Dissertationes Forestales 244

Ecological effects of disturbance-based restoration in boreal forests

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Academic dissertation

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ABSTRACT

The degradation and disappearance of natural ecosystems and habitats – including forests – is one of the most important factors behind the current global decline in biological diversity. Since most of terrestrial biodiversity is found in forests, restoration of these ecosystems or their natural characteristics has been proposed as one of the main strategies to counteract global species loss.

In this thesis, I examined the ecological effects of forest restoration in disturbance-driven boreal conditions. The applied restoration methods (prescribed burning; creation of canopy gaps; dead wood restoration) used natural forest disturbances as the reference point. Specifically, I focused on the effects that restoration has on tree species composition, age-class structure, and the amount and diversity of dead wood in forest ecosystems. In addition to examining the changes in these structural attributes, I investigated dead-wood-associated fungal communities in the restored substrates, and assessed whether dead wood restoration could be used to conserve rare and threatened fungal species.

Of the examined restoration treatments, the combination of prescribed burning and the creation of canopy gaps was found to be the most promising measure for the restoration of age-class structure and tree species composition in pine-dominated forests. Dead wood restoration – by artificially creating standing and fallen large-diameter dead trees – clearly enhanced the amount of dead wood in both pine and spruce dominated forests. Although dead wood restoration increased the abundance of fungal species in the examined forests, all aspects of the qualitative variation in dead wood was found to be difficult to restore in the short-term, since the restored dead wood was mainly in the initial stage of decomposition. The use of various restoration treatments (e.g. the creation of both standing and fallen dead wood) can compensate for some of the missing variation in fungal communities in the restored substrates.

Based on my results, disturbance-based restoration produces promising results by the rapid re-introduction of some of the most important structural attributes that have been lost from forests previously managed for timber production. Although the findings in this thesis show the clear positive effects that restoration has on the re-creation of naturally occurring forest characteristics, it appears difficult to restore all the inherent variability of natural forests. A particular challenge originates from the extended time scale of the natural processes, which have created and maintained the full array of ecological structures in forests, including the generally slow processes of stand succession and wood decomposition. To build a more comprehensive understanding of the potential of forest restoration for the conservation of endangered forest-associated species, a substantially longer monitoring period of restored forests would be useful in future studies.

Keywords: Forest restoration, fungal diversity, natural disturbance emulation, sustainable forest management

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I required a lot of help from numerous people to being able to finish this project and to understand the complexity of my research area. Most of the help I received was from my supervisors Prof. Jari Kouki (School of Forest Sciences, University of Eastern Finland) and Dr. Kaisa Junninen (Metsähallitus Parks & Wildlife Finland). I undertook my Masters' thesis under their supervision, and this doctoral thesis represents a natural continuum to our earlier work. As my main supervisor, Jari helped me sketch the original idea for this thesis, and has provided excellent guidance in all parts of the process; both relating to practical aspects but also in aiding my understanding of science in general. I highly appreciate his skills in leadership and his ability to keep a cool head in all kinds of situations. As my second supervisor, Kaisa helped me to understand the peculiar and interesting life of polypore fungi. She had the sharpest eyes for spotting inconsistencies in various parts of my manuscripts and she provided indispensable help with microscopy. Altogether, I think we made a solid team where each of us provided important input for this work. Thank you for all the support.

I thank my co-authors Shinichi Tatsumi, Seppo Rouvinen, Johanna Boberg, Jan Stenlid, and Virve Rehu for collaborating with me. In particular, the work with Jan, Johanna, and the people at the Swedish University of Agricultural Sciences gave me a highly valuable perspective on DNA-based fungal sampling.

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I thank Juha Varis and all the nice people at Pandia for arranging an office-room for me to work in during the first year of working with this thesis.

Last autumn I did field sampling in Isojärvi, where Jari Kulmala kindly arranged accommodation for me. Thanks for the good company during those couple of months.

This work would not have been possible without the experimental sites provided by Metsähallitus.

I'm grateful for my parents; Antero and Raija and the rest of my family for providing such a good ground to start from. I use this opportunity to thank all my friends for all the great things that have happened over the years. Finally, Annamaria, my partner in life, is thanked for all her love, patience, and understanding.

Joensuu, May 2017

Hannes Pasanen

"Conservation is getting nowhere because it is incompatible with our Abrahamic concept of land. We abuse land because we regard it as a commodity belonging to us. When we see land as a community to which we belong, we may begin to use it with love and respect." –Aldo Leopold (1948)

LIST OF ORIGINAL ARTICLES

This thesis is a summary of the following articles, which are referred to in the text by the Roman numerals. Studies **I–III** are reprints of previously published articles reprinted with the permission of the publishers. Study **IV** is a manuscript.

I Pasanen H., Rehu V., Junninen K., Kouki J. (2015). Prescribed burning of canopy gaps facilitates tree seedling establishment in restoration of pine-dominated boreal forests. Canadian Journal of Forest Research 45: 1225-1231. https://doi.org/10.1139/cjfr-2014-0460

II Pasanen H., Rouvinen S., Kouki J. (2016). Artificial canopy gaps in the restoration of boreal conservation areas: long-term effects on tree seedling establishment in pine-dominated forests. European Journal of Forest Research 135: 697-706. https://doi.org/10.1007/s10342-016-0965-8

III Pasanen H., Junninen K., Kouki J. (2014). Restoring dead wood in forests diversifies wood-decaying fungal assemblages but does not quickly benefit red-listed species. Forest Ecology and Management 312: 92-100. https://doi.org/10.1016/j.foreco.2013.10.018

IV Pasanen H., Junninen K., Boberg J., Tatsumi S., Stenlid J., Kouki J. (2017). Life after tree death: does restored dead wood host different fungal communities to natural woody substrates? Manuscript.

