Acta Universitatis Agriculturae Sueciae

Doctoral Thesis No. 2025:35
Faculty of Forest Sciences

Effectiveness of prescribed burning as a conservation tool in boreal forests

The role of time, weather and site attributes

Ellinor Ramberg

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Ellinor Ramberg
Faculty of Forest Sciences
Department of Ecology
Uppsala

SLU
SWEDISH UNIVERSITY
OF AGRICULTURAL
SCIENCES

DOCTORAL THESIS
Uppsala 2025

Acta Universitatis Agriculturae Sueciae
2025:35

Cover: Photo of prescribed burning in progress in a nature reserve.
Photo: Ellinor Ramberg

ISSN 1652-6880
ISBN (print version) 978-91-8046-470-3
ISBN (electronic version) 978-91-8046-520-5
https://doi.org/10.54612/a.7r7ltu7875

Swedish University of Agricultural Sciences, Department of Ecology, Uppsala, Sweden

Print: SLU Grafisk service, Uppsala 2025

Effectiveness of prescribed burning as a conservation tool in boreal forests – the role of time, weather and site attributes

Abstract

Prescribed burning is used as a conservation tool in Fennoscandia to create and restore fire-associated structures and processes, aiming to benefit biodiversity. However, knowledge on when and where prescribed burns should be applied to be most efficient in terms of promoting biodiversity is lacking. In this thesis I examine how stand and landscape characteristics, weather, season and time since burning influences the outcomes of prescribed burns. I studied saproxylic fungal communities in spruce dominated stands in Finland 16 years after burning. I inventoried deadwood, basal area, potential fires-scars and seedling regeneration in 32 prescribed burn sites in Sweden. In 23 of the 32 sites, I surveyed saproxylic beetles. My results show that prescribed burn outcomes vary considerably among sites. I found that burning forests with high spruce proportions can create large volumes of deadwood, facilitate deciduous tree regeneration and promote red-listed saproxylic fungi. The red-listed fungi were present 16 years after burning, but not in previous inventories, highlighting the importance of long-term studies. Burning forests as opposed to clear-cuts benefited different types of saproxylic beetles, suggesting that these burn types are not interchangeable but instead complementary. Beetle species richness was also positively correlated to the proportion of protected forests in the landscape. The composition of the surrounding landscape should therefore be considered when planning burns. Weather and season differed between prescribed fires and wildfires, with wildfires occurring in drier weather conditions and later in the summer. Several Fire Weather Indices were positively correlated with the amount of deadwood created and establishment of deciduous seedlings. But in comparison to wildfires, few sites had high values of either, indicating that many burns are suboptimal in terms of creating structures and processes that benefit biodiversity. Burning later in the season when the ground is drier may be one way to improve outcomes. My results demonstrate that the conservation value of prescribed burns can be improved by more carefully considering forest type, landscape context, weather and seasonal factors.

Keywords: Prescribed burning, Conservation, Saproxylic species, Deadwood, Restoration, Boreal forests

Analys av naturvårdsbrand som skötselåtgärd i borealskog – betydelsen av tid, väder och platsegenskaper

Sammanfattning

I Fennoskandien används naturvårdsbränningar för att skapa brandpräglade miljöer med målsättningen att gynna biodiversitet. Det är dock fortfarande oklart om var och när naturvårdsbränningar ska genomföras för att vara mest gynnsam för biodiversitet. I denna avhandling undersöker jag hur skogsbeståndets och landskapets sammansättning, väder, årstid och tid sedan brand påverkar nyttan av naturvårdsbränder. Jag studerade vedlevande svampar i grandominerande skogar in Finland 16 år efter bränning. Jag inventerade död ved, grundyta, potential för brandljud och föryngring av träd i 32 naturvårsbränder i Sverige. I 23 av dessa 32 bränder inventerande jag vedlevande skalbaggar. Mina resultat visar att effekterna av naturvårdsbränder är väldigt variabla. Att bränna grandominerade skogar skapar död ved, gynnar föryngring av lövträd och rödlistade vedlevande svampar. De positiva effekterna på de rödlistade svamparna fanns inte vid en tidigare inventering, utan uppstod först 16 år efter bränningen. Det visar på att vissa naturvårdseffekter blir synliga långt efter branden, och understryker vikten av långtidsuppföljningar. Bränningar av skog och hyggen gynnade olika typer av vedlevande skalbaggar, vilket tyder på att dessa två brännings typer inte är utbytbara. Artrikedomen av skalbaggar varierade beroende på andelen skyddad skog i landskapet runt de brända områdena. Det omkringliggande landskapets naturvårdskvalité borde därmed beaktats vid planering av naturvårdsbränder. Väder och årstid i samband med branden skilde sig mellan vildbränder och naturvårdsbränder. I jämförelse med vildbränder, genomförs naturvårdsbränningar när det är blötare och tidigare på året. Flera Fire Weather Indices var positivt korrelerade med volymen av död ved och föryngring av lövträd efter branden. För många bränder var dock både mängden skapad död ved liten och föryngringen låg, vilken indikerar att många bränder utförs under suboptimala väderförhållanden. Att bränna senare på året under torrare perioder kan vara ett sätt att förbättra utfallet. För att öka naturvårdsnyttan med bränningar bör de utföras med noggrannare hänsyn till skogsbeståndets karaktär, landskapets sammansättning, väderförhållanden och vilken årstid de genomförs.

Nyckelord: Naturvårdsbrand, Naturvård, Vedlevande diversitet, Restaurering, Dödved, Boreal skog

Dedication

To Clara and Norah -
For finding joy in the small things and sharing them with me.

And

For Hanna -
“Her memory will ever shine like golden embers in the night” Andrew Marlin

Photo: Ellinor Ramberg

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Ellinor Ramberg, Håkan Berglund, Reijo Penttilä, Joachim Strengbom, Mari Jönsson (2023). Prescribed fire is an effective restoration measure for increasing boreal fungal diversity. Ecological applications, 33 (6):e2892. https://doi.org/10.1002/eap.2892

II. Ellinor Ramberg, Mattias Edman, Gustaf Granath, Jörgen Sjögren, Joachim Strengbom. Prescribed burning for boreal forest restoration: Evaluating challenges and conservation outcomes. (under revision)

III. Ellinor Ramberg, Joachim Strengbom, Lars-Ove Wikars, Thomas Ranius. Surrounding landscape composition influences saproxylic beetle assemblages after prescribed burning. (Accepted for publication in *Journal of Applied Ecology*)

IV. Ellinor Ramberg, Jonas Hagge, Mat Jonsell, Mari Jönsson, Thomas Ranius, Diana Rubene, Joachim Strengbom. Both trait and taxonomic composition of saproxylic beetles differ between burned forests and burned clear-cuts. (manuscript)

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The contribution of Ellinor Ramberg to the papers included in this thesis was as follows:

I. Participated in the development of ideas and in data processing, led the analyses, writing and revisions of the manuscript.

II. Participated in the development of ideas and study design, conducted the fieldwork, led the analyses, writing and revisions of the manuscript.

III. Participated in the development of ideas and study design, conducted the fieldwork, led the analyses, writing and revisions of the manuscript.

IV. Led the development of ideas and study design, processed the data, led the analyses and writing of the manuscript.

1. Introduction

1.1 The role of fire in the boreal forests of Fennoscandia

Boreal forests are historically shaped by disturbance events and successional processes, creating dynamic mosaic landscapes (Kuuluvainen & Aakala 2011; Aakala et al. 2023). Wildfire is recognised as a pivotal disturbance in boreal forests, acting on a range of temporal and spatial scales. In Fennoscandia fire-driven cohort dynamics have dominated, creating heterogeneous forest stands with a diversity of tree ages and species, and a range of dead, dying and injured trees (Kuuluvainen & Aakala 2011; Lunde et al. 2025). Wildfire can also be stand-replacing, essentially killing all trees, resetting the successional cycle. Additionally, wildfire events are stochastic in nature, most commonly ignited by lighting (Granström 1993). The variations in fire frequency thereby resulted in forests at different successional stages, creating heterogeneity at a landscape scale.

1.1.1 Wildfire behaviour and the fire triangle

The effects wildfire has on forests can be discussed in terms of fire severity, which is the loss or change in organic matter above or below ground (Keeley 2009). How severe a fire is in turn determined by key components of fire behaviour: fire intensity, depth and rate of spread. Fire intensity is the energy released at the flame front, with a more intense fire consuming more organic matter (Granström 2005; Keeley 2009). Burn depth is a measure of how much organic matter in the ground layers that a fire consumes (Ryan 2002; Granström 2005). Besides direct combustion of organic matter below ground, deep burns can also indirectly affect above ground survival, through for example combustion of roots (Ryan 2002; Granström 2005). Rate of spread is simply how fast the fire spreads.

Weather, fuel characteristics and topography, also known as the fire triangle, all affect wildfire behaviour (Ryan 2002). For example, longer periods of dry weather reduces the moisture content in the organic ground layer (humus), thereby increasing burn depth (Granström 2005). Once a fire has been ignited, wind speed is paramount to the rate of spread and intensity of the fire. With increasing wind speed the flames are at a narrower angel to the ground, which heats fuels more efficiently and increases the rate of ignition (Ryan 2002; Granström 2005). Other important weather variables are relative humidity, precipitation and temperature, which impact moisture levels and evaporation rates in fuels. The vegetation in a forest act as fuels. In Fennoscandia surface fuels such as porous mosses (e.g. *Hylocomium splendens*) and lichens (*Cladonia spp.*) common in Scots pine (*Pinus sylvestris*) forests generally sustain fires and, canopy fuels i.e. tree crowns only support fires in the rare event of high fire intensity under high wind-speed conditions (Granström 2005; Tanskanen 2007; Lindberg et al. 2021). However, vegetation structure also affects fire behaviour, as tree spatial distribution and different species combinations can affect microclimate, wind speed and direction, impeding or facilitating fire (Loudermilk et al. 2022). Likewise, topography can impact fire behaviour by facilitating it through funnelling wind or steep slopes increasing fire intensity, or impede it with mires or lakes acting as fire breaks (Hellberg et al. 2004; Granström 2005). The severity of the wildfire therefore depends on a combination of weather conditions, forest characteristics and the surrounding landscape.

1.1.2 The effect of wildfire on forest structure

The most dramatic effect of fire in forests is tree mortality, which can be a result of both burn depth and burn intensity. Deep burns cause root-necrosis, and high intensity burns damages above-ground tree structures beyond repair, killing the tree (Bär et al. 2019). Trees injured by fire are also vulnerable to secondary disturbances such as insect attacks and fungi, which kill the tree over time (Bär et al. 2019). How susceptible a tree is to burning is, however, largely dependent on the tree species and its adaptions to fire.

In Fennoscandia, two conifer species dominate, Scots pine (*Pinus sylvestris*) and Norwegian spruce (*Picea abies*). Scots pine, with its thicker bark, deeper roots, and elevated crown, are more resistant to fire. Thereby, though pine forests are more prone to burning due to suitable surface fuels and more open stands, tree mortality would be variable, leaving larger trees with thick bark alive (Esseen et al. 1997; Kuuluvainen 2009). Injured pines die over time creating a continuity of deadwood. On injured, but surviving, pines fire-scars can form over time, which is the trees reaction to heat damage to the cambium (Baker & Ehle 2001). Norwegian spruce have thin bark, shallower roots and lower crowns, characteristics that make the trees more susceptible to fire-induced mortality (Ryan 2002; Bär et al. 2019). Though spruce trees are sensitive to fire, spruce forests are often dense and moist with more compact surface fuels (*Dicranum spp.*) and therefore burned only after longer dry periods (Esseen et al. 1997; Kuuluvainen 2009). Though generally recognized that high deadwood volumes can be created by disturbances (Siitonen 2001; Kuuluvainen 2009; Swanson et al. 2011), surprisingly few studies in Fennoscandia have reported deadwood volumes created after wildfires. A study in Russian Karelia 30 years after a mixed-severity wildfire found a mean volume of 95 m^3 ha^1 (ranging from 16 to 201 m^3 ha^{-1}) deadwood in pine-dominated forests, which was comparable to the living tree volume of 112 m^3 ha^{-1} (Lampainen et al. 2004). Ylisirniö et al. (2012) found deadwood volumes with a mean of 98 m^3 ha^{-1} in spruce-dominated forests 15 years after stand-replacing fire in northern Russia and Finland. In mid-boreal Sweden mean volumes of 92 m^3 ha^{-1} deadwood have been reported in pine-dominated stands four years after high-intensity wildfires (Jakob 2023). For perspective, boreal old-growth spruce forests are estimated to sustain 90−120 m^3 ha^{-1} of deadwood and pine old-growth forests 60−120 m^3 ha^{-1} (Siitonen 2001).

Tree mortality also alters shade, nutrient and moisture conditions on the forest floor, benefitting early successional deciduous species such as birch (*Betula spp.*) and aspen (*Populus tremula*). Burn depth is also important for the establishment of these deciduous species. Gustafsson et al. (2019), reported that in areas where the remaining humus layer exceeded 2 cm after a wildfire almost no deciduous seedlings had established. Aspen can also reproduce vegetatively from burned parent tree stumps, which is a regeneration form that is not dependant on humus depth, but facilitated by disturbance (Rogers et al. 2020). The early successional habitats created after fire can be structurally complex, with a rich and varied composition of deadwood, and represents a more open habitat type than surrounding forests, benefitting species specialised to this habitat (Swanson et al. 2011).

1.1.3 Species that are tied to and benefit from fire

Generally, some species benefit from disturbances whilst others respond negatively (Pastro et al. 2011; Eales et al. 2018; Viljur et al. 2022). According to the intermediate disturbance hypothesis (Connell 1978), a disturbance of intermediate magnitude is expected to support the highest biodiversity. Viljur et al. (2022) found that in disturbed forest stands the highest α-diversity across 26 species groups (fungi, plants, invertebrates and vertebrates) occurred at intermediate disturbance intensity, which was defined as when approximately 55% of trees had been killed by the disturbance. The cohort dynamics which dominated Fennoscandia boreal forests, can be considered an intermediate disturbance, creating heterogenous habitats. Nevertheless, many species are adapted to, and dependant on the substrates and forest types that fire creates. The large volumes and diversity of deadwood created by fire, and specialized substrates formed by fire such as fire-scars and charred wood, benefit many species (Hjältén et al. 2018; Gustafsson et al. 2019).

Saproxylic (i.e. deadwood dependent) species are a diverse group estimated to include at least 7500 species in northern Europe, of which insects and fungi are the most species rich (Stokland et al. 2012). Amongst saproxylic insects, beetles are by far the most studied, and more than a thousand species have been documented. Saproxylic fungi are equally species rich, with approximately 1500 identified species. In addition, many interactions between saproxylic beetles and fungi have been recorded (Birkemoe et al. 2018), increasing the complexity in post-burn habitats.

Polypores (*Basidiomycota,* 'bracket fungi') are saproxylic fungi that are key decomposers of deadwood in boreal forests, as well as being an important food source for many beetles (Stokland et al. 2012). Many are specialized to a specific decay stage, tree species or size of deadwood (Penttilä et al. 2004; Berglund et al. 2011a; Junninen & Komonen 2011). Polypores as sessile and thereby fire has a direct negative effect on them. However, polypore assemblages usually recover within a few years, utilizing the deadwood created by fire, and diversify over time (Penttilä et al. 2013; Koivula & Vanha-Majamaa 2020). Polypores are therefore most abundant at intermediate decay stages (Junninen & Komonen 2011). Burning also modifies the chemical and structural composition of wood, which has an influence on polypore composition (Edman & Eriksson 2016).

Saproxylic beetles (*Coleoptera*) are a heterogenous group with species tied to different deadwood decay stages, tree species, sizes and microhabitats (Siitonen 2001; Stokland et al. 2012). For example, many species of bark beetles (*Scolytinae*) larvae feed on the inner bark of newly dead trees (Stokland et al. 2012). Deadwood and injured trees created by burning thereby represent a large and continual source of niches available to saproxylic beetles. In addition, many saproxylic beetles are specifically favoured by fire, responding to smoke or found in higher abundances in burned forests, drawn by the large volume of newly dead trees and open environment (Bell 2023). A specialized group, pyrophilic (fire-dependant) beetles have evolutionary adaptions to fire, and utilize substrates that fire creates (Wikars 2006; Bell 2023). For example, two *Stephanopachys* species in Sweden utilise the fire damaged area in pine trees that precedes fire-scar formation (Wikars 2006). Many of the saproxylic, fire-favoured and fire-dependant species are also known to have good dispersal capabilities, tracking suitable substrates across the forest landscape (Bell 2023).

Other species groups that are affected positively after wildfires are for example ungulates that browse on early-succession deciduous saplings (Fredriksson et al. 2023) and woodpeckers that feed on the large number of saproxylic insects (Gustafsson et al. 2019).

1.1.4 Consequences of forestry

Over the last century in Fennoscandia wildfire extent has decreased markedly as a result of effective fire suppression (Zackrisson 1977; Ramberg et al. 2023). This developed alongside the rise of large-scale production forestry, which heightened the economic incentive to suppress forest fires. In addition, clear-cutting has been the dominating harvesting practise since the 1950’s, which has had extensive effects on forest ecosystems (Lunde et al. 2025). This intensive forest management system has resulted in forests lacking in structural diversity and generally deficient in deadwood (Jonsson et al. 2016; Lunde et al. 2025). The mean deadwood volume in production forest in Sweden is approximately 6−10 m^3 ha^{-1} (Jonsson et al. 2016; Kyaschenko et al. 2022), which is far below deadwood volumes in old-growth forests, or the ones created by fire. As a result, populations of many species groups that rely on deadwood or substrates created by fire have declined and are today threatened and red-listed (Wikars 2006; SLU Artdatabanken 2020; Lunde et al. 2025). Conservation measures to counteract the negative effects of wildfire exclusion and clear-cutting practises are therefore necessary.

1.2 Prescribed burning as a conservation tool

Prescribed burning is used in Fennoscandia as a conservation tool to restore key structures (e.g. deadwood) and dynamics (e.g. successional processes) that have been degraded by intensive forest management practises and fire suppression. The overarching goal of these prescribed burns is to benefit biodiversity (FSC Sweden 2020; Life Taiga 2023). Although specific goals of prescribed burning may vary, many of these prescribed burns have three general objectives: create multilayered forests, create deadwood and promote fire scars on pines, which benefits saproxylic and fire-dependant species.

Prescribed burning for conservation purposes within forests has been applied in Sweden and Finland since the 1990's (Cogos et al. 2020; Lindberg et al. 2020). Currently prescribed burning is conducted by governmental organisations and by forestry companies within forest certification schemes (FSC Sweden 2020; Life Taiga 2023). In Sweden, many of the most recent burns have been applied within the EU funded project Life Taiga, which had its first round between 2015 and 2020, burning over 2000 ha standing forest in protected areas across Sweden (Life Taiga 2023). The second round to the project, Life2Taiga, is currently underway (2022-2028), with the aim to burn approximately 3400 ha in Sweden and Finland (Länsstyrelsen Västmanland 2025). Prescribed burns performed by forestry companies and within restoration programmes often lack both pre- and post-burn surveys of forest vegetation and structures. Post-burn surveys that are conducted are often done soon after burning, so many longer-term changes are not captured. Indeed, though prescribed burns have been applied for several decades for conservation purposes, few assessments of their effectiveness as conservation tools have been conducted.

