for most of the vegetation biomass and cover parameters, the variability differed between sites. Variability of vegetation parameters was higher than that of soil parameters. In addition, I found a difference between the more pronounced impacts of silvicultural prescribed burning and the milder impacts of restoration burning used in nature conservation (**I**). The findings of the study that focused on detailed spatial analyses of a few case sites need to be verified in a rigorous replicated manner across multiple regions and site types. For that purpose, the simulations of statistical power carried out can guide the planning of future studies on active restoration or in the compilation of existing data for meta-analyses. It has been suggested that a database on active restoration interventions in the boreal zone is needed (Ramberg et al. 2017) and I highly recommend that soil parameter data be added to such a database whenever possible. Further, it would be beneficial to study the balance and turnover of C and nutrients in actively restored ecosystems in an integrated way, i.e. by observing and quantifying net primary production, litterfall, litter decomposition, humus formation and changes in SOM stocks.

The results of the study on vegetation diversity (**II**) in actively restored sites showed that fire homogenizes the understory vegetation and this effect is seen up to 10 years after disturbance. Study **II** also adds to the mounting evidence that the retention of gaps of live trees during forest logging is highly important in sustaining important biological properties and ecosystem functioning in boreal forests. Retention gaps influenced the post-disturbance vegetation biodiversity noticeably and this variation is most likely related to non-random colonization-extinction dynamics and retention patches acting as refugia for plant species. These results can give further insight to how green tree retention affects the processes and mechanisms that maintain biodiversity in boreal managed forests and lay a foundation for future studies that would examine a broader spectrum of disturbances and a wider range of disturbance intensities.

My results also showed increased decomposition rates of standard substrate placed next to non-charred logs as compared to decomposition rates in microsites located further away from downed logs (**III**). Interestingly, no such increase in decomposition rates occurred next to charred logs. There are several possible mechanisms to be considered in future studies as the cause of this spatial pattern of decomposition, such as priming, microclimate regulation or fungal N translocation in relation to CWD fragments, or spatially varying burning severity of the forest floor and CWD. To ascertain the relative importance of these mechanisms, I suggest further studies that combine a distance gradient from logs with several sample plots and molecular tracing methods. Nevertheless, my findings on the role that proximity to charred and non-charred dead wood may have on soil processes are novel and may also have consequences as to how C dynamics should be estimated after wildfires.

My results from the passive restoration study (**IV**) confirmed that disturbed forests still had lower SOM stocks and a higher volume of birch trees and standing dead wood after more than a century of recovery than the less disturbed reference forests nearby. The results also suggest that while current active restoration burnings affect soils to a small degree or for short periods of time (**I**), the impacts of historical intensive slash-and-burn regimes are much more pronounced and long-term (**IV**). This would suggest that the restoration of primeval soils in the boreal region is probably more complicated than previously known. In the context of long-term recovery from past land use, it is imperative to preserve protected areas into the future for ongoing studies and for the monitoring of natural recovery. However, observation of actively restored forests over a longer successional time frame is also necessary in order to compare the long-term pathways and outcomes in active and passive restoration.

It is especially important to note that while passive restoration aims to achieve a holistic natural self-regulation of the ecosystem with a “hands-off” approach, active restoration often explicitly aims to (re-)establish known species, habitats, structures and processes in the ecosystem, and as such, the initial focus of the two restoration approaches is fundamentally different. Whether the outcomes of active and passive restoration eventually converge at longer successional timescales across multiple ecological parameters and processes in currently unknown and should be the focus of future studies.

REFERENCES

Abiven S., Hengartner P., Schneider M.P.W., Singh N., Schmidt M.W.I. (2011). Pyrogenic carbon soluble fraction is larger and more aromatic in aged charcoal than in fresh charcoal. Soil Biology and Biochemistry 43(7): 1615-1617. https://doi.org/10.1016/j.soilbio.2011.03.027.