The contribution of Hannes Pasanen to the studies included in this thesis was as follows:

Study **I**: Analyzed the data and wrote the manuscript together with co-authors.

Study **II**: Participated in field sampling. Analyzed the data and wrote the manuscript together with co-authors.

Study **III**: Participated in field sampling. Analyzed the data and wrote the manuscript together with co-authors.

Study **IV**: Participated in developing the original idea and the study design**.** Did most of the field sampling and laboratory work. Analyzed the data and prepared the manuscript together with co-authors.

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TERMINOLOGY

Natural disturbance: "Any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, and substrate availability or the physical environment" (Pickett & White 1994). Disturbances can arise from within or from outside the system (Perera et al. 2004).

Natural forest: "A forest that has evolved and reproduced itself naturally from organisms previously established, and that has not been significantly altered by human activity" (Rouvinen & Kouki 2008).

Resilience: "The capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks" (Walker et al. 2004).

Red-Listed species: A species with an enhanced risk of disappearance in a defined area over a certain period of time. The probability of disappearance is expressed by assessing threat status for species (or taxa). The following categories are used to define Red-Listed species in Finland: regionally extinct (RE), critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NE), and data deficient (DD). Species belonging to categories CR, EN, and VU are considered threatened (IUCN 2017).

Restoration: Practice that aims at bringing back the assumed former state of an object or a system. Ecological restoration has been defined as "…the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER 2004).

1. INTRODUCTION

1.1 Background

During the course of history, foresters have developed principles to avoid the over-exploitation of forests, in order to achieve a sustainable level of resource use (Kimmins 2004; Morgenstern 2007). With concepts such as normal forest and sustained yield, it has been possible to resolve many of the earlier problems concerning the continuous temporal supply of timber (Burton et al. 2003; Puettman et al. 2008). Sustaining all the inherent variability of forest ecosystems, however, has proven difficult with traditional approaches. The main problem is that the conventional methods generally do not take into account the long-term issues in forest resilience and adaptation to changes in external conditions, let alone the problems associated with the loss of biological diversity (Brandt et al. 2009; Ceballos et al. 2015) – the importance of which has only been more widely understood in the past few decades.

Ecological theory and its emerging convergence with silviculture have provided widened understanding and new methods to incorporate aspects other than timber yield into forest management (Hunter 1999; Puettman 2008). This development has now resulted in a more holistic view that does not see forests merely as a stock of trees, but as complex systems where management should be reconciled with an understanding of natural forest dynamics (Kimmins 2004; Puettman 2008). A management approach that attempts to take into account all the natural variability of forests is often referred to as forest ecosystem management (Kohm & Franklin 1997; Gauthier et al. 2009; Kuuluvainen 2017).

Despite the recent scientific advances in our understanding of the structure and functioning of forest ecosystems, several major problems remain to be solved. Primarily, the structural changes caused by forest management continue to negatively influence biological diversity, and solving this problem requires a better integration of theoretical advances into practice. Due to the complexity of forest ecosystems, the practical application of novel management methods requires continuous monitoring in order to assess both the short- and long-term effects of the treatments, which is a prerequisite for adaptive management (Walters & Holling 1990; Williams 2011).

1.2 Disturbance dynamics of natural forests as a reference in forest ecosystem management

The initial ideas on the use of natural forests as a reference in forestry (nature-based forestry) were developed in central Europe in the 19th century (Johann 2006; Kuuluvainen 2017). Similar ideas also inspired forestry practices and science in northern Europe, where competition among trees was used to build the foundations for various silvicultural operations (Kalela 1948). However, there are differences between the initial and the more recent versions of the concept; connected with the accumulated understanding of the role of stochastic events – and not merely deterministic processes such as competition – in shaping the structures and the dynamics of forest ecosystems (Attiwill 1994; Kuuluvainen & Grenfell 2012).

In the first half of the 20th century, the dominating paradigm in the study of ecological succession suggested that plant communities would reach a climax state mostly through deterministic sequences of seral stages, which was seen as an analogy to the development of an individual organism (Pickett et al. 2009; Kuuluvainen 2002). In particular, systems science and chaos theory have shaped the understanding of forest ecosystems towards a direction that is more coherent with the general scientific development (Filotas et al. 2014; Messier et al. 2013). Perhaps the most influential change has been a better acknowledgment of forests as open systems prone to stochastic events that originate both within and outside of the system (Filotas et al. 2014). Consequently, forests are currently seen as complex adaptive systems that do not approach equilibrium in their development, but are in a constant state of change between order and disorder (Messier et al. 2013). Therefore, it is difficult – and very likely impossible – to make exact, long-term predictions on their functioning and development (Landres 1999; Kuuluvainen 2002; Messier et al. 2013). It follows that all definitions that describe nature-based management are vague and cannot be used without due consideration of the disturbance dynamics that affect the system behavior in a given space (Rouvinen & Kouki 2008; Shorohova 2011; Kuuluvainen & Grenfell 2012; Gauthier et al. 2015).

