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Research article

Wildfires provide more diverse habitats than prescribed burns for saproxylic beetles and wood decay fungi in Swedish boreal landscapes

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ABSTRACT

Boreal forests provide important ecosystem services such as climate regulation, wood production and biodiversity. Fire determines forest dynamics and generates habitat for many species but fire frequency and severity are expected to increase as a result of global warming. In Fennoscandian boreal forests forest management and fire suppression have reduced the burnt areas and amount of deadwood since early 1900s, causing habitat loss and subsequent declines of many saproxylic fungi and beetles. Here, prescribed burns are used as a tool to restore habitats of crucial importance for biodiversity and are well-documented to promote fire associated insects in the short term and fungi in the long run. As the first study to compare wildfires and prescribed burns in landscapes with a long history of fire suppression we examine how large wildfires and prescribed burning contribute to biodiversity of saproxylic fungi and beetles after a decade by addressing the question: How does deadwood volume and composition, and species richness, abundance and assemblage composition of wood fungi and beetles differ between a) wildfires and prescribed burns and b) between burned areas and unburned areas. We use a study design with three large wildfires paired with three unburnt controls, and five prescribed burns. We sampled beetles with flight intercept traps and conveyed detailed deadwood and polypore field inventories. We found that the prescribed burns incompletely mimicked wildfire, with prescribed burns only containing half the volumes of deadwood with significantly lower volumes of decidouous wood but significantly more highly decayed deadwood.and only hosting a subset of the wood fungi assemblages. Beetle assemblages recovered largely after 12 years with similar species richness, abundance and assemblage composition, but species associated with old-growth stands were still rare in burned areas. For wood fungi, assemblage composition differed between burned and unburned stands and species associated with decayed wood were not detected in burned areas after 12 years. We show that to meet biodiversity goals with prescribed burning it is important to aim for higher tree mortality and higher deadwood production than was achieved in this study. This can be done by burning larger areas to include more variation, to burn at dryer conditions, and/or to combine burning with the creation of deadwood. We show that wildfires will provide high volumes of deadwood that provide valuable substrates for saproxylic species for many years to come.To facilitate conservation it is thus also important to protect wildfire areas and avoid salvage logging, especially when old forests burn.

1. Introduction

The circumpolar boreal zone represents one of the largest terrestrial biomes, encompassing approximately 30 % of the global forest area and delivering critical ecosystem services, including climate regulation and the maintenance of biodiversity. At present, nearly two-thirds of the boreal forest is subject to management, primarily for timber production. Although boreal forests exhibit adaptations that enable persistence under prevailing disturbance regimes, projected environmental changes pose significant threats to their resilience and ecological integrity.

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(Gauthier et al., 2015; Boucher et al., 2018). Forest fires is the disturbance that have largely determined the post-glacial forest dynamics in the boreal region (Zackrisson, 1977; Niklasson and Granström, 2000; Gauthier et al., 2015; Berglund and Kuuluvainen, 2021). Fire results in large inputs of deadwood, form stand structural diversity and initiate succession of saproxylic (deadwood associated) organisms (Hjältén et al., 2018; Eisenberg et al., 2019; Fredriksson et al., 2020).

In pre-industrial times, up to 2 % of the Swedish boreal forest landscape burned annually (Zackrisson, 1977), compared with <0.02 % today (Niklasson and Granström, 2004). Historical wildfires were spatially heterogeneous in size and severity producing a wide range of types of habitats that influenced abundances and distributions of species (Kuuluvainen and Aakala, 2011). In boreal Fennoscandia, covering over 50 million hectares, forest management and efficient fire suppression during the last century has altered the landscape and largely affected the biodiversity by reducing the amount of important structures such as deadwood and burnt areas (Esseen et al., 1997). Here, habitat restoration is needed to halt biodiversity loss.

Ecological restoration theory is generally based on the assumption that it is efficient to mimic natural processes and disturbances (Lindenmayer et al., 2006). Restoration efforts often return some elements of prior biotic conditions, but success is reliant on both natural recolonization and species interactions (Hägglund et al., 2015; Hjältén et al., 2017). It is established that burning, tree retention and dead wood creation has profound positive effects on wood living assemblages (Johansson et al. 2007, 2011; Olsson et al., 2011; Hjältén et al., 2017) including both rare species (Hjältén et al., 2012; Hägglund et al., 2015) and functional diversity, suggesting that there is environmental filtering so that species associated with open habitat and fresh deadwood are favoured by both burning and tree retention (Heikkala et al., 2016b). However, burning has more long-lasting effects and might favor predators to a larger extent (Heikkala et al., 2016a).A key challenge in restoration is the "Field of Dreams" assumption: simply providing habitat (deadwood) will lead to species recolonization (Palmer et al., 1997). This overlooks key processes like dispersal abilities, habitat preferences, and interspecies interactions, which can affect restoration success (Arroyo-Esquivel et al., 2023).

Reintroduction of fire is based on the arguments that restoration measures should resemble natural disturbances, and recent studies show that such measures are efficient, at least in the short term (Junninen et al., 2008; Heikkala et al., 2016a; Hägglund et al., 2020; Koivula and Vanha-Majamaa, 2020). During the last 25 years, prescribed burning has been used to promote biodiversity in protected forest areas and is a part of the FSC certification in managed forest (Forest Stewardship Council, 2019; Anonymous, 2021a). Prescribed burns are performed both in standing forest and on clear cuts with only few retained trees and are generally smaller in size and performed during less warm and dry weather conditions compared to most historical wildfires. However, there is a lack of knowledge about biodiversity response to large scale wildfires in landscapes subjected to fire suppression, how well prescribed burns may mimic natural wildfires, and how different fires might maintain diverse saproxylic communities in the long-term.

Previous studies, spanning multiple regions and taxa, show that wildfires and prescribed burns yield distinct effects on biodiversity. Prescribed burns are associated with positive or neutral changes in native plant composition over short (less than 1 year) to moderate (up to 1 year) time scales. For example, prescribed burns enhanced native plant composition in North America and Australia (Alba et al., 2014) and supported higher native plant diversity in Californian grasslands (Glassman et al., 2021), while another indicates a significant increase in vertebrate alpha diversity after burning (Pastro et al., 2011). In contrast, wildfires show mixed outcomes. Several studies report that wildfires yield neutral or negative effects on native plant performance (Alba et al., 2014) and a decline in soil fungal richness (Glassman et al., 2021). In bird communities, wildfires affect a greater number of species and produce more pronounced shifts in community composition compared with prescribed burns (Latif et al., 2021).

Beta diversity patterns diverge similarly. Studies indicate that prescribed burns lead to minor shifts in community composition and lower beta diversity (Pastro et al., 2011; Alba et al., 2014), whereas wildfires result in higher species turnover and greater alterations in community structure. Responses vary with ecosystem type and geography; for instance, wildfire effects on birds in dry conifer forests and native species in arid shrublands contrast with the more moderated changes produced by prescribed burns in temperate grasslands and heathlands (Pastro et al., 2014; Latif et al., 2021). To our knowledge, no studies compare wildfires and prescribed burns in boreal forest.

Two organism groups that are negatively affected by forest management and are in focus for restoration measures are polypores and saproxylic beetles. These taxa include many species that are affected by or dependent on fire and they impact the post-fire environment by controlling decomposition rates and nutrient availability (Geiszler et al., 1980; Kluting et al., 2023). These groups respond to fire in different ways. The consumption of deadwood by fires results inevitably in an immediate decline in occurrences and species of wood-inhabiting fungi (Penttilä et al., 2013; Koivula and Vanha-Majamaa, 2020). However, fire may also form large inputs of dead wood, the basis for wood-inhabiting communities, to develop during many decades (Ylisirniö et al., 2012). The amount of dead wood is the strongest factor related to abundance and species richness of polypores (Junninen and Komonen, 2011; Ylisirniö et al., 2012). The short-term effects of wildfire or prescribed burning on wood-inhabiting species including beetles (Hyvärinen et al., 2009; Johansson et al., 2011) and wood fungi (Penttilä and Kotiranta, 1996; Junninen et al., 2008; Olsson and Jonsson, 2010) are relatively well studied. However, long term effects of forest fire remain a knowledge gap. The few existing studies consist of retrospective chronosequence studies of beetles, 29 (Boulanger and Sirois, 2007) and 16 (Toivanen and Kotiaho, 2007) years after fires and two experimental studies of wood fungi 1–22 years (Junninen et al., 2008) and 1–16 years after prescribed fire (Ramberg et al., 2023).