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

Angelstam P.K. (1998). Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. Journal of Vegetation Science 9(4): 593–602. https://doi.org/10.2307/3237275.

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

Anselin L., Ibnu S., Youngihn K. (2006). GeoDa: An Introduction to Spatial Data Analysis. Geographical Analysis 38(1): 5-22. https://doi.org/10.1111/j.0016-7363.2005.00671.x.

Barnosky A.D., Brown J.H., Daily G.C., Dirzo R., Ehrlich A.H., Ehrlich P.R., Eronen J.T., Fortelius M., Hadly E.A., Leopold E.B., Mooney H.A., Myers J.P., Naylor R.L., Palumbi S., Stenseth N.C., Wake M.H. (2014). Introducing the scientific consensus on maintaining humanity's life support systems in the 21st century: Information for policy makers. The Anthropocene review 1(1): 78-109.

Bates D., Maechler M., Bolker B., Walker S. (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67(1): 1-48. https://doi.org/10.18637/jss.v067.i01.

Beale C.M., Lennon J.J., Yearsley J.M., Brewer M.J., Elston D.A. (2010). Regression analysis of spatial data. Ecology letters 13(2): 246-264. https://doi.org/10.1111/j.1461-0248.2009.01422.x.

Berg A., Ehnstrom B., Gustafsson L., Hallingback T., Jonsell M., Weslien J. (1994). Threatened plant, animal and fungus species in Swedish forests: Distribution and habitat associations. Conservation biology 8(3): 718-731. https://doi.org/10.1046/j.1523-1739.1994.08030718.x.

Bergeron Y., Leduc A., Harvey B.D., Gauthier S. (2002). Natural fire regime: a guide for sustainable forest management of the Canadian boreal forest. Silva Fennica 36: 81–95. https://doi.org/10.14214/sf.553.

Bernes C., Jonsson B.G., Junninen K., Lõhmus A., Macdonald E., Müller J., Sandström J. (2015). What is the impact of active management on biodiversity in boreal and temperate forests set aside for conservation or restoration? A systematic map. Environmental Evidence 4: 25. https://doi.org/10.1186/s13750-015-0050-7.

Brown J.K., Smith J.K. (eds.). (2000). Wildland fire in ecosystems: effects of fire on flora. General Technical Report RMRS-GTR-42-vol. 2. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 257 p. https://doi.org/10.2737/RMRS-GTR-42-V2.

Brūmelis G., Jonsson B.G., Kouki J., Kuuluvainen T., Shorohova E. (2011). Forest Naturalness in Northern Europe: Perspectives on Processes, Structures and Species Diversity. Silva Fennica 45(5): 807-821. https://doi.org/10.14214/sf.446.

Cajander A.K. (1949). Forest types and their significance. Acta Forestalia Fennica 56: 1-71. https://doi.org/10.14214/aff.7396.

Certini G. (2005). Effects of fire on properties of forest soils: a review. Oecologia 143: 1-10. https://doi.org/10.1007/s00442-004-1788-8.

Chapin F.S. III, Kofinas G.P., Folke C. (eds.). (2009). Principles of ecosystem stewardship: Resilience-based natural resource management in a changing world. Springer, New York, USA. 401 p.

Chapin F.S. III, Matson P.A., Vitousek P.M. (2011). Principles of terrestrial ecosystem ecology. Springer, New York, USA. 529 p. https://doi.org/10.1007/978-1-4419-9504-9.

Chivian E., Bernstein A. (eds.). (2008). Sustaining life: How human health depends on biodiversity. Center for Health and the Global Environment. Oxford University Press, New York.

Clemmensen K.E., Bahr A., Ovaskainen O., Dahlberg A., Ekblad A., Wallander H., Stenlid J., Finlay R.D. Wardle D.A., Lindahl B.–D. (2013). Roots and associated fungi drive long-term carbon sequestration in boreal forest. Science 339: 1615–1618.