To study the potential for prescribed burns to promote biodiversity several experimental studies, some long-term, have been implemented in Fennoscandia (Vanha-Majamaa et al. 2007; Hjältén et al. 2017; Koivula & Vanha-Majamaa 2020; Kouki 2024). Results from these experiments show positive effects of prescribed burning on several species groups, for example, saproxylic beetles (Hyvärinen et al. 2006; Heikkala et al. 2016a; Hjältén et al. 2017) and polypores (Olsson & Jonsson 2010; Suominen et al. 2018). Prescribed burning has often resulted in higher species richness and abundances, increased numbers of red-listed and/or pyrophilic species and diverging species composition compared to not burning (Hyvärinen et al. 2006; Sandström et al. 2019). However, many knowledge gaps remain in terms of where and when prescribed burns should be applied to be most efficient in terms of promoting biodiversity.

1.2.1 Site attributes

Stand characteristics

Where to burn is determined by the stakeholder conducting the burn, based on the framework within which they are burning. For example, Life Taiga burns are within Natura 2000 areas in western taiga forest types (boreal conifer forest) and burning within FSC should be on ‘dry and mesic forest land’ prioritising land that has been affected by fire previously (FSC Sweden 2020; Länsstyrelsen Västmanland 2025). Pine-dominated forests are often targeted as they were maintained by fire historically. Safety and practical issues, such as water and road access, are also given substantial consideration when planning burn locations.

Though stand and vegetation characteristics are known to be important for wildfire behaviour and thereby fires effect on forests (Ryan 2002; Loudermilk et al. 2022), there is a lack of research on how these characteristics relate to and impact on prescribed fire. Prescribed fires are applied in a systematic and controlled way, with ignition often in a horseshoe pattern or applied in points that burn to meet a backing fire (burning against the wind), which is significantly different to how wildfires behave (Similä & Junninen 2012; Boby et al. 2023). How stand structure would subsequently interact with fire behaviour is therefore ambiguous. In addition, though pine-dominated forests are targeted for burning, spruce trees are often present. Patches with spruce trees can foster a more humid micro-climate than surrounding pine forests, affecting burn intensity negatively. Spruce trees are however also more prone to burning, even acting as ladder fuels to overhead pine trees, which would increase fire intensity (Granström 2005). How spruce proportions in prescribed burn sites affect fire behaviour and the subsequent fire severity is largely unknown. In addition, as pine has been the dominating forest type to conduct prescribed burns in, both experimentally and for conservation, there is limited knowledge about the effects of burning spruces forests for biodiversity (but see the EVO experiment (Lilja et al. 2005; Vanha-Majamaa et al. 2007)).

Prescribed burning is not only conducted on standing forest but also on clear-cuts. In Sweden, prescribed burning on clear-cuts has been documented since the 1920's, with its peak in use during the 1950's and 1960's, and is still applied today (Ramberg et al. 2018; Cogos et al. 2020). Initially it was only use as site preparation technique for forest regenerating (Cogos et al. 2020). Today, FSC certification includes burning clear-cuts within their definition of burning forest land, which allows forest companies to harvest valuable timber before burning, thereby maintaining the practise (FSC Sweden 2020). Burned clear-cuts and burned standing forests are similar in several ways, both are disturbed early successional habitats that are open and sunlit. The most pronounced difference between them, however, is the potential to create high volumes of deadwood of diverse types. In clear-cuts, timber is removed leaving retention trees, stumps and logging residue, deadwood volume is thereby low, and the potential to create deadwood by burning is limited. Prescribed burning in standing forests, however, can potentially create both high volumes and diversity of deadwood (Eriksson et al. 2013; Hekkala et al. 2016). This has implications for saproxylic species. A few experimental studies have studied differences between burning forests, different retention levels and/or created deadwood volumes and burning clear-cuts in relation to saproxylic beetles (Hyvärinen et al. 2006; Toivanen & Kotiaho 2007; Heikkala et al. 2016a). In general species richness seems to increase with increasing tree cover of the burned area, and species composition differs between burned clear-cuts and burned forests (Hyvärinen et al. 2006; Toivanen & Kotiaho 2007; Heikkala et al. 2016a). Only one study has examined the functional diversity of beetles of beetles in burned forests, clear-cuts and across retention levels. They found that burning favoured certain traits, but that at low tree-retention levels the effect of fire was reduced (Heikkala et al. 2016b). To my knowledge, no studies have compared if and how the effect on saproxylic beetle assemblages differs between burned clear-cuts and burned forests conducted as conservation or management measures. Further insight into how stand characteristics relate to subsequent effects of prescribed fires can help improve its application.

Location in the landscape

The ecological resilience of an ecosystem after a disturbance is largely determined by its capacity to recover i.e. its ecological memory (Bengtsson et al. 2003). Biological legacies within sites (e.g. deadwood) promotes regeneration and colonisation after burning (internal ecological memory), and the surrounding landscape is a source of dispersal to sites (external ecological memory) (Bengtsson et al. 2003). Consequently, post-burn communities are not only influenced by stand characteristics, but the surrounding landscape is likely to be important. A better understanding of how the landscape composition influences communities after burning is therefore important when planning the location of prescribed burns.

For prescribed burning there is limited knowledge about how the surrounding landscape affects beetle assemblages after burning (but see: (Kouki et al. 2012; Ranius et al. 2014; Rubene et al. 2017). Additionally, it is unclear if local (site) habitat amount in terms of deadwood volume is more important for forming communities (Species-energy hypothesis (Wright 1983) or if landscape habitat amount, i.e. deadwood rich habitats in the landscape, is paramount (Habitat amount hypothesis (Fahrig 2013). It is also important to know at what scale species respond to habitat amount in the landscape i.e. the spatial scale of effect (Jackson & Fahrig 2012), to be able to make evidence-based decisions on what landscape scale to consider when planning prescribed burns.

1.2.2 Weather and season

At high precipitation levels, high relative humidity and low temperatures igniting and sustaining a fire is unfeasible. On the opposite end of the scale, high wind speeds, low relative humidity and high temperatures can lead to a volatile fire that is hard to control. Prescribed burning is conducted somewhere between these two extremes, in 'burn/weather windows', were burn viability and risk are balanced. Weather conditions are therefore carefully monitored before, and during, a prescribed burn (Life Taiga 2023). In Sweden, the Canadian Fire Weather Index (FWI) system has been adopted to assess fire risk (Granström 2005). FWI indices are also monitored prior to burning. Despite weather having a pivotal role in prescribed burn planning, assessments relating burn outcomes to weather conditions are lacking (but see (Hermanson 2020)). To set realistic goals when conducting prescribed fires knowledge about what fire effects can be achieved when burning within 'weather windows' is highly relevant.

The season in which burns are conducted may also be of importance. Ryan et al. (2013) illustrated differences between the historical wildfire season and the prescribed burn season in North America. In Sweden, a similar pattern has been observed (Granström 2001), but so far not verified with data. Burning outside of the main wildfire seasons may not benefit species as intended if their activity patterns do not align with the altered timing. It also has implications on fire behaviour. For example, burning in spring or early summer entails high moisture in the humus layer, resulting in shallow burns with consequences for both deciduous seedling establishment and tree mortality.

1.2.3 Time since burning

Studying prescribed burn effects at regular intervals and in the long-term after a burn is essential as fire has direct effects but also leads to successional processes. This is especially important for species that utilise substrates in later successional stages such as polypores. Penttilä et al. (2013) found that for polypore communities in pine-dominated forests in Finland it took 13 years after burning to observe a clear positive effect of fire, and the effects were still apparent 22 years after fire. In fact, it took approximately ten years after the fire before red-listed species started to appear (Penttilä et al. 2013; Suominen et al. 2015). Knowledge on long-term effects on polypore communities of burning in spruce forests is limited, nevertheless relevant as red-listed species are common targets of conservation efforts.

Saproxylic beetle assemblages also follow successional patterns as different species utilise different deadwood stages. Most studies have studied saproxylic beetle communities directly after prescribed burns and up to a few years after (e.g. Hyvärinen et al. 2005; Heikkala et al. 2016b), and a few have looked at communities over longer time periods (Heikkala et al. 2016a). The lack of studies examining the later post-fire development of biodiversity may have contributed to the dominance of short-term effects, more directly linked to the fire event, when evaluating the potential benefits of prescribed burning, while long-term effects, which may be even more important, have largely been overlooked.

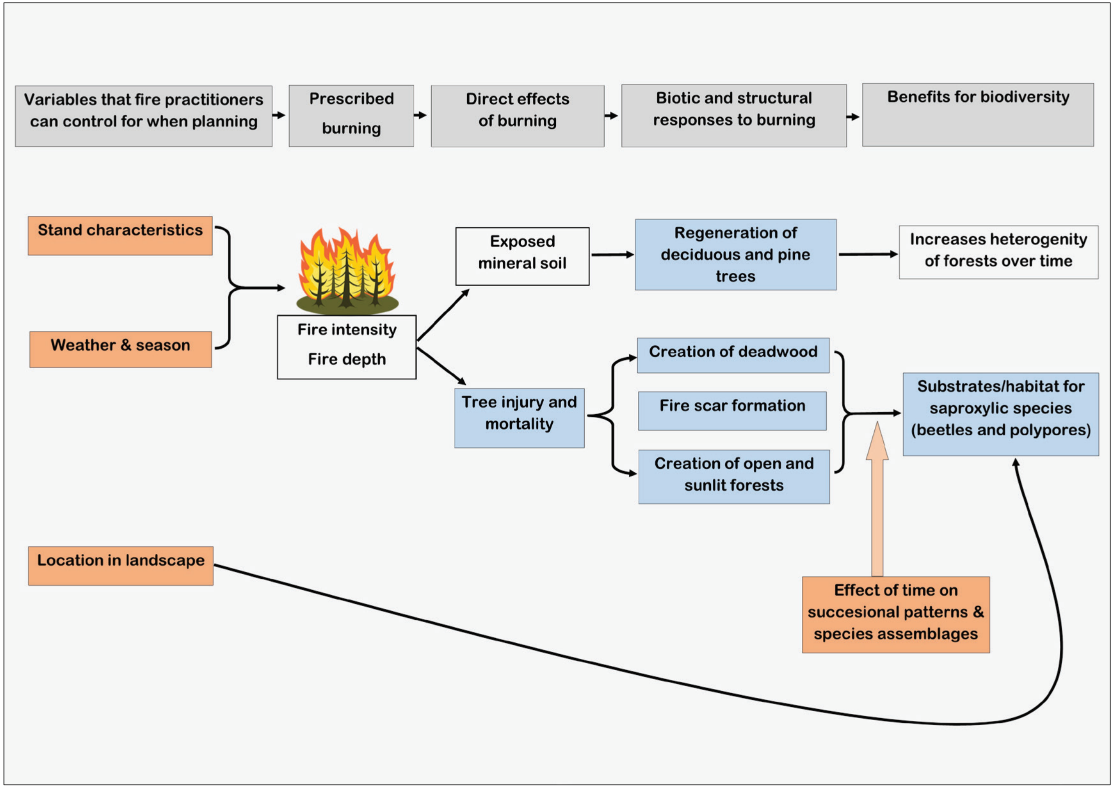


Figure 1. Schematic overview of prescribed fire that this thesis considers, from the planning stage through to the effects of prescribed burning on biodiversity. Orange coloured boxed are connected to aims of the thesis, blue boxes have been inventoried within the study and uncoloured boxes are hypothesised links/effects.

2. Aims

The overarching aim of my thesis is to examine where and when prescribed burning should be applied to be most efficient in terms of promoting biodiversity. I examine how both spatial factors—such as stand and landscape characteristics—and temporal factors—like weather, season, and time since burning—influences the outcomes of prescribed burns. These post-burn outcomes include structural features (e.g., deadwood), ecological processes (e.g., tree regeneration), and the composition of polypore and saproxylic beetle communities. In addition to this I also aim to describe the status of three general objectives of prescribed burns (creating deadwood, creating multilayered forests and potential formation of fire-scars) in burn sites.

The specific aims of each paper are:

I. To investigate the long-term effects of prescribed burning on polypore community composition, abundance and richness in spruce-dominated forests.

II. To assess the effects of prescribed burning in relation to three prescribed burn objectives (creating deadwood, creating multilayered forests and potential formation of fire-scars) and analyse how they relate to weather conditions and stand characteristics prior to burning. In addition, to illustrate the differences between wildfires and prescribed burns in terms of weather and season.

III. To investigate how local and landscape characteristics shape saproxylic and fire-favoured beetle communities after burning, comparing species abundances, richness and species composition.

IV. To examine how burning in clear-cuts differs from burning in forests in relation to saproxylic and fire-favoured beetle taxonomic and trait richness and composition.

3. Materials and Methods

3.1 Study sites and study design

All data used for this thesis was collected from within the southern and mid boreal zones (Ahti et al. 1968) of Sweden and Finland (Fig. 2a). For **Paper I** data was collected from the Evo-Vesijako area in southern Finland. For **Papers II** data was collected from three areas across Sweden, spanning a latitude from 56º 55'N in the south to 62º39'N in the north. Sites in **Paper III & IV,** were subset of the sites from **Paper II**. Additional sites were added in the centre of Sweden for **Paper IV**.

3.1.1 Paper I: The Finnish experiment

The data used in **Paper I** were collected within the EVO experiment in Finland which was set up in 2001 (Lilja et al. 2005; Vanha-Majamaa et al. 2007). The experimental forest was dominated by mature Norway spruce (*Picea abies*) trees and all stands had been influenced by forest management prior to treatment. A full factorial design was employed, with a total of 18 stands and three replicates of each possible treatment combination (Fig. 2b). Treatments were randomized among stands. Two main treatments were applied, creation of deadwood and prescribed burning. In early 2002 all stands were subjected to partial cutting, resulting in a standing tree retention of 50 m^3 ha^{-1} across all stands. The felled trees were used to create three levels of deadwood: 5, 10 and 60 m^3 ha^{-1}. In the summer of 2002 half of the stands were burned, (N=9, three of each deadwood level). Polypore data used in **Paper I** was collected in 2018, 16 years after the treatments had been applied (inventory details can be found in section 3.2.2).

3.1.2 Paper II−IV: Swedish prescribed burns

For **Paper II,** I identified 32 prescribed burn sites in Sweden that were larger than 4 ha, conducted between 2014−2019 and Scots pine-dominated (*Pinus sylvestris*) (Fig. 3). The rationale for these restrictions was to reduce among-site variation in relation to time since burning and tree species composition. Sites were grouped in three areas in Sweden: North, Central and South (Fig.2a), which resulted in a larger pool of sites and created a climatic and biogeographical gradient. In the North and South, eight burns per area were included, whereas in the Central area 16 burns were included (Fig.2b). This was largely based on available burns fitting the criteria.

Most burns were within the Life Taiga project, an EU funded project that conducted prescribed burns in 14 counties across Sweden between 2015−2020. One burn was conducted in 2014 by the county board (Västmanland) and was included as it was adjacent to another Life Taiga burn. The general aim of all the prescribed burns was to benefit biodiversity in taiga forests. All burns were within protected areas (nature reserves, national parks and Natura 2000 areas). The 32 burn sites were surveyed in 2020.

A subset of 24 sites were chosen for the beetle survey used in **Paper III** (Fig.2b). Originally all sites in the North and South, and eight sites in the Central region were chosen. One site in the North fell away during fieldwork as it was difficult to access, leaving 23 sites. The sites in the central region were selected to match the burn year of sites in the other regions (2015-2018) and based on logistics (travel distances). Beetle sampling was done in 2022, 4-7 years after burning.

For **Paper IV** I focused on the differences between burning in forests versus clear-cuts. Here I used data from the Northern and Central sites in **Paper III**, resulting in 15 prescribed burns in forests. This was done to match data collected in an earlier study (Rubene et al. 2017) that had surveyed beetles in clear-cut sites overlapping and further north of my Central region (Fig 2a). A total of 32 clear-cuts sites were included. The 15 clear-cuts had either been clear-cut before prescribed burning or salvage-logged after wildfires. The remaining 17 clear-cuts were unburned and included as controls for the effect of clear-cutting. All sites had been clear-cut/burned 3−5 years prior to sampling. The clear-cuts were located in a landscape dominated by managed pine and spruce forests. Forest managers from the companies Bergvik and Sveaskog had applied the prescribed burns. All beetle sampling details can be found in section 3.2.2.

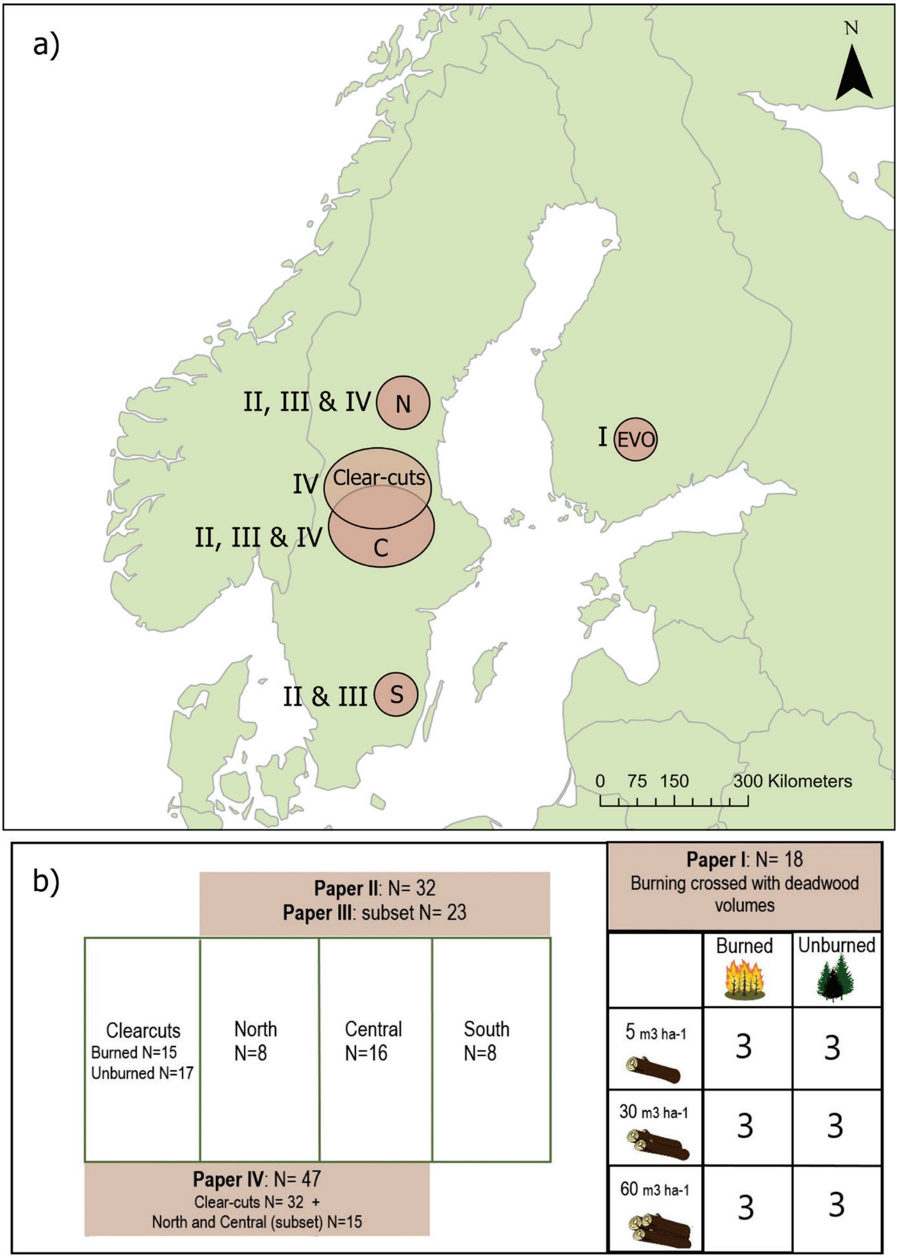


Figure 2. a) Map of the study site areas in Sweden and Finland. Roman numerals correspond to thesis papers. N: North, C: Central, S: South, Clear-cuts: Clear-cuts sites, EVO = EVO sites. b) Graphical description of the study design and number of sites in each study.

