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Harvested and burned forests as habitats for polypore fungi

Mai Suominen

School of Forest Sciences
Faculty of Science and Forestry
University of Eastern Finland

Academic dissertation

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Author: Mai Suominen

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Thesis supervisors:
Professor Jari Kouki
School of Forest Sciences, University of Eastern Finland, Joensuu, Finland

Dr. (Docent) Kaisa Junninen
Metsähallitus Parks & Wildlife Finland, Joensuu, Finland

Pre-examiners:
Assistant Professor Jodi Forrester
Department of Forestry and Environmental Resource
College of Natural Resources
North Carolina State University, Raleigh, USA

Associate Professor Jacob Heilmann-Clausen
Natural History Museum of Denmark
University of Copenhagen, Copenhagen, Denmark

Opponent:
Professor Anders Dahlberg
Department of Forest Mycology and Plant Pathology
Swedish University of Agricultural Sciences, Uppsala, Sweden

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ABSTRACT

This thesis explores the effects of controlled burning and logging intensity on wood-decaying polypore fungi 10 years after the treatments. Intensive forest management, where most of the wood is removed from harvested sites, has resulted in many dead-wood-dependent species becoming Red-listed. The role that managed forests and novel, more biodiversity-oriented silviculture could play in safeguarding fungal diversity has remained largely unclear.

This thesis is based on data sets collected from five years: 2000, 2003, 2005, 2008 and 2011 from the same study areas. A large-scale, replicated experiment was established on 24 forest sites that were exposed to logging and burning treatments. The data comprised 98,136 observations of dead wood pieces and 22,150 observations from a total of 122 polypore species.

The main findings in this thesis were;

1) Retention tree levels need to be high in order to maintain polypore diversity. I observed more polypore species on sites with 50 $m^3 ha^{-1}$ of retention trees than sites with 10 $m^3 ha^{-1}$. The burning of retention harvested sites accelerates the death and fall of retention trees and diversifies the dead wood quality at a managed site. Red-listed species were found chiefly on the burned sites with the higher retention level.

2) Harvested sites comprise widely different types of dead wood substrates: old natural dead wood, stumps, slash and retention trees, and all these contribute to polypore diversity in managed forests. The response of polypore species to management can typically be seen only after a longer period of time. After a disturbance, such as logging or fire, these four different dead wood substrates are available for polypores over different periods of time.

3) Burning harvested and unharvested sites increases the number of polypore species and diversifies the polypore assemblages. Of the four dead wood types, burning specifically leads to an increase in the number of polypores on stumps.

These results demonstrate new possibilities for the conservation of dead-wood-dependent species outside protected areas. Leaving retention trees, abstaining from the extraction of logging residuals and maintaining old naturally formed dead wood are beneficial for polypore species. Prescribed fire can be utilized as an effective method to modify dead wood dynamics and for the creation of more variable dead wood substrates on managed forest sites.

Keywords: bioenergy, boreal forest, dead wood, fire, old natural dead wood, pine, prescribed fire, retention trees, slash, stumps.

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Turku, November, 2018

Mai Suominen

LIST OF ORIGINAL ARTICLES

This thesis is a summary of the following articles, which are referred to in the text with the Roman numerals. Studies **I**, **II** and **III** are published articles that are reprinted here with the permission from the publishers. Study **IV** is a manuscript.

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

II 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(4): 1001-1008. https://doi.org/10.1111/1365-2664.12447

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

IV Suominen, M., Junninen, K., Kouki, J. Diversity of fungi in harvested forests 10 years after logging and burning: polypore assemblages on different woody substrates. Manuscript.

The contribution of Mai Suominen to the studies included in this thesis was as follows:

Study **I**: Participated in the coordination and sampling in the field work and in the data management. Contributed to data analyses and wrote the manuscript together with co-authors.

Study **II**: Coordinated and participated in the field work. Identified the species with microscopy. Conducted the data management. Analyzed the data and wrote the manuscript together with co-authors.

Study **III**: Coordinated and participated in the field work. Identified the species with microscopy. Conducted the data management. Analyzed the data and wrote the manuscript together with co-authors.

Study **IV**: Coordinated and participated in the field work. Identified the species with microscopy. Conducted the data management. Analyzed the data and wrote the manuscript together with co-authors.

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1. INTRODUCTION

1.1 Changes in the forest ecosystem and the importance of dead wood and fire

Globally, forest loss and degradation have been rapid during the past century (Heino *et al.*, 2015). In the northern hemisphere, intact forest landscapes can be found only in some parts of Russia, Canada and Alaska (Potapov *et al.*, 2017). Elsewhere, the remaining natural forests are small in size. At this time, forests that host higher levels of biodiversity are located in fragmented landscapes, and are usually isolated patches.

Because of the scarcity of natural forests and uncertainties in the quality of protected area networks (Lindenmayer and Franklin, 2002; Orlikowska *et al.*, 2016) it is crucial to develop forest management methods that assist in species conservation in the managed forests that surround protected areas. The management methods vary from country or region although clear-cutting is practiced globally, and the ecological consequences of this method are severe as most of the wood is removed from a harvested site on one occasion. During forest rotations, forests are thinned and in these phases wood is also removed from a site, and thus the formation of dead wood is mainly largely prevented at several points during the rotation, with the exception of logging residuals that are maintained at harvested sites.

Under natural conditions, a similar large-scale disturbance comparable to clear-cutting is stand-replacing fire, but there are obvious differences between clear-cuts and wildfires. In particular, most of the wood after a wildfire remains on the site and typically only small branches and needles are completely burned, although the effects clearly depend on the severity of the fire (Ryan, 2002). Hunter (1993) argued that forest fires burn all the wood on a forest site, and this resembles the effects of clear-cutting. However, such severe fires are very rare and forest fires typically have a highly variable severity (Pitkänen and Huttunen, 1999; Kafka *et al.*, 2001; Bergeron *et al.*, 2002). In natural environments, the dead wood remains in the forest after the death of a tree, whereas in managed forests these trunks are often removed. The dead wood is an obligatory resource for dead-wood-dependent species. Such species are estimated to include 20-25 % of forest dwelling species (Siitonen, 2001), and in managed forests several forest dwelling species have become endangered.