Cole D.N., Yung L. (eds.). (2010). Beyond naturalness: rethinking park and wilderness stewardship in an era of rapid change. Island press, Washington DC, USA. 287 p.

Crutzen P.J. (2002). Geology of mankind. Nature 415: 23. https://doi.org/10.1038/415023a.

DeLuca T.H., Boisvenue C. (2012). Boreal forest soil carbon: distribution, function and modelling. Forestry 85(2): 161-184. https://doi.org/10.1093/forestry/cps003.

Eales J., Haddaway N.R., Bernes C., Cooke S.J., Jonsson B.G., Kouki J., Petrokofsky G. (2016). What is the effect of prescribed burning in temperate and boreal forest on biodiversity, beyond tree regeneration, pyrophilous and saproxylic species? A systematic review protocol. Environmental Evidence 5: 24. https://doi.org/10.1186/s13750-016-0076-5.

Finér L., Messier C., De Grandpré L. (1997). Fine-root dynamics in mixed boreal conifer – broad-leafed forest stands at different successional stages after fire. Canadian Journal of Forest Research 27(3): 304-314. https://doi.org/10.1139/x96-170.

Finér L., Ohashi M., Noguchi K., Hirano Y. (2011). Factors causing variation in fine root biomass in forest ecosystems. Forest Ecology and Management 261(2): 265-277. https://doi.org/10.1016/j.foreco.2010.10.016.

Finér L., Jurgensen M.F., Palviainen M., Piirainen S., Page-Dumroese D. (2016). Does clear-cut harvesting accelerate initial wood decomposition? A five year study with standard wood material. Forest Ecology and Management 372: 10-18. https://doi.org/10.1016/j.foreco.2016.03.060.

Gauthier S., Bernier P., Kuuluvainen T., Shvidenko A.Z., Schepaschenko D.G. (2015). Boreal forest health and global change. Science 349(6250): 819-822. https://doi.org/10.1126/science.aaa9092.

Gonzalez-Polo M., Fernandez-Souto A., Austin A.T. (2013). Coarse woody debris stimulates soil enzymatic activity and litter decomposition in an old-growth temperate forest of Patagonia, Argentina. Ecosystems 16: 1025-1038. https://doi.org/10.1007/s10021-013-9665-0.

Halme P., Allen K.A., Auniņš A., Bradshaw R.H.W., Brūmelis G., Čada V., Clear J.L., Eriksson A., Hannon G., Hyvärinen E., Ikauniece S., Iršėnaitė R., Jonsson B.G., Junninen K., Kareksela S., Komonen A., Kotiaho J.S., 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. Biological Conservation 167: 248-256. https://doi.org/10.1016/j.biocon.2013.08.029.

Harmon M.E., Nadelhoffer K.J., Blair J.M. (1999). Measuring decomposition, nutrient turnover, and stores in plant litter. In: Robertson G.P., Coleman D.C., Bledsoe C.S., Sollins P. (eds.) Standard soil methods for long-term ecological research. Oxford University Press, New York. pp. 202-240.

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

Heikkala O., Martikainen P., Kouki J. (2016). Decadal effects of emulating natural disturbances in forest management on saproxylic beetle assemblages. Biological Conservation 194: 39-47. https://doi.org/10.1016/j.biocon.2015.12.002.

Helmisaari H.-S., Lehto T., Makkonen K. (2000). Fine Roots and Soil Properties. In: Mälkönen E. (eds.). Forest Condition in a Changing Environment. Forestry Sciences, vol. 65. Springer, Dordrecht. https://doi.org/10.1007/978-94-015-9373-1_24.

Hobbs R.J., Higgs E., Harris J.A. (2009). Novel ecosystems: implications for conservation and restoration. Trends in Ecology and Evolution 24(11): 599-605. https://doi.org/10.1016/j.tree.2009.05.012.