An accumulated understanding of the significant role of disturbances implies that a rational approach to securing the natural diversity of ecosystems requires the integration of disturbances into forest management (Attiwill 1994; Hunter 1999; Perera et al. 2004). During the last decades, several management approaches have been developed under the natural disturbance paradigm, of which natural disturbance emulation (NDE) is perhaps the most general one (Perera 2004; Kuuluvainen & Grenfell 2012). In essence, the NDE concept is based on the assumption that species with different life-history strategies have adapted to utilizing the spatial and temporal niches that the interplay between forest succession and disturbances create over various temporal and spatial scales (Kuuluvainen 2002). The strength of the NDE approach is that it provides a comprehensive framework that can bridge the gap between different management objectives (Kuuluvainen & Grenfell 2012). With increased understanding of the relative importance of different disturbance types across the boreal zone, it is now possible to develop practical applications in their integration to forest management (Gromtsev 2002; Kuuluvainen & Aakala 2011; Shorohova et al. 2011). So far, NDE has been utilized both in the development of silvicultural systems that better take into account the ecosystem perspective (Hyvärinen et al. 2005; Koivula et al. 2014; Rodríguez et al. 2015; Heikkala et al. 2016; Suominen et al. 2016), but also as a guide to forest restoration treatments (Kuuluvainen 2002; Similä & Junninen 2012; Halme et al. 2013).

1.3 Boreal forests and their management

Boreal forests comprise one of the largest terrestrial biomes on earth, covering ca. 30% of the global forest area (Burton et al. 2005; Brandt et al. 2013; Gauthier et al. 2015). Forests in the boreal zone are characterized by tree species that tolerate low winter temperatures and short growing seasons, mainly belonging to the Genera *Abies*, *Betula*, *Larix*, *Picea*, *Pinus*, and *Populus* (Brandt 2009). Soils in the boreal forests are typically podzol-type and are relatively poor in nutrients. Although generally uniform, the boreal zone encompasses distinct and variable ecosystems due to geographic variation in historical glacial processes, climate, edaphic conditions and disturbance dynamics (Mönkkönen 2004; Shorohova et al. 2011).

Approximately two-thirds of the forest area in the boreal zone is managed for timber production: ca. 90% in northern Europe, followed by Russia (ca. 60%) and Canada (ca. 35-40%) (Gauthier et al. 2015). Management history, intensity, and practices vary depending on the region within the zone. My studies focus on boreal Fennoscandia where forest use and management has a long history extending back over centuries (e.g. Tasanen 2004).

Geographically, boreal Fennoscandia includes Norway, most of Sweden, Finland, and the northwestern part of Russia. Climate in the western parts of boreal Fennoscandia is strongly influenced by the Atlantic Ocean but in the eastern parts is intermediate between oceanic and continental climates. Prior to World War II, timber harvesting in the area was mainly based on selective cuttings in which little consideration was given to the regeneration of the forest stands (Kuuluvainen et al. 2012). To improve the quality of forest management, selective cuttings were officially banned in Finland and Sweden by the end of the 1940s, after which the emphasis in forestry practice shifted from uneven-aged management to even-aged management with the application of clear-cutting and thinning from below (Esseen et al. 1997; Kuuluvainen et al. 2012).

Development of even-aged silvicultural systems and large-scale draining of peatlands increased the volume of the growing stock in boreal Fennoscandian forests in the latter part of the 20th century (Henttonen et al. 2017). The drawback, however, has been the simplification of forests and the decline of their associated species (Esseen et al. 1997; Raunio et al. 2008; Rassi et al. 2010). Although the loss of biological diversity in forests, as such, is obviously partly an ethical issue that forest managers should resolve, a growing emphasis has been placed on the estimation of risks that simplification of forest ecosystems has on long-term resilience and adaptation, and the ecosystem services that forests provide for society (Cardinale et al. 2012; Mori et al. 2017). Although boreal forests have thus far retained much of their health and functioning, the conditions brought about by a changing climate may bring unexpected threats to their future resilience (Gauthier et al. 2015).

1.4 Forest restoration in Fennoscandia

Human land-use has modified most of the terrestrial biosphere (Ellis & Ramankutty 2008; Ellis 2011). Although forest utilization has led to a decrease in forest coverage, particularly in the tropics, recent changes in higher-latitude forests mainly concern their transformation into structurally simplified ecosystems that are managed for economic purposes (Keenan 2011; Sloan & Sayer 2015). In boreal Fennoscandia, the main structural differences between natural and managed forests are in tree species composition, age-class structure, and the amount and diversity of dead wood (Esseen et al. 1997; Raunio et al. 2008). The origin of the differences can be understood by comparing the variable disturbance dynamics of natural forests (Kuuluvainen & Aakala 2012) to the dynamics created by even-aged forestry, where only stand-replacing disturbances are emulated in a simplified manner and most of the trees are extracted from the stands. Restoration of human-modified ecosystems is one of the main strategic goals to meet the objectives of the Convention on Biological Diversity; where the current target is to restore at least 15% of the degraded ecosystems by 2020 (SCBD 2010).

Changes in forest structures are still visible in many protected areas due to their historical use for commercial timber production. In southern Finland, for example, approximately 75% of the forests within currently protected areas have been managed for timber production (Similä & Junninen 2012). To improve the ecological quality of degraded forests, various restoration treatments have been applied during the last decades (Djupström et al. 2012; Similä & Junninen 2012; Halme et al. 2013; Hekkala et al. 2016). Conceptually, the restoration approach in Fennoscandia relies on the natural disturbance paradigm, and aims at emulating natural disturbances in forests subjected to restoration (Kuuluvainen 2002; Halme et al. 2013). The rationale behind the various restoration treatments is to increase the structural diversity of essentially single-cohort forests, which are then expected to restore the native biota over time. In this thesis, I examine changes in forest structures by assessing the regeneration of trees and the amount and quality of dead wood in the restored forest stands. The structures together with the species that are dependent on them are assumed to restore some of the ecological processes and the functioning of the forests (Brūmelis et al. 2011).