The difference between a natural disturbance, such as wildfire, and clear-cutting is widely accepted (Kuuluvainen and Grenfell, 2012). Despite the growing interest in dead wood in harvested sites, and the impact of fire on tree dynamics (Bunnell and Houde, 2010; Burrows *et al.*, 2012; Sensenig *et al.*, 2013; Brazee *et al.*, 2014), the actual ecological impact of these effects remains unclear. Moreover, this has also hindered the development of novel forestry practices and a robust estimation of their efficiency.

1.2 Dead wood amount, quality and dynamics in natural and managed forests

1.2.1 Difference in the dead wood dynamics and quality in natural forests vs. clear-cut forests

In natural boreal forests, the amount of dead wood is often more than 100 $m^3 ha^{-1}$ (Siitonen, 2001) and typically includes a wide range of dead wood types: standing snags and lying logs in different decay stages, representing several different tree species. Moreover, the pieces of dead wood can be found in different sizes. Trees die continuously or during a single small-scale event (e.g. windthrow, fungal outbreak or flooding) or during a large scale disturbance event (e.g. insect outbreaks, large storms and fire). Between 1950-2000, storms in Europe accounted for 53 % of the total annual tree mortality due to natural disturbances, fires accounted for 16 %, snow damage 3 %, other abiotic causes 5 %, and biotic factors affected 16 % (Schelhaas *et al.*, 2003).

The amount of dead wood in managed forests can be less than 10 % of that found in natural forests (Siitonen, 2001). In managed boreal forests, the highest amount of dead wood is usually found in forests where the dominant tree cohort is mature, whereas in natural forests the largest amount of dead wood is found in early successional stages after a stand-replacing disturbance (Kouki *et al.* 2001, Junninen *et al.* 2006). Indeed, this kind of forest habitat is almost completely absent from intensively managed forests. Managed forests are clear-cut long before the age of the forest when the accumulation of dead wood is at its highest. In recent times, rotation times have become shorter and, as a consequence, dead wood amounts have also decreased. The quality of dead wood is less diverse in managed forests compared to natural forests. As only one or two tree species are typically grown, the availability of different tree species is scarce. Managed forests are thinned at regular intervals and, therefore, tree sizes at a site are similar. The majority of dead wood in managed forests is small in diameter and will decay faster than a large sized piece of wood. Larger diameter logs in advanced decay stages are seldom found in managed forests (Siitonen *et al.*, 2000). These kind of differences in forest structure are found in managed and natural forests globally (Burrascano *et al.*, 2013).

1.2.2 Dead wood addition and maintenance in managed forests

The amount of dead wood in managed forests is low compared to natural forests (Siitonen, 2001), and under current forest management practices very little is left in treated sites. Based on the observed occurrence of species, at least 20-40 m^3 ha^{-1} of dead wood should be maintained in order to host Red-list species on a managed site (Penttilä *et al.*, 2004; Hottola *et al.*, 2009). Although dead wood addition benefits several species, the knowledge of long-term effects of maintaining dead wood for biodiversity are still scarce (Seibold *et al*. 2015). To alleviate the negative effects of cutting, dead wood can be added or maintained in many ways in forest management:

1) Retention forestry was introduced in North America 30 years ago (Franklin, 1989) and since the 1990s it has been practiced globally in different forest habitats (Gustafsson *et al.*, 2012; Mori and Kitagawa, 2014). In this system, green retention trees are left in clear-cut sites, in order to reduce the negative impact of clear-cutting on species (Lindenmayer *et al.*, 2012). Retention trees are used for at least five objectives (Gustafsson *et al.*, 2010): 1) to assist species survival on a stand over the regeneration period, 2) to create variability in the tree structure, 3) to provide connectivity between similar sites at the landscape level (Franklin, 1997), 4) to provide substrates for species that utilize dead wood and live trees during the early-successional period, and 5) to maintain ecosystem functions such as nutrient retention, provide seeds for the establishment of new saplings and enhance the productivity of the new tree cohort (Gustafsson *et al.*, 2010). As retention trees are initially alive, they provide habitats for species such as ectomycorrhizal fungi (Rosenvald and Lõhmus, 2008), lichens (Gustafsson *et al.*, 2013; Hämäläinen *et al.*, 2014), some mammals (Holloway *et al.*, 2012) and cavity nesting birds (Lance and Phinney, 2001). After their death, dead-wood-dependent species may benefit from the retention trees (Hyvärinen *et al.*, 2006; Junninen *et al.*, 2007).

Despite the wide use of retention forestry, the effect of retention trees at the stand and the individual trunk levels is still largely unknown. Several studies have investigated the effects of retention trees on different species groups (e.g. Fedrowitz *et al.*, 2014) although knowledge of the long-term effects is low (Jönsson *et al.*, 2007; Halpern *et al.*, 2012; Runnel *et al.*, 2013) and the significance on rare and threatened species, in particular, is poorly studied and documented. In addition, very few studies have examined retention tree dynamics together with disturbances in forests, such as fire, wind and insect outbreaks (see Hämäläinen *et al.*, 2016). The amount of retention trees left on harvested sites, together with the different external and internal disturbances, affects tree dynamics and the availability of living and dead trees over different periods of time. Currently, the amount of trees left on a harvested site is often very low (Gustafsson *et al.*, 2012), and may provide only short-term benefits for fauna and flora. The level of retention is much lower than the amount of dead wood in natural forests, which could be more than 100 m^3 ha^{-1}.