Figure 3. Examples of prescribed burn sites at time of inventory. Photos: Ellinor Ramberg and Matilda Karlsson.

3.2 Data collection

3.2.1 Site attributes

Local environmental variables

In all 32 prescribed burns sites data on environmental variables were collected to describe the effects of burning, which was assessed in **Paper II.** Data were collected in circular plots (5 m radius) arranged 100 m apart in a grid pattern covering each site (averaging one plot per ha). Four main variables were of interest: changes in basal area, tree regeneration (deciduous and pine seedlings), potential fire-scar formation and created deadwood. In each plot, all dead and living trees were identified to species and measured for diameter at base height (DBH: 130 cm). Dead trees were categorized as dead before or at/after burning based on charring, decay stage, absence of bark and needles, and presence of wood-boring insects. The categorisation facilitated the characterisation of the stands before and after burning. Data on all trees (DBH ≥ 1 cm) was used to calculate the pre-burn basal area and mean diameter of trees per site, whilst only living trees were used for post-burn basal area and mean tree diameter. All seedlings within the plots (max height 130 cm), were counted to estimate tree regeneration. Potential fire-scar formation was estimated by examining all pine trees within the plots and counting the trees with visual resin flow on the outside of the tree trunk (resin flow is a sign of injury which can lead to fire-scar formation) (Fig. 4a). The explanatory variables (**Paper II**) pre-burn basal area and spruce proportion were obtained from the data collected.

Deadwood was estimated along 50 m transects which were placed between plots (Fig. 4b). Each transect began at a plot centre and the direction of transects was alternated to minimize the impact of the direction of wind-felled trees. For fallen deadwood the line transect method was used (Van Wagner 1968), which entailed measuring the diameter of the deadwood (estimated DBH ≥ 10 cm) that intersected with the transect. The volume of the deadwood ($m^3\ ha^{-1}$) was then calculated using the equation:

$$V = \pi^2 \times \sum_{i=1}^{n} \left(\frac{{DT_i}^2}{8L} \right)$$

Equation 1.Where DTi = diameter of wood item i at transect crossing, and L = transect length (Van Wagner 1968).

Standing deadwood diameter (DBH ≥ 10 cm) and height (using a clinometer) was measured within 2.5 m on each side of the transect. The volume of standing deadwood ($m^3\ ha^{-1}$) was calculated using the equation of a cylinder. The same method described above for plots was used to categorize if tree mortality was pre- or post-burn. Deadwood identified as dead before burning was used to calculate pre-burning volumes and all deadwood was used to estimate post-burning volumes, with the difference between the two being the volume created by burning.

In **Paper III** & **Paper IV** deadwood volumes were used to represent the local habitat amount, as the beetles studied were dependant on deadwood. Estimated deadwood volumes for clear-cuts were extracted from measurement done by Rubene et al. (2017). All standing and fallen deadwood had been measured within a circular plot (50 m radius, mean area 2.3 ha, SD ± 0.5 ha) in the centre of clear-cuts and recalculated to site level.

Figure 4. a) A pine with resin flow used to identify possible fire scar formation. b) Example of a transect used to estimate deadwood volumes in sites, the white line on the ground is the transect. Photos: Ellinor Ramberg

Weather data

In **Paper II** weather conditions prior to, and during burning were of interest. The included weather variables were: Fire Weather Index (FWI), Fine Fuel Moisture Code (FFMC), Duff Moisture Code (DMC), Drought Code (DC), temperature (°c), wind speed (m/s), relative humidity (RH), millimetres rain 14 days prior to burning and number of rain-free days prior to burning (Details can be found in **Paper II**, supplementary Table 2). Of the 32 sites, 28 had weather data in their reports from the county administrative boards. For the other four sites weather data was extracted from the Swedish Civil Contingencies Agency (MSB) database, by matching site coordinates to the nearest point with modelled weather and FWI indices data for the same time frame. I also wanted to compare weather conditions and seasonality of wildfires to the prescribed fires. For this, I used data on all wildfires larger than 50 hectares in Sweden reported to MSB between 2012 and 2021, resulting in 31 wildfires. Weather and FWI indices data for wildfires was retrieved using the same method as described above.

Landscape environmental variables

Data on several landscape variables that potentially can be important for saproxylic beetles were collected for **Paper III**. I used the following variables: the area of burned forest (wildfires and prescribed), area of protected forest, area of clear-cuts, area of forest older than 120 years, and the standing volume per hectare of spruce, pine and deciduous trees. To account for both landscape habitat amount and the spatial scale of effect, landscape variables were calculated in circular landscapes surrounding sites at four spatial scales (2, 5, 10 and 20 km radius from the site perimeter). ArcMap 10.8 (ArcGIS, ESRI, Redland, CA, USA) was used to synthesize and calculate data for each of the landscape variables at each scale.

Wildfire coordinates and size was retrieved from MSB and circular polygons created to estimate area of wildfires within the defined landscapes. Prescribed burn data was collected from county boards, Life Taiga and larger forestry companies (Sveaskog, Holmen, SCA, and Stora Enso). As fire-favoured beetles can be found on burn sites up to ten years after burning (Wikars 2006), data for fires was collected for between 2012 – 2021, as they could be possible source habitats for beetles occurring in the study sites (burned 2015 – 2018, beetles surveyed in 2022).

The area of protected forests (national parks, nature reserves, Natura 2000 and woodland key habitats) was collected from the Swedish Environmental Protection Agency and Swedish Forest Agency. Clear-cut area (logged during 2012-2021) was obtained from Swedish Forest Agency. The area of forest older than 120 years, and the standing volume per hectare of spruce, pine and deciduous trees, was downloaded from (SLU Forest Map 2010), and is based on a combination of satellite imagery and field data form the Swedish National Forest Inventory program.

In **Paper IV** the landscape habitat amounts were represented by circular landscapes with a radius of 5 km from the site perimeter, which was a spatial scale found to be important for beetles in **Paper III**, and matched the largest landscape measured by Rubene et al. (2017). The protected forest area was combined with the deciduous forest area to create a new category ‘deadwood rich forest area’ to match a similar category in Rubene et al. (2017). Burned forest area was also included, as it is potentially important for fire-associated beetles.

3.2.2 Species sampling, identification and traits

Polypores

Polypores in **Paper I** were inventoried by M. Jönsson, H. Berglund and R. Penttilä. Ten experimentally cut logs and ten naturally fallen logs were inventoried per site (were possible), resulting in a total of 349 logs in the 18 sites. The logs were randomly selected. The diameter at breast height (DBH=

1.3 m from the base) and decay class (Karjalainen & Kuuluvainen 2002) of each log was measured. The polypore species were identified based on their fruiting bodies (example Fig. 5a), which is effective for sampling dominant species (Allmer et al. 2006). A few red-listed corticoid fungi were also included if they were found. Polypore nomenclature followed (Niemelä 2016) and corticoid fungi (Kotiranta et al. 2009). The Finnish red-lists for 2000, 2010 and 2019 (Hyvärinen et al. 2019) were used to classify species. An example of what the sites looked like and how the polypores were inventoried can be seen in Figure 5b.

Figure 5. Photos of a) a Rhodofomes roseus (Fomitopsis rosea), a red-listed polypore found predominantly in burned sites; b) inventory of polypores 16 years after burning. Photos: Mari Jönsson.

Beetles

Window traps were used for sampling beetles (Coleoptera) for **Paper III & IV**. They consisted of a 30 x 60 cm transparent plastic sheet fitted above an aluminium tray (Fig. 6). The trays were half-filled with propylene glycol and water to preserve fallen insects. A minimum of four traps were placed centrally in each study site (prescribed burns in the North and Central areas, Fig. 2a), 25 m apart in different directions. They were fastened to nearby trees, approximately 1.5 m above the ground to avoid disturbance by wildlife. The traps were up for approximately six weeks during the summer (late-May to mid-July). Canopy cover (%) was also measured above each trap using CanopyApp (For Apple iOS, Version 1.0.3, University of New Hampshire). After collecting the samples, the beetles were sorted and identified to species level by taxonomic expert Hans-Erik Wanntorp.

For **Paper IV** beetle data collected by Rubene et al. (2017), was also utilised. Sampling had been done using similar methods. Three window traps had been placed centrally in each clear-cut attached to available snags, at least ten meters apart and 1.5 m above the ground. Propylene glycol was used as a preservative in traps. Traps were up from the beginning of June to mid-July. As it was a summer with high rainfall, the traps were in addition to the final collection also emptied in late-June to avoid overflow. Beetles were sorted to species level by Olof Hedgren.

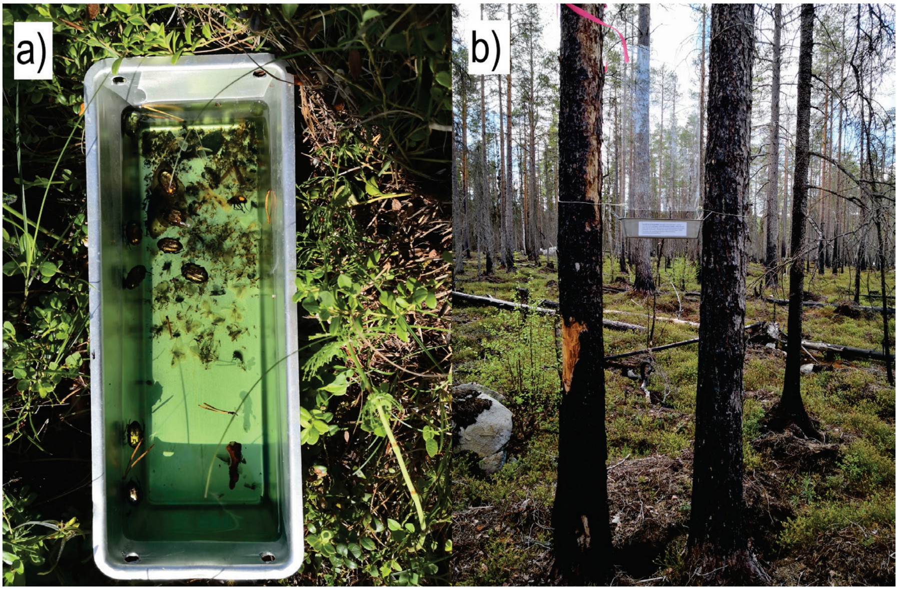


Figure 6. Photos of a) one of the trays used to collect beetles, the greenish colour is from propylene glycol; b) one of the window traps used to collect beetles. Photos: Ellinor Ramberg

All Beetles were classified as saproxylic based on an unpublished list by Mats Jonsell, grounded on own expert knowledge and taxonomic literature (Palm 1959; Hansen 1964; Koch 1989). In **Paper III** classification of beetles as fire-favoured was based on a list published by Rubene et al. (2017). In **Paper IV** two additional sources, Wikars 2006 & Bell 2023, were used to classify beetles as fire-favoured and fire-dependant. Beetles were classified as fire-dependant if they were classified as such by Lars-Ove Wikars (expert on fire-associated beetles) and/or if they had evolutionary adaptions to fire

(Bell 2023). Fire-favoured species were all other species that had been classified as fire associated by (Wikars 2006; Rubene et al. 2017; Bell 2023).

Besides more traditional descriptions of diversity with taxonomic richness and composition, functional diversity in terms of trait richness and composition are increasingly used to described communities. Beetle morphological traits used in **Paper IV** were extracted from a database published by Hagge et al. (2021). Approximately 80% of all beetle species in my total dataset were accounted for in the trait database. I used eight traits: body length, body width, body roundness, wing length, wing load, wing aspect, mandibular aspect and colour lightness (Table 1). This selection was based on previous studies showing that these traits were associated with extinction risk (Hagge et al. 2021), dispersal capabilities (Hassall 2015; Burner et al. 2023), forest naturalness (Wetherbee et al. 2023) and cryptic colouration (Wikars 1997; Roulin 2014). Wing length and wing load were standardised by dividing by body length. In a few cases species-specific traits were not available, in which case the family mean trait value was used.

Table 1. The eight morphological traits of saproxylic beetles included in **Paper IV**, the unit they are measured in and hypothesised functional role. Sources: (Wikars 1997; Roulin 2014; Hassall 2015; Birkemoe et al. 2018; Hagge et al. 2021; Bell 2023; Traylor et al. 2024).

Morphological trait	Unit	Hypothesised functional role
Body length	mm	Longer beetles are tied to larger diameter deadwood and larger home-ranges. Body size may also be tied to diet, with smaller beetles feeding largely on fungi (on deadwood) and larger beetles directly on deadwood. Greater body length increases extinction risk.
Body width	mm	Wider beetles are tied to habitats outside of the phloem layer such as more decayed deadwood or tree hollows, as well as larger diameter deadwood. Greater body width increases extinction risk.
Body roundness	Ratio mm/mm (body height/ body width)	Rounder beetles are tied to habitats outside of the phloem layer such as more decayed deadwood or tree hollows. Greater body roundness increases extinction risk.
Wing length	mm	Longer wings are associated with higher dispersal abilities and a lower extinction risk.
Wing load	mg/mm^2 (mass/ wing area)	Lower wing loads are associated with high dispersal abilities. Greater wing load decreases extinction risk.
Wing aspect	Ratio mm/mm (wing length/ wing width)	High wing aspects increase manoeuvrability, whereas lower wing aspects increases dispersal abilities.
Mandibular aspect	Ratio mm/mm (mandible width/length)	High mandibular aspect is tied to hard deadwood (i.e. many deciduous species). Greater mandibular aspect ratio increases extinction risk.
Colour lightness	RGB (high values are lighter)	Dark individuals are tied to burned environments and have a higher resistance to UV radiation and pathogens.

3.3 Data analyses

All statistical analyses were done in R studio within the statistical programming environment R (R Core Team 2024).

In **Paper I** the response variables were polypore species richness and abundance. I tested how the variation in the response variables were associate with the two main treatments, different deadwood volumes (5, 30 and 60 m^3 ha^{-1}) and burning in stands. I also analysed if the effect of burning on species richness and abundance was associated with log origin (cut vs naturally fallen). GLMs with a Poisson and quasi-Poisson distribution were used as they are appropriate for count data, and the latter is preferred when data is overdispersed. Differences in polypore species composition between the treatments was explored using nonmetric multidimensional scaling (NMDS) ordination, and differences statistically tested using permutational multivariate analyses (PERMANOVA) (Oksanen et al. 2020). All analyses were done for both all polypores and for red-listed polypores separately.

In **Paper II** four objectives of prescribed burning (response variables: created deadwood, tree seedlings, changes in basal area and potential fire scar formation) were assessed with a series of regression models to test for relationships with weather and stand variables, and interactions. Tree regeneration and changes in basal area were together used to describe the objective multilayered forests. The explanatory weather variables were: FWI, DMC, DC, FFMC, relative humidity, wind speed, temperature, mm rain 14 days before burning and number of rain free days. The explanatory stand variables were pre-burning basal area and spruce proportion. Due to correlations between explanatory variables, each model was limited to one response variable, one stand variable and one weather variable. Beta regression models were used for basal area change as it is a proportion (Cribari-Neto & Zeileis 2010). Negative binomial GLMs were used for the variables tree seedlings and fire scars, as is appropriate for count data with large overdispersion (Venables & Ripley 2002). For deciduous seedlings I used zero-inflated negative binomial models when zero-inflation was detected (Zeileis & Hothorn 2002). Deadwood volume was log-transformed (to fit model assumptions of normality) and analysed with linear models with a Gaussian distribution.

Differences between pre- and post-burn basal area, mean diameter of all trees and deadwood volumes were assessed using paired t-tests. Differences in weather between wildfires and the prescribed burns was examined using Welch two-sample t-tests.

In **Paper III,** I explored relationships between local and landscape variables for post-burning assemblages of saproxylic and fire-favoured beetles. Differences between regions (areas S, C and N, Fig. 2a) were also assessed. The response variables were rarefied species richness and mean abundance per trap (for each site). Rarefaction was done to account of for any differences in sampling efficiency between sites (Hsieh et al. 2024). Correlation between landscape scales (2, 5, 10 and 20 km) and variables resulted in the adoption of single-variable models. For rarefied species richness GLMs with a Poisson distribution were used and for abundance per trap negative-binomial GLMs. To identify the spatial scale of effect model AIC and ΔAIC were extracted (Jackson & Fahrig 2012). To account for spatial autocorrelation Morans I for model residuals was calculated (Bivand & Wong 2018). Patterns in species composition were explored using NMDS ordination, and differences between regions assessed with PERMANOVA. Local and landscape variables correlations with ordination axes was tested for, and significant variables fitted onto the ordination plot (Oksanen et al. 2020).

In **Paper IV,** two datasets, my own beetle data from burned forests and Diana Rubene's beetle data from clear-cuts (Rubene et al. 2017), were combined to examine the effect of burning on forest versus clear-cuts on beetle richness and composition. All analyses were done for both all saproxylic beetles and fire-favoured beetles separately. As sampling effort differed between the two studies, species richness was rarefied to the same coverage based on the smallest maximum coverage (50%). Differences in rarefied species richness between the burned forests and burned clear-cuts (and control unburned clear-cuts) were assessed with quasi-Poisson GLMS. Principal coordinate analysis (PCoA) was used to visualise differences in species composition between the site types (burned clear-cut, unburned clear-cut and burned forest). PERMANOVA was used to statistically test differences between site types. The correlation between three environmental variables, local deadwood, landscape deadwood rich forests and landscape burned area, and ordination axes were assessed and fitted onto the ordination if significant.

In addition to the analyses of taxonomic richness and species composition described above, I also analysed trait richness and composition (**Paper IV**).

To control of for sampling differences, trait and abundance data from forest sites was subsampled to match clear-cut sample sizes and bootstrapped. Three commonly used measures of functional diversity functional richness (FRic), evenness (FEve) and divergence (FDiv) were calculated (Laliberté et al. 2014), see **Paper IV** Table 3 for definitions. The differences between site types were then analysed using GLMs with a Gaussian distribution for FRic and beta regression models for FEve and FDiv (as they are proportions). Trait composition was quantified using community weighted means (CWM) of the eight included traits. Differences between site types were then visualised with principal component analysis (PCA) ordination and PERMANOVAS run to ascertain statistical differences. Again, the relationships between the ordination axes and the three environmental variables were tested and significant variables plotted.

4. Results and discussion

In this section, I summarize my main results and discuss how they relate to the aims of this thesis, both independently and collectively. I found that the efficiency of prescribed burning as a conservation tool is influenced by stand and landscape characteristics, weather and season, as well as time since burning.

4.1 Prescribed burn objectives

In general, prescribed burning is an efficient measure to increase the amount of deadwood and promote the development of multilayered forest and fire-scars (**Paper II**). However, variation among burns was considerable (Fig. 7).

Creating multilayered forests, that are open and sunlit with pine and deciduous trees of different ages, requires both relatively high tree mortality and seedling regeneration. Although there was considerable variation among sites, I found that prescribed burning always resulted in some tree mortality and that reduced the basal area of the forests (Fig. 7a). The mean diameter of trees was higher after burning, suggesting that mostly smaller trees were killed. As prescribed burns often are of low intensity this can be expected and has been found in other studies (Linder et al. 1998; Sidoroff et al. 2007). In relation to the goal of creating deadwood that can promote biodiversity this is sub-optimal, as large-diameter deadwood are tied to higher species richness and rare species (Siitonen 2001; Junninen & Komonen 2011; Löfroth et al. 2023). In the short-term, the size-based mortality also reduces structural heterogeneity. However, if fire can be applied recurrently it will promote diverse age-cohorts at the landscape level, and thereby heterogeneity can be established on a larger scale.