From both management and theoretical perspectives, the challenge is to determine how precisely natural disturbances can, or should, be emulated in disturbance-based restoration. Due to practical reasons, the currently applied treatments most often differ to some extent from natural disturbances. For this reason, the application of restoration treatments is often referred to as being “artificial”, such as the artificial creation of canopy openings or dead wood. A topical problem in this regard is to understand whether more or less artificial treatments also result in forest structures (and thus species communities) that differ from those that appear in forests after natural disturbances. In this thesis, I examine the problem by comparing the communities of wood-inhabiting fungi in artificially created logs with logs of a natural origin.

1.5 Wood-inhabiting fungi and dead wood

Several ecological and taxonomic groups are affected by forest management and the consequent lack of structures created by natural disturbances. Wood-dependent fungi, for instance, appear particularly sensitive to forest management. Currently, these fungi are one of the most clearly declined groups of species in boreal Fennoscandian forests (Kotiranta et al. 2010). Thus, these fungi can be regarded as a key taxon when exploring how forest management – including restoration – influences forest biodiversity.

In addition to being widely endangered, fungi also have several important ecological roles in forest ecosystems (Harmon et al. 1986; Boddy & Heilmann-Clausen 2008; Stokland et al. 2012). Because fungi are heterotrophs, they rely on autotrophs for their resources. Some species use a strategy whereby they obtain energy by forming symbiotic associations with plants, which at the same time increases the nutrient intake of the plant roots. Another important strategy is to enzymatically degrade structural cell wall components of plant residues, for example woody debris (Baldrian 2008; Stokland et al. 2012). Decomposition of organic structures is important in understanding how matter, such as carbon and nutrients, cycle in forest ecosystems (Stenlid et al. 2008). This thesis mainly deals with those fungal species that have adapted to utilizing the cell walls of coarse woody debris as their resource.

In boreal Fennoscandia, the amount of dead wood in commercially managed forests is reduced by ca. 90-98% compared to natural forests (Siitonen 2001; Stokland et al. 2012). Thus, it is only logical that there has been a concurrent decline in the populations of fungal species that are dependent on dead wood (Kotiranta et al. 2010). The quantity of dead wood largely determines the amount of energy that is available for saproxylic food webs to consume (Wright 1983), but this only partly explains the structure of the fungal communities due to the high variation in niche requirements between species (Stokland et al. 2012; Kunttu et al. 2016). Qualitative variation (e.g. decay stage, diameter, host-tree species) of dead wood is an equally important aspect in understanding the composition of fungal species in a given forest, and is particularly important for species with narrow ecological niches (Stenlid et al. 2008; Stokland et al. 2012).

In addition to dispersal and environmental constraints, internal dynamics are a principal determinant in the community assembly (Belyea & Lancester 1999). For example, the life-history traits of fungi, such as the strategy for capturing resources and competitive ability, have an effect on how different species are able to colonize dead trees (Cooke & Rayner 1984; Stenlid et al. 2008). The strategy that different fungal species utilize in resource capture is linked with the mortality factor of a tree (Stokland et al. 2012; Ottosson et al. 2015). For this reason, it is assumed that various treatments to create dead wood may also result in differences in the quality of dead wood and consequently in the community composition of fungi; a process that is reminiscent of the effect of disturbance type in determining post-disturbance tree succession in forests, but at a different spatial scale.

In this thesis, wood-decaying fungi were chosen as a target group for an examination of the effects of dead wood restoration on species diversity since they are closely dependent on the restored substrates as a resource. By assessing fungal diversity in the restored forests, it is possible to assess whether the structural restoration of forests can also aid in the restoration of the native biota.

1.6 Aims of the thesis

The general objective of my thesis is to assess the ecological outcomes of emulating natural disturbances in the restoration of intensively managed forests closer to their natural state. The question is approached from four aspects, three of which focus on the main structural differences between natural and managed forests in Finland: (1) tree species composition, (2) tree age-class structure, and (3) the amount and diversity of dead wood. In addition to examining the change in the structural diversity of live and dead trees following restoration, I examine whether the restoration of dead wood can be beneficial in the conservation of (4) fungal diversity.

The aspects concerning the diversification of tree species composition and the age-class structure of trees were examined in studies **I** and **II**, in which tree regeneration following restoration measures was monitored. The amount and diversity of dead wood, and its associated fungal species, were investigated in studies **III** and **IV**.

The specific questions addressed in this thesis are:

1. Do various restoration treatments result in the diversification of the age-class structure and the tree species composition in pine dominated forests? (**I** and **II**)
2. What is the effect of artificially increasing the amount of dead wood on saproxylic fungi in pine and spruce dominated forests? (**III** and **IV**)
3. How do the various tree-level restoration treatments affect the fungal communities on Scots pine logs? Are these communities different from those that occur in natural dead wood? (**III** and **IV**)

2. MATERIAL AND METHODS

2.1 Study sites

The four data sets included in this thesis were collected from the boreal and the hemi-boreal vegetation zones in Finland (Fig. 1). Studies **I**, **II**, and **IV** were conducted in Scots pine (*Pinus sylvestris* L.) dominated forests; study **III** included both Norway spruce (*Picea abies* [L.] Karst.) and Scots pine dominated forests. Forests in the study area were growing on podzol soils, and the sites belonged to the *Vaccinium*-type (**I**, **II**, and **IV**) and to the *Myrtillus*-type (**I**), according to the to the Finnish site type classification (Cajander 1949; Kuusipalo 1996). More detailed information on the characteristics of the study areas is described in the various studies.