Many insect species are directly attracted to burned areas and some breed almost exclusively in burned forest (Saint-Germain et al., 2008; Hjältén et al., 2018). Fire immediately induces changes in the beetle communities where beetle richness and abundances increase the first few years after fire (Hyvärinen et al., 2005; Saint-Germain et al., 2008). After a few years species richness and abundance decrease to pre-disturbance levels although species composition might still differ after a decade (Hekkala et al., 2014; Heikkala et al., 2016a; Fredriksson et al., 2020). Importantly, the habitat qualities and the species pool of the surrounding landscape are important drivers for the polypore and beetle species compositions formed after disturbance (Saint-Germain et al., 2008; Kouki et al., 2012; Moor et al., 2021). Large scale fires in human altered landscapes and comparisons between wildfires and prescribed burns in boreal ecosystems remain unstudied.

In this study we take advantage of a unique event with three large wildfires and five prescribed burns of similar age in northern Sweden where natural fires have been suppressed since early 1900s. The wildfires occurred in landscapes with different management history providing the opportunity to study whether prescribed burns may provide similar habitat qualities for saproxylic organism as wildfires and to investigate the variation of beetle and polypore assemblages among wildfires. While immediate positive effects of prescribed burning on saproxylic beetles (including pyrophilic species) are well documented, decadal or longer impacts are not. We were particularly interested in species known to be favoured by fire and by species of conservation concern, i.e. nationally red-listed species, fire associated species, species in management programmes and species under the EU habitat directive. We compared beetle and polypore assemblages on 12 years old wildfires in northern Sweden with prescribed burns of similar age and unburnt forests.

This study explored to what extent deadwood volume and composition of dead woodand abundance, richness and diversity and assemblages of polypores and saproxylic beetles differ between a) wildfires and prescribed burns, and b) between burned areas and unburned areas.

We hypothesize that:

1. Wildfires provide a variety of different habitats because of the structure of the pre-fire forest. Prescribed burns will only capture parts of this variation and provide lower amounts and different composition of deadwood than wildfires.
2. As a consequence, abundance, richness and diversity of polypores and saproxylic beetles will be lower at prescribed burns compared with wildfires and lower in unburned than in burned plots.
3. Assemblages will be affected by fire and the effects will differ between wildfires and prescribed burns. Prescribed burns will overlap with unburned controls and wildfire. Beta-diversity will be lower in prescribed burns than in wildfires for both polypores and beetles. Wildfires will only to a small extent overlap with unburned controls after 12 years
4. The successional stage of polypore and saproxylic beetle communities will differ a decade after fire although a large proportion of the communities will overlap. Polypores will still be dominated by early successional species while the saproxylic beetles will have entered an intermediate phase and be dominated by fungivores. Pyrophilous species will not be present after 12 years.
5. Total numbers and frequencies of species of conservation interest will be higher at unburnt conditions although taxa favoured by fire will occur in higher abundances after wildfire and to a lesser degree after prescribed burning.

2. Method

2.1. Study areas and design

In this study we sampled three wildfires, three unburned control areas and five prescribed burns in Norrbotten County, northern Sweden (Fig. 1). All study areas are in the northern boreal zone (Ahti et al., 1968) and represent a gradient from the dominant managed forest landscape to old-growth stands. The wildfires occurred in 2006 and the prescribed burns between 2005 and 2008. The prescribed burns included all prescribed burns performed during that time by Sveaskog, the main forest owner in the area. The wildfire in Lainio was located in a landscape with a mosaic of wetlands and old-growth forests dominated by spruce with presence of birch. The fire originated from burning a clear-cut which is used as soil preparation method in the area. The fire was a crown fire with very high tree mortality. The wildfire in Muddus (Muttus) National

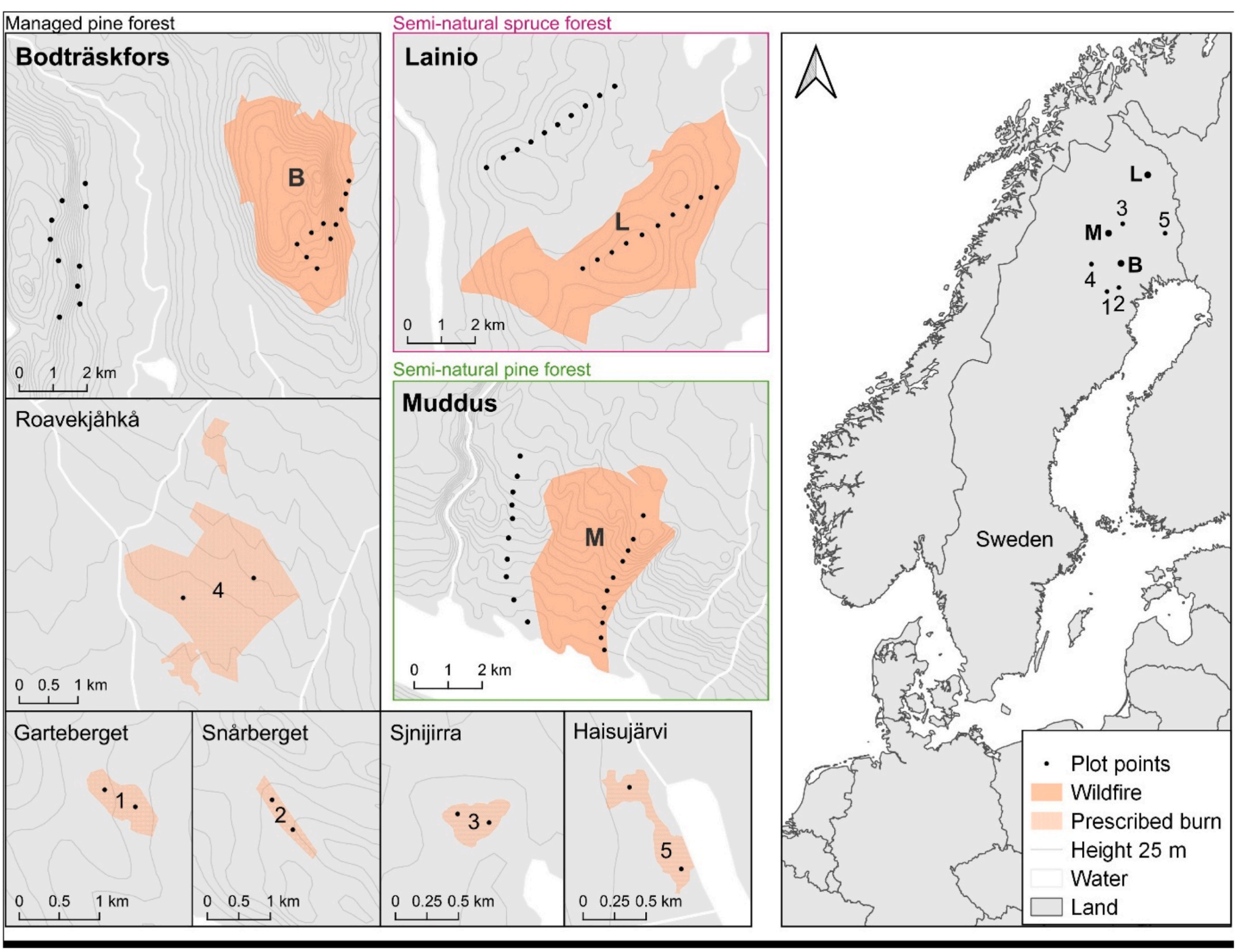

Fig. 1. Study area in northern Sweden with the three wildfire areas; Lainio (L), Muddus (M) and Bodträskfors (B), with unburnt forest comparisons and the five prescribed burns 1–5. Two main comparisons forest were made; 1) wildfire and unburnt forests and 2) managed pine forest including only Bodträskfors and the prescribed burns.