2) There is growing demand for the production of energy from renewable sources, including bioenergy. This has led to increased extraction of stumps and slash from harvested sites (Routa *et al.*, 2013; de Jong *et al.*, 2017). Abstaining from the collection of stumps and slash for bioenergy is crucial for the maintenance of their function in forest ecosystem. They provide nutrients in harvested sites and enrich the growing conditions for living trees. Extraction of stumps should be considered with caution as knowledge of the impact of stump removal on soil properties is still inadequate (Achat *et al.*, 2015). Similarly, the impacts of biofuel harvest on biodiversity are scarce and contradictory (Dahlberg *et al.*, 2011; Toivanen *et al.*, 2012; Vasaitis *et al.*, 2016; de Jong and Dahlberg, 2017). For dead-wood-dependent species, the extraction of stumps and slash may have severe consequences in managed forests, where they are the main dead wood substrate available. The importance of small-diameter slash has probably been underestimated but these substrates form a diverse set of dead wood types (Eräjää *et al.*, 2010), and small diameter dead wood can host a unique set of species (Juutilainen *et al.*, 2011). However, it is not known how much slash contributes to overall polypore assemblages on cut sites.

3) In addition to the extraction of logging residuals, large-sized logs (both newly formed and older, more decayed logs) may be intentionally removed from harvested sites (Rudolphi and Gustafsson, 2005) or accidentally destroyed during soil scarification (Ranius and Kindvall, 2004). Naturally formed logs that are retained on harvested sites add notably to the total dead wood volume (Ranius and Kindvall, 2004; Ranius *et al.*, 2005), which suggests that modification in silvicultural technologies needs more attention. Moreover, formation of dead wood can be also promoted by prolonging the rotation period, which has been found to add 11 % of dead wood compared to shorter rotation periods (Ranius and Kindvall (2004).

Besides the methods directly related to cutting, key woodland habitats that are left unharvested also add to the amount of dead wood in managed forests (Jönsson and Jonsson, 2007), and buffer zones along water bodies (lake and sea shores, streams, mires) have more dead wood than the surrounding forest matrix (Komonen *et al.*, 2008; Komonen, 2009). These biotopes have been found to be beneficial for polypore conservation (Junninen and Kouki, 2006; Hottola and Siitonen, 2008; Komonen *et al.*, 2008).

1.3 Fire in forest ecosystems

Fires are naturally occurring disturbance events that affect tree dynamics, the physical conditions of a forest site and, consequently, species assemblages. Nowadays, wildfires occur frequently and widely in the forest areas of Russia and Canada (Johnson *et al.*, 1998; de Groot *et al.*, 2012). However, fire prevention has been effectively practiced for decades in the Nordic countries (Zackrisson, 1977; Esseen *et al.*, 1997), and thus wildfires are rare and cover only marginal areas (Lindberg, 2017). As a consequence, the processes and structures created by fire are almost completely absent in the forest landscape of the Nordic countries. In the future, fire frequency will most likely increase in many regions globally because of climate change (Seidl *et al.* 2017) but whether this will also happen in the intensively managed forests in boreal Europe is unclear (Abbott, 2016).

Fire is an important process in natural forest conditions (Rowe and Scotter, 1973). Fires occur at different intervals (Bergeron *et al.*, 2004) and over variable sized areas (Niklasson and Granstom, 2000). Fires vary in severity but often they have a clear influence on tree mortality and growth dynamics. Severe stand-replacing fires that reach the canopy can kill trees and form a large amount of dead wood, whereas milder ground fires only char the surface of a trunk and leave most of the trees alive, although part of the trees may be weakened.

In Finland, lack of forest fires and lack of habitats that fires create is estimated to be the primary cause of threat for 7 % of all the forest-dwelling threatened species (Rassi *et al.*, 2010). Additionally, other specialized dead-wood-dependent species also benefit from fire directly (Penttilä and Kotiranta, 1996) or indirectly (Saint-Germain *et al.*, 2008). Substrates and habitats created by fire are often highly variable, and this allows the species assemblage to become more diverse, provided that there are dispersal sources in close vicinity of a burned site. In natural forest landscapes, large-scale fires create early-successional forests that are sun-exposed and have much dead wood. Such habitats are valuable for dead-wood-dependent species (Kouki, 2001; Swanson *et al.*, 2011) but are almost absent in protected areas (Similä and Junninen, 2012). Emulating the natural forest disturbances so that natural or semi-natural early-successional habitats are also maintained would be a valuable goal for forest management, both in protected areas and managed forests.

Although wildfires are now rare in many areas, fires may still occur occasionally. Traditionally, prescribed fire has been used to prepare the soil and to enhance tree regeneration after a clear-cut, but this method is seldom utilized anymore. Prescribed burning has also been conducted in order to reduce the risk of wildfires, for example in Australia (Burrows and McCaw, 2013). The influence of these fires on biodiversity and especially on threatened and endangered species is largely unknown. Yet, it is known that fire, in general, also benefits biodiversity in managed forests (Hyvärinen *et al.*, 2006; Toivanen and Kotiaho, 2007; Heikkala *et al.*, 2016) and therefore could be an effective tool for achieving several forest management goals.

However, the application of fire is a challenging task in forest ecosystems. How it should be applied and under what circumstances are largely unresolved issues at present. Similarly, prescribed fire should also be conducted in various ways: severe and mild fires would create different kinds of conditions, and burning different aged and structured forests would create different dead wood types in the landscape. However, it would be difficult to conduct a severe prescribed burning because of the high risk of fire spreading from the burned site.