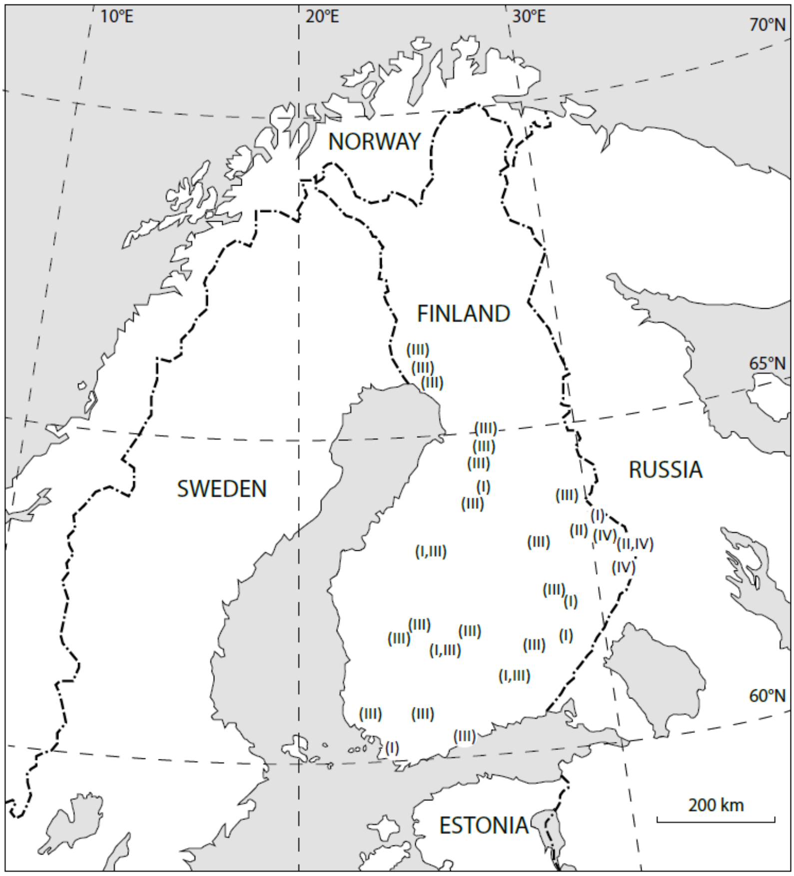

Figure 1. The location of study areas. The Roman numerals within parenthesis indicate the approximate locations of the sampling areas for each study (**I**-**IV**) included in this thesis.

2.2 Experimental treatments

All my studies are based on experimentation and include active manipulation of trees or forest structures. Restoration treatments were applied in the experimental sites to initiate the successional processes of live and dead trees. The focus in studies **I** and **II** was on the regeneration of trees following the creation of canopy openings and/or the use of prescribed burning (Fig. 2A). Fire treatments were applied in areas that ranged from 2 to 10 ha in size. Canopy openings in **I** and **II** were created by chainsaw-felling (Fig. 2B) or by girdling (Fig. 2C) healthy coniferous trees. In studies **III** and **IV**, which focused on the effects of dead wood restoration, trees were killed either by chainsaw-felling, girdling or by pushing them down with the bucket of an excavator (Fig. 2D). Chainsaw-felling and uprooting of trees were considered as analogs to the snapping of trees or tree uprooting following a strong wind for example. Ring-barking was used to create standing dead wood that, in turn, is expected to resemble mortality caused by insects or fungi. Trees were generally killed in clusters so that they formed canopy openings of various sizes and shapes. A detailed description of the rationale and practical application of the restoration treatments used in Finland can be found in Similä & Junninen (2012). All experimental treatments were conducted by Metsähallitus, a state-run enterprise that administrates state-owned land and water areas in Finland.

2.3 Sampling and data analysis

Sampling was carried out between 5 and 10 years after the treatments. To study the effects of restoration on tree regeneration, circular sample plots with a radius of 10 m were used in study **I** and smaller 40 x 60 cm quadrats in study **II**. Larger sample plots were used to represent the general effect of the treatments on seedling density, and smaller quadrats were used to account for within gap differences in position and soil disturbance.

To explore the effects of dead wood manipulation, dead trees and their polypore fungi were sampled from circular plots within a radius of 10 m (**III**). In study **IV**, logs that were of similar size and quality in terms of their decay stage and diameter were randomly chosen from the restored stands. Height and diameter were recorded for all dead wood units to calculate their volume. Measured qualitative features of dead wood included decay stage and the position of the tree (**III** and **IV**) as well as bark cover, ground contact, and the maximum height from the soil in study **IV**.

Fungi on dead wood were sampled using two approaches. Firstly, polypores, a morphological group of Basidiomycetes, were sampled based on their visible sporocarps (**III** and **IV)**. Secondly, the whole fungal community was sampled based on the extraction of DNA from wood dust samples taken from the logs (**IV**). Sampling of fungi was conducted between early September and late November using single surveys. The mean probability of detecting polypores within the sampling time frame used is approximately 70-75% for annual and 90-95% for perennial species (Halme et al. 2012). Polypores that could not be reliably identified in the field were collected and identified microscopically based on Niemelä (2011) and Niemelä (2016). Delineation and nomenclature of polypores mostly follows Niemelä (2016), and the Red List categories are according to Kotiranta et al. (2010).

In the data analyses, I applied quantitative, numerical statistical methods. Between group differences were tested either with parametric tests (analysis of variance, t-test, and linear models; **I**, **II**, **III**, **IV**) or with non-parametric alternatives (Mann–Whitney's U test; **III**). Differences in the compositional dissimilarity of fungi were examined using non-metric multidimensional scaling (NMDS; **III** and **IV**). A more detailed description of the applied statistical tests can be found in the original studies **I-IV**.