Park, was started by lightning and comprise a pine forest on a south-facing slope where selective felling of large trees had occurred historically. The area has a long-documented fire history where the last large wildfire before 2006 occurred in 1933 (Uggla, 1958; Engelmark, 1984). The wildfire in 2006 was a low-intense ground fire with intermediate mortality and damaged trees died the years following the fire. The wildfire in Bodträskfors and the prescribed burns occurred in managed forest landscapes, with clear-cuts, forests of different successional stages and patches of mature coniferous forest. The Bodträskfors wildfire was started after an accidental ignition by a forestry machine and caused high tree mortality. An area of ~900 ha was salvage logged. Our sampling was performed in an area of 300 ha set aside for conservation that was not salvage logged. Nearby each wildfire an unburnt area with similar topography and stand characteristics was selected as a control (Table 1). The prescribed burns in Garteberget, Snårberget and Roavejahka were situated in coniferous dominated managed landscapes. The stands were silviculture stands with low natural values. The prescribed burns in Sjnijrra and Varjisån are situated in Ecoparks that are landscapes where 50 percent of the area are managed for biodiversity conservation. The prescribed burn in Sjnijrra was a mixed coniferous forest and Varjisån was pine dominated with some old growth characters. For all prescribed burns tree mortality and post-fire deadwood volumes were relatively low (Fig. 1; Table 1).

2.2. Inventory of stand characteristics

We surveyed deadwood in 10 sample plots at each wildfire and unburned forest and 2 plots in each prescribed burn (this gives in total 10 plots in prescribed burns) in 2018, 12 years after the wildfires. Sample plots were placed along transects, at least 140 m apart and had a radius of 25 m (Fig. 1). In the plots, we measured all deadwood items with the base inside the plot, a minimum base diameter of >10 cm and length >1.3 m (Gibb et al., 2005). The length was measured from the base to the spot where the diameter equalled 5 cm. For each log, tree species identity, the maximum diameter, the minimum diameter (>5 cm), length, proportion burnt (%), ground contact (%), type of stem breakage (at base, at stem, or sawed). For standing dead trees with a height >1.3 m we recorded diameter at breast height (DBH), their total height, type (i.e., snag or high stump). Decay class was classified in four categories for logs and 5 categories for snags (Gibb et al., 2005). The decay classes for logs were; 1 = bark intact or starting to loosen,>50 % bark remaining, wood hard; 2=<50 % bark remaining, surface of wood smooth, but beginning to soften, wood hard; 3 = lacking bark, surface of wood soft, some crevices and some small pieces of wood lost or bigger wood fragments lost with a deformed surface; and 4 = lacking bark, wood soft, but still possibly having a heart of hard wood, surface of object hard to define, outline of object indefinable. For snags categories were; 1 = All bark and branches intact, 2=<50 % bark remaining, fine branches intact, 3 = bark gone, coarse branches left, 4 = Wood hard, no branches but top intact, 5 = No branches, top broken. When more than one decay class was present, we recorded the dominant decay class in respect to volume. We also calculated the basal area (m^2) of living trees within a smaller subplot (r = 10 m) by measuring the DBH. Three trees representative of the plot (of different tree species if relevant) were measured for age and height. Heights above 2 m were measured using a clinometer and age by counting tree rings using an increment borer at DBH height. For plots with a high density of logs and/or snags, and where the deadwood was evenly distributed in the plots, only 25 or 50 % of the plot areas were surveyed due to time constraints. In those cases, the numbers were multiplied to represent the total plot area. This was done at 8 plots for snags and 13 plots for logs, of a total of 70 plots. Wood volume was calculated for the snags, high stumps and logs separately in accordance with the method used by the 'The Swedish National Forest Inventory' (Näslund, 1947; Edgren and Nylinder, 1949; Ollas, 1980).

2.3. Inventory of polypores and insects

Sporocarps of polypores and the fire-associated ascomycete *Daldinia loculata*, hereafter collectively termed 'polypores', were recorded as presence and not counted on wood units. The inventory took place in the beginning of September of 2018. We limited our inventory to only logs >15 cm in diameter and >1.3 m in length, hence excluding smaller logs and snags. Sporocarps were surveyed in the entire plot also when deadwood was measured in half or one quarter of the plot part due to high density of logs. A small mirror was used to survey the underside of the logs whenever possible. Polypores were identified to species in field or collected if microscope was needed for identification. Species identification was made using Ryvarden and Melo (2017) and by consulting expertise when needed. Traits and red-list category were compiled from SLUArtdatabanken (2023) and Ottosson et al. (2014). Voucher specimens have been deposited in the Herbarium UME, Department of Ecology and Environmental Science, Umeå University.

We collected beetles in flight intercept traps (Polish IBL2) placed in the centre of each plot (Appendix 1). The traps consist of a triangular semi-transparent plastic intercept of ~0.35 m^2. The traps were tied between two living trees using ropes. If no living trees were close to the plot position we used standing dead trees. The traps had a water removing funnel and a collecting bottle of 600 ml that was filled to a third with propylene glycol mixed with water (50/50) and a small amount of detergent (Johansson et al., 2010). The traps were put up in the beginning of June 2018 and taken down in the beginning of September the same year. All beetles were identified by experts. Taxonomy and nomenclature for all species follow (SLUArtdatabanken, 2023). Saproxylic beetles were identified based on literature (Speight,

Table 1
Description of sampled burned areas including type of fire, forest type, management history and size of the burned area.

	Lainio	Muddus	Bodträskfors	Garteberget	Snårberget	Sjnijirra	Roavekjåhkå	Haisujärvi
Fire size [ha]	400	300	300 (1800)[a]	6	5	2	83	3
Year burned	2006	2006	2006	2008	2005	2006	2006	2006
Coordinates [WGS84]	67.90°N, 22.16°E	66.76°N, 20.16°E	66.15°N, 20.82°E	65.57°N, 20.07°E	65.65°N, 20.67°E	66.95°N, 20.87°E	66.13°N, 19.27°E	66.76°N, 23.03°E
Management history	Selective felling, clear-cut burning, reindeer herding,	National park, reindeer herding	Rotation forestry, reindeer herding	Rotation forestry, reindeer herding	Rotation forestry, reindeer herding	Selective felling, reindeer herding	Selective felling, reindeer herding	Rotation forestry, reindeer herding
Tree mortality, fire type	High, crown fire	Medium, ground fire	High, mixed ground and crown fire	Low, ground fire	Low, ground fire	Medium, mostly ground fire	Medium, mostly ground fire	High, mostly crown fire
Forest type	Spruce, semi-natural	Pine, semi-natural	Pine/mixed coniferous, managed forest	Pine, managed forest	Pine, managed forest	Mixed coniferous, Ecopark[b]	Pine, Ecopark[b]	Pine, managed forest

[a] Area with retained forest and in brackets the total area burned.
[b] Ecopark = a landscape where 50 % of the area is managed for biodiversity and 50 % for biomass production.

1989; Stokland et al., 2012) and red-list category was based on SLUArtdatabanken (2020). Fire-dependence was based on Wikars (2006) and include "**fire-dependent insects"** defined as species that exhibit strong behavioural specialization for fire and/or have the majority of their known occurrences on recently burned sites; "s**trongly fire-favoured insects (0–5 years)" that are** species that either exhibit a behavioural response to smoke, fire, or ash, or are significantly more abundant in burned compared to unburned habitats or substrates (Combination of class 2 and 3 from Wikars (2006)). and "**fire-favoured insects (>5 years)"**. This category includes species for which fire creates optimal development conditions, often through increased sun exposure and specific wood substrates from fire-killed trees.