Fire may also be detrimental to biodiversity. For example, depending on the intensity of a fire, existing dead wood on a burned site may be consumed to different extents. Eriksson *et al.* (2013) studied the loss of different dead wood types in restoration fires and found that fire decreased the total volume of pre-fire dead wood by 23-41 %, and logs in late decay stages by 26-54 %. However, the new dead wood exceeded the amount of lost dead wood, and was formed mainly by snags killed by fire. Fire also changes the micro climatic conditions of logs by decreasing their ground contact, increasing the area of charred wood and reducing the vegetation coverage. Fire has also been found to reduce the stand scale diversity of lichen species (Hämäläinen *et al.*, 2014).

1.4 Polypore fungi – the study species group

For this thesis, I examined wood-decaying polypore fungi. Polypores are taxonomically polyphyletic group of Basidiomycota (Hibbet *et al.* 2014). Some of the species are soil-inhabiting whereas most of them consume wood causing brown or white rot which degrade the wood structure in different ways (Rayner and Boddy 1988). Polypores, among other Basidiomycota, are the main wood decomposers (Stokland *et al.* 2012). Polypores are excellent species to indicate conservation value (Heilmann-Clausen *et al.*, 2014), and moreover to assess the impact of forest management actions, as several of these species are highly specialized in their habitat and substrate associations (Junninen and Komonen, 2011). This is a useful feature when evaluating the importance of different dead wood substrates produced in harvested sites. Most of the polypore species in Finland are found only on deciduous or conifer tree species, and most of the species on conifers are confined either to spruce or pine (Niemelä, 2016). The quality of a tree (e.g. stump, tree top, trunk, snag, branch, living tree) may determine which particular species occurs on a decaying piece of wood (Stokland *et al.*, 2012). Most of the species utilize dead wood, especially lying logs, as only a few species are found on living trees (Junninen and Komonen, 2011). However, less is known about the ability of polypores to utilize stumps and slash (see Sippola and Renvall, 1999). A larger diameter tree (> 20 or 30 cm) has been found to be beneficial in terms of a higher number of polypore species (Junninen and Komonen, 2011) but this relationship is not straight forward as small diameter pieces of wood have a higher surface area per volume than large diameter logs, and can thus provide more niches for dead-wood fungi (Kruys and Jonsson, 1999).

In Finland, there are 251 polypore species (Niemelä, 2016) of which approximately 50 % only occur in the south of the country where they utilize "noble" broadleaved tree species whose geographical range limits the occurrence of these polypores. Part of the species occurs only in the north of the country. Stand level properties affect species colonization on a site: sun-exposed sites and moist closed forests both have some species that can be found only in these habitats.

In addition to their biodiversity value, wood-decaying fungi, such as polypores, play an important role in recycling nutrients from a dead tree back to the soil, thereby improving the quality of the soil for new tree saplings. There are strong associations between fungal species in the soil and dead wood at all stages of wood decay: Mäkipää *et al.* (2017) found unique sets of species underneath dead wood logs compared to the surrounding areas of soil in the forest floor, and also observed that the species assemblages in the final stages of decay were the same on the dead wood and the soil. However, among polypore species only a few species utilize the very final stages of decay. The rate of decay and fungal growth depends on the temperature and moisture content of a piece of wood. These conditions can vary between different forest habitats. Forrester *et al.* (2012) found that dead wood logs in forest canopy gaps had increased respiration, and that temperature and moisture content were affected in a complex way. In addition to the environmental factors also the trunk properties and the cause of tree death have an impact on the fungal community on a trunk (Pouska *et al.* 2011).

Many polypores have become endangered due to intensive forestry: In Finland, over 40 % of polypores are Red-listed (Kotiranta *et al.*, 2010) and the reduction in the amount and quality of dead wood in managed forests is one reason for this. Commonly, the available dead wood at a managed forest site can consist of one tree species, all pieces of wood can be similar in size and the majority of the dead wood may have originated from a single event, and thus, each piece of dead wood is at the same decay stage. Given the demands of polypores for dead wood quality it is important to consider what kind of dead wood pieces are maintained and produced in forest sites.

The spores colonize a trunk and then grow as mycelia that decay the wood. Eventually, polypore produces sporocarps on the surface of the wood that functions as their reproductive organs. At a time of a spore arriving on a piece of dead wood it can be already colonized by another fungal individual. This might affect the capabilities of a new species to establish. Although fungal spores can travel long distances with the wind (Hallenberg and Küffer, 2001), the majority of the spores produced by one sporocarp are known to disperse only short distances, which has been demonstrated with a number of species (Norros *et al.*, 2012). Based on the results from those studies, polypores may require suitable habitats in close vicinity in order to colonize a new substrate. In many cases, the landscape in managed forests consists of a matrix of forest sites where the amount of dead wood is low. Protected areas are small in size and the distance between them may be too long for successful colonization.

1.5 Aim of my thesis

My overall aim was to study methods of forest management that could be utilized in managed forests outside protected areas, to facilitate polypore diversity. In study **I**, I investigated the longevity of green retention trees on harvested sites and examined the impact of burning on the timing of tree death and fall. In addition, I examined whether there is a difference in these processes between retention levels of 10 $m^3 ha^{-1}$ and 50 $m^3 ha^{-1}$. Study **II** was conducted to determine the polypore assemblages that utilize retention trees on harvested sites with different retention levels, either with or without burning. In study **III**, I asked what kind of polypore assemblages are hosted by post-harvest stumps and slash, and whether burning alters these substrates for polypores. Furthermore, in study **IV**, I compared the differences in polypore communities on natural dead wood that exist on harvested sites before treatments and on artificially created dead wood (e.g. retention trees, stumps and slash) left on harvested sites after cutting. In this study, I also compared the differences between polypore communities in near-natural forests without burning and with burning to those communities on harvested sites. I discuss these topics of polypore conservation in managed forests in the four articles included in this thesis, and to which I hereafter refer with Roman numerals (the original articles are listed on page 5).