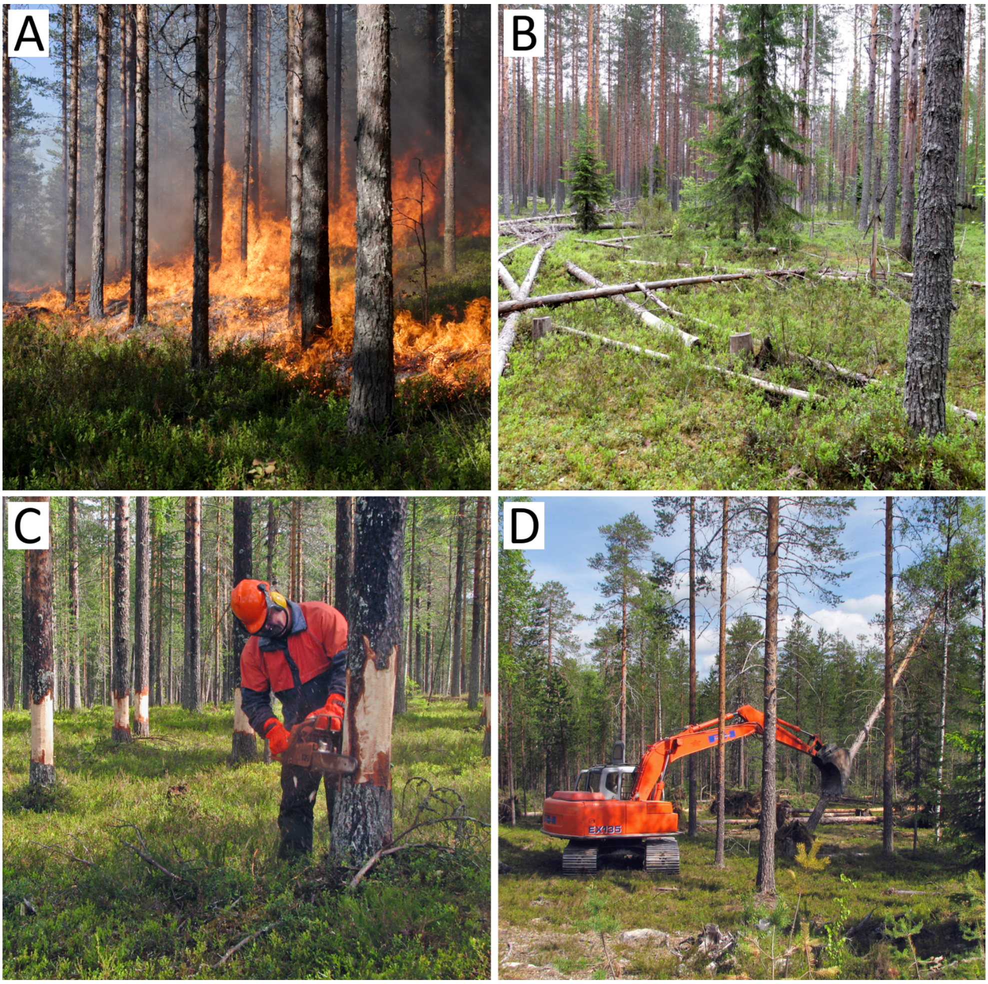

Figure 2. Some of the experimental treatments used in this thesis, (A) prescribed burning (Photo: Mika Pirinen); (B) chainsaw-felling to create fallen dead wood (Photo: Jari Kouki); (C) girdling to create standing dead wood (Photo: Juha Siekkinen); (D) pushing trees with an excavator to create uprooted trees (Photo: Juha Siekkinen).

3. MAIN RESULTS AND DISCUSSION

3.1 Prescribed burning, canopy gaps and soil disturbance may aid in the diversification of age-class structure and tree species composition (I and II), but longer than decadal effects still remain unverified

In boreal Fennoscandia, forests subjected to restoration most often consist of essentially single-aged cohorts of trees, and the main focus in assessing the short-term changes in forests' age-class structure and tree species composition is related to the emergence of new generations of trees. In this thesis, the combination of prescribed burning and the creation of canopy openings appeared the most promising method to improve tree regeneration (**II**). The total density of seedlings in the canopy gaps located within the burned areas (c. 2500 seedlings/ha) was approximately four times higher than the control forests (c. 600 seedlings/ha). The result is most likely caused by the various effects that fire have on soil properties; the most important being the reduction in the depth of the organic layer, the decrease in vegetation competition, and the increase in nutrient availability (Lehto 1956; Yli-Vakkuri 1961; Certini 2005; Pitkänen et al. 2005). Changes in soil properties also provide the most probable explanation for the difference in seedling density between burned and unburned canopy gaps.

The sole use of prescribed burning, however, was not found to promote seedling emergence if it was not combined with the prior removal of trees in the canopy. Because prescribed burning (surface fire) did not result in significant mortality of the dominant trees in the restored sites, the low amount of solar radiation that reaches the field layer probably hindered the establishment and growth of shade-intolerant pine and birch. Hence, prescribed burning, if combined with the creation of canopy openings, appears to be a promising method when the age-class structure of pine-dominated forests is restored closer to its natural condition.