2.4. Statistical analysis

All analyses were performed in R (Posit Team, 2025) and included all saproxylic species. To analyse differences between wildfires and unburned areas we included all three physical locations (Lainio, Muddus and Bodträskfors). The prescribed burns were only compared with the unburnt and wildfire areas of Bodträskfors, because the prescribed burns were located in pine dominated and managed landscapes similar to Bodträskfors. For this comparison we included 10 sample plots in each treatment (wildfire, prescribed burn, unburned control) which means that the analysis was based on a balanced design. In the NMDS-plot all data is included.

To test differences in deadwood volumes, abundance and richness among treatments we used a negative binomial generalized linear model in the *MASS* package (Venables and Ripley, 2002) and performed Tukey's tests in *multcomp* (Hothorn et al., 2008). Abundance was defined as number of individuals for beetles and frequency i.e., the number of logs on which the species occurred, for polypores. We calculated Shannon diversity index in the *vegan* package (Oksanen et al., 2017) and analysed differences in diversity with a one-Way ANOVA and Tukey's test for polypores and a Kruskal Wallis test, followed by Wilcoxon-Mann-Whitney tests with Bonferroni corrections for beetles (Iversen, 2011; Rey and Neuhäuser, 2011).

We tested for differences in species composition and beta-diversity among treatments with Permanova and betadisper in the "Vegan" package (Oksanen et al., 2017). Beta-disper also provide a dispersion-test of the Permanova. We then visualized the results using two-dimensional non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities in the "MASS" package (Venables and Ripley, 2002). A dummy-species was added to the polypore species matrix as NMDS cannot handle plots without records. The NMDS plot for the beetles presented in the results have three sample plots removed, classified visually as outliers, i.e., because the NMDS including all plots (Appendix 2) was hard to visually evaluate, we removed the three sample plots that was furthest away from the centre of the graph. However, all plots were included in the Permanova.Indicator species analysis was performed with the package "indicspecies" (De Cáceres and Legendre, 2009).

3. Results

In total, we recorded 50 polypore species and the ascomycete *Daldinia loculata*, and 331 saproxylic beetle species of which 18 and 21 were nationally red-listed (SLUArtdatabanken, 2020), respectively, and one beetle species, *Stephanopachys substriatus*, was listed in the habitat directive annex 2 species list and included in a Species Action Program for conservation of fire-dependent insects in boreal forests (Wikars, 2006). Three of the polypores species and *D. loculata* and 22 beetle species were classified as fire associated. The total number of polypore occurrences and beetle individuals were 829 and 9116, respectively. Overall, the three most abundant polypore species were *Trichaptum fuscoviolaceum*, *T. abietinum*, and *Fomes fomentarius*, and made-up 42 % of the sporocarp occurrences, while the most abundant beetle species'; *Cryptophagus lapponicus*, *Euplectus mutator* and *Enicmus* spp.*;* made up 30 % of the captures (Appendix 3–5).

3.1. Volume and composition of deadwood

After 12 years the volume and composition of deadwood differed among wildfires and prescribed burnings and unburned controls. Our results confirmed our first hypothesis and the 22 m^3ha^{-1} total deadwood volume in prescribed burned areas comprised around half of volume in the wildfire or in the unburned control in Bodträskfors. The prescribed burns contained only one m^3ha^{-1} deciduous logs, which was significantly lower than the wildfire (Fig. 2). In prescribed burns the proportions of deadwood of decay stage 4 comprised 25 % of the total deadwood volume while for wildfire decay stage 4 comprised less than 5 % (Fig. 3).

For pine logs average volumes were significantly higher in wildfires and prescribed burns compared with unburned control (11 ± 5, 14 ± 8 and 20 ± 20 m^3ha^{-1}, for control, prescribed burns, and wildfires, respectively). On average the wildfire areas had twice as much total volume of deadwood per ha than the unburnt forests, 45 m^3ha^{-1} vs 23 m^3ha^{-1}. The wildfire in Lainio had significantly higher volumes of logs and snags of spruce than the control. For Muddus the volume of pine snags was significantly higher in the wildfires while the volumes of pine logs did not differ. In Bodträskfors the control had lower amounts of pine logs than both wildfires and prescribed burns. Wildfires had significantly higher volumes of coniferous logs, snags and deciduous snags (only Lainio and Muddus), but similar amounts of deciduous logs (Fig. 2) compared with unburnt forests. The wildfire in Lainio caused higher tree mortality than in Muddus and Bodträskfors and hence contained higher volume of snags (Fig. 2). In the wildfires and prescribed burns deadwood of decay stage 1 and 2 comprised between 60 (for prescribed burns and Muddus) and 90 percent (Bodträskfors) (Fig. 3).

3.2. Species richness, abundance and diversity

Hypothesis 2 was partly supported for polypores. Across all areas, polypore abundance was higher in wildfires than in unburned controls, and species richness tended to be higher overall, while species diversity did not differ between wildfire and unburned areas (Table 2; Fig. 4). The higher richness in wildfire was significant in Muddus but not in Lainio or Bodträskfors (Table 2), whereas abundance was higher in wildfire in all three areas (Table 2). In the managed pine forest (Bodträskfors), prescribed burns had lower polypore abundance and richness than both wildfire and control (Table 2), and lower diversity than both (Fig. 4), contrary to the expectation that prescribed burns would exceed the unburned forest. Wildfire also was higher than the control for polypore abundance in Bodträskfors (Table 2).

For beetles, hypothesis 2 was not supported. Beetle abundance and richness did not differ between wildfires and unburned controls, and species diversity likewise did not differ (Table 2; Fig. 4). No area showed a significant wildfire effect on beetle richness or abundance (Table 2). Within Bodträskfors, beetle abundance was marginally higher in the control than in the prescribed burns (Tukey $p = 0.0504$), while prescribed burns did not differ from wildfire; richness and diversity did not differ among treatments (Table 2; Fig. 4).

3.3. Assemblage composition

In Bodträskfors, assemblage composition differed among wildfire, unburned forest and prescribed burns for both polypores (Permanova, $p < 0.001$) and beetles (Permanova, $p < 0.001$). The variation explained by treatment was 30.0 % for polypores and 17.5 % for beetles (Fig. 4). Hypothesis 3 were partly supported. Beta-diversity of polypores were lower in the prescribed burns than in both wildfire and control (beta-disper, $p=0.012$). For beetles, beta-diversity was higher in wildfires and prescribed burns compared with the control (beta-disper, $p=0.019$).