Reduction in basal area also facilities the growth of seedlings as nutrient, moisture and light conditions are altered on the forest floor. Again, I found that seedling counts varied greatly among sites (Fig. 7b). The mean seedling density per hectare, 1 430, is far below what has been reported after wildfires which can result in densities of up to 17 000 seedlings per ha (Gustafsson et al. 2019). Fredriksson et al. (2023) found similar results, with higher numbers of deciduous and pine seedlings in wildfires sites. The long-term implication of high variability of seedling counts in sites, and generally low numbers of seedling germinating in relation to wildfires, is that the establishment of cohort-dynamics will be tentative. In addition, old deciduous trees are important for biodiversity (Esseen et al. 1997) but are lacking in the forest landscape. The primary reasons for this is a low frequency of wildfires and legacy effects from past forest management practises (e.g. Östlund et al. 1997), that have and still influence the rate of recruitment of for example aspen (Hardenbol et al. 2020). The modest regeneration of deciduous seedlings that I observed after prescribed fires is therefore of concern, as conservation actions targeting deciduous seedling regeneration need to be successful to benefit associated species in the long-term.

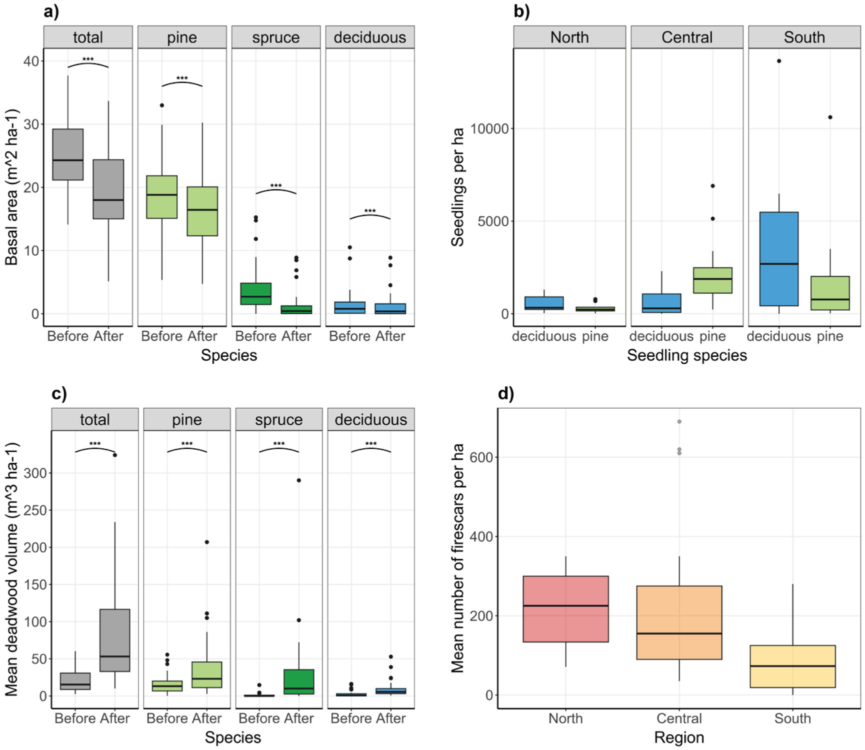


Figure 7. Boxplots of a) basal area per site before and after burning, b) number of seedlings per ha after burning, c) volume of deadwood (DBH > 10 cm) before and after burning and d) the mean number of potential fire-scars per ha after burning. Species group colours: total=grey, pine=light green, spruce=dark green and deciduous=blue (birch, aspen, sallow, rowan). Region colours: North=red, Central=orange and South=yellow. Whiskers correspond to +/-1.5* Inter quartile range. *** = $p<0.001$ for a paired t-test. (adapted from **Paper II**)

I estimated pre-burn mean volumes of coarse deadwood (DBH > 10 cm) per site to 20 m^3 ha^{-1}. This may have been higher initially as fire may also consume part of the deadwood (Eriksson et al. 2013), but as most prescribed fire is relatively low intensity this is probably negligible in relation to the volumes that the burn generates at most sites. Pre-burn volume (20 m^3 ha^{-1}) is also in line with estimated deadwood volumes in protected areas across Sweden (Kyaschenko et al. 2022). This deadwood amount is far below what is estimated in old-growth forests (Siitonen 2001), and at the lower end of the 20-30 m^3 ha^{-1} threshold needed to support forest biodiversity in the long term (Müller & Bütler 2010; Junninen & Komonen 2011). My results show that prescribed burning created a mean total volume of 55 m^3 ha^{-1} of coarse dead wood per site. This volume is substantially higher than what is typically in most forest types in Sweden (Jonsson et al. 2016; Kyaschenko et al. 2022), but much lower than the volumes created by wildfires (e.g. Ylisirniö et al. 2012; Jakob 2023). I however also found large variability among sites in created deadwood volume (2.5 m^3 ha^{-1} to 283 m^3 ha^{-1}), as well as in deadwood tree species (Fig. 7c). This demonstrates that in some sites, with low levels of dead wood creation, the effectiveness of prescribed burning for promoting saproxylic species is likely very small, whilst it in other sites it may be substantial.

I found that the prescribed burning may be an efficient tool to promote formation of fire-scars as on average 46 % of the surviving pines across sites had visible resin flow. However, once again, there was considerable variation among sites in the number of pine trees with visible resin flow (Fig. 7d). Fire-scars are created through heat induced injuries to the tree cambium (Baker & Ehle 2001). The tree's response to the injury is to produce resin to cover the exposed injured area. The resin-impregnated wood gives the tree an enhanced protection against decay, which is more or less a prerequisite for the formation of so called kelo trees. Kelo trees are important structural elements for maintaining high forest biodiversity, particularly of rare lichens and fungi, and are declining at a rapid rate (Niemelä et al. 2002; Larsson Ekström et al. 2023). In early stages, the site of injury is also a habitat for pyrophilious beetles such as *Stephopachys.* The creation of fire-scars is therefore important in both short and long timescales. The large variability I observed, and the low frequency of scarring in some sites are likely due to too low fire intensity. This was further supported by a positive correlation between the number of smaller diameter pines in a site and the number of fire-scars, as higher fire intensities are needed to scar thick-barked older trees.

My results are likely a realistic picture of the variability across prescribed burns in general as they are conducted by several different stakeholders, under different weather conditions, site-types and in different regions of Sweden. Subsequently, the rather small impact of prescribed fire in some sites, along with the large variation across sites, may from a conservation management perspective need more attention. In my thesis this is supported by the results presented in **Paper II**, and further reinforced by results from **Papers III & IV**, which draw on data from **Paper II** as explanatory variables.

4.2 Site attributes

4.2.1 Stand characteristics

Spruce trees

The proportion of spruce in stands before prescribed burning was important in relation to several outcomes of burning (**Paper II**). High spruce proportions correlated with larger changes in basal area, higher volumes of deadwood created and more deciduous seedlings. In many of the burn plans issued by county boards for the 32 fires I studied, high spruce mortality was an explicit goal, with the aim to restore pine-dominated open forests. Spruce trees are sensitive to fire, and spruce mortality was high. Thereby in sites with initial high spruce proportion, consequent changes in both basal area and deadwood can be expected. Spruce can also serve as ladder fuel (Granström 2005), increasing burn intensity around pine tree crowns and potentially promoting pine mortality, increasing overall deadwood volume. Spruce generally thrive under mesic conditions, which also favours establishment of deciduous seedlings (Latva-Karjanmaa et al. 2006), which may explain why high initial share of spruce resulted in more deciduous seedlings. These results suggest that targeting stands with initial high spruce proportions may be effective in creating deadwood and promoting establishing deciduous seedlings.

In **Paper I,** I found that red-listed polypores were present and thriving on spruce deadwood created by burning. For beetles Toivanen & Kotiaho (2007) found that burning had a positive effect on saproxylic, red-listed and pyrophilous richness in the same spruce-dominated stands. Most prescribed burns are applied in pine-dominated forests as they are more adapted fire. However, as my results in **Paper I & II** indicate, burning spruce forest or mixed-conifer forest is effective and benefits many species. In addition, as spruce trees generally die from fire, burning spruce-dominate stands creates early successional habitats, which can be both species and structurally rich (Swanson et al. 2011).

Clear-cuts versus forests

I found that both trait and taxonomic composition of saproxylic beetles differed significantly between burned forests and burned clear-cuts (**Paper IV,** Fig. 8). Differences in taxonomic species composition has been shown in a few previous experimental studies (Toivanen & Kotiaho 2007; Hyvärinen et al. 2009; Heikkala et al. 2016a) and functional composition in one previous study (Heikkala et al. 2016b). However, my study is the first to test differences between burns conducted within conservation and management schemes, thereby solidifying that the results from the experimental studies also have practical application. Within FCS certification burning within different types is tied to an upward adjustment factor, so more value is given to standing forest compared to clear-cuts, i.e. burning a larger clear-cut area is given the same value as a smaller forest area (FSC Sweden 2020). My results show that the two burn types are not interchangeable, which means that burning larger clear-cut areas, which may be tempting from an economical perspective, cannot compensate for a smaller forest area as it is not the same type of species and diversity that is influenced.

As sourced from **Paper II** and Rubene et al. (2017), both local deadwood amount and deadwood rich forest area in the landscape were higher for forest sites compared to clear-cuts. As saproxylic species respond to deadwood volumes and diversity (Seibold et al. 2016; Seibold & Thorn 2018), these habitat variations may explain the differences found in trait and taxonomic diversity between the burn types.

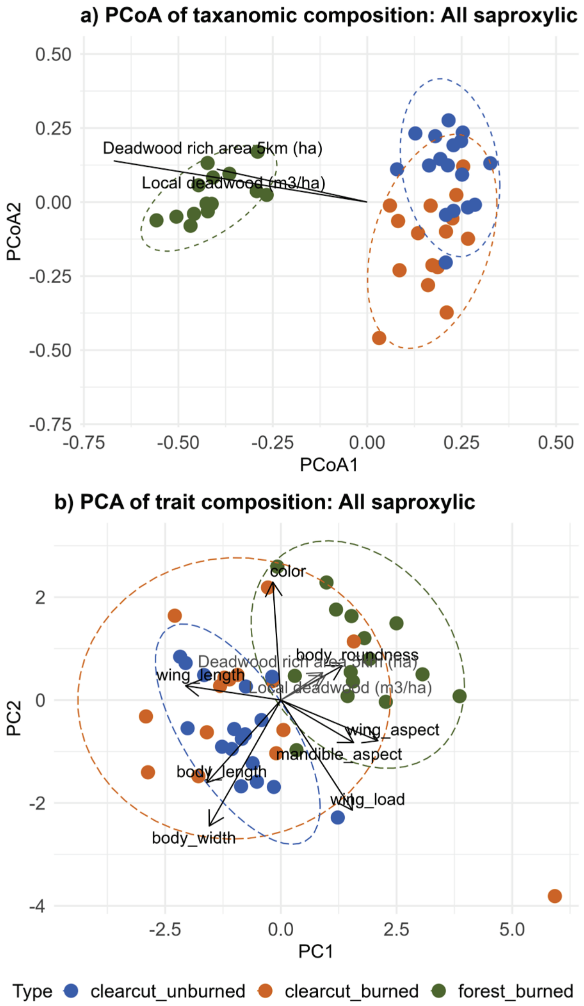


Figure 8. **a)** PCoa ordination plots showing differences in taxonomic composition for all saproxylic beetles between burned clear-cuts, unburned clear-cuts and burned forests (PERMANOVA $R^2 = 0.28$. $F_{2,44}= 8.56$, $p = 0.001$). The first principal coordinate (PCoA1) explained 25% of the variance in saproxylic species composition, while the second principal coordinate (PCoA2) explained 7% of the variance. **b)** PCA plot showing the differences in trait composition (community weighted means) for all saproxylic beetles between burned clear-cuts, unburned clear-cuts and burned forests (PERMANOVA $R^2 = 0.133$. $F_{2,44}= 3.38$, $p = 0.015$). PC1 explains 41 % of the variance and PC2 explained 20%. Black trait arrows show the direction and magnitude of the contribution of each trait to the principal components. In both **a** and **b** deadwood rich forest area within 5 km (ha) and local deadwood volume (m^3 ha^{-1}) that had significant correlations with axes are fitted as vectors, where the length of the vectors indicates their importance and their position indicates the direction of change. (adapted from **Paper IV**)

I found that taxonomic species richness was higher in burned forests than burned clear-cuts, but not functional richness (**Paper IV**). Higher taxonomic richness of saproxylic beetles was expected as forest sites generally had higher volumes of deadwood, which implies that they can support higher species diversity, and concurs with previous studies (Toivanen & Kotiaho 2007; Heikkala et al. 2016a). The higher taxonomic richness, but similar functional richness in forests compared to clear-cuts suggests that forests may be more functionally redundant, with more species sharing similar traits. Fire-favoured species responded in a similar way to saproxylic species, mirroring the many disturbance adapted species in this group.

4.2.2 Landscape composition

In **Paper III** analysis of landscape and local environmental variables in relation to saproxylic beetle communities revealed that landscape variables seemed to have a stronger effect on species richness and abundance than local variables after burning. For saproxylic beetles both landscape (Seibold et al. 2017; Hallinger et al. 2018) and local (Seibold et al. 2016; Larsson Ekström et al. 2021) deadwood amounts and heterogeneity have been shown to be important in other contexts. i.e. not related to fire, and but also in a limited number of studies involving burned habitats (Ranius et al. 2014; Rubene et al. 2017).

I found that saproxylic beetle species richness increased with increasing area of protected forests in the landscape and decreased with increasing area of clear-cuts in the landscape (Fig. 9). Protected forests have larger volumes and diversity of deadwood compared to clearcuts and production forests (Siitonen 2001; Kyaschenko et al. 2022; Lunde et al. 2025) and can support a higher species richness and abundance of saproxylic species (Paillet et al. 2010; Stenbacka et al. 2010). The protected forests may therefore act as source habitats for colonization after burning, and possibly explaining the higher richness found on burned sites in such landscapes.

For total abundance, I observed the opposite pattern (Fig. 9), with higher abundances in landscapes that had a larger clear-cut area. As many saproxylic species are disturbance adapted, the habitats on clear-cuts and burn sites should favour many of the same species. Some of the most abundant species I found, such as *Hylastes brunneus* confirm this. However, I found in **Paper IV** that species composition differed between burned sites and unburned clear-cuts. Which implies that though some species may be common between clear-cuts and burned forests, they also harbour distinct communities.

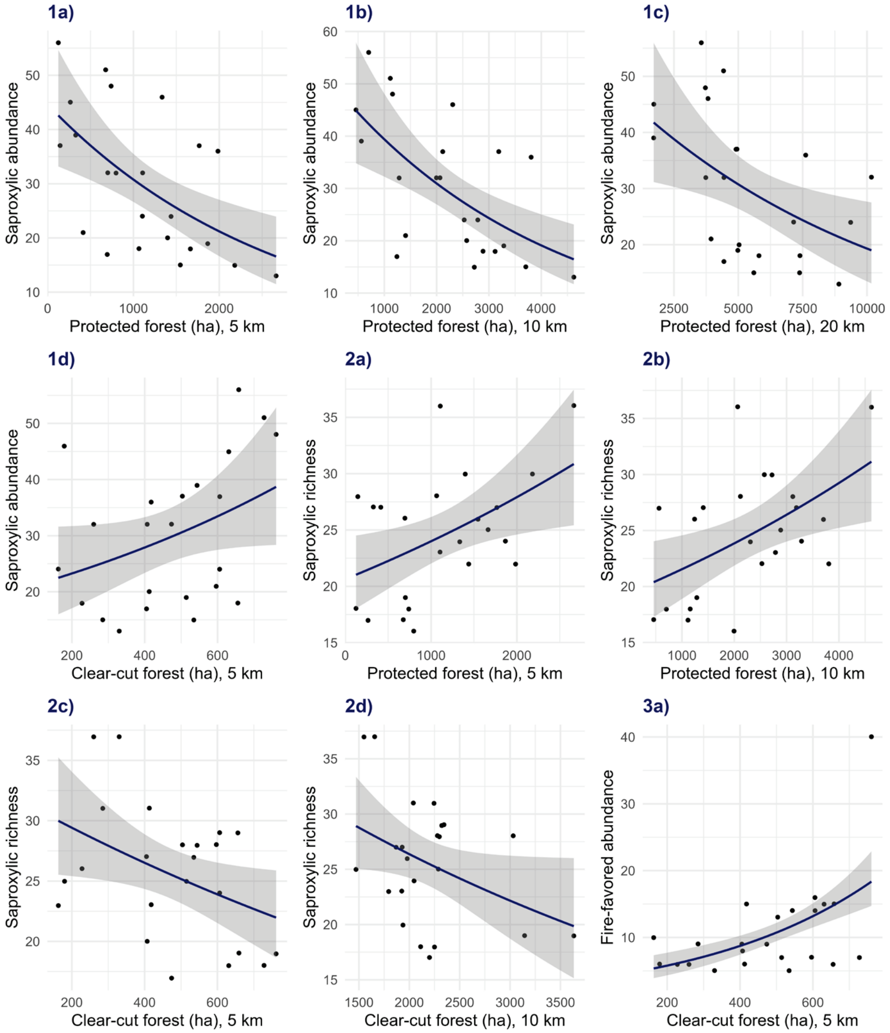


Figure 9. Effect plots for: 1) the saproxylic abundance in relation to protected forest area at 1a) 5 km 1b) 10 km and 1c) 20 km, and 1d) clear-cut forest area at 5 km; 2) the saproxylic richness in relation to protected forest area at 2a) 5 km and 2b) 10 km, and clear-cut forest area at 2c) at 5 km and 2d) 10 km; 3a) the fire-favoured abundance in relation to clear-cut forest area at 5 km. Black dots are data points, the blue line shows the predicted value and the grey areas depict 95 % confidence intervals. Only statistically significant positive and negative relationship are depicted (**Paper III**).

I studied landscape effects between 2 km and 20 km (buffers with a radius of 2, 5, 10 and 20 km from the burn perimeter, **Paper III**). The strongest effects were evident within 5 and 10 km, suggesting that the scale of effect may be within this span. Many saproxylic and fire-favoured species have high dispersal capabilities (Bell 2023), and colonization of a burned area may thus be influenced by source areas rather far away. Taken together, this demonstrates that when planning prescribed burns, it may be important to consider the composition of the landscapes up to at least 5-10 km around the sites. Selecting sites with a high proportion of potential source habitats for beetles within 5-10 km may increase effectiveness of conservational prescribed burns.