Most of the tree seedlings recorded in the restored sites were deciduous species (87%; **I**). In particular, birch was found to benefit from the combination of prescribed burning and the creation of canopy gaps. Therefore, the applied treatments can also be expected to contribute to the diversification of tree species composition in pine-dominated forests. Aside from birch, the effect of fire was only moderately beneficial for other deciduous trees, such as the European aspen, possibly due to the lack of adjacent seed sources and living aspen trees in the restored stands from which root suckers could arise (**I**). Moreover, as the drier stands (*Vaccinium*-type) in particular are a non-optimal growth site for aspen, it is likely that location may have played a role. Therefore, it appears that it may be difficult to restore aspen (or any other species) in forests if the ecosystem (and its surrounding matrix) is very far from its natural state. Because the dispersal ability varies greatly depending on the species to be restored (Jonsson et al. 2005; Kouki et al. 2012; Norros et al. 2012), the effect of dispersal constraint is species-specific. Since aspen often regenerates through root suckers, a better result in terms of reaching restoration targets could perhaps be achieved by introducing the species by highly artificial means, for instance by the planting of trees.

Although prescribed burning showed promising results in terms of enhancing tree regeneration and diversifying tree species composition, the results from the five-year monitoring period should be interpreted with caution. The importance of long-term monitoring was demonstrated in study **II**, in which the density of seedlings displayed a clear decline five years after the creation of the canopy openings. New seedlings of pine and birch do appear in canopy gaps if disturbed soil patches are available, but the seedlings are unable to establish and grow (study **II**). Because the effect of browsing was minor, the reasons are likely related to the competitive environment in the gaps. Due to the shade-intolerance of pine and birch, it is apparent that their niche requirements are not met in small canopy gaps, particularly in nutrient-poor soils in which the competition for belowground resources also plays an important role (Björkman and Lundeberg 1971; Axelsson et al. 2014).

Since the majority (ca. 90%) of the pine and birch seedlings were found on the plots where the mineral soil was exposed (**II**), the results of my thesis emphasize the importance of soil disturbance. It follows that the treatments should not focus merely on the openings in the canopy, but also on the "gap dynamics" in the soil, which provide suitable seedbeds for germination and allow the initial development of tree seedlings (Kuuluvainen 1994; Kuuluvainen & Juntunen 1998; de Chantal et al. 2009). To compensate for this missing variation in soil microtopography it is necessary to artificially expose the mineral soil if the canopy openings are created by the chainsaw-felling of trees rather than by uprooting (Hekkala et al. 2014). An alternative is to use prescribed burning, which may also reduce the effect of root competition, at least temporarily in nutrient-poor sites, due to increased availability of soluble nutrients in the soil (Kuuluvainen & Ylläsjärvi 2011).

3.2 Restoration of dead wood increases the richness of polypore fungi but does not benefit rare and threatened species in the short-term (III and IV)

One of the main structural differences between managed and natural forests in boreal Fennoscandia is the quantity and quality of dead wood (Siitonen 2001; Stokland et al. 2012). An increase in the amount of dead wood is, therefore, expected to result in an increase in saproxylic species in the restored sites (Similä & Junninen 2012). Based on my results, dead wood restoration has indeed enhanced the possibilities for polypores to thrive in both pine and spruce dominated forests (**III**). Most of the polypores found in the restored substrates, however, were common species. Since the main goal in restoration is not to maximize species richness, but to restore the native biota in the area, a more general understanding of the reasons that affect species composition requires that habitat heterogeneity is also considered (Seibold et al. 2016).

The heterogeneity of dead wood is based on many features, and mainly includes decomposition stage, diameter of the log, moisture content, and wood density (Renvall 1995; Rajala et al. 2012). The restored dead wood was found to consist mainly of substrates that were in the initial stage of their decay succession (**I**), which explains why many of the polypore species in the restored substrates were pioneer decomposers. The lack of substrates in more advanced decay stages has very likely limited the occurrence of Red-Listed polypore species, as they are mainly decomposers of dead wood in the middle and the final stages of the decay succession (Tikkanen et al. 2006; Junninen and Komonen 2011). Because the decomposition stage of a substrate is mostly determined by the time since tree mortality, all aspects of structural heterogeneity are difficult to achieve simultaneously in dead wood restoration. To restore the characteristics of dead wood that occur in the advanced decay stage, it may be that the only alternative is to wait until the restored substrates become more decomposed over time. Based on the findings in study **IV**, it can be expected that the first threatened species begin to appear on the substrates approximately ten years following the restoration treatments. However, as the decomposition of pine and spruce may take up to 80 years (Mäkinen et al. 2006), species that require substrates in the advanced stages of decay may only appear several decades after the treatments.

3.3 Fungal communities in restored logs differ from those in natural logs, and the specific method of restoration causes differences in fungi that occur in restored substrates (III and IV)

In studies **III** and **IV**, our results suggest that restoration of dead wood can provide substrates for many fungi, including Red-Listed polypores, and successfully contribute to achieving restoration targets. However, the fungal communities in naturally occurring dead wood were more diverse in comparison to the restored substrates. The result poses a challenge for restoration and implies that the full array of fungal diversity in naturally originated woody substrates is difficult to re-create with the restoration of dead wood (**III** and **IV**; Komonen et al. 2012). The actual mechanisms and processes for this are beyond the scope of my thesis, but are very likely linked to more complex mortality patterns that result from the uprooting of natural logs. One possible solution to this restoration challenge is to apply several mortality agents simultaneously and, thus, to mimic the natural dying processes more closely, for example by the creation of standing dead wood and fallen dead wood with chainsaw-felling and uprooting of trees. Although I was only able to look at the relatively short-term effects of initial colonization, they may be highly influential because several fungal species rely on predecessor species either directly or because they modify the substrate (Renvall 1995; Niemelä et al. 1995; Kubartová et al. 2012). While the observed differences may also result in different successional trajectories for fungi in the later stages of decomposition, increased competition pressure along the decomposition succession may even out some of the stochastic effects caused by tree mortality (Stokland et al. 2012; Ottosson et al. 2015).