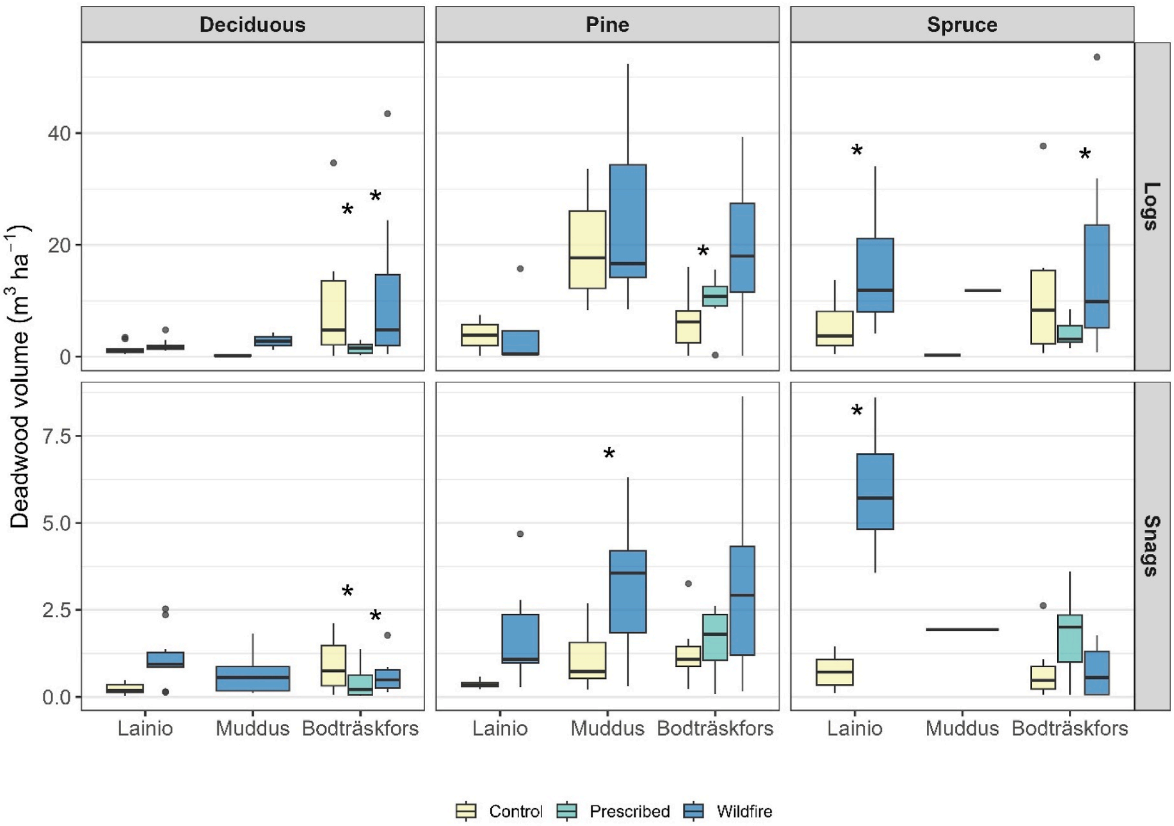

Fig. 2. Log and snag volume per area and treatment, divided among deciduous trees, pine and spruce. Each individual boxplot has an n = 10. P-values refer to results from GLM and reflect differences within each study area and dead wood type.

When comparing all wildfires to their unburned controls, assemblage composition differed between wildfire areas and unburnt forests for polypores (Permanova, $p < 0.001$) and beetles (Permanova, $p < 0.001$), supporting hypothesis 3. Beta-diversity did not differ between wildfires and unburnt controls for beetles (beta-disper $p = 0.112$) but did for polypores (beta-disper, $p = 0.008$). Assemblage composition differed among study areas for both taxa (polypores; F = 6.8694, $p < 0.001$, beetles; F = 5.284, $p < 0.001$). For polypores 15,9 % and 16,6 % of the variation in the polypore community was explained by the treatment (wildfire vs. unburned control) and the study area, respectively. For beetles treatment explained 4.8 % of the variation while study area explained 15.6 % (Fig. 5).

The indicator species largely confirmed hypothesis 4 where early successional species were expected as indicators for polypores and mid-successional fungivores were expected to be indicators for beetles. The indicator species analysis showed that six polypores were indicators of burned areas (wildfire areas and prescribed burns); *Trichaptum fuscoviolaceum, T. abietinum, Gloeophyllum sepiarium, Amyloporia sinuosa, Amyloporia xantha* and *Daldinia loculata*, having 82–100 % of their records at the wildfires or prescribed burns (Appendix 6). They constituted 54 % of the sporocarp records and were among the 11 most frequently recorded fungi. The first two are pioneer generalist species, the latter frequently occurring generalists and the last two specialised and dependent on burned wood. One species, *Fuscoporia viticola*, was associated with unburned forest conditions.

For beetles 5 species were indicators for wildfire areas and 17 species were indicators of unburned control areas (Indicator species analysis, S4). The indicator species for burned areas was mainly fungivores such as *Anomognathus cuspipdatus* and *Sericus brunneus*. The indicator species for control areas included several common bark beetles that frequently occur in shaded conditions e.g., *Dryocoetes autographus* and *Polygraphus poligraphus* but also several fungivores and predators. Within the managed pine forest, one species was a significant indicator for the prescribed burns; the cambivore *Epuraea silacea,* known to be linked to younger forests (SLUArtdatabanken, 2025).

3.4. Red-listed and fire-associated species

For polypores a total number of six fire-associated and 18 red-listed species were found. The red-listed species were more species rich in unburned control areas and many of the red listed species only occurred in unburned controls. However, some species, e.g. *Diplomitoporus crustulinus,* occurred only in the wildfires. Fire-associated species occurred in all forest types and while most species occurred in low number some species like *Amyloporia sinuosa* occurred on 35 substrates in wildfires, one in prescribed burns and two in unburned controls and *Daldinia loculata* occurred on 19 substrates, only in wildfires. (Appendix 3, Appendix 4).

For beetles we encountered 3 fire dependent, 13 strongly fire-dependent and 6 fire dependent species. All species categories were present in all forest types. For some more frequent species it was clear that abundance was much higher in wildfires than prescribed burns or unburned controls. For example, the strongly fire-favoured *Anomognathus cuspidatus* were around 5 times as abundant in wildfires and *Dacne hispidulus* showed double abundance in wildfires compared with unburned controls. In contrast, *Phloeostiba lapponica* were equally abundant in the wildfires and unburned controls and was much more abundant in Muddus than in Lainio and Bodträskfors. We encountered 19 red-listed species also spread over all forest types and burned areas (Appendix 3, Appendix 4).

The 19 red-listed beetle species were evenly distributed on all forest types and most species were represented by only a few specimens. However, some red-listed species were more frequent and the fire-dependent and red-listed *Stenotrachelus aeneus* occurred with 29