Hollander M., Wolfe D.A. (1973). *Nonparametric Statistical Methods.* New York, John Wiley & Sons. pp. 68-75.

Hotanen J.-P., Nousiainen H., Mäkipää R., Reinikainen A., Tonteri T. (2008). Metsätyypit – opas kasvupaikkojen luokitteluun. [Forest types – A guide for classification of site-types]. Metsäntutkimuslaitos. 182 p. ISBN-13: 978-952-5694-22-2.

Hurlbert S.H. (1984). Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187-211. https://doi.org/10.2307/1942661.

Hyvärinen E., Kouki J., Martikainen P., Lappalainen H. (2005). Short-term effects of controlled burning and green-tree retention on beetle (Coleoptera) assemblages in managed boreal forests. Forest Ecology and Management 212: 315-335. https://doi.org/10.1016/j.foreco.2005.03.029.

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 forests. Conservation Biology 20: 1711-1719. https://doi.org/10.1111/j.1523-1739.2006.00511.x.

IBM Corp. Released 2012. IBM SPSS Statistics for Windows, Version 21.0. Armonk, NY: IBM Corp.

Johnson D.W., Curtis P.S. (2001). Effects of forest management on soil C and N storage: meta analysis. Forest ecology and management 140: 227-238. https://doi.org/10.1016/S0378-1127(00)00282-6.

Johnstone J.F., Chapin F.S. III, Hollingsworth T.N., Mack M.C., Romanovsky V., Turetsky M. (2010). Fire, climate change, and forest resilience in interior Alaska. Canadian Journal of Forest Research 40: 1302-1312. https://doi.org/10.1139/X10-061.

Jones H.P., Jones P.C., Barbier E.B., Blackburn R.C., Benayas J.M.R., Holl K.D., McCrackin M., Meli P., Montoya D., Mateos D.M. (2018). Restoration and repair of Earth's damaged ecosystems. Proceedings of Royal society B 285: 20172577. https://doi.org/10.1098/rspb.2017.2577.

Junninen K., Kouki J., Renvall P. (2008). Restoration of natural legacies of fire in European boreal forests: an experimental approach to the effects on wood-decaying fungi. Canadian Journal of Forest Research 38: 202–215. https://doi.org/10.1139/X07-145.

Keuskamp J.A., Dingemans B.J.J., Lehtinen T., Sarneel J.M., Hefting M.M. (2013). Tea Bag Index: a novel approach to collect uniform decomposition data across ecosystems. Methods in Ecology and Evolution 4: 1070–1075. https://doi.org/10.1111/2041-210X.12097.

Knicker H. (2007). How does fire affect the nature and stability of soil organic nitrogen and carbon? A review. Biogeochemistry 85: 91-118. https://doi.org/10.1007/s10533-007-9104-4.

Köster K., Berninger F., Heinonsalo J., Lindén A., Köster E., Ilvesniemi H., Pumpanen J. (2015). The long-term impact of low-intensity surface fires on litter decomposition and enzyme activities in boreal coniferous forests. International Journal of Wildland Fire 25(2): 213-223. https://doi.org/10.1071/WF14217.

Kouki J. (2017). http://forest.uef.fi/jarikouki/project_fire.htm. [Cited 9 August 2017].

Kouki J., Löfman S., Martikainen P., Rouvinen S., Uotila A. (2001). Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. Scandinavian Journal of Forest Research 16(sup003): 27-37. https://doi.org/10.1080/028275801300090564.

Kouki J., Arnold K., Martikainen P. (2004). Long-term persistence of aspen and its associated threatened species are endangered in old-growth conservation areas in Finland. Journal for Nature Conservation 12(1): 41–52. https://doi.org/10.1016/j.jnc.2003.08.002.

Kuuluvainen T. (2002). Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fennica 36(1): 97–125. https://doi.org/10.14214/sf.552.