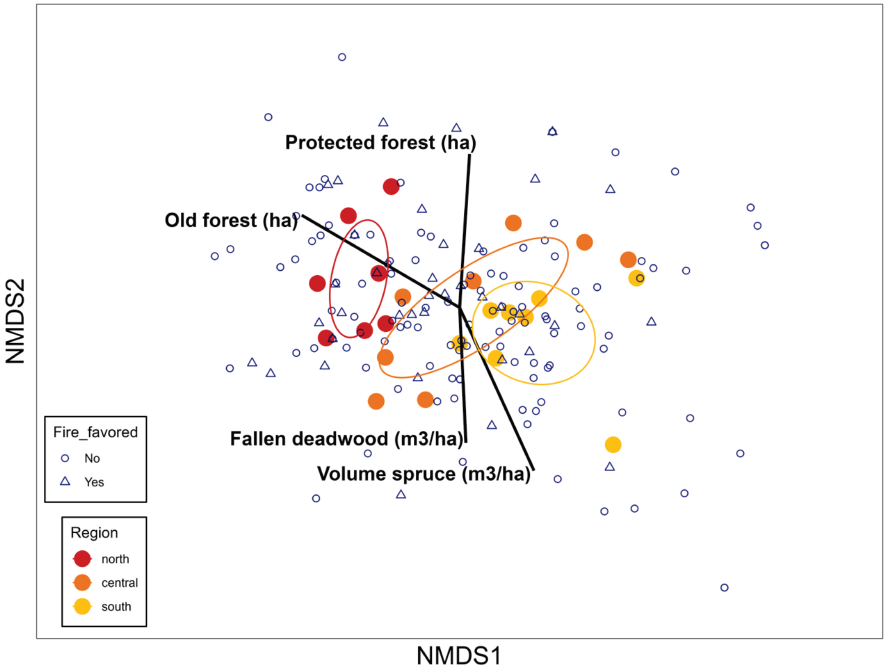


Figure 10. NMDS ordination plot showing differences in saproxylic beetle species composition between three Swedish regions, North, Central and South (PERMANOVA $R^2 = 0.18$. $F_{2,22} = 2.24$, $p = 0.001$). Fire-favoured beetles are indicated with triangles, whereas other saproxylic beetles are represented by circles. Environmental variables are fitted as vectors, where the length of the vectors indicate their importance, and their position indicates the direction of change. The two-dimensional stress ratio is 0.14. (**Paper III**)

In **Paper III,** I found differences in saproxylic and fire-favoured species composition between the three study regions (Fig. 10). This result probably reflects differences in both current and historic land-use (Östlund et al. 1997; Josefsson & Östlund 2011) and climate induced differences in geographical distribution of the beetles (Gossmann et al. 2024). Similar to results from **Paper IV,** both local deadwood amount and landscape deadwood rich habitats were important for shaping the differences in species composition in **Paper III**. In **Paper IV,** forest sites (the same sites as North and Central in **Paper III**) were associated with both higher local and landscape deadwood proxies. In contrast, in **Paper III,** I found the Southern sites to be associated with local deadwood and the Central and Northern sites to be more associated with landscape variables. These seemingly contradictory results are likely a result of context specific effects, with the importance of local and/or landscape deadwood amount for saproxylic beetles depending on what is being is being compared. For example, as in my study, if clear-cuts are being compared to forests sites, or if different forest sites are being compared to each other.

4.3 Weather and season

In **Paper II** I show that post-burn outcomes commonly were explained by several of the Fire Weather indices (FWI) tested for. I found a positive relationship between Drought Code (DC) and deadwood volume. DC describes the moisture conditions of the deeper organic layer. A higher DC therefore indicates a dryer organic layer, which could result in deeper burns, which could lead to root necrosis, killing more trees and subsequently creating more deadwood (Bär et al. 2019). I found higher deciduous seedling densities in sites that were burned under days with higher Duff Moisture Code (DMC). High DMC indicates dry conditions in the shallow organic layer, which leads to deeper burns. It has been established that deciduous seedling establishment is impeded if the humus depth exceeds 2 cm and that establishment is positively correlated with burn depth (Johnstone & Chapin 2006; Gustafsson et al. 2019). This may explain the relationship between DMC and seedling establishment that I observed. For FWI, which is an index that describes both potential fuel stock and risk of a fire spreading, I found two relationships. A bit surprisingly I found a negative correlation between density of pine seedlings and FWI, with lower pine seedling densities at high

FWI. One possible explanation for the observed relationship could be that burning consumed surface fuels but not the ground organic layer leaving a charred, hydrophobic layer which could hamper germination (Johnstone & Chapin 2006). FWI was positively related to volume of deadwood. Which can be expected as high fire intensity indicated by high FWI typically results in high tree mortality (Ryan 2002; Granström 2005), which would create more deadwood and explain the correlation that I found.

The positive correlations between FWI indices and the post-burn structures and processes suggests that the FWI system may be useful for predicting post-burn outcomes. Correlation between FWI indices and wildfire behaviour in Canada (where the system originated), has been established (Coogan et al. 2021). Although it is likely that the relationships between the FWI system and fire ignition potential, behaviour and seasonal activity also are valid for Fennoscandia, such correlations are not that well studied in this region (Granström & Schimmel 1998; Tanskanen 2007; Lindberg et al. 2021). My results therefore contribute to the current limited evidence base and supports the use of the FWI system. However, for some weather variables, such as wind speed and precipitation amount prior to burning, I found no correlation with any burn outcomes. This may seem counterintuitive, but it is possible that prescribed burns are conducted under such consistently unfavourable weather conditions that small variations within this limited range make it difficult to detect any correlations. For example, if the precipitation level prior to a burn is already high, minor changes are unlikely to significantly affect burn outcomes, thereby making it harder to identify significant relationships.

Wildfires occurred under drier, more extreme weather conditions than prescribed fires (**Paper II**). For wildfires included in my comparisons, all the three FWI indices mentioned above were significantly higher than for prescribed fires. As prescribed burn practitioners need to balance safety with conservation goals, burning in ‘weather windows’, this result may not be that surprising. Yet, if burn objectives cannot be reached while burning within this ‘weather window’, prescribed burning may not be an effective restoration measure. As my results above indicate there are correlations between FWI indices and outcome for some of the objectives. It is for example, more likely to get high deciduous seedling regeneration under drier weather conditions. Many prescribed burns, however, fall short of reaching the objectives. My results suggest that one reason may be that burns are often conducted at low DC and DMC, which is more common in late spring/early summer. DMC is high after several weeks with little or no precipitation and DC is only high following extended drought periods (Granström 2005). Therefore, both these indices are often only high well into the summer.

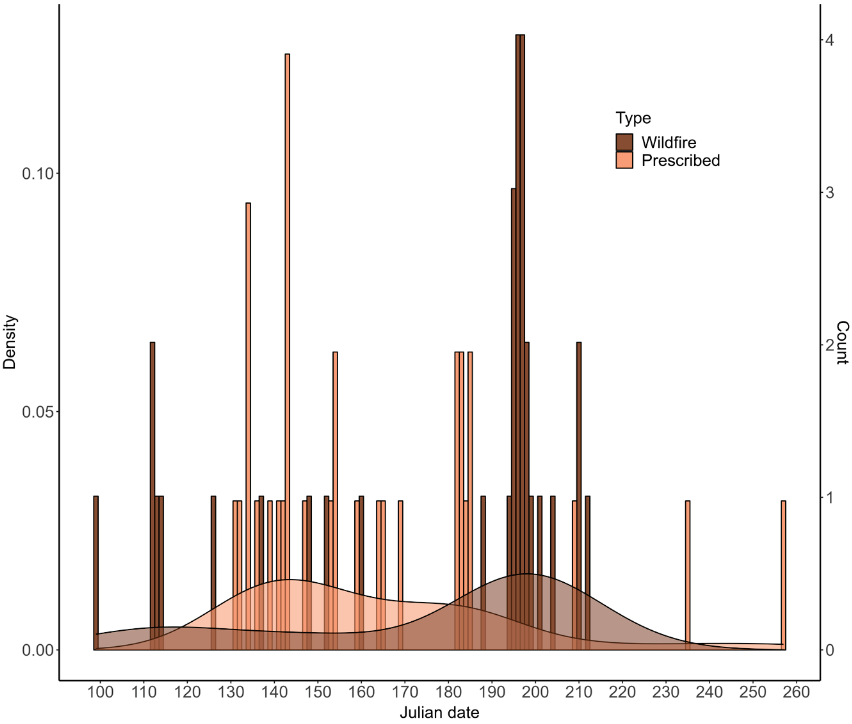


Figure 11. Histogram and density plot showing the distribution of the Julian dates of prescribed burns (N=32) and wildfires (N=31) which occurred during the same years (**Paper II**).

As seen in Figure 11, the main prescribed burn season in Sweden does not align with the main wildfire season. Burning earlier in the year when the ground moisture levels are high will influence burn behaviour with subsequent results on structures and processes post-burn, as described above. Burning early in the season may also diverge from seasonal patterns of species that are conservation targets. For example, Wikars et al. (2005) found strong seasonal patterns for saproxylic insects with the most active period in

June to July. There have however, been suggestions that pyrophilic species may have an extended phenology, a strategy that coincides with the stochastic nature of fire (Bell 2023). More research is clearly needed to study the response of species to early-season burns.

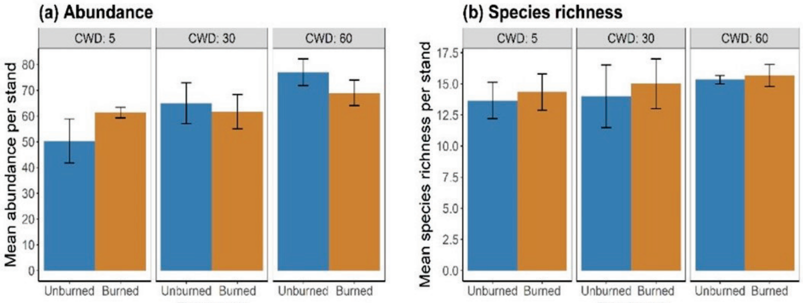
4.4 Time since burning

Differences between polypore communities in burned and unburned stands were more pronounced after 16 years than after 5 years (**Paper I**). I found that red-listed species had higher richness and abundances in burned stands compared to unburned stands (Fig. 12), which Berglund et al. (2011b) had not found 5 years after burning. My results therefore highlight the importance of long-term studies to capture effects that may only be evident at longer timescales. This is a unique result as previous studies on polypores at longer timescales were focused on pine-dominated forests (Junninen et al. 2008; Penttilä et al. 2013; Suominen et al. 2015).

I did not find any differences between burned and unburned stands when looking at all saproxylic polypores. The experiment also included different volumes of added deadwood (artificially cut); however, no differences were found between the volumes in terms of polypores (Fig. 12). Cut logs were more decayed than logs that had naturally fallen after burning. This had an impact, as most red-listed species were recorded on the natural logs, at intermediate decay stages.

Deadwood creation after a fire event can be continuous with injured trees dying overtime, in synergy with secondary disturbances such as insects and fungi (Bär et al. 2019). This may be especially true for prescribed burns with low fire intensity, which often does not lead to high direct tree mortality but may injure trees. A recent publication (Shorohova et al. 2024), has described the deadwood characteristic of the study sites used in **Paper I**. They found that 16 years after the treatments, i.e. the same year as my polypore inventory, prescribed burn sites were characterised by much higher deadwood volumes and higher heterogeneity than unburned sites. This variation included decay stages and both standing and lying deadwood.

1) All species



2) Red-listed species

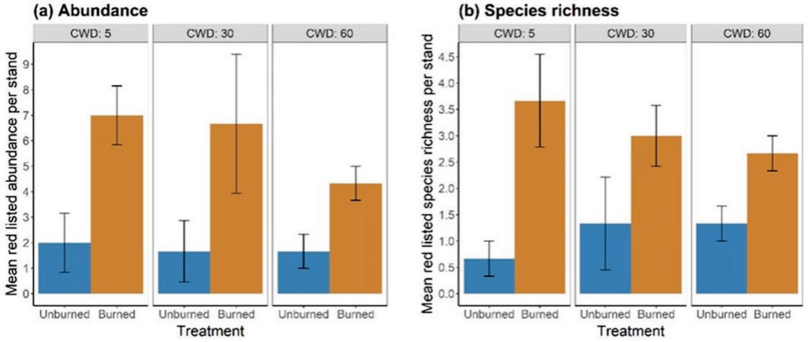


Figure 12. Response of 1) all polypore species and 2) red-listed polypore species to prescribed burning and created coarse woody debris levels (5, 30 and 60 m^3 ha^{-1}), showing mean and ±SE of a) abundances and b) species richness per stand (20 logs). Modified from **Paper I,** which is published under CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/)

In addition, though direct bark beetle damage to surviving trees was relatively low in the first few years after burning (Eriksson et al. 2006), it is likely that insects have had an effect on fire-damaged trees in the subsequent years after burning. It is therefore not surprising that deadwood amounts increase overtime. However, for my prescribed burns in **Paper II**, I found little overall effects of time on deadwood creation. This does not imply that deadwood is not created over time in individual sites. Rather, it is likely that some of the burns conducted have caused minimal fire damage to living trees. Thereby, when comparing all sites over time, those early in the time series with negligible deadwood created may obscure the expected increase in deadwood over time.

I also found difference in polypore species composition between burned and unburned stands (**Paper I**, Fig. 13). This is in line with the results found five years after the burn in the same stands (Berglund et al. 2011b). This initial difference found by Berglund et al (2011b) may have a long-term impact, as polypore communities are known to be influenced by priority effects, i.e. earlier fungal and insects assemblages affect later assemblages (Ottosson et al. 2014; Jacobsen et al. 2015). In addition, fire can affect wood characteristics, such as hemicellulose structure (Alen et al. 2002), and create a habitat type that favours certain polypore species over others (Edman & Eriksson 2016).

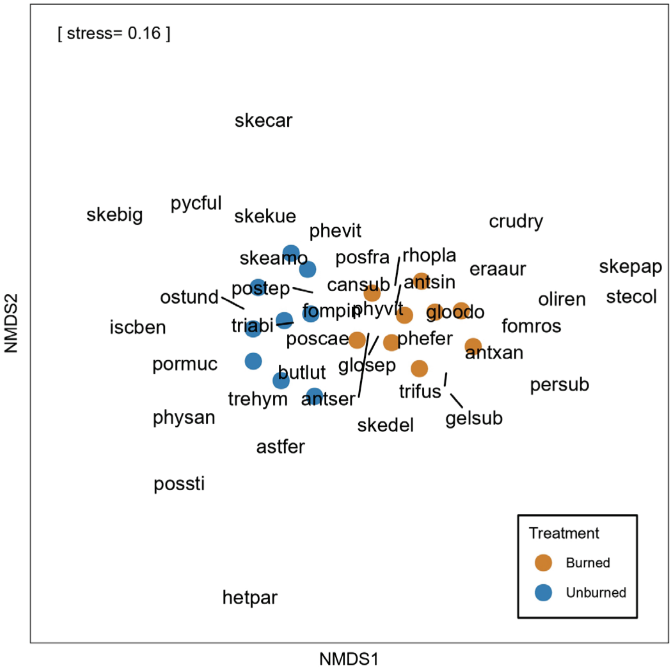


Figure 13. NMDS ordination plot showing differences in polypore species composition between burned and unburned stands (PERMANOVA R^2=0.41, $F_{1,16}$=11.13, p=0.001). The two-dimensional stress ratio is 0.16. Species abbreviations can be found in **Paper I** appendix Table 2. Modified from **Paper I,** which is published under CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/)

It is clear that time since burning has an impact on communities and successional processes. I found that beetle communities 3-7 years after burning differed between regions, and between forests and clear-cuts (**Paper III & IV**). Many studies have focused on early effects, 1-2 years after burning (Hyvärinen et al. 2005; Heikkala et al. 2016b), and very few studies have examined the long-term effects, however see (Heikkala et al. 2016a). My results suggest that early differences observed between burned and unburned communities (see studies above) are sustained several years after burning. However, whether these differences persist over longer timescales remains uncertain.

5. Conclusions and implications for conservation

The results presented in this thesis highlight several key variables that can help improve the efficiency of prescribed burns. I found that both where and when a prescribed fire is applied has effects on its potential to promote biodiversity. One of the most striking results is the large variability amongst prescribed burn sites in terms of creating structures and process that relate to conservation objectives. This suggests that as currently applied, the value of some burns for promoting fire-associated biodiversity may be limited. Given that prescribed burning is a costly conservation measure, it is important to assess whether and how its value can be enhanced.

Both stand characteristics and landscape composition were important for post-burn outcomes. The importance of spruce forests and spruce deadwood are largely overlooked both within prescribed burn application and studies. However, my results suggest that burning mixed-conifer or spruce forests can create large volumes of deadwood, encourage deciduous seedling regeneration and harbour several red-listed polypore species. Within pine-dominated forests the aim is often to restore and maintain open, multi-storied forest stands and create fire-affected deadwood, that were historically typical for pine forests. With spruce, the opportunity lies not in restoring, but in creating early successional habitats with large amounts of dead wood, thereby facilitating conditions and processes that are important for many threatened species.

Burning in forests versus clear-cuts benefitted different types of saproxylic beetle species, and traits associated with the species. This indicates that the two burn types are not interchangeable. From a management perspective, this is particularly important within FSC certification, as my results show that a small, burned area of standing forest cannot be compensated for by burning a larger clear-cut area, as they do not affect the same saproxylic beetles. Landscape composition also seems to be important for saproxylic beetle populations after burning. I found that species richness of saproxylic beetles on burned sites increased with increasing area of protected forests but decreased with increasing clear-cut area in the landscape. The effects were strongest for 5-10 km circular landscapes around burn sites. Thereby, selecting sites for prescribed burning with high proportions of protected forests within 5-10 km should be considered when planning burns aimed at promoting saproxylic beetles.

Weather conditions and season differed largely between wildfires and prescribed burns. Prescribed burns are generally conducted under cooler, wetter and less windy conditions than wildfires occur, and earlier in the year. I found that Fire Weather Index, Duff Moisture Code and Drought Code indices positively correlated with the creation of deadwood and regeneration of deciduous seedlings. The FWI index system may therefore be useful for predicting post-burn outcomes. Low volumes of created deadwood and poor seedling regeneration at low FWI indices values implies that burning under marginal conditions will result in limited possibilities to reach conservation objectives. As safety aspects need to be considered when conducting prescribed burns, it may be unrealistic to burn in the same weather conditions as wildfires. One approach could be to burn later in the season, when the ground layer in general is drier. However, this may put an added pressure on prescribed burn practitioners as deep burns require more intensive work to secure burn boundaries. In addition, deep burns need longer post-burn monitoring as embers may be difficult to see but can flare up to a ground-fire in favourable weather conditions. Cost and safety issues in relation to the conservation outcomes therefore need to be carefully evaluated, but it is important not to neglect the conservation outcome. Under some conditions it may be better to search for alternative management options rather than to apply prescribed burns under suboptimal conditions. For example, it may be more efficient to mechanically remove humus layers to promote deciduous trees establishment than to burn when the humus layer is too wet to be combusted.

My thesis also underscores that some conservation values resulting from prescribed burning have long delivery times, implying that long-term monitoring is essential to fully understand and capture their benefits. I found red-listed polypores on spruce logs 16 years after burning, which were not present in a inventory conducted 5 years after burning. Many studies are restricted to the early post-fire succession stages because of lack of funding for long-term monitoring and due to the pressure of demonstrating the usefulness of the applied measure. However, there is a need to study and evaluate long-term effects of prescribed burning, as successional processes after fire span for decades, with deadwood being continuously created and habitat conditions changing over time, thereby benefitting different species at different points of time,

To conclude, prescribed burning can be made more efficient and can be better tailored to meet conservation goals by considering forest type, landscape context, weather, and seasonal factors.

6. Future perspectives

During the process of this thesis several gaps in knowledge, challenges and questions have arisen, both in relation to prescribed burns but also within fire research in general.

- One challenging part of my thesis was the lack of detailed surveys on structures and species done before burning. This meant that though reconstruction of pre-burn conditions was possible through inventory, utilizing charring, decay stage etc, I could not calculate how much deadwood was consumed by burning, or how beetle communities had changed after burning. A before, after, control and impact, i.e. B.A.C.I. design would have been a prefered way to evaluate the effects of prescribed burning. Therefore, implementing pre-burning inventories for prescribed burns applied by county boards and forestry companies is something that I think should be prioritised, facilitating future studies and monitoring programs aiming to evaluate this conservation method.
- There is a lack of studies comparing wildfires and prescribed fires in Fennoscandia. I know of two recent studies one a master project (Jakob 2023) and one a PhD study (Fredriksson 2021) that have addressed this topic, and both demonstrate large differences between prescribed burns and wildfire. Knowledge on how these burn types differ can be instrumental for aligning expectations and goals of prescribed burns with their ability, or lack of ability, to mimic wildfires. Since prescribed burning is intended to create biological legacies similar to those produced by wildfire, its value as a conservation measure may be limited if the two burn types differ substantially.
- Since effects of fire can be seen several decades after burning, long term monitoring is necessary to capture successional processes. Large wildfires, such as the one that occurred in Västmanland, Sweden in 2014 gives a rare opportunity for long-term monitoring of a wildfire. Studying how such wildfires compare to prescribed burns overtime can give insights into the long-term value of prescribed burning in relation to wildfires.