The specific questions asked in this thesis were:

1) Are retention trees beneficial for polypores? And if they are, how and when? (**I, II & IV**)
2) Do different dead wood types (old natural dead wood, stumps, slash and retention trees) all contribute to the diversity of polypore assemblages? (**III & IV**)
3) What effect does prescribed burning have on the polypore assemblages in unharvested and harvested forests, and on the different substrates found in harvested sites? (**I, II, III & IV**)

2. MATERIALS AND METHODS

2.1 Study area and experimental design

This thesis is based on datasets that were collected from a large-scale experimental study from eastern Finland. The study area is located on the transition zone between the southern and middle boreal zones (Ahti *et al.*, 1968) (63 10'N, 30 40'E) (Fig. 1.). All the datasets were collected from forest sites that were dominated by *Pinus sylvestris* with a mixture of *Picea abies, Betula* spp. and other deciduous tree species. More detailed information on the study sites can be found in the four studies included in this thesis (see also http://forest.uef.fi/jarikouki/project_fire.htm).

The experimental design is a two-factor factorial with orthogonal factor levels. The study plots were established in 24 forests, each 3-5 ha in area. Six of the sites were unharvested and three of these were burned. 18 sites were cut with different levels of green retention trees: 0 m^3 ha^{-1}, 10 m^3 ha^{-1} and 50 m^3 ha^{-1}. Nine of these sites were burned after cutting creating three replicates of each treatment. The cuttings were conducted in the winter 2000-2001 and the sites were burned during the following summer 2001 (over a two day-period at the end of June). The sites were randomly allocated to different cutting and burning treatments, except that unharvested sites were all in Patvinsuo National Park, in order to guarantee that they will not be harvested in the future. Burning treatments also on these unharvested sites were randomly allocated to experimental units. All the treatments were conducted by Metsähallitus, which administrates state owned land in Finland, in close collaboration with research project coordination.

2.2 Sampling

Studies **I** and **II** were conducted on the sites that had retention trees (n=12 sites). Study **III** was conducted on 18 cut sites and the data was collected from 1 ha study plots that were located in the center of each study stand. Study **IV** was conducted on all 24 sites and sampling was from the same 1 ha study plots. However, the second part of the study **IV** was conducted only on 12 sites because only these sites included all four examined dead wood substrates: old natural dead wood, stumps, slash and retention trees. The 1 ha permanent study plots were sampled before the treatments in 2000 and two, four and 10 years after the treatments.

All the living trees and dead wood (minimum diameter >5cm) were counted and measured from the 1 ha study plots. The wood items were classified into live and dead standing trees, fallen trunks, slash (all wood items produced with a saw) and stumps. Trunks were divided into old natural dead wood that existed on the sites before logging and into retention trees that were left alive on the harvested sites. For studies **I** and **II**, the retention trees were individually marked and the same trees were repeatedly monitored during the 10-year study period.

In addition to *Pinus sylvestris* and *Picea abies,* dead wood pieces of deciduous tree species were identified to the species level. However, the number of deciduous tree species was so low that they were pooled (**I**). The polypore occurrences recorded on deciduous tree species were considered when describing the complete polypore assemblages (**II**), while separate analyses were done only on polypores found on *Pinus sylvestris* and *Picea abies* (**II** and **III**). In study **IV,** the host tree species were not considered separately, because of difficulties in identifying the species on the smaller wood pieces.

Polypores were inventoried on all retention trees that occurred in each study stand. The individually marked retention trees were investigated for polypores in the first autumn (2001) after cutting and burning, and then again two (2003), four (2005) and 10 (2011) years after the treatments (**I** and **II**). All tree components (incl. stumps and slash) were sampled for polypores 10 years after the treatments (**III** and **IV**).