The specific cause of mortality of trees is known to affect the initial fungal communities in dead wood (Stokland et al. 2012; Ottosson et al. 2015). Therefore, it can be expected that different treatments to restore dead wood may also result in differences in the fungal communities in the created substrates. In this thesis, restoration treatment affected how fungi appear on decaying wood (**III** and **IV**). For instance in study **III**, no observations of *Phellinus ferrugineofuscus* were recorded in the restored spruce logs, even though the species is a common pioneer decomposer of natural substrates (Niemelä 2016). In a comparable study, Komonen et al. (2012) also found *P. ferrugineofuscus* in the restored (girdled) logs, but at a much lower probability compared to the natural logs of a similar decay stage. According to my results, and also supported by earlier findings (e.g. Komonen et al. 2012), it appears that some fungal species are specialized to colonize trees that have experienced a specific mortality factor, and that the level of specialization varies depending on the fungal species. The number of species that have specialized to favoring a particular mortality factor was examined in study **IV**, which showed that approximately 15% of all the fungal species in pine logs showed an association only to one specific type of tree mortality.

Most of the tree-mortality related variation in fungal community composition among the restored logs was found between trees that had been initially felled and trees that were girdled and left standing (**IV**). As tree position is expected to cause differences, especially in the initial moisture content in the restored snags, girdling probably favors species that have adapted to dry conditions and temperature fluctuations (stress-tolerant strategy; Cooke and Rayner 1984). This is also likely the mechanism that explains why girdled and later fallen trees hosted, on average, a lower number of fungal species compared to trees that had been felled (**III** and **IV**).

4. MANAGEMENT IMPLICATIONS

According to my results, restoration that is based on emulating natural disturbances and natural ecological processes provides promising results in terms of bringing back some of the key structural attributes in previously managed forests. However, a more challenging question is whether the restored structures can also aid in the restoration of threatened species over time. In this context, at least two aspects must be considered. Firstly, the inherent variability in forests is difficult to re-create using purely artificial treatments. Secondly, to fully determine how species respond to increased structural heterogeneity a longer time-scale (than the 10 year period examined in this thesis) is required.

My results emphasize the challenges faced in the restoration of forests based on natural disturbance emulation. In fact, natural disturbances are often complex phenomena leading to wide variation in forest structures and processes. In practice, this implies that combinations and compromises are also necessary. Of the treatments included in this thesis, the use of prescribed fire is perhaps the closest analog to a natural disturbance, although its effects can be expected to differ markedly from wildfires that have a greater variability in their extent and severity (Zackrisson 1977; Pennanen 2002; Kuuluvainen & Aakala 2011). Therefore, if high-intensity crown fires cannot be prescribed, as they are often difficult to control, it is advisable to kill some of the trees prior to burning the forests, either by the creation of canopy gaps or by thinning the forests to varying degrees (**I**).

The situation is slightly different in canopy gaps that are created without fire by cutting the trees; without available seedbeds, the increase in above-ground resources does not compensate for the missing variation in ground microtopography (**II**). This missing factor could, therefore, be replaced by artificially exposing the mineral soil from small patches (**II**). To better capture all the variation in pit-and-mound microtopography, an alternative would be to artificially uproot the trees when canopy openings are created (Hekkala et al. 2014). Heterogeneity should also be the target in tree-level treatments where various mortality factors are emulated; to account for the natural variation in dead wood, different methods should probably be used together, to provide substrates for species with different life-history strategies and substrate requirements (Berglund et al. 2011; Eriksson et al. 2013; Komonen et al. 2014).

Since much of the variation in structural heterogeneity is connected with successional processes, both in dead and living trees, it takes time for these successions to reach more advanced stages. For this reason, it is challenging to create variation in the decay stages of restored dead wood (**III**) or to create a multi-cohort age-class structure of trees in the short-term (**II**). These can only develop with time. Moreover, the historical use of the ecosystem and its surrounding landscape can be expected to have an effect on the ability of species to colonize the forest. The further the structures, and hence the source populations, are from natural forests, the longer it will take for the species to appear in the restored forest.

5. CONCLUDING REMARKS

Natural and anthropogenic disturbances form a continuum in their level of naturalness, and all disturbance-based treatments can be placed at some point along this continuum. The closer the treatments are to natural disturbances, and the closer the current forest structure is to a natural one, the more likely that the structures and species in the forest can be restored. How closely natural disturbances can be emulated in the current forest structure will depend on the management objective. Given the lack of detailed knowledge on species-level responses to restoration, the safest strategy would be to emulate natural disturbances as closely as is practically possible, as we can expect that the species will have adapted to, or can benefit from, these disturbances. Such a strategy could be used in protected areas, where the main function is to provide habitats for endangered species that cannot survive in managed forests. In forests where the main function is to produce timber, disturbances cannot be closely emulated due to different management goals. However, some restorative actions – such as prescribed burning and increasing the amount of dead wood – may also be applied in managed forests, to facilitate emulation of natural disturbances and to maintain biodiversity.

Although the evidence I have gathered in this thesis show the clear positive effects that restoration has on the re-creation of naturally occurring forest characteristics, restoration of the full array of structural heterogeneity of natural forests appears to be difficult with the methods that are currently applied. The discrepancy in the structures between natural and managed forests, however, can be greatly diminished with careful planning of the restoration treatments. A particular challenge comes from inherently long processes that create and maintain the ecological structures in boreal forest ecosystems, including the generally slow process of stand succession or wood decay. Some of my results are clearly limited due to the relatively short monitoring period. Whether the situation will change as time passes can only be answered by longer-term monitoring of the restored forests.

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