- Sweden has adopted the Fire Weather Index system to predict wildfire risk. This is a system developed based on Canadian forest types, and though there are similarities to Fennoscandian forest types, confirmation and alterations to the system based on research on forest types in Fennoscandia is limited (but see Plathner et al. 2022). The FWI systems relationship to fire ignition potential and fire behaviour are also understudied in Fennoscandia, which is relevant both for wildfires and prescribed burning. For example, the FWI system is currently used when planning prescribed burns to find appropriate ‘weather windows’, however as my study show, it can also be used to predict outcomes.
- The effects of landscape composition and connectivity are also understudied in relation to prescribed burning and associated species. Such knowledge would help improve in planning and can develop and refine strategies to improve the conservation status for threatened species. To date, there is still no nationally coordinated database of wildfires and burns, despite that its importance for both conservation and wildfire management has been underlined for some time (Ramberg et al. 2018; Granström 2023). Such a database would simplify both planning and studying landscape scale fire dynamics.

These are only some of the many ways forward and puzzle pieces that are needed to understand wildfire behaviour and improve prescribed burning implementation and research. In addition, climate change will likely impact wildfire frequency and intensity. Already in the past recent decades we have had some large fire years in Sweden. How this will manifest in coming years, and how it will affect the use of prescribed burning as a conservation tool, is difficult to anticipate.

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Popular science summary

Where there's smoke, there's fire? For prescribed burns, not quite — more like embers. Wildfire is a natural disturbance in boreal forests that not only kills trees but also resets successional cycles, creating new life. By killing trees, it generates deadwood and increases forest heterogeneity, promoting biodiversity. Many species such as deadwood-dependent beetles and fungi are adapted to the environments that follow a fire. However, fire suppression over the past century has resulted in the loss of such environments, posing a threat to biodiversity. Prescribed burning aims to mimic wildfire, creating and restoring the lost environments, benefitting biodiversity. But where and when should we apply prescribed fire to make the greatest impact on biodiversity? That is the focus of this thesis. The 'where?' referred to forest characteristics and surrounding landscape, while the 'when?' involved time, weather and season. I examined the effect of these variables on deadwood-dependant beetles and fungi after prescribed burning. I also investigated how the 'where' and 'when' aspects of prescribed fires influence key structures and functional outcomes, including deadwood production and forest regeneration. To address this, I collected data from 18 prescribed burn sites in Finland and 32 in Sweden. I found that the proportion of spruce trees in forests is an important factor to consider as spruce trees are sensitive to fire and are therefore often killed by the fires. This creates deadwood and gaps within forest, which in turn facilitates the establishment of new trees. Spruce trees were also an important habitat for wood-inhabiting fungi nearly two decades after burning, which led me to conclude that it is important to consider long-term effects to fully capture the conservation benefits of prescribed burns. Beetle populations after burning were affected by both forest characterises at the site of the burn and the composition of the surrounding landscape. I found different beetle species on burned clear-cuts compared to forests. I also found that the area of protected forests in the landscape influenced the species richness in prescribed burn sites. This means that both local habitat conditions and the surrounding landscapes are important for the outcome and should be considered when planning prescribed burns. Weather is crucial for how fire behaves. I found that indices used to predict fire risk, that describe how dry the ground is and how fast fire will spread, were correlated with the amount of deadwood that was created by the fire and number of new trees germinating after the burn. Burning under drier conditions resulted in larger amounts of deadwood and higher numbers of tree seedlings. This means that weather conditions influence how effective the burns are in creating structures important for biodiversity. To summarise, burning forests with many spruce trees, under dry weather conditions, in landscapes with high proportions of protected areas is preferable, if you want a fire and not just embers.

Populärvetenskaplig sammanfattning

Ingen rök utan eld? Inte riktigt för naturvårdsbränder— snarare glöd. Brand är en naturlig störning in den boreal skogen. När skogen brinner dör träd som skapar död ved. Variationen av död ved, och döende och levande träd skapar heterogena skogar, vilket gynnar biologisk mångfald. Många arter, bland annat många skalbaggar och svampar som är beroende av död ved, är anpassade till brandskapade miljöer. Under de senaste 100 åren har skogsbruk och effektiv brandbekämpning medfört att brand inte längre är en viktig störningsfaktor i skogslandskapet. Detta har påverkat många arter i en negativ riktning. Naturvårdsbrand är en skötselmetod som används för att återskapa brandpräglade miljöer, med målsättningen att gynna biodiversitet. Var och när ska man bränna för att skapa störst nytta för biodiversitet är fortfarande öppna frågor. Dessa frågor är några av de som den här avhandlingen försöker svara på. För att svara på ’var?’ studerade jag skogsbestånden karaktär och sammansättningen av landskapet runt brandområden. För att svara på ’när?’ undersökte jag hur utfallet av naturvårdsbränningar påverkades av väder och under vilken årstid bränderna genomfördes, samt för hur länge sedan de genomfördes. Jag studerade hur dessa variabler påverkade förekomsten av vedlevande skalbaggar och svampar. Dessutom undersökte jag hur dessa ’var’ och ’när’ variabler påverkade brandskapade strukturer och processer, som mängden död ved och föryngringen av lövträd. Jag samlade data från 18 naturvårdsbränder i Finland och 32 i Sverige. Mina resultat visar att man kan skapa stora mängder död ved om man bränner grandominerade skogar; Granar är brandkänsliga och dör ofta även vid lågintensiva bränder. Detta skapar luckor i skogen vilket gynnar föryngringen av lövträd. Döda granar är också ett viktigt habitat för rödlistade vedlevande svampar. Dessa koloniserar dock inte de brända skogarna på en gång efter brand. Mina resultat visar att 16 år efter brand så hade brända skogar signifikant mer rödlistade svampar än obrända skogar. När samma jämförelse gjordes fem år efter branden fanns ingen skillnad i förekomsten av sådana arter, vilket tyder på att det är viktigt att beakta långa tidsperspektiv i relation till naturvårdsbrand för att förstå den långsiktiga nyttan med brand. Populationer av vedlevande skalbaggar efter brand påverkades av både skogens karaktär och landskapets sammansättning. Jag hittade olika typer av skalbaggar på brända hyggen och i bränd skog. Arikedomen av skalbaggar efter brand var högre för de bränningar som hade högre andel skyddad skog i det kringliggande landskapet. Detta tyder på att både lokala egenskaper, d.v.s. skogens karaktärer och landskapets sammansättning är viktiga för utfallet av bränningar. Eftersom dessa variabler påverkar hur skalbaggssamhället påverkas av bränningen borde de i större utsträckning än i dag övervägas vid planering av naturvårdsbränder. Väder är en viktig faktor som styr hur en brand beter sig. I Sverige används en modell för att utvärdera brandrisk med ett antal olika variabler som beskriver hur torrt det är i marken och hur snabbt en brand kan spriddas. Jag fann att flera av dessa variabler korrelerade med mängden dödved som skapades efter brand och hur många nya lövträdsplantor som fanns på området efter bränningen. Bränder som utfördes under torrare väderförhållande skapade större mängder död ved och gynnade föryngringen av lövträd. Detta visar att väder är viktigt för vilka värden som skapas efter branden. Sammanfattningsvis, receptet för att få eld och inte bara glöd är att bränna i skogar med hög andel gran, att genomföra bränningar under torra väderförhållande och välja skogar i landskap med hög andel skyddad skog.

Acknowledgements

Firstly, I would like to thank my supervisor team **Joachim**, **Mari** and **Thomas** for your support and guidance throughout these years. **Joachim** many years ago you led an excursion to the fire site in Västmanland that I as a bachelor student attended, and your fascination with fire as a disturbance was inspiring, starting me down this path. Thank you for letting me work independently, for challenging me and guiding me. Your understanding of the trials (and joys) of juggling work, commuting and having young children at home has made this PhD possible. I could not have asked for a better supervisor! **Mari** thank you for always coming with input, ideas and critique that none of the others thought of; it has made my work better and given me new perspectives. **Thomas**, I appreciate your direct manner, you don't mince words, and I think that is a great quality! Thank you for pushing me to be clearer and holding me back when I suggest crazy things in manuscripts.

A big thank you to all my co-authors, field assistants and colleagues. A special thanks to: **Göran Thor** for asking me if I had considered doing a PhD, which made me consider doing a PhD; **Gustaf Granath** for your good statistical advice and advice in general; **Mats Jonsell** for equipment, sharing knowledge on bugs, chats and teaching experience; **Aino Hämäläinen** for guiding me through R struggles; **Jan Bengtsson, Erik Öckinger, Lena Gustafsson** and **Joakim Hjältén** for giving me useful feedback at my yearly seminars; **Elin** and **Andy** for being good office roommates; **Oliver**, **Matilda** and **Pernilla** for soldiering on in the field; **Ly** for utilising all available daylight for fieldwork and **Virginia,** your master thesis was my pilot study, which gave me invaluable insights and necessary adaptions to my study design. To **Life Taiga** thank you for giving me access to your data and sites. I would also like to acknowledge **Holmen**, **Sveaskog**, **SCA** and **Stora Enso** for providing burn data.

Thank you, **Astrid Taylor**, and everyone at the ecology department for creating a positive work atmosphere. I would especially like to thank the Conservation Biology Unit: **Thomas, Joachim, Erik, Malin, Aino, Lena, Göran, Simon, Anika, Elin, Elodie, Andreas, Carl, Svenja, Julia, Alwin, Ly, Andy, Margaux, Juliana,** for your inclusiveness and giving me a work context despite my sporadic appearances over the years. I have enjoyed our shuffleboard dinners, meetings and conferences together. To **Anika** and **Andreas** stay strong! and good luck in the final months/year of your PhDs.

And to all the other PhDs that have crossed my path during the past few years, thank you for lunches, breakfasts and chats. To the **current PhDs** the best advice I can give is this: *Writing a first draft is like hitting a beach on D-Day. You don't stop to tend the wounded or mourn the dead. If you don't get off the beach, you'll die there….The point of the first draft is not to get it right, but get it written. Get off the beach. (Matt Hughes 2011).* Maybe it will help you get out of a first draft swamp like it did for me. I wish you well on your continued PhD journey!

Finally, I would like to thank my family. **Rasmus**, **Norah** and **Clara** thank you for giving my life outside of work meaning, for our adventures together and for giving me the space to do this PhD. To my parents **Lars** and **Susanna,** you instilled in me a love for the natural world from an early age, thank you for that, as well as for your support, and many conversations about my work that have helped me untangle tangled thoughts. A special thanks to my siblings **Anna**, **David** and **Mats** for being there when it matters. Last but not least, I would like to thank my mother-in-law **Carina**, and again my mother **Susanna,** for your invaluable help with the kids during these PhD years.

Received: 12 January 2023 | Revised: 24 April 2023 | Accepted: 11 May 2023

DOI: 10.1002/eap.2892

ECOLOGICAL APPLICATIONS
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ARTICLE

Prescribed fire is an effective restoration measure for increasing boreal fungal diversity

Ellinor Ramberg[1] | **Håkan Berglund**[2] | **Reijo Penttilä**[3] | **Joachim Strengbom**[1] | **Mari Jönsson**[2]

[1]Department of Ecology, Swedish University of Agricultural Science, Uppsala, Sweden

[2]Swedish Species Information Centre, Swedish University of Agricultural Science, Uppsala, Sweden

[3]Natural Resources Institute Finland (LUKE), Helsinki, Finland

Correspondence
Ellinor Ramberg
Email: ellinor.karin.ramberg@slu.se

Funding information
Skogssällskapet, Grant/Award Number: 2019-655-Steg 2 2018

Handling Editor: Carolyn Hull Sieg

Abstract

Intensive forestry practices have had a negative impact on boreal forest biodiversity; as a consequence, the need for restoration is pressing. Polypores (wood-inhabiting fungi) are key decomposers of dead wood, but, due to a lack of coarse woody debris (CWD) in forest ecosystems, many species are under threat. Here, we study the long-term effects on polypore diversity of two restoration treatments: creating CWD by felling whole trees and prescribed burning. This large-scale experiment is located in spruce-dominated boreal forests in southern Finland. The experiment has a factorial design ($n = 3$) including three levels of created CWD (5, 30, and 60 m^3 ha^{-1}) crossed with burning or no burning. In 2018, 16 years after launching the experiment, we inventoried polypores on 10 experimentally cut logs and 10 naturally fallen logs per stand. We found that overall polypore community composition differed between burned and unburned stands. However, only red-listed species abundances and richness were positively affected by prescribed burning. We found no effects of CWD levels created mechanically by felling of trees. We show, for the first time, that prescribed burning is an effective measure for restoring polypore diversity in a late-successional Norway spruce forest. Burning creates CWD with certain characteristics that differ from what is created by CWD restoration by felling trees. Prescribed burning promotes primarily red-listed species, demonstrating its effectiveness as a restoration measure to promote diversity of threatened polypore species in boreal forests. However, because the CWD that the burning creates will decrease over time, to be functional, prescribed burns need to be applied regularly on the landscape scale. Large-scale and long-term experimental studies, such as this one, are invaluable for establishing evidence-based restoration strategies.

KEYWORDS
boreal forest, coarse woody debris, long-term experiment, polypore, prescribed fire, restoration

INTRODUCTION

Globally, the degradation of ecosystems due to human activities has led to a decline in biodiversity, and consequently, the need to restore natural habitats is recognized globally (European Commission, 2022; IPBES, 2018). However, to be successful, restorations need to be tailored to fit the specific habitat type, and for this, in-depth knowledge of species ecology is necessary (Halme et al., 2013).

In boreal forests of northwestern Europe, there is a great need to restore values lost due to the long history of large-scale forestry (Halme et al., 2013; Kuuluvainen & Gauthier, 2018; Östlund & Zackrisson, 1997). Practices such as clear-cutting and planting of monocultures have degraded boreal forest landscapes such that there is a lack of key structural components (e.g., dead wood) and functions (e.g., natural processes such as disturbances) (Jonsson et al., 2016; Lindberg et al., 2020; Ramberg et al., 2018; Siitonen, 2001). Consequently, many species associated with these structures and functions are threatened, including many saproxylic (wood-inhabiting) species (Hyvärinen et al., 2019; SLU Artdatabanken, 2020; Tomao et al., 2020).

Polypores (saproxylic fungi with poroid hymenophore) play a key role in the decomposition of dead wood in boreal forest ecosystems (Siitonen, 2001). Due to the aforementioned lack of dead wood, several polypore species are red-listed in Fennoscandia. Many have specific habitat quality requirements and are confined to dead wood of particular size, decay stage, and tree species (Berglund, Hottola, et al., 2011; Junninen & Komonen, 2011; Penttilä et al., 2004). The diversity and abundance of polypores also increase with increasing local abundance of coarse woody debris (CWD) (Junninen & Komonen, 2011; Penttilä et al., 2004; Tomao et al., 2020). Therefore, restoration of polypore communities needs to target both the quality and quantity of CWD.

In forests with natural dynamics, disturbances such as wind throws and fire create large amounts of CWD. Restoration of CWD volumes in degraded forests commonly aims to emulate these natural disturbances by, for example, mechanical felling of living trees (Sandström et al., 2019; Similä & Junninen, 2012). Although CWD created by felling trees promotes overall species richness of saproxylic species (Koivula & Vanha-Majamaa, 2020; Sandström et al., 2019), such measures tend to deliver a rather uniform type of CWD that lacks much of the variation in quality that is characteristic of naturally generated CWD. Hence, the benefit of this type of measure for red-listed polypores seems limited (Pasanen et al., 2014, 2019; Sandström et al., 2019). Prescribed burning (hereafter burning) is another way of emulating a natural disturbance that creates CWD. Besides generating a pulse of CWD by instantly killing many trees, fire also injures trees, which successively die and fall down, creating CWD several years after the initial disturbance. Although many polypores seem to die from the fire, and so burning in general has an immediate negative effect, polypore communities usually recover quickly and commonly diversify within a few years after a burn (Berglund, Jonsson, et al., 2011; Koivula & Vanha-Majamaa, 2020; Penttilä et al., 2013). Additionally, burning modifies the characteristics of the dead wood itself (e.g., hemicellulose structure), which has shown to influence polypore community composition (Alen et al., 2002; Carlsson et al., 2012; Edman & Eriksson, 2016; Kamdem et al., 2002).

Although adding CWD and burning are commonly used restoration measures in boreal forests that appear to promote polypore diversity, their effectiveness in promoting threatened species, especially in the long term, is surprisingly poorly understood (however, for pine forests see Junninen et al., 2008; Penttilä et al., 2013; Suominen et al., 2015). In managed spruce forests, long-term and large-scale experimental studies that compare different restoration measures are particularly lacking, especially considering the importance of spruce forests for highly specialized species (such as red-listed polypore species) (Hyvärinen et al., 2019; SLU Artdatabanken, 2020). Nevertheless, identifying the long-term responses of biological communities to restoration under field experimental conditions is fundamental to inform and refine evidence-based conservation strategies (Halme et al., 2013; Seibold et al., 2015).

In this study we analyzed the long-term effects on polypore community composition (abundance and species richness) by restoration of CWD by felling of whole trees and by prescribed burning in spruce-dominated boreal forests. For this we utilized a unique large-scale and long-term forest restoration experiment (the Evo experiment; Lilja et al., 2005; Vanha-Majamaa et al., 2007) located in a managed landscape in southern Finland. In particular, we examined whether the effects on diversity of red-listed and specialized polypore species differed depending on CWD levels (from cut logs) and if effects depended on whether or not CWD levels were crossed with burning. Finally, we addressed the extent to which log origin (i.e., cut logs compared to naturally fallen logs) influenced the polypore community.

MATERIALS AND METHODS

Study area

The study was located in the Evo-Vesijako region of Finland (61° N, 25° E). The region is within the southern boreal vegetation zone (Ahti et al., 1968) and has an annual average precipitation of ~670 mm, a mean annual temperature of +3.1°C, and a growing period of 160 days. The region is dominated by forests, mostly publicly owned, and has a long tradition of ecological research (Vanha-Majamaa et al., 2007). The Evo-Vesijako region has a long history of the use of prescribed fire in the landscape, and burns have been executed on both standing forest and clear-cuts in the area for at least 70 years (Hyväluoma et al., 2022).

For this study, we included the same 18 experimental stands studied by Berglund, Jonsson, et al. (2011). The forest stands are located within an area of 25 × 15 km, and each stand has an area of 1–3 ha. Prior to treatment in 2001, all stands had been influenced by forest management, and their average stand age was 80 years (60–100 years). The stands were predominantly of the mesic type, dominated by mature Norway spruce (*Picea abies*), with no significant pretreatment differences in volume of living trees or dead wood among stands (Lilja et al., 2005).

Experimental design and polypore inventory

The 18 stands are part of a field experiment set up in 2001 (Lilja et al., 2005; Vanha-Majamaa et al., 2007). The stands were subjected to different treatments following a standard factorial design with three replicates of each treatment. All treatments were randomized among the stands. First, in the winter of 2002, all stands were subjected to partial cutting, maintaining a constant volume of standing retention trees of 50 m^3 ha^{-1}. A portion of the felled trees was then used to create three CWD levels (5, 30, and 60 m^3 ha^{-1}, six stands per level) by retaining the cut trees on the forest floor. The remaining timber was removed from the stands. Second, in the summer of 2002, half of the stands (three of each CWD level, nine in total), were burned, while the other half remained unburned.