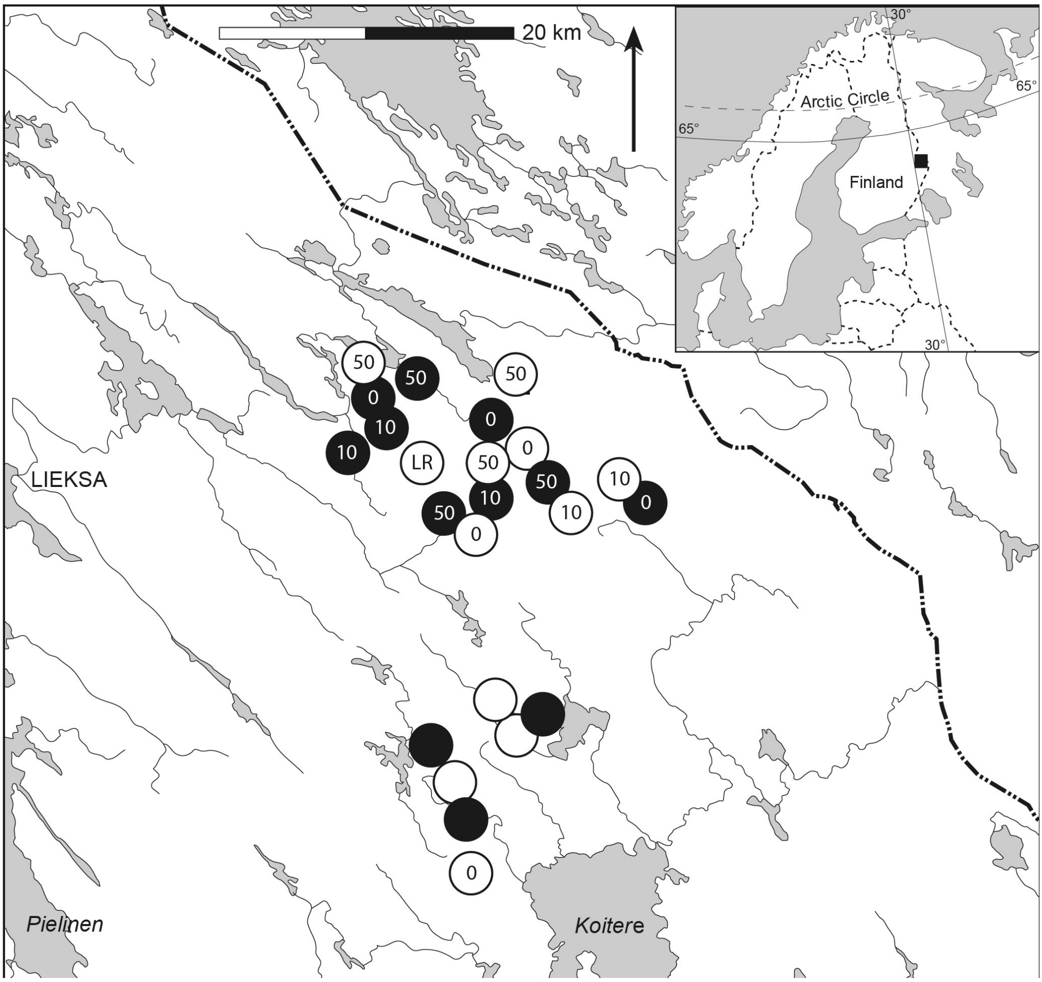

Figure 1. Map of the study area. Black = burned sites, white = unburned sites. The numbers refer to the retention levels of 0, 10 and 50 m^3 h^{-1}. The empty circles are control sites with no cuttings.

All polypore surveys were conducted in September and October during peak sporocarp production season. One record of a species was made from one piece of wood even though there would have been several sporocarps on the same trunk. It is possible that there were two or more individuals on the same trunk but it is also very likely that the sporocarps were produced from the same mycelia, and thus, belonged to the same individual. Red-listed species classification was according to Kotiranta *et al.* (2010).

3. MAIN RESULTS AND DISCUSSION

3.1 Fire modifies retention trees dynamics and diversifies polypore assemblages 10 years after retention harvest on managed sites (I and II)

Dead wood dynamics on retention harvested forests are different on burned sites compared to unburned sites (**I** & **II**). On the unburned sites, most of the retention trees (76 % of the total number of trees) were still standing and majority of then as snags 10 years after the treatments and thus would provide dead wood substrates for a longer period of time. In contrast, most of the retention trees (95 %) on the burned sites had fallen 10 years after the treatments. There was also a clear difference in stand level dynamics between the two different levels of retention trees after burning: on sites with 10 m^3 ha^{-1} of retention trees, almost all the trees had fallen 10 years after the treatments and, thus, there would not be more new fresh dead wood over many years, whereas on the sites with 50 m^3 ha^{-1} retention, the trees formed a longer continuum during the early successional stages and were a source of new dead wood even 10 years after the treatments, even on the burned sites. The higher level of retention trees, together with tree-level differences in fire-caused mortality, produced a highly diversified assemblage of dead and living retention trees (**I**). In addition to the direct effect of fire killing the trees, damaged trees have a lower capacity to resist insect outbreaks, fungal colonization and desiccation (Dixon *et al.*, 1984; Harrington, 1996; Rasmussen *et al.*, 1996). These effects cause longer-term tree mortality and probably also modify the quality of the dead wood that is eventually available. However, windthrow also affects the post-fire dynamics of retention trees on a cut site. The various qualities of a site (e.g. edaphic variables, topography, tree properties: diameter and tree species) strongly determine the probability of trees falling during winds (Lavoie *et al.*, 2012).

The number of polypore species increased 10 years after the treatments and Red-listed species generally appeared at this time as well. Ten years after the treatments the polypore assemblages were significantly different between the retention trees on burned and unburned sites. In total, 13 species favored burned sites, and six species favored unburned sites (**II**). Red-listed species are likely to appear on a forest site when there is at least 20 m^3 ha^{-1} of dead wood (Penttilä *et al.*, 2004). A similar pattern can also be seen with Red-listed species in my study, especially on burned sites that had more than 20 m^3 ha^{-1} of dead wood ten years after the treatments (**I**). It takes a number of years for retention trees to die and fall (although parts may fall soon after a fire, **I**) and time to reach the middle stage of decay and host species that require more advanced decay stages (**II**). In the 10 years after the treatments, several dead wood types developed from the retention trees on burned sites (**I**), and provided niches for various species, resulting in diverse polypore assemblages. Indeed, pioneer polypore species had utilized retention trees abundantly 10 years after the fire. Furthermore, species that occur on the more advanced decay stages were found on these trunks at this time (**II**). Trunks that are in the middle stages of decay host more species than other trunks (Renvall, 1995). I expect that species that demand more advanced stages of decay will appear on the trunks as long as there are colonization sources in close vicinity of the managed sites (Penttilä *et al.*, 2013).

I was able to follow the retained trees for 10 years after the treatments (**I** & **II**). Although this is a rather long-term study, and is longer than any other polypore study on retention cuts, it may still be too short to reveal all the significant effects. In particular, the decay dynamics are much longer than 10 years. Part of the old natural dead wood may already be in an advanced decay stage, and it will take years for green retention trees to reach a similar stage and provide resources for species utilizing this substrate. Further, following retention tree dynamics over even longer periods, especially on the unburned sites (where 76 % of the trunks were still standing 10 years after the treatments; **I**), would provide critical data on the long-term possibilities of providing new dead wood. Runnel *et al.* (2013) concluded in their study that retention trees do not provide a continuum at the stand level, and it is more appropriate to consider retention trees in relation to the landscape scale, not focusing only on the stand-scale as was done in my studies.