Kuuluvainen T. (2009). Forest management and biodiversity conservation based on natural ecosystem dynamics in Northern Europe: The complexity challenge. Ambio 38(6): 309-315. https://doi.org/10.1579/08-A-490.1.

Laiho R., Prescott C. (2004). Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. Canadian Journal of Forest Research 34: 763-777. https://doi.org/10.1139/x03-241.

Lankia H., Wallenius T., Várkonyi G., Kouki J., Snäll T. (2012). Forest fire history, aspen and goat willow in a Fennoscandian old-growth landscape: are current population structures a legacy of historical fires? Journal of Vegetation Science 23(6): 1159–1169. https://doi.org/10.1111/j.1654-1103.2012.01426.x.

Larjavaara M., Berninger F., Palviainen M., Prokushkin A., Wallenius T. (2017). Post-fire carbon and nitrogen accumulation and succession in Central Siberia. Scientific Reports 7: 12776. https://doi.org/10.1038/s41598-017-13039-2.

Lassauce A., Paillet Y., Jactel H., Bouget C. (2011). Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecological Indicators 11(5): 1027-1039. https://doi.org/10.1016/j.ecolind.2011.02.004.

Lavoie M., Mack M.C. (2012). Spatial heterogeneity of understory vegetation and soil in an Alaskan upland boreal forest fire chronosequence. Biogeochemistry 107(1): 227–239. https://doi.org/10.1007/s10533-010-9547-x.

Lehtonen H. (1997). Forest fire history in North Karelia: a dendroecological approach. Doctoral dissertation. University of Joensuu, Faculty of Forestry.

Lehtonen H., Huttunen P., Zettenberg P. (1996). Influence of man on forest fire frequency in North Karelia, Finland, as evidenced by fire scars in Scots Pines. Annales Botanici Fennici 33: 257-263.

Liski J. (1995). Variation in soil organic carbon and thickness of soil horizons within a boreal forest stand – effect of trees and implications for sampling. Silva Fennica 29(4): 255-266. https://doi.org/10.14214/sf.a9212.

Liu J., Dietz T., Carpenter S.R., Alberti M., Folke C., Moran E., Pell A.C., Deadman P., Kratz T., Lubchenco J., Ostrom E., Ouyang Z., Provencher W., Redman C.L., Schneider S.H., Taylor. W.W. (2007). Complexity of Coupled Human and Natural Systems. Science 317: 1513-1516.

Makkonen K., Helmisaari H.-S. (2001). Fine root biomass and production in Scots pine stands in relation to stand age. Tree Physiology 21(2-3): 193-198. https://doi.org/10.1093/treephys/21.2-3.193.

McDonald T., Gann G.D., Jonson J., Dixon K.W. (2016). International standards for the practice of ecological restoration – including principles and key concepts. Society for Ecological Restoration, Washington, D.C. http://c.ymcdn.com/sites/www.ser.org/resource/resmgr/docs/SER_International_Standards.pdf. [Cited 20 July 2017].

Myers J.A., Chase J.M., Crandall R.M., Jiménez I. (2015). Disturbance alters beta-diversity but not the relative importance of community assembly mechanisms. Journal of Ecology 103: 1291–1299. https://doi.org/10.1111/1365-2745.12436.

Neary D.G., Ryan K.C., DeBano L.F. (eds.). (2005). (revised 2008). Wildland fire in ecosystems: effects of fire on soils and water. General Technical Report RMRS-GTR-42-vol.4. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 250 p. https://doi.org/10.2737/RMRS-GTR-42-V4.

Palviainen M., Pumpanen J., Berninger F., Ritala K., Duan B., Heinonsalo J., Sun H., Köster E., Köster K. (2017). Nitrogen balance along a northern boreal forest fire chronosequence. PLoS ONE 12(3): e0174720. https://doi.org/10.1371/journal.pone.0174720.

Pasanen H. (2017). Ecological effects of disturbance-based restoration in boreal forests. Dissertationes Forestales 244. 29 p. https://doi.org/10.14214/df.244.