In 2018, 16 years after the treatments, we inventoried polypores on 10 experimentally cut logs and 10 naturally fallen logs per stand. However, in three stands we were unable to find 20 logs, so there we inventoried all available logs (14, 16, and 19 logs, respectively). Broken logs (with stem breakage at ≥2.5 m height) or logs lying on top of each other were excluded. All logs were randomly selected based on the nearest distance to the center point of each stand. The dbh (cm) and decay class according to Karjalainen and Kuuluvainen (2002), modified from Renvall (1995), was measured for each log.

In total, we surveyed 349 Norway spruce logs in 2018. The polypore species were recorded by the presence of fruiting bodies per log, an efficient method of surveying dominant species (Allmer et al., 2006). Besides polypore species, we also followed and recorded a few red-listed or indicator corticoid fungi (Corticiaceae) if they were found. Dead identifiable fruiting bodies were also included, as we focused on the general temporal effect rather than records for a specific year. The nomenclature of polypores follows Niemelä (2016), while that of corticoid fungi follows Kotiranta et al. (2009). Red-listed species were classified according to Finnish red lists for 2019, 2010, and 2000 (Hyvärinen et al., 2019).

Statistical analyses

Data collected from a total of 20 logs of different origin (10 cut, 10 natural) were compiled and analyzed for each stand. In this way, all results per stand were based on the 20 logs, except for the aforementioned three stands with fewer logs. All analyses were done in RStudio in the statistical programming environment R (version 4.1.2; R Core Team, 2021). We analyzed different measures of polypore species diversity. First, we analyzed the abundance and species richness when considering all species, but also when considering red-listed species only. The abundance of species was measured as the total number of species records made in each stand, and one record corresponded to a finding of an individual species on a single log. The species richness was measured as the total number of species recorded across all the logs sampled in each stand. Second, we analyzed the species composition of stands considering all species and red-listed species.

We tested how the variation in polypore species diversity between stands was explained by the two main experimental treatment factors: (1) CWD level (5, 30, and 60 m^3 ha^{-1}) and (2) burning (burned vs. unburned). The effects of the main factors were thus tested using independent measures of species diversity from each stand. The effects of the main treatment factors and their interaction on abundance and species richness were analyzed with generalized linear models ("glm" function, MASS package; Venables & Ripley, 2002). Poisson models with a log-link function are appropriate for count data and were therefore first used. However, to account for overdispersion and underdispersion (a dispersion parameter 0.5 above or below 1, respectively) quasi-Poisson models were often more appropriate and therefore used for analyzing the abundance and species richness of all species and the abundance of red-listed species. To assess model validity, Fisher-Pitman permutation tests based on 10,000 Monte Carlo resamplings were run ("oneway_test" function, coin package; Hothorn et al., 2006).

To test whether species composition differed between main treatments, we used nonmetric multidimensional scaling (NMDS) ordination ("metanmds" function, vegan package; Oksanen et al., 2020) with Euclidean distances on Hellinger transformed data. Assumptions of homogeneity of spread were tested ("betadisper" functions, vegan package; Oksanen et al., 2020). Dissimilarities detected between main treatments were tested with permutational multivariate analyses of variance (PERMANOVA; "Adonis" function, vegan package; Oksanen et al., 2020). As significant dissimilarities were found only between burned and unburned stands, and not across stands of different CWD levels, only the ordination for burning was included in the results. Finally, the relative contribution of each species (%) to the dissimilarity between ordination groups was analyzed ("simper" function, vegan package; Oksanen et al., 2020).

To further explore the effects of burning, the effects of the subfactor log origin (cut vs. naturally fallen) were tested on species abundance and richness. This was done in a separate set of analyses, including two measures from each stand, one for species found on cut logs and one for species found on naturally fallen logs. Thus, this test included two correlated measures from each stand. Again, generalized linear models were fitted using Poisson or quasi-Poisson with a log-link function. Models were compared with and without the random effect of stand identity to assess the impact of the correlation. As there was no significant difference between the models, the simpler model without the random effect (stand identity) was used. To assess model validity, Fisher-Pitman permutation tests were run ("oneway_test" function, coin package; Hothorn et al., 2006). Additionally, the polychoric correlation between log origin and decay class was tested ("polychor" function, polycor package; Fox, 2022).

RESULTS

Effects of CWD and burning on all species

In total, we recorded 1153 fruiting bodies of 39 species (Appendix S1: Tables S1 and S2). There were no significant differences between CWD levels, though there was a tendency toward increasing abundance at higher levels of CWD (Figure 1, Table 1). Likewise, we found no difference between burned and unburned stands, either for abundance or richness (Figure 1, Table 1). Altogether 576 records of 32 species were made in the burned stands and 577 records of 33 species in the unburned stands (Appendix S1: Table S1). We found no interaction between burning and CWD levels (Table 1).

Effects of CWD and burning on red-listed species

In total we recorded 70 fruiting bodies of nine red-listed species (Appendix S1: Tables S1 and S2). No significant differences were found between the three CWD levels, that is, varying levels of downed logs by felling alive trees, had no significant effect on either the abundance or richness of red-listed species (Figure 2, Table 2). By contrast, the burned stands had generally both higher species abundance and richness in comparison to unburned stands (Figure 2, Table 2). In total, 54 records of nine red-listed species were made in burned stands and 16 records of five red-listed species in unburned stands (Appendix S1: Table S1). Additionally, we found no significant interaction between the main treatment factors burning and CWD level (Table 2).

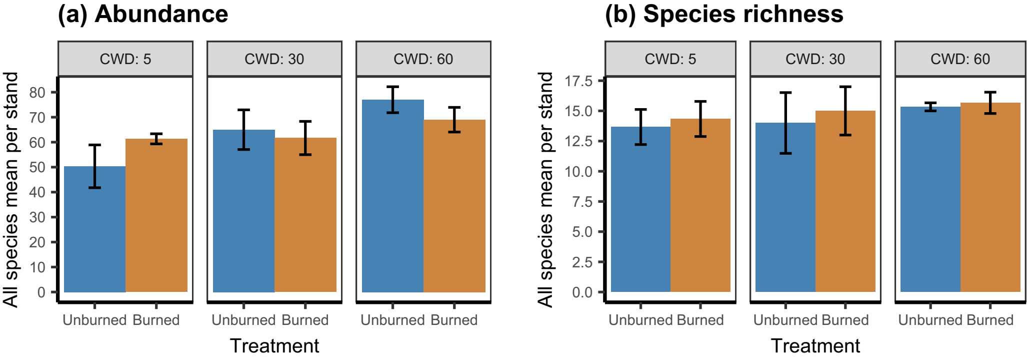

FIGURE 1 Response of polypores to main treatment factor creation of coarse woody debris (CWD) at levels 5, 30, and 60 m^3 ha^{-1} and prescribed burning (burned vs. unburned) showing mean and ± SE ($N = 1153$) of abundance (a) and species richness (b) per stand (20 logs).

TABLE 1 Results of generalized linear model (Quasi Poisson with log link function, *F* test) ANOVAs for effects of the main treatment factors coarse woody debris (CWD) levels (5, 30 vs. 60 m^3 ha^{-1}) and burning (burned vs. unburned) on the abundance and species richness of all polypore species.

Diversity measure	Treatment	df	Deviance	Residual df	Residual deviance	*F* value	*p* value	Resampling *p*-value
Abundance	CWD level	2	13.84	14	28.57	3.53	0.062	**0.042**
Abundance	Burning	1	9 e-04	16	42.41	4 e-04	0.98	1
Abundance	CWD-level × burning	2	4.93	12	23.73	1.23	0.33	...
Species richness	CWD-level	2	0.47	14	6.33	0.44	0.65	0.59
Species richness	Burning	1	0.14	16	6.81	0.25	0.62	0.64
Species richness	CWD-level × burning	2	0.025	12	6.31	0.024	0.98	...

Note: Dispersion parameter for abundance is 1.96 and species richness is 0.54. The last column shows results of Fisher-Pitman permutation tests with 10,000 Monte Carlo resamplings. Statistically significant results are written in bold. Model coefficients can be found in Appendix S1: Table S3.

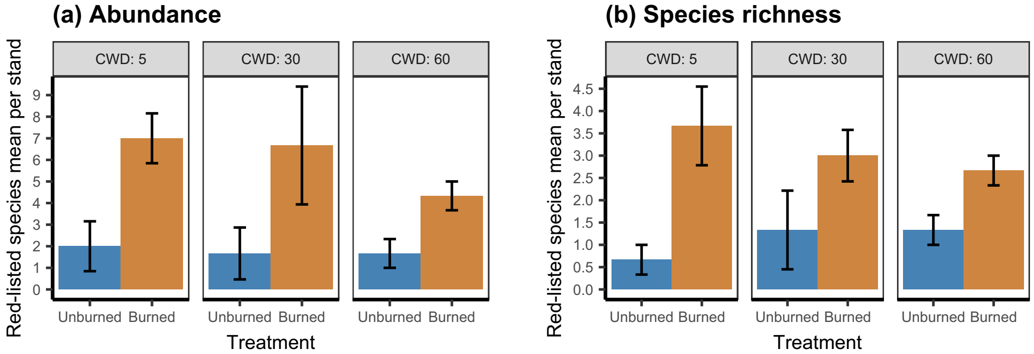

FIGURE 2 Response of red-listed polypores to main treatment factor creation of coarse woody debris (CWD) at levels 5, 30, and 60 m^3 ha^{-1} and prescribed burning (burned vs. unburned) showing mean and ± SE ($N = 70$) of abundance (a) and species richness (b) per stand (20 logs).

TABLE 2 Results of generalized linear model ANOVAs for effects of the main factors coarse woody debris (CWD) levels (5, 30 vs. 60 m^3 ha^{-1}) and burning (burned vs. unburned) on the abundance (Quasi Poisson with log link function, *F* test) and species richness (Poisson with log link function, χ^2 test) of red-listed polypore species.

Diversity measure	Treatment	df	Deviance	Residual df	Residual deviance	*F* value	*p* value	Resampling *p* value
Abundance	CWD level	2	1.99	14	21.63	0.62	0.55	0.73
Abundance	Burning	1	21.78	16	23.62	13.57	**0.003**	**0.001**
Abundance	CWD level × burning	2	0.36	12	21.26	0.11	0.89	...
Species richness	CWD level	2	0.05	14	10.01	...	0.97	1
Species richness	Burning	1	8.88	16	10.07	...	**0.003**	**0.002**
Species richness	CWD level × burning	2	1.31	12	8.70	...	0.52	...

Note: Dispersion parameter for abundance is 1.6 and species richness is 0.6. The last column shows results of Fisher-Pitman permutation tests with 10,000 Monte Carlo resamplings. Statistically significant results are written in bold. Model coefficients can be found in Appendix S1: Table S4.

Community composition

The main factor burning had a strong effect on the polypore community, resulting in a difference in community composition between burned stands and unburned stands (Figure 3; PERMANOVA $R^2 = 0.41$, $F_{1,16} = 11.13$, $p = 0.001$). The five most influential species contributing to the dissimilarity were *Trichaptum abietinum*, *Fomitopsis pinicola*, *Gloeophyllum sepiarium*, *Antrodia serialis*, and *Antrodia sinuosa* (SIMPER analysis; Table 3).

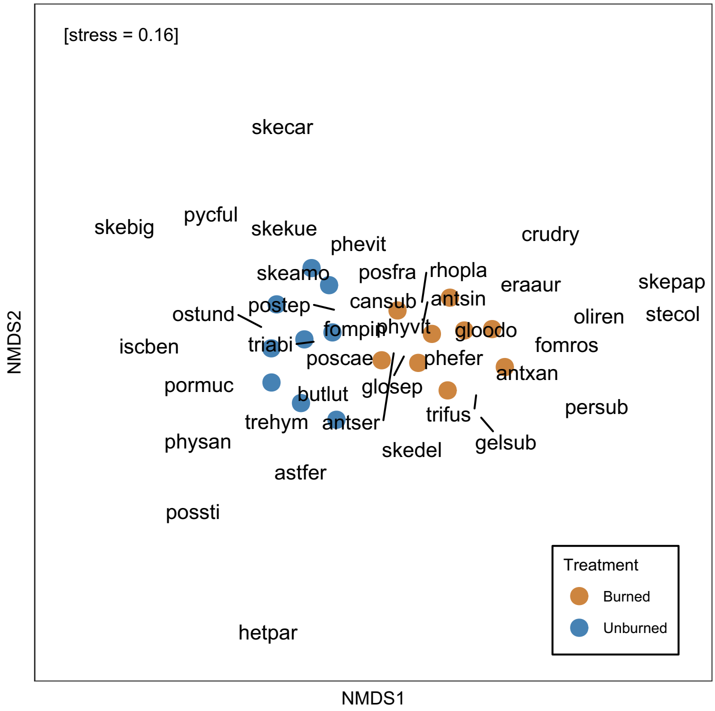

FIGURE 3 Nonmetric multidimensional scaling ordination plot showing polypore communities in burned (orange) and unburned (blue) stands. The two-dimensional stress ratio was 0.16. Species abbreviation explanations can be found in Appendix S1: Table S2.

TABLE 3 Results of SIMPER analysis for the five most influential species, showing the species contribution to average between-treatment dissimilarity, the cumulative contribution, and the average abundances in the burned and unburned stands.

Species	Abbreviations used in Figure 3	Average	Cumulative	Average abundance	
				Burned stands	Unburned stands
Trichaptum abietinum	triabi	0.07	0.15	4	12.89
Fomitopsis pinicola	fompin	0.06	0.27	5.78	12.78
Gloeophyllum sepiarium	glosep	0.05	0.39	13.44	7.00
Antrodia serialis	antser	0.05	0.50	15.78	10.22
Antrodia sinuosa	antsin	0.03	0.57	6.11	2.33

Log origin and decay class

Though we found no effect of burning alone on the whole community (Figure 1), we detected effects of burning when we accounted for log origin (cut vs. naturally fallen) (Appendix S1: Figure S1). For abundance, we found a significant interaction between burning and origin, which was that the effect of burning depended on log origin (Appendix S1: Figure S1 and Table S5). Burning was negative for species abundance on cut logs, and there was a tendency toward the same pattern for species richness (Appendix S1: Figure S1 and Table S5). The opposite was true of natural logs, with burning increasing mean responses.

For red-listed species, we detected positive treatment effects of burning even when controlling for origin, with no significant interaction between burning and log origin (Figure 4, Table 4). Burning and natural log origin had independent significant positive effects on abundance and species richness of red-listed species (Figure 4, Table 4).

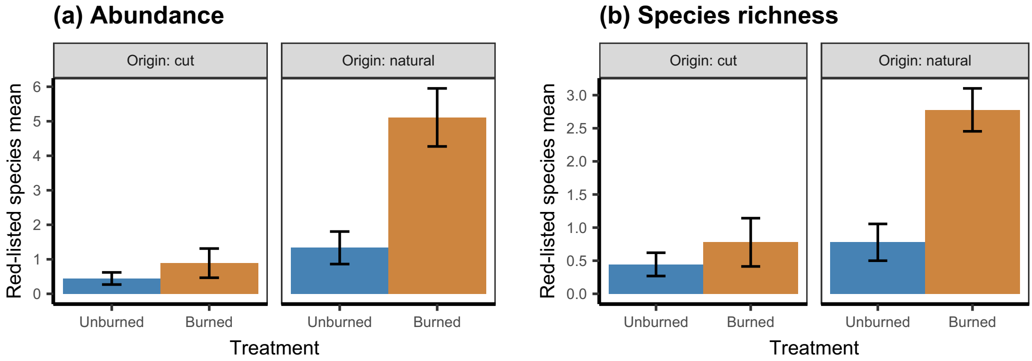

FIGURE 4 Response of red-listed polypores to main treatment factor prescribed burning (burned vs. unburned) and the subfactor log origin (cut vs. natural) showing mean and ± SE ($N = 70$) of abundance (a) and species richness (b).

TABLE 4 Results of generalized linear model (Poisson with log link function, χ^2 test) ANOVAs for effects of main treatment factor burning (burned vs. unburned) and subfactor log origin (cut vs. natural) on abundance and species richness of red-listed polypore species.

Diversity measure	Treatment	df	Deviance	Residual df	Residual deviance	*p*-value	Resampling *p*-value
Abundance	CWD level	1	21.78	34	80.69	**3.05 e-06**	**0.007**
Abundance	Burning	1	32.90	33	47.79	**9.70 e-09**	**4 e-04**
Abundance	CWD level × burning	1	0.84	32	46.94	0.36	...
Species richness	CWD level	1	10.71	34	32.65	**0.001**	**0.006**
Species richness	Burning	1	10.71	33	31.94	**0.001**	**0.005**
Species richness	CWD level × burning	1	0.86	32	31.08	0.35	...

Note: Dispersion parameter for abundance is 1.3 and species richness is 0.8. The last column shows results of Fisher-Pitman permutation tests with 10,000 Monte Carlo resamplings. Statistically significant results are written in bold. Model coefficients can be found in Appendix S1: Table S7.

With regard to log origin alone, natural logs in general had higher species richness and abundance with regard to both the entire community (Appendix S1: Figure S1 and Table S5) and red-listed species (Figure 4, Table 4), though not always significantly so. Log origin was negatively correlated with log decay class (−0.85), with cut logs being more decayed (median decay Stage 3 to 5) than natural logs (median decay stage 2 to 3.5) in unburned and burned stands at time of inventory (Appendix S1: Table S1).

DISCUSSION

Our study reveals that the mechanical creation of CWD (by felling whole trees) and CWD generated by prescribed burning results in different effects on polypore communities. Prescribed burning promoted higher species diversity of wood-inhabiting fungi, especially red-listed species, which had both higher abundance and higher species richness in burned stands compared to unburned stands. Our results highlight that fire can also be important for restoring high species diversity in habitats traditionally perceived as less fire adapted and underlines the long time scales needed for understanding polypore community-level responses to restoration.

Responses to CWD levels

In our experiment, the creation of different CWD levels by felling whole trees and leaving them as cut logs did not affect the diversity of polypores over time, which is in accordance with the findings of Berglund, Jonsson, et al. (2011), who reported the same effects 5 years after the treatments. The lack of effect from CWD levels was consistent irrespective of burn treatment, and for both the entire community and red-listed species. Thus, restoration in terms of increasing local CWD levels (5–60 m^3 ha^{-1}) in ecologically degraded forests by just felling live trees appears to have limited long-term conservation benefits with regard to the restoration of polypore diversity.

These findings are surprising since others have demonstrated positive responses; species diversity among polypores increases with local CWD availability in both descriptive (Junninen & Komonen, 2011; Penttilä et al., 2004) and experimental studies (Koivula & Vanha-Majamaa, 2020; Sandström et al., 2019; Seibold et al., 2015; Suominen et al., 2015). Essentially, a positive relationship is expected from general theory. The species–energy hypothesis (Stokland et al., 2012; Wright, 1983) states that increasing volume results in more available energy, which can sustain a higher abundance and richness of species. In addition, according to the species–area relationship (MacArthur & Wilson, 1967), an increase in volume entails more area and resources for colonization and growth of species.

What might explain our contradictory findings? The CWD in this study was created by felling trees and leaving them as cut logs at one time point, resulting in a homogeneous addition of CWD with similar characteristics. The trees' great qualitative similarity may in turn limit differentiation of polypore communities among cut logs and explain why increasing CWD levels alone has no clear effect on overall species diversity. Previous studies showed that CWD heterogeneity was an important predictor of polypore diversity, especially for rare species, which generally have more specific habitat requirements (Berglund, Hottola, et al., 2011; Junninen & Komonen, 2011). This is also supported by theory, with the habitat–heterogeneity hypothesis stipulating that species diversity will increase with habitat diversity (MacArthur & MacArthur, 1961; Seibold et al., 2016). In addition, earlier experimental studies revealed short-term positive biodiversity effects of CWD enrichment (e.g., Sandström et al., 2019; Seibold et al., 2015), but those studies did not examine long-term persistence. Polypores are known to experience succession and colonization on a decadal time scale (Penttilä et al., 2013; Suominen et al., 2015). As a result, long-term studies, such as this one, are essential to fully understand the ecology of polypores.