In this thesis, I show that retention trees can be colonized by polypores (**II**). However, when applying a retention harvest to a particular forest site, it is important to take into account the quality of the surrounding landscape. If the surrounding forests are poor in quality there will not be source populations from where species could colonize the retention trees. Our study area is located in a landscape with a rather good continuum compared to southern-western parts of Finland with longer management history (Kouki *et al.*, 2012). Therefore, some of the Red-listed species especially may not be found in other regions. Abrego *et al.* (2015) showed that in order to conserve polypores in beech forests, it is crucial to enlarge the size of present protected areas and establish new areas close to the existing ones. In addition to this, retention trees provide support for the species survival in protected area networks.

Retention trees have been found to benefit polypores on aspens (*Populus tremula*) (Junninen *et al.*, 2007) and some moss and lichen species (Arseneault *et al.*, 2012) but they do not benefit all species or they provide only partial support for species communities (Pengelly and Cartar, 2010; Löbel *et al.*, 2012; Otto and Roloff, 2012; Oldén *et al.*, 2014). Similarly, the burning of retention trees may not be useful to all species groups, or burning could even harm some species, especially at the stand level (Hämäläinen *et al.*, 2014) or initially after the fire (Hautala *et al.* 2010). Nevertheless, my results on long-term patterns of and dynamics of retention trees provides insights into how clear-cutting can be improved, in order to maintain biodiversity on harvested sites. Despite some potentially negative effects that fire may have, the use of fire on harvested sites with higher retention appears generally beneficial for the species that I studied.

3.2 Burning unharvested and harvested sites diversifies polypore assemblages (I, II, III, IV)

For the first time, I was able to simultaneously follow the long-term impacts of fire on dead wood dynamics and polypore assemblages both in unharvested and harvested forests (**I**, **II**, **III**, **IV**). In addition, it was possible to experimentally manipulate the conditions on managed sites, and compare polypore assemblages with those that occur on burned and unburned unharvested sites (**IV**). The long-term (> 10 years) influence of fire on polypores in uncut forests is relatively unknown, with only one study published thus far (Penttilä *et al.*, 2013). In managed and harvested forests, the effects of fire have been explored more often but these studies are limited in their temporal coverage (Penttilä and Kotiranta, 1996; Junninen *et al.*, 2008; Olsson and Jonsson, 2010; Berglund *et al.*, 2011) and those conducted in managed forests comprise four or five year study periods. My study on dead wood dynamics and polypore assemblages covered a 10-year period, which is much more relevant from a biological perspective, because this period potentially includes not only pioneer species but also successor species. Due to the large sampling effort, I was also able to collect some observations of Red-listed polypore species.

The number of species was similar on the unburned and burned harvested sites, and also on the burned unharvested sites ten years after the treatments, although there were more recordings on the harvested sites and the species assemblages were different in all treatment categories (**IV**). Red-listed species appeared on the study sites ten years after the treatments, especially on the burned sites. Physical conditions on a sun-exposed harvested site are different from that in a closed forest, and this influences the moisture and temperature conditions of logs (Forrester *et al.*, 2012), and likely has an impact on dead-wood-dependent species assemblages as well. The diversifying impact of fire on polypores was already apparent four years after the treatments and was very evident after ten years (**II**, **III**, **IV**). This is to be expected as the trees were weakened after the fire but may have stayed alive or occurred as dead-standing snags. Most of the polypore species would only begin to utilize them after they had fallen down. Slash and stumps are fresh dead wood that is utilized by primary colonizers. The differences in the species assemblages between sites and treatments can be explained by the difference in the dead wood types on the harvested and unharvested sites, e.g. stumps and slash were absent from unharvested sites. On the other hand, no living trees were recorded on harvested sites, except for a few retention trees, and as a consequence a continuity of large-diameter dead wood was not a feature of these sites. The various dead wood substrates host different polypore assemblages (**IV**) and living trees also host different polypore species to dead wood (Niemelä, 2016). The physical conditions on the harvested sites favor species that benefit from heat, such as *Dichomitus squalens* (**II**). Burning an unharvested forest increased the number of polypore species and records ten years after the treatments compared to the pre-treatment numbers (**IV**). This was also expected because burning clearly affects the diversity of the available dead wood (**I**) (Mattson *et al.*, 1988; Nuopponen *et al.*, 2004).

Prescribed burning increased the number of species and records on stumps (**III**, **IV**), but not on slash or old natural dead wood. Fire is known to affect wood quality in many ways and has an impact on fungal decay rates (Carlsson *et al.*, 2017) as well as on the whole fungal assemblage (Carlsson *et al.*, 2012). The first species that colonize a freshly cut stump could determine the succession of the following species (Ottosson *et al.*, 2014), thus creating a different polypore assemblage on burned and unburned stumps. However, this was not seen on slash or old natural dead wood in my study, which can be due to several differences between these substrate types and stumps. Slash is smaller in diameter than stumps, and the temperature inside a piece of slash when burned can get high throughout the wood. A stump might stay cooler in fire, and that could have an impact on the mycelium, which grow at different speeds at different temperatures (Fukasawa, 2018). This in turn could affect species succession on a piece of dead wood. The old natural dead wood was larger in diameter and thus resembled the stumps. However, this substrate had already hosted several different species before the treatments (**IV**), whereas the stumps were newly produced dead wood. Therefore, species interaction could have been different on these substrate types thereby affecting the species assemblages. Fire did not increase the number of species on retention trees in study **IV** but did so in study **II**. This was due to the different sample sizes in these two studies. In study **II**, I compared high levels of retention trees (10 and 50 m^3 ha^{-1}) whereas in study **IV** there were only a few retention trees at each one ha sized study plot.

In my study, 18 Red-listed species were recorded 10 years after the treatments, and of these, seven occurred only in the burned unharvested sites, whereas 17 were found on the burned harvested sites (**IV**), and many of these species were found on slash (**III**, **IV**). Five years after logging and burning, both Berglund *et al.* (2011) and Olsson and Jonsson (2010) found only three Red-listed species on burned sites. Their results are similar to my results for four years after the treatments. Thus, relatively more Red-listed species appear at these sites ten years after the treatments and not before.