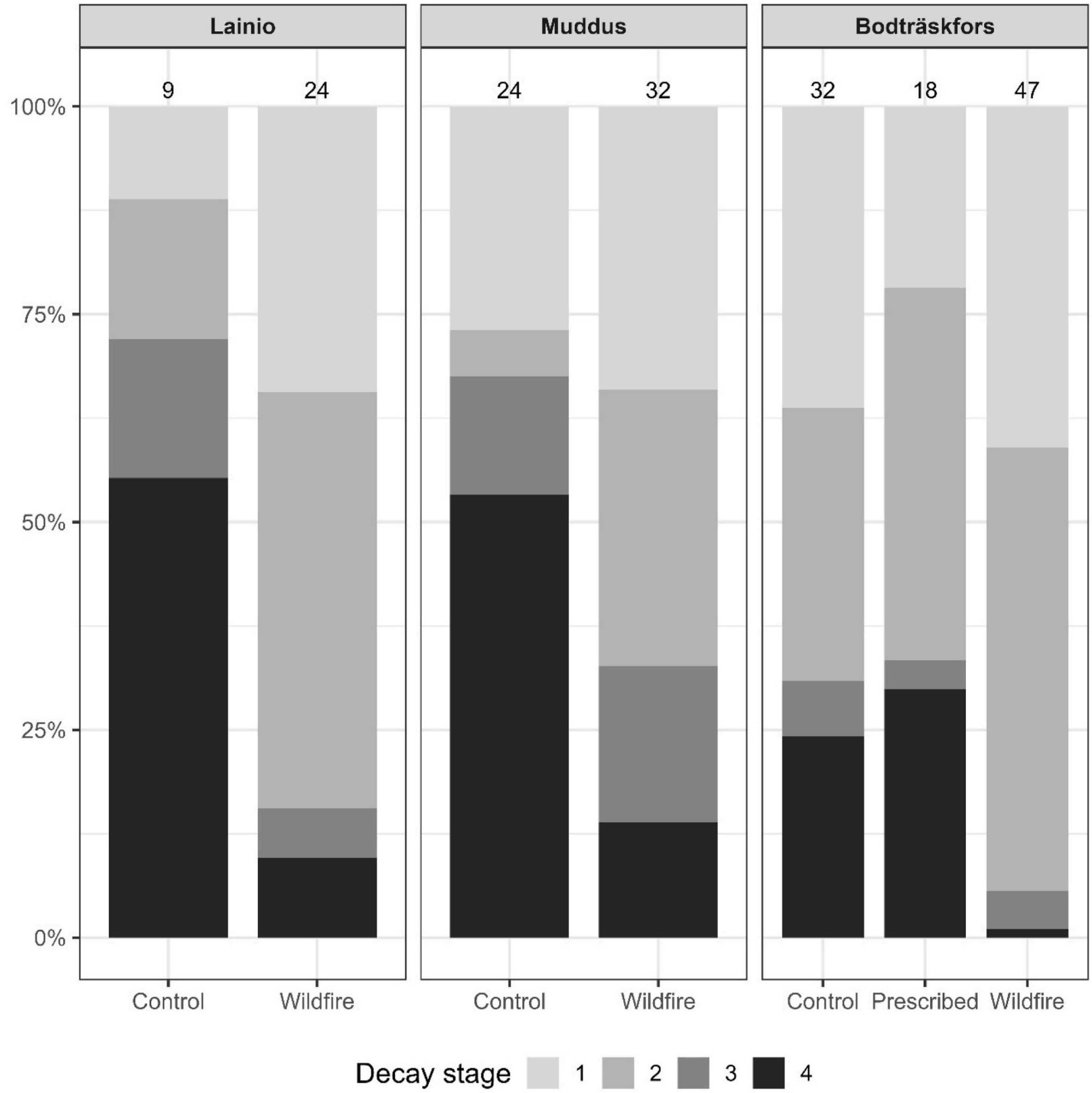

Fig. 3. Proportions of coniferous logs of different decay stages in the different burned areas. Total volumes (cubic metres summed over the 10 sampling plots) are given above each bar.

specimens in wildfires, 10 in prescribed burns and 11 in unburned controls (Appendix 3, Appendix 4).

4. Discussion

We studied decadal effects of wildfires and prescribed burns and show that wildfires and prescribed burning affect both the habitat structure and community composition of polypores and saproxylic beetles in northern Sweden. The study include fires that occurred in standing forest and no area was salvaged logged. Thus, our results are not comparable with prescribed burning of clear-cuts. Neither salvage logged wildfires nor prescribed burning of clear-cuts provide high volumes of deadwood for saproxylic beetles and polypores and burned clear-cuts have been suggested to act as ecological traps, attracting species that cannot reproduce there (Wikars, 1995; Robertson and Hutto, 2007; Robertson, 2012). For polypores stumps on burned clear-cuts have been shown to potentially host red-listed species (Suominen et al., 2018) but higher numbers of species occurred in sites with higher retention levels (Suominen et al., 2015). Thus, although we do not compare with salvage logged areas in this study, we expect the effect size of burning on saproxylic species to be much more pronounced.

4.1. *Volume and composition of deadwood*

Consistent with prediction 1, we found higher volumes of logs and snags in the wildfire areas compared with the prescribed burns and unburned controls. However, more decayed deadwood was less abundant in the burned areas, as it was consumed by fire. In the prescribed burns the small volumes of deadwood in later decay stages were probably a result of low pre-burning deadwood volumes but the relatively high proportion of decayed wood was a result of low burning intensity. For both the wildfires and the prescribed burns the amount and types of deadwood was a result of the conditions of the pre-fire forests and the fire characteristics. The fact that we do not have data on the stand structure and deadwood composition before fire limit the possibilities to disentangle these effects but some conclusions can be drawn based on the postfire forest. The high number of snags that originated from the

Table 2
Model output from negative binomial tests (4 models, one comparing the wildfires (model 1) and the others per area (model 2–4)) and a pairwise Tukey test in the managed pine forest (Bodträskfors) on richness and abundance of beetles and polypores among treatments. Intercept representing unburned control.

Taxa	Test	Predictors	Estimate	SD/SE	Z-value/Z-ratio	P-value
Beetles	*neg. glm*	**Richness** ~ Treatment				
		1. Wildfire (All)	−0.07004	0.12244	−0.572	0.567
		2. Wildfire (Muddus)	0.14290	0.11876	1.203	0.229
		3. Wildfire (Lainio)	−0.05158	0.18906	−0.273	0.785
		4. Wildfire (Bodträskfors)	−0.3391	0.2623	−1.293	0.196
		Prescribed burns	−0.2546	0.2619	−0.972	0.331
	neg. glm	**Abundance** ~ Treatment				
		1. Wildfire (All)	−0.1574	0.1747	−0.901	0.367
		2. Wildfire (Muddus)	0.01124	0.23627	0.048	0.962
		3. Wildfire (Lainio)	0.1304	0.3004	0.434	0.664
		4. Wildfire (Bodträskfors)	−0.3943	0.3136	−1.257	0.2087
		Prescribed burns	−0.7348	0.3141	−2.339	**0.0193**
	pairwise tukey	Abundance ~ Treatment (Bodträskfors)				
		Control – Prescribed burns	0.735	0.314	2.339	*0.0506*
		Control – Wildfire	0.394	0.314	1.257	0.4196
		Prescribed burns - Wildfire	−0.341	0.322	−1.058	0.5402
Polypores	*neg. glm*	**Richness** ~ Treatment				
		1. Wildfire (All)	0.2967	0.1523	1.948	*0.0514*
		2. Wildfire (Muddus)	0.5500	0.2359	2.332	**0.0197**
		3. Wildfire (Lainio)	0.1886	0.2127	0.887	0.375
		4. Wildfire (Bodträskfors)	0.2567	0.1951	1.316	0.1883
		Prescribed burns	−0.8804	0.2409	−3.654	**<0.001**
	pairwise tukey	Richness ~ Treatment (Bodträskfors)				
		Control – Prescribed burns	0.880	0.241	3.654	**0.0008**
		Control – Wildfire	−0.257	0.195	−1.316	0.3864
		Prescribed burns - Wildfire	−1.137	0.235	−4.836	**<0.001**
	neg. glm	**Abundance** ~ Treatment				
		1. Wildfire (All)	1.0261	0.2153	4.766	**<0.001**
		2. Wildfire (Muddus)	1.2358	0.3650	3.386	**<0.001**
		3. Wildfire (Lainio)	0.7928	0.2396	3.308	**<0.001**
		4. Wildfire (Bodträskfors)	1.0642	0.2838	3.75	**<0.001**
		Prescribed burns	−0.8630	0.3104	−2.78	*0.00543*
	pairwise tukey	Abundance ~ Treatment (Bodträskfors)				
		Control – Prescribed burns	0.863	0.310	2.780	**0.0150**
		Control – Wildfire	−1.064	0.284	−3.750	**<0.001**
		Prescribed burns - Wildfire	−1.927	0.302	−6.380	**<0.001**

fire suggest that mortality was higher in the wildfire. The wildfire in Bodträskfors had areas with 80–100 % tree mortality and areas where many snags had fallen over. There were also visible remnants of peat combustion. Together this suggests an intensive fire. In the prescribed burns, the field layer had largely recovered, the remaining trees had no emerging fire scars, tree-mortality was low and deadwood in late decay comprised relatively high proportions. Together with the fact that there were very few signs of combusted deadwood (like linear, scarred cavities on the ground), this suggest that the burning intensity was low.

The crown fire in Lainio and the intense fire in parts of the Bodträskfors area caused high mortality resulting in a pulse of added fresh deadwood. A decade later the deadwood in these areas was dominated by intermediate decay classes. In Muddus the less intense ground fire resulted in gradual mortality of the pines and deadwood was added over time. Natural forest fire in Fennoscandian forests were typically low intense with a high tree survival although stand replacing fires also occurred (Berglund and Kuuluvainen, 2021). The wildfire in Muddus is probably the wildfire that was most similar to a historical wildfire. Our results are consistent with Ramberg et al. (2023) showing that burning of spruce dominated forests results in large volumes of deadwood that benefit biodiversity in the long term. In addition, we show that prescribed burns rarely contribute with similar amounts of deadwood as a wildfire.