Effects of prescribed burning

Our study is the first large-scale experimental study to show that CWD restoration by prescribed burning has strong, unique, and long-lasting (up to 16 years) effects on polypore diversity in Norway spruce-dominated forests. The great majority of earlier studies focused on the importance of prescribed burning in fire-prone Scots pine-dominated forests (Junninen et al., 2008; Penttilä et al., 2013; Suominen et al., 2015), where species are considered to be adapted to reoccurring wildfires (Zackrisson, 1977). In pine-dominated forests, fire has been shown to have positive effects on polypore community diversity, especially on longer time scales (Junninen et al., 2008; Penttilä et al., 2013; Suominen et al., 2015). Our results show that prescribed burning also promotes diversity of red-listed polypores in less fire-prone spruce-dominated forest. We found, as in a few previous studies (Penttilä et al., 2013; Ylisirniö et al., 2012), that species (e.g., *Fomitopsis rosea*) earlier thought to be mainly confined to old-growth forests seemed to also thrive well on CWD in burned and open forest habitats.

There are several potential explanations of the positive effects of burning on both abundance and species richness of red-listed polypores. First, the community assembly may be a legacy of the heating effect fire generates, with species that have more heat-resistant mycelia gaining an advantage (Carlsson et al., 2012). In addition, heat can affect wood characteristics, such as moisture content, hemicellulose structure, and organic compounds (Alen et al., 2002; Kamdem et al., 2002), and create a habitat type that favors certain polypores over others (Edman & Eriksson, 2016).

Second, it is likely that the community assemblages that we observed are shaped by priority effects, that is, that pioneer wood-inhabiting fungal communities determine the assemblages of secondary communities (Fukami et al., 2010; Weslien et al., 2011). It is well known that wood-inhabiting fungal communities are influenced by such priority effects (Ottosson et al., 2014; Rajala et al., 2015). Community assembly trajectories have not been specifically tested for burned CWD. However, in controlled laboratory conditions, both temperature and assembly history jointly appear to determine dead-wood decomposition rate and polypore community assembly trajectories (Edman et al., 2021). In addition, Komonen et al. (2014) found differences in polypore communities between natural and created spruce logs after 8 years, suggesting that the manner in which dead wood is created (i.e., tree mortality mode) affects community trajectories. Thus, the initial differences in community composition found by Berglund, Jonsson, et al. (2011) may have been instrumental in determining the community composition observed in the present study.

Finally, burning not only creates a pulse of CWD but also injures trees, killing them gradually. The burn treatment results in a more continuous addition of CWD over a longer period than adding cut logs, creating a diversity of CWD, allowing for more specialized substrates that red-listed species often need (Berglund, Hottola, et al., 2011; Junninen & Komonen, 2011). A longer continuity of CWD also means that suitable habitat is available for a longer time (on the stand and landscape scales). Ylisirniö et al. (2012), for example, concluded in their study that CWD created by fire provided habitat for wood-inhabiting fungi for up to 70 years. In our study, the experimentally cut logs were often decayed to such a degree that the habitat quality of the logs was diminished for most polypores. However on naturally generated CWD, the positive effects we found for red-listed species remained significant decades after burning, indicating that burning has long-term conservation benefits with regard to restoration of polypore diversity. The continuity of CWD that fire creates seems to be necessary for promoting the diversity of red-listed polypore species, which is in accordance with previous studies in which red-listed species have often started to occur first 10 years or so after a fire (Junninen et al., 2008; Penttilä et al., 2013; Suominen et al., 2015). The significance of the continuous addition of CWD for diversity also underlines the importance of reoccurring fires in the landscape. This might be especially important for spruce-dominated forest, where fires are more likely to be stand-replacing, which implies that, although the addition of CWD may occur over decades, it will eventually end, and the wood-inhabiting species will need to relocate to more recently disturbed areas. In the Evo-Vesijako region, fire has occurred in the landscape at fairly regular intervals (Hyväluoma et al., 2022). In an intensively managed landscape without fire continuity, the occurrence and dispersal of rare species is likely to be lower (see e.g., for beetles; Kouki et al., 2012) as appropriate habitats are lacking.

Our findings regarding the effects of burning may to some extent be confounded by the fact that the local CWD volumes in burned stands increased due to the high mortality of the retained trees. The higher abundance and species richness of red-listed species in burned compared to unburned stands may therefore be related to the higher stand-level resource (energy) availability (Stokland et al., 2012; Wright, 1983), in combination with the trait-dependent colonization rates of different species (Moor et al., 2021). However, we compared fungal communities in standardized samples, that is, 10 cut and 10 natural logs, and found no effect of increasing stand-level volumes in either unburned or burned stand treatments. It is therefore more likely that the CWD qualities created by burning (discussed earlier) account for the positive relationships found between burning and red-listed polypore diversity.

Conclusions and implications

This study shows that prescribed burning is an effective restoration measure that can promote species diversity of polypore communities. Restoration by burning in boreal forests previously primarily targeted pine-dominated forest, but our results demonstrate that it is also an effective measure to promote red-listed species in forests less adapted to recurring fires, such as spruce-dominated forests. Burning results in the continuous addition of CWD and creates CWD of different characteristics, compared to CWD that is generated by felling trees. Thus, restoring CWD by burning is more beneficial for conserving polypore biodiversity. Our results underscore how managed Norway spruce forests should also be included in forest fire restoration programs. However, because the resource pulse that burning generates will be fairly short-lived, prescribed burning needs to be applied with regular intervals on a landscape scale. It is common practice to combine forest restoration treatments with partial cuttings, where the harvested wood covers the costs of restoration actions without compromising the restoration goals (Vanha-Majamaa et al., 2007). Future studies need to investigate whether CWD restoration treatments affect fungal communities similarly in uncut, closed forest stands. Lastly, this study confirms that red-listed polypore species recruitment works on a decadal time scale, and therefore it is not possible to understand the effectiveness of prescribed burning as a restoration measure over shorter periods. Our study highlights that long-term experimental studies, such as this one, are invaluable for establishing evidence-based restoration strategies necessary for the successful conservation of biodiversity in boreal forests.

AUTHOR CONTRIBUTIONS

Ellinor Ramberg, Håkan Berglund, Reijo Penttilä, Joachim Strengbom, and Mari Jönsson conceived the ideas of the study. Håkan Berglund, Reijo Penttilä, and Mari Jönsson designed the methodology. Håkan Berglund, Mari Jönsson, and Reijo Penttilä collected the data. Ellinor Ramberg and Mari Jönsson analyzed the data. Ellinor Ramberg, Joachim Strengbom, and Mari Jönsson interpreted the initial results. Ellinor Ramberg led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for the article's publication.

ACKNOWLEDGMENTS

HAMK, University of Applied Sciences, Metsähallitus, UPM-Kymmene Ltd., the City of Hämeenlinna, and the Finnish Forest Research Institute (Metla) provided the stands for the study and implemented the treatments. Burning activities were organized by Timo Heikkilä. We thank Ilkka Vanha-Majamaa, Saara Lilja, and Timo Kuuluvainen who planned and initiated the Evo experiment. We also thank Henrik Lindberg for his help with practical issues and Elisabet Ottosson for her field assistance. The study was financially supported by

Skogssällskapet (Grant 2019-655-Steg 2 2018) to Joachim Strengbom.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Ramberg et al., 2023) are available in Dryad at https://doi.org/10.5061/dryad.g1jwstqw9.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Ramberg, Ellinor, Håkan Berglund, Reijo Penttilä, Joachim Strengbom, and Mari Jönsson. 2023. "Prescribed Fire is an Effective Restoration Measure for Increasing Boreal Fungal Diversity." *Ecological Applications* 33(6): e2892. https://doi.org/10.1002/eap.2892

Ecological Applications

Appendix S1

Supplementary material for:

Prescribed fire is an effective restoration measure for increasing boreal fungal diversity

Ellinor Ramberg, Håkan Berglund, Reijo Penttilä, Joachim Strengbom, Mari Jönsson

Table S1. Summary per stand of the main treatment factors burning and created coarse woody debris (CWD) level, the total number of logs, the number of logs per origin, the decay class median per origin, the log diameter per origin, total abundance, red listed abundance, total species richness and red listed species richness.

Stand ID	Burning treatment	CWD level	Total number of logs	Number of logs cut:natural	Log decay class cut:natural median	Log diameter (cm) cut:natural median	Abundance Total	Abundance Red list	Species richness Total	Species richness Red list
165	Burned	5	20	10:10	4:3	26.0:31.5	65	5	12	2
250	Burned	5	20	10:10	4:3	23.5:23.0	61	7	17	5
301	Burned	5	16	5:11	4:3	26.0:31.0	58	9	14	4
41	Burned	30	19	11:8	4:3	22.0:23.0	55	5	13	3
85	Burned	30	20	10:10	4:3	29.5:28.0	75	12	19	4
203	Burned	30	20	10:10	5:3	26.5:29.5	55	3	13	2
55	Burned	60	20	10:10	4:3	27.5:27.0	68	5	16	2
205	Burned	60	20	10:10	4:3	24.0:24.5	61	3	14	3
327	Burned	60	20	10:10	4:2.5	25.0:25.0	78	5	17	3
Total			**175**				**576**	**54**	**32**	**9**
230	Unburned	5	20	10:10	4:3	21.5:32.0	63	2	16	1
291	Unburned	5	14	12:2	4:3.5	20.0:22.0	34	0	11	0
552	Unburned	5	20	10:10	4:3	20.0:25.5	54	4	14	1
168	Unburned	30	20	10:10	4:3	23.5:21.5	62	1	12	1
271	Unburned	30	20	10:10	4:2.5	27.0:25.5	80	4	19	3
496	Unburned	30	20	10:10	3:3	21.5:21:5	53	0	11	0
37	Unburned	60	20	10:10	4:3	24.0:26.5	68	1	15	1
196	Unburned	60	20	10:10	4:2	28.0:27.0	77	3	15	2
617	Unburned	60	20	10:10	3:3	24.0:28.5	86	1	16	1
Total			**174**				**577**	**16**	**33**	**5**

*Table S2. Polypore and corticoid (Corticiaceae, marked with *) species names, the abbreviations used in figures and the total abundance of the species in burned and unburned stands. Species in red text are and have been red listed in Finnish red lists made in 2019, 2010 and 2000. Species names are according to Niemelä (2016) and Kotiranta et al. (2009).*

Species		Abbrevation	Burned	Unburned
Antrodia	*serialis*	antser	142	92
	sinuosa	antsin	55	21
	xantha	antxan	19	2
*Asterodon**	*ferruginosus*	astfer	8	11
Butyrea	*luteoalba*	butlut	6	14
Canopora	*subfuscoflavida*	cansub	28	36
*Crustoderma**	*dryinum*	crudry	2	0
Erastia	*aurantiaca*	eraaur	1	1
Fomitopsis	*pinicola*	fompin	52	115
	rosea	fomros	21	1
Gelatoporia	*subvermispora*	gelsub	1	0
Gloeophyllum	*odoratum*	gloodo	12	3
	sepiarium	glosep	121	63
Heterobasidion	*parviporum*	hetpar	0	1
Ischnoderma	*benzoinum*	iscben	0	2
Oligoporus	*rennyi*	oliren	3	0
Osteina	*undosa*	ostund	2	5
Perenniporia	*subacida*	persub	5	0
Phellinus	*ferrugineofuscus*	phefer	20	12
	viticola	phevit	3	8
Physisporinus	*sanguinolentus*	physan	0	2
	vitreus	phyvit	1	1
Porpomyces	*mucidus*	pormuc	0	5
Postia	*caesia*	poscae	11	9
	fragilis	posfra	5	6
	stiptica	possti	0	2
	tephroleuca	postep	8	17
Pycnoporellus	*fulgens*	pycful	1	8
Rhodonia	*placenta*	rhopla	2	1
Skeletocutis	*amorpha*	skeamo	2	3
	biguttulata	skebig	0	1
	carneogrisea	skecar	0	1
	delicata	skedel	1	1
	kuehneri	skekue	1	3
	papyracea	skepap	1	0
Steccherinum	*collabens*	stecol	1	0
Trechispora	*hymenocystis*	trehym	2	13
Trichaptum	*abietinum*	triabi	36	116
	fuscoviolaceum	trifus	3	1

Table S3. Generalized linear model (Quasi Poisson with log link function) coefficients for the effects of the main treatment factors coarse woody debris (CWD) levels (5, 30 vs 60 m^3 ha^{-1}) and burning (burned vs unburned) on the abundance and species richness of all polypore species. Dispersion parameter for abundance is 1.96 and species richness is 0.54.

Variable	Estimates	SE	t value	Pr (>|t|)
Abundance				
Intercept	3.92	0.11	34.39	2.3 e-13
Burning	0.19	0.15	1.29	0.22
CWD 30	0.26	0.15	1.69	0.12
CWD 60	0.43	0.15	2.90	0.01
Burning x CWD 30	-0.25	0.21	-1.19	0.26
Burning x CWD 60	-0.31	0.20	-1.51	0.16
Species richness				
Intercept	2.61	0.11	22.81	2.9 e-11
Burning	0.05	0.16	0.29	0.77
CWD 30	0.03	0.16	0.15	0.88
CWD 60	0.12	0.16	0.73	0.48
Burning x CWD 30	0.02	0.23	0.09	0.93
Burning x CWD 60	-0.03	0.22	-0.12	0.91

Table S4. Generalized linear model coefficients for the effects of the main treatment factors coarse woody debris (CWD) levels (5, 30 vs 60 m^3 ha^{-1}) and burning (burned vs unburned) on the abundance (Quasi Poisson with log link function) and species richness (Poisson with log link function) of red-listed polypore species. Dispersion parameter for abundance is 1.6 and species richness is 0.6.

Variable	Estimates	SE	t value	Pr (>|t|)
Abundance				
Intercept	0.69	0.52	1.34	0.21
Burning	1.25	0.59	2.13	0.05
CWD 30	-0.18	0.77	-0.24	0.82
CWD 60	-0.18	0.77	-0.24	0.82
Burning x CWD 30	0.13	0.86	0.16	0.87
Burning x CWD 60	-0.29	0.88	-0.34	0.74
Species richness				
Intercept	-0.41	0.71	-0.57	0.57
Burning	1.70	0.77	2.22	0.03
CWD 30	0.69	0.87	0.80	0.42
CWD 60	0.69	0.87	0.80	0.42
Burning x CWD 30	-0.89	0.96	-0.92	0.36
Burning x CWD 60	-1.01	0.98	-1.03	0.30

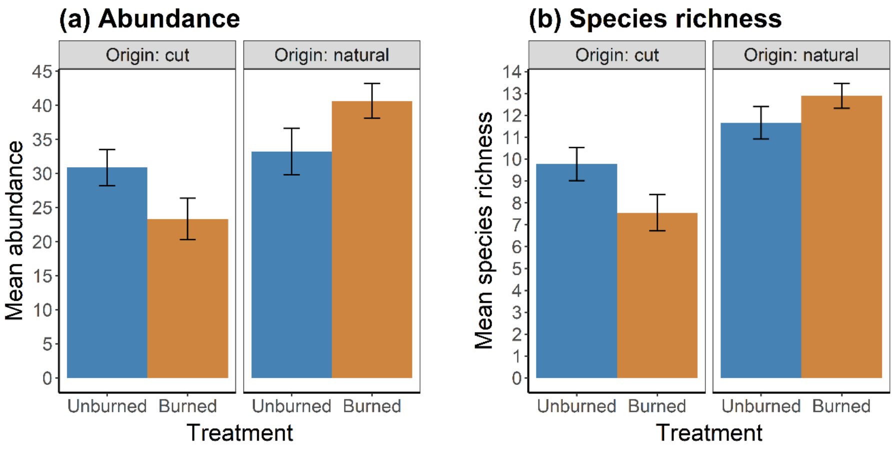

*Figure S1. Response of all polypores to the main treatment factor prescribed burning (burned vs unburned) and the sub-factor log origin (cut vs natural) showing the mean and ± se (N=1153) of the **abundance (a)** and **species richness (b)**.*

Table S5. Results of generalized linear model ANOVAs for effects of the main treatment factor burning (burned vs unburned) and sub-factor log origin (cut vs natural) on the abundance (Quasi poisson with log link function, F test) and species richness (Poisson with log link function, chi-squared test) of all polypore species. Dispersion parameter for abundance is 2.6 and species richness is 0.5. The last column shows results of Fisher-pitman permutation tests with 10000 montecarlo re-samplings. Statically significant results are written in bold. Model coefficients can be found in Table S6.

Variable	DF	Deviance	Residual DF	Residual Deviance	P value	Resampling P value
Abundance						
Burning	1	9 e-04	34	136.62	0.98	1
Origin	1	27.28	33	109.34	**0.003**	**0.004**
Burning x Origin	1	16.27	32	93.08	**0.02**	-
Species richness						
Burning	1	0.21	34	30.49	0.64	0.66
Origin	1	11.26	33	19.23	**7 e-04**	**1 e-04**
Burning x Origin	1	2.90	32	16.32	0.08	-

Table S6. Generalized linear model coefficients for the effect of the main treatment factor burning (burned vs unburned) and sub-factor log origin (cut vs natural) on the abundance (Quasi poisson with log link function) and species richness (Poisson with log link function) of all polypore species. Dispersion parameter for abundance is 2.6 and species richness is 0.5.

Variable	Estimates	SE	t value	Pr (>|t|)
Abundance				
Intercept	3.43	0.09	35.79	2 e-16
Burning	-0.28	0.14	-1.92	0.06
Origin	0.07	0.13	0.54	0.59
Burning x Origin	0.19	0.19	2.51	0.01
Species richness				
Intercept	2.28	0.11	21.39	2 e-16
Burning	-0.26	0.16	-1.59	0.11
Origin	0.18	0.14	1.22	0.22
Burning x Origin	0.36	0.21	1.70	0.09

Table S7. Generalized linear model (Poisson with log link function) Coefficients for the effect of the main treatment factor burning (burned vs unburned) and sub-factor log origin (cut vs natural) on the abundance and species richness of red-listed polypore species. Dispersion parameter for abundance is 1.3 and species richness is 0.8.

Variable	Estimates	SE	t value	Pr (>|t|)
Abundance				
Intercept	-0.81	0.50	-1.62	0.10
Burning	0.69	0.61	1.13	0.26
Origin	1.09	0.57	1.90	0.06
Burning x Origin	0.65	0.69	0.94	0.34
Species richness				
Intercept	-0.81	0.50	-1.62	0.10
Burning	0.56	0.63	0.89	0.37
Origin	0.56	0.63	0.89	0.37
Burning x Origin	0.71	0.76	0.94	0.35

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Prescribed burning is used as a conservation tool in Fennoscandia. However, knowledge on when and where prescribed burns should be applied to be most efficient for promoting biodiversity is lacking. In this thesis I examine how site attributes and temporal variables influence the outcomes of prescribed burns. My results show that prescribed burn outcomes vary considerably among sites, but that the conservation value of prescribed burning can be improved by more carefully considering forest type, landscape context and weather.

Ellinor Ramberg received her PhD education from the Department of Ecology at SLU, Uppsala. She obtained her MSc degree from the Biology Education Centre at Uppsala University, and her BSc from the Swedish University of Agricultural Sciences.

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ISSN 1652-6880
ISBN (print version) 978-91-8046-470-3
ISBN (electronic version) 978-91-8046-520-5