My results in regard to the diversifying effect of fire on polypores are similar to Penttilä *et al.* (2013) who were able to follow the development of polypore assemblages 13 years after a fire, although their study did not include different management treatments. As longer periods of sampling are absent from the scientific literature, it would be invaluable to further follow the development of species assemblages both in unharvested burned sites and harvested burned sites, and to also investigate dead wood dynamics to determine how far the impacts of fire and retention logging extend temporally.

3.3 Old natural dead wood, retention trees, stumps and slash all host diverse polypore assemblages (III, IV)

Cut stumps, slash, natural dead wood and retention trees are all important substrates for polypores in managed forests (**III**, **IV**). Ten years after the treatments they were all hosts to different sets of polypore species, and in many cases were also host to several Red-listed species. Polypores were more abundant on slash and retention trees than on old natural dead wood and stumps (**IV**).

While only one species on the harvested sites was found exclusively on stumps, I observed 43 species using stumps in total on all harvested sites (**IV**). This shows that this substrate is valuable, in particular as they remain at harvested sites for a long period of time (Shorohova *et al.*, 2012), and thus, stumps may act as life-boats for several species. The importance of slash has probably not been fully realized so far, although there are some studies on dead-wood-dependent species on slash (Juutilainen *et al.*, 2014). I found that slash was host to Red-listed species, especially when burned (**III**, **IV**). This is opposite to the findings of De Jong and Dahlberg (2017) who observed only few occurrences of species of conservation interest on small diameter slash. Slash was numerous on my study sites compared to the number of other substrates (**IV**). The high amount of this substrate could have resulted in high numbers of polypore species. Also, the proportional surface area of slash is high compared to larger pieces of dead wood (Kruys and Jonsson, 1999), thus providing an enhanced area for colonization. On the other hand, it could be that slash, as a small diameter piece of wood, is colonized relatively rapidly and competition between different species is scarce. Moreover, the production of sporocarps could be faster on slash as less time might be utilized for growing the mycelium. As a result, species (sampled as sporocarps) appear more quickly on slash than on the larger diameter dead wood pieces.

Dead wood that originates before harvest may be accidentally destroyed during the management operations that follow harvest (Hautala *et al.*, 2004). In my study sites, no such operations were conducted, and old natural dead wood did host a different polypore assemblage than the other substrates. These trunks hosted species that were already present at the harvested sites before the treatments (**IV**) and these trunks may act as life-boats. Many of these species occur only at the more advanced decay stages, and as the fallen retention trees decay over time the species from old natural dead wood may be able to colonize these new trunks. Thus, old dead wood is a likely life-boat and maintains a continuum for dead-wood-dependent species on a managed site. As the old natural dead wood is formed by trees dying and falling without human intervention it is also useful to note that the green retention trees are left alive at the harvested sites and that they too will die and fall naturally, thereby forming similar qualities of dead wood as that of the old natural dead wood already present at the harvested sites before the treatments. However, because the majority of the retention trees die and fall quite soon after the treatments, new dead wood will not be formed later during the complete rotation period. Furthermore, because the trees die and fall relatively soon, these trunks do not reach old age, which may have a subsequent impact on dead wood quality.

My results imply that it is possible to also host some Red-listed polypore species in managed forests if a representative set of different dead wood types can be maintained at the harvested sites (**IV**). Even though slash hosted most of the recorded Red-listed species (**III** & **IV**), retention trees are likely to provide substrates for these species further in the future (**I**). Slash is a short-lasting substrate that is rapidly consumed (Hyvönen *et al.*, 2000), thus, it will not provide a continuum of suitable substrates for polypore species.

3.4 Implications for forest management and species conservation

In general, my results include several new aspects that can be used to facilitate the maintenance of biodiversity in managed boreal forests. Based on my results, I suggest the following recommendations for the conservation of polypore species in managed forests outside of protected areas. Three general rules or recommendations could be particularly useful.

First, the amount of retention trees should be increased from current levels in clear-cut forests. In my study, the level of 10 m^3 ha^{-1} was insufficient for providing a continuum of dead wood over the early-successional stage of a forest rotation, not to mention further into the future as most of the trunks had fallen 10 years after the treatments. Thus, I recommend leaving retention trees at a level closer to 50 m^3 ha^{-1}, which in our study forests was about 17 % of the pre-harvest volume. However, it is important to note that this is probably not necessary in every harvested stand. The concentration of retention trees in selected stands, while maintaining enough dead wood at the landscape level, may be the most efficient solution. However, the optimal arrangement of retention trees at different spatial scales needs further study.

Second, stumps, slash, and the old natural dead wood that originated before the harvest should be maintained at clear-cut sites, to provide necessary substrates for several polypore species. These substrate types, together with retention trees, provide a diverse set of substrates for polypore species, which seems to be a pre-requisite for high fungal diversity.

Third, burning can be used on retention harvested sites with a higher level of retention trees (in my study 50 m^3 ha^{-1} of retention trees) in order to diversify the dead wood quality and to provide a greater variety of dead wood substrates so as to provide continuum in dead wood availability at the stand level. Burning harvested sites increases the number of polypores on stumps and retention trees, and consequently these dead wood substrates in particular should be maintained on burned harvested sites.

My results give support to the idea that a continuity of dead wood substrates can be much improved on harvested sites for the early-successional years and that this continuity will facilitate polypore diversity. A key element is that there is sufficient dead wood available and that different types of dead wood are also accessible. It is likely that a sufficient amount of dead wood during the early successional years can act as a life-boat for species in the 10-year period after a disturbance. Therefore, in order to maintain polypore in managed forests all the major substrates should be maintained on harvested sites. In particular, longer lasting pieces of dead wood e.g. stumps and retention trees should be carefully preserved on cut sites to provide substrates for longer periods after clear-cutting.

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