Pennanen J., Kuuluvainen T. (2002). A spatial simulation approach to natural forest landscape dynamics in boreal Fennoscandia. Forest Ecology and Management 164(1–3): 157–175. https://doi.org/10.1016/S0378-1127(01)00608-9.

Pickett S.T.A., White P.S. (eds.). (1985). The ecology of natural disturbance and patch dynamics. Academic Press, New York, USA. 472 p.

PKMMKA (1899). Pohjois-Karjalan maanmittauskonttorin arkisto, Lieksa. Kartanosa 5. Pielis-järven eteläisemmästä kruununmaasta, Rek. nro. 29:5. [North-Karelian land survey bureau archive, Lieksa. Map unit 5. Pielisjärvi southernmost crownland, Reg. No. 29:5.] [In Finnish].

Pinheiro J., Bates D., DebRoy S., Sarkar D., R Core Team (2017). nlme: linear and nonlinear mixed effects models. R package version 3.1-131. https://CRAN.R-project.org/package=nlme.

Preston C.M., Schmidt M.W.I. (2006). Black (pyrogenic) carbon: a synthesis of current knowledge and uncertainties with special consideration of boreal regions. Biogeosciences 3(4): 397-420. https://doi.org/10.5194/bg-3-397-2006.

Puhlick J.J., Fraver S., Fernandez I.J., Weiskittel A.R., Kenefic L.S., Kolka R.K., Gruselle M.-C. (2016). Factors influencing organic-horizon carbon pools in mixed-species stands of central Maine, USA. Forest Ecology and Management 364: 90-100. https://doi.org/10.1016/j.foreco.2016.01.009.

R Development Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.R-project.org.

Ramberg E., Strengbom J., Granath G. (2017). Coordination through databases can improve prescribed burning as a conservation tool to promote forest biodiversity. Ambio 47(3): 298-306. https://doi.org/10.1007/s13280-017-0987-6.

Raup D.M., Crick R.E. (1979). Measurement of faunal similarity in paleontology. Journal of Paleontology 53: 1213-1227.

Rinne K.T., Rajala T., Peltoniemi K., Chen J., Smolander A., Mäkipää R. (2017). Accumulation rates and sources of external nitrogen in decaying wood in a Norway spruce dominated forest. Functional Ecology 31(2): 530-541. https://doi.org/10.1111/1365-2435.12734.

Rouvinen S., Kouki J. (2008). The natural northern European boreal forests: Unifying the concepts, terminologies, and their application. Silva Fennica 42(1): 135-146. https://doi.org/10.14214/sf.270.

Ruxton G.D. (2006). The unequal variance t-test is an underused alternative to Student's t-test and the Mann-Whitney U test. Behavioral Ecology 17: 688-690. https://doi.org/10.1093/beheco/ark016.

Sarkkola S. (2006). Stand structural dynamics on pristine and managed boreal peatlands. Doctoral dissertation. University of Helsinki, Department of Forest Ecology. 78 p. ISBN-13:978-951-651-146-0.

Schimmel J., Granström A. (1996). Fire severity and vegetation response in the boreal Swedish forest. Ecology 77(5): 1436-1450. https://doi.org/10.2307/2265541.

Shorohova E., Kapitsa E., Vanha-Majamaa I. (2008). Decomposition of stumps in a chronosequence after clear-felling vs. clear-felling with prescribed burning in a southern boreal forest in Finland. Forest Ecology and Management 255: 3606–3612. https://doi.org/10.1016/j.foreco.2008.02.042.

Similä M., Junninen K. (2012). Ecological restoration and management in boreal forests – best practices from Finland. Metsähallitus, Natural Heritage Services, Vantaa. 54 p.

Šmilauer P. (2016). Canoco5 Support Site. http://www.canoco5.com/. [Cited 16 February 2017].