4.2. Species richness, abundance and diversity

For polypores but not for beetles our results were in line with our hypothesis that prescribed burning does not reach similar effects as a wildfire. We hypothetizised that abundance, richness and diversity of polypores and saproxylic beetles would be lower at prescribed burns compared with wildfires. We found that for polypores prescribed burning had lower richness, abundance and diversity while for beetles these was no or marginal differences. For polypores these patterns is probably a direct effect of the higher volumes of deadwood in the wildfire. This is supported by the strong effect for the abundance that is directly associated with the volume of deadwood in the sampling plots. We measured abundance of polypores as the number of deadwood substrates a species occur on. Richness and diversity are more limited by the local species pool and thus respond less dramatic to increased deadwood volumes. Similar results have been shown by (Suominen et al., 2015) in a controlled experiment where plots with higher deadwood volumes supported higher abundance and richness of polypores.

The lack of differences between wildfires and prescribed burns for beetles suggests that the peak of cambivores and fungivores that colonise burned areas immediately after fire has levelled off and the available deadwood is now suitable for wood-boring species and fungivores that are less abundant. Similar patterns have been shown when analysing decadal beetle succession in the wildfire area in Muddus (Fredriksson et al., 2020) and for prescribed burns (Larsson Ekström et al., 2024).

We hypothesised that wildfires would have higher abundance, richness and diversity than the unburned controls. This hypothesis was partly supported for polypores with higher abundance and similar richness and diversity in the wildfires as in the unburned controls. This shows that the deadwood created by the wildfires suits many polypores. This is in accordance with other studies on prescribed burned sites showing that burned areas start to develop suitable habitat for polypores to form sporocarps after 10–15 years (Suominen et al., 2019; Ramberg et al., 2023).

For beetles our hypothesis was rejected, and the only detected

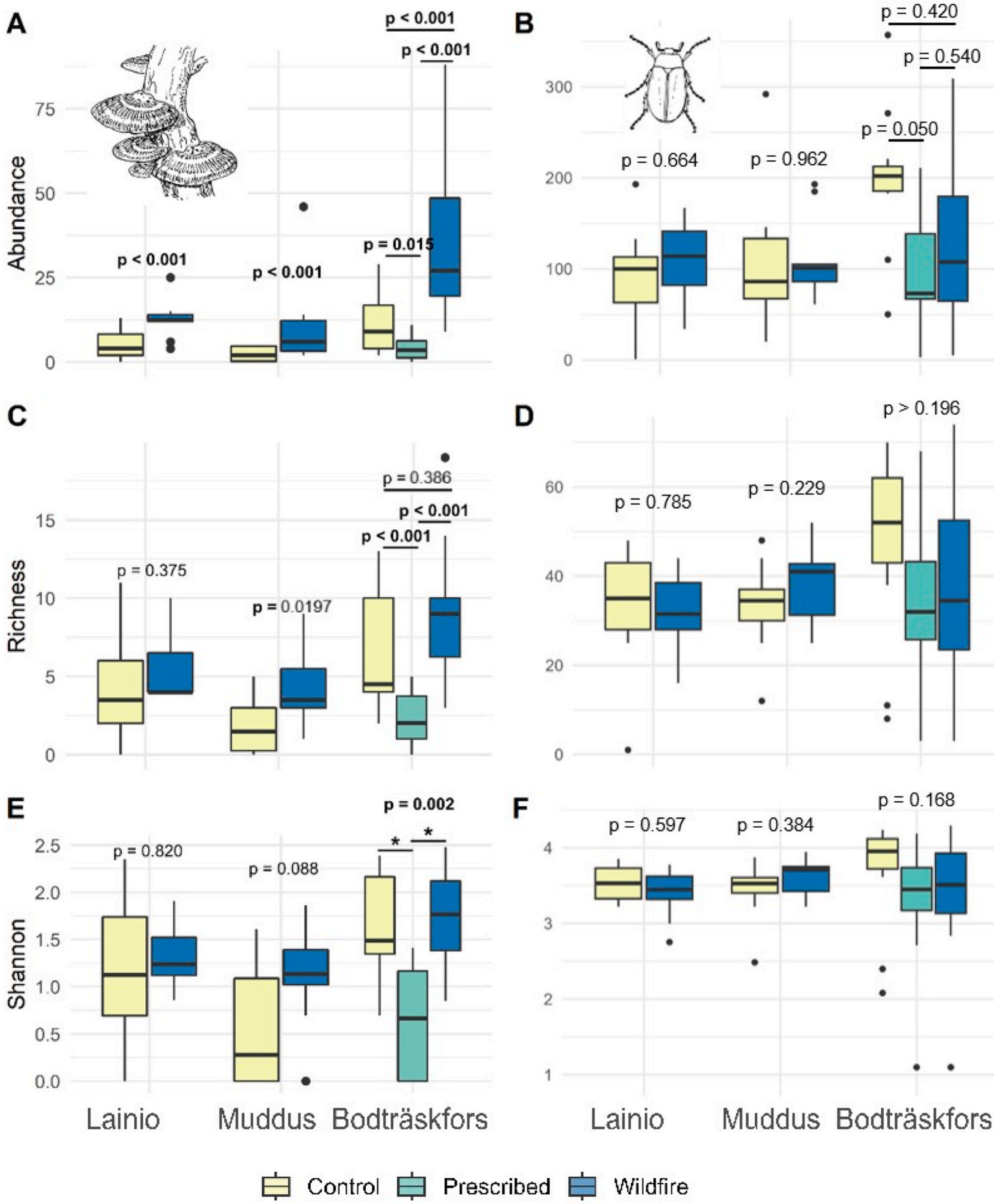

Fig. 4. Abundance, richness and Shannon-Wiener index of polypores (left column) and beetles (right column) at the three areas and among treatments. Note the different scales on the y-axis for polypores and beetles. Significant differences (p-value) are based on the result of negative binominal generalized linear model (with Tukey HSD pairwise test) for abundance and richness, and Kruskal Wallis test and Wilcox pairwise comparisons for the Shannon-Wiener index (denoted by a '*'). Bold letters indicate a p-value of less than 0.05. Each individual boxplot has an n = 10.

difference was higher abundance in the control than in both the wildfire and the prescribed burning in Bodträskfors. The higher abundance in the unburned control can be attributed to the generalist fungivores such as *Cerylon histeroides*, *Cryptophagus lapponicus*, *Euplectuss* spp. and *Enicmus rugosus*. All these species clearly favoured the unburned control in Bodträskfors but in the other burned areas they were more evenly distributed on wildfire areas and unburned controls. The reason for the differences among wildfires could be that the burned area in Bodträskfors contained less spruce and were thus less attractive for the spruce associated species and that Bodträskfors burned more severly than the Muddus ground fire and thus suitable habitat for these species were destroyed in Bodträskfors. Another explanation is that the unburned control in Bodträskfors contained relatively high volumes of suitable substrate for fungivores. Since the surrounding landscape is a mosaic of clear-felled areas and retention patches with high-quality deadwood and high edge density, it likely provides a continuous input of deadwood for fungivores.