Smithwick E.A.H., Mack M.C., Turner M.G., Chapin III F.S., Zhu J., Balser T.C. (2005). Spatial heterogeneity and soil nitrogen dynamics in a burned black spruce forest stand: distinct controls at different scales. Biogeochemistry 76(3): 517–537. https://doi.org/10.1007/s10533-005-0031-y.

Steffen W., Sanderson R.A., Tyson P.D., Jäger J., Matson P.A., Moore III B., Oldfield F., Richardson K., Schellnhuber H.-J., Turner B.L., Wasson R.J. (2004). Global change and the Earth system: a planet under pressure. Springer-Verlag, New York. 332 p.

Stutz K.P., Lang F. (2017). Potentials and unknowns in managing coarse woody debris for soil functioning. Forests 8(2): 37. https://doi.org/10.3390/f8020037.

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

Suominen M., Junninen K., Heikkala O., Kouki J. (2018). Burning harvested sites enhances polypore diversity on stumps and slash. Forest Ecology and Management 414: 47-53. https://doi.org/10.1016/j.foreco.2018.02.007.

Team R.C. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

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. Annales Zoologici Fennici 43: 373-383.

Turetsky M.R., Kane E.S., Harden J.W., Ottmar R.D., Manies K.L., Hoy E., Kasischke E.S. (2011). Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands. Nature geoscience 4: 27-31. https://doi.org/10.1038/ngeo1027.

Turner II B.L., Lambin E.F., Reenberg A. (2007). The emergence of land change science for global environmental change and sustainability. Proceedings of the National Academy of Sciences 104(52): 20666–20671. https://doi.org/10.1073/pnas.0704119104.

UN environment (2017). Aichi biodiversity targets. https://www.cbd.int/sp/targets/. [Cited 26 April 2018].

Uotila A., Kouki J., Kontkanen H., Pulkkinen P. (2002). Assessing the naturalness of boreal forests in eastern Fennoscandia. Forest ecology and management 161(1-3): 257-277. https://doi.org/10.1016/S0378-1127(01)00496-0.

van der Plas F., Manning P., Soliveres S., Allan E., Scherer-Lorenzen M., Verheyen K., Wirth C., Zavala M.A., Ampoorter E., Baeten L., Barbaro L., Bauhus J., Benavides R., Benneter A., Bonal D., Bouriaud O., Bruelheide H., Bussotti F., Carnol M., Castagneyrol B., Charbonnier Y., Coomes D.A., Coppi A., Bastias C.C., Dawud S.M., Wandeler H.D., Domisch T., Finér L., Gessler A., Granier A., Grossiord C., Guyot V., Hättenschwiler S., Jactel H., Jaroszewicz B., Joly F-x., Jucker T., Koricheva J., Milligan H., Mueller S., Muys B., Nguyen D., Pollastrini M., Ratcliffe S., Raulund-Rasmussen K., Selvi F., Stenlid J., Valladares F., Vesterdal L., Zielínski D., Fischer M. (2016). Biotic homogenization can decrease landscape-scale forest multifunctionality. Proceedings of the National Academy of Sciences of the United States of America 113(13): 3557-3562. https://doi.org/10.1073/pnas.1517903113.

Vellend M., Verheyen K., Flinn K.M., Jacquemyn H., Kolb A., Van Calster H., Peterken G., Graae B.J., Bellemare J., Honnay O., Brunet J., Wulf M., Gerhardt F., Hermy M. (2007). Homogenization of forest plant communities and weakening of species-environment relationships via agricultural land use. Journal of Ecology 95(3): 565-573. https://doi.org/10.1111/j.1365-2745.2007.01233.x.

Wake D.B., Vredenburg V.T. (2008). Are we in the midst of the sixth mass extinction? A view from the world of amphibians. Proceedings of the National Academy of Sciences of the United States of America 105(suppl. 1): 11466-11473. https://doi.org/10.1073/pnas.0801921105.