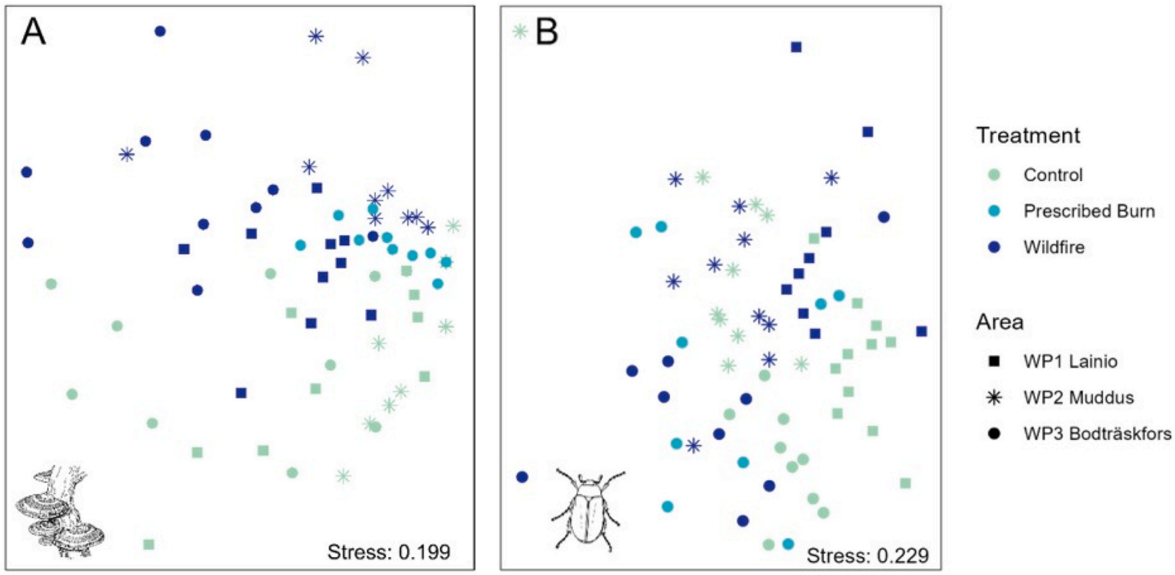

Fig. 5. NMDS ordination of the polypore (A) and saproxylic beetle (B) community compositions at unburnt forests or subjected to wildfire or prescribed burning a decade before the study at the three study areas; Laino, Muddus and Bodträskfors. Each symbol represents the species composition in one plot.

4.3. Assemblage composition, red-listed and fire-associated species

Our results were partly in line with our hypothesis that prescribed burning result in assemblages that overlap with both wildfire and unburned control. Assemblage composition differed between wildfire and prescribed burns for both polypores and beetles. For polypores the beta diversity was smaller in the prescribed burns than in unburned controls and wildfires which show that there is less variation among plots for the prescribed burns. This probably contributed to the significant differences in assemblage composition. The position of the prescribed burns in between the wildfire and the unburned control in the NMDS-plot suggest that for polypores the assemblage composition in prescribed burns is a mix of wildfire and unburned controls. For beetles there was considerate overlap in assemblage composition suggesting that the beetle assemblages to a large extent have recovered in both wildfire and prescribed burns. However, the higher beta-diversity in wildfires and prescribed burns indicate that both types of fire contribute with variation also after a decade. The prescribed burns were more spread out in the landscape than the wildfire and part of the beta-diversity for prescribed burns can most probably be assigned to the geographical location and variation in time for the burning. This indicate that wildfires generate more variation within each burned area but that variation from prescribed burns can be achieved by adding a higher number of burns. The higher beta diversity in burned areas might also suggest that the burned areas still have characteristics from intermediate successional stages where later successional species have colonised but earlier successional species, including many fungivores, are still abundant (Fredriksson et al., 2020). The fact that there were indicator species for unburned forest and that these included bark beetles associated with mature forest suggest that neither wildfires nor prescribed burns provide habitat for mature forest specialists after 12 years. For polypores indicator species of unburned forest included species associated with decayed wood, a substrate that was absent in wildfires. Furthermore, the indicator species for wildfire (both polypores and beetles) were not abundant in prescribed burns and the diversity of polypores in prescribed burns were significantly lower than in wildfire areas. These more limited effects of prescribed burning are most probably explained by the lower amount of deadwood and more limited wood qualities. Such differences can also explain why species indicators of unburned forest are less abundant and species indicating wildfire are not benefitted by prescribed burning. In a well replicated experiment, both species richness and abundances of red-listed polypores, particularly at naturally formed wood, was shown to be favoured by burning in stands with 5–50 m^3 wood ha^{-1} in managed spruce forests after 16 years (Ramberg et al., 2023). Similarly, red-listed polypores in burnt pine-forests are reported to increase with time since disturbance (Penttilä et al., 2013). The reason for this not being found in this study is probably lower pre-fire populations of red-listed polypores and lower volumes of deadwood at the prescribed burns and in their nearby landscapes. Furthermore, the deadwood created in the prescribed burns might not provide the qualities needed for more specialised polypores, namely course wood in suitable moist conditions. We lack data on the microclimate in prescribed burns compared with wildfires but potentially the wildfires could provide a higher variation in microclimate because of their larger size and thus also a wider range of moisture conditions for the deadwood generated by the fire. Previous studies have shown that although polypore spores can spread over considerable distances the chance of colonisation is much higher close to dispersal sources (Edman et al., 2004b) and in landscapes rich in old forest containing a continuous supply of dispersal sources and suitable substrates (Edman et al., 2004a). In such forests, abundant beetles like *Dryocoetes autographus*, is attracted to wood infested with polypore species that are now rare in the managed landscape (Johansson et al., 2006) and potentially the beetle can facilitate spread of polypores. The lack of such polypore-beetle associations in managed landscape might contribute to limited dispersal of some polypore species to the prescribed burns in this study.

Fewer pyrophilous and red-listed polypores were found in the managed pine forest compared to the semi-natural study areas, however there were only small differences in beetles. This is consistent with a previous study from the same area (Johansson et al., 2011) showing that pyrophilous species might have lower chance of colonizing burned areas in landscapes with a long history of fire suppression. Other studies show that prescribed burns may have positive short-term effects on beetle abundance and diversity (Hjältén et al., 2017; Hägglund et al., 2020). Polypores respond negatively the first years but many species reappear within five years (Olsson and Jonsson, 2010) and in the long-term polypores benefit from the deadwood generated by fire (Ylisirniö et al., 2012; Ramberg et al., 2023). A recent review shows that prescribed burning in protected areas generate higher quality habitat than prescribed burns in managed stands. In landscapes dominated by managed forest like Fennoscandia, it is however not possible to conserve disturbance dependent species only in protected areas and it is thus necessary to perform prescribed burns outside formally protected areas (Tälle et al., 2023). Thus, the effects of prescribed burning are context dependent and the results depend on e.g. pre-fire conditions, area burned, and the surrounding landscape (Ramberg, 2025). The reason why the prescribed burns in this study show less pronounced effects than in other studies is thus probably a combination of the low production of deadwood and the targeted stands with low natural values and surrounded by heavily managed landscapes.

Consistent with hypothesis 4, burned areas and unburned areas to a large extent shared the same polypore assemblage comprising mainly of species that are not fire-dependent. Differences in assemblage composition and diversity were mainly explained by changed occurrence patterns for these species. However, three fire-favoured fungi (*Amyloporia sinuosa*, *A. xantha* and *Daldinia loculata*) occurred almost exclusively in the wildfire areas. These results suggest that the polypore assemblage in our study is still in an early successional phase and we can expect more species of conservation concern to colonise as the deadwood generated by the fires enter later decay stages, as shown for prescribed burning (Koivula and Vanha-Majamaa, 2020; Ramberg et al., 2023).

Our results for beetles show that there are still differences in assemblage composition between wildfires and unburned controls after 12 years and the indicator species show that late seral species are more frequent in the unburned control. However, there is a large overlap in assemblage composition between wildfire and controls suggesting that the assemblages largely have recovered from the fire. Our results are in line with succession theory where is expected that the abundance, richness and assemblage composition were largely explained the geographical position and the different initial conditions for each wildfire area. Previous studies have found short-term effects, with higher abundance and species richness the first few years after fire (Hyvärinen et al., 2005; Hjältén et al., 2017), but that these initial differences level off after five years (Hekkala et al., 2014; Heikkala et al., 2016a) although differences still exist after 8 years (Larsson Ekström et al., 2024). We show that in northern boreal forests, full recovery after fire might take more than a decade.

We consider the prescribed burns in this study to be comparable to the wildfire in Bodträskfors because they are located in similar forest types, i.e., in a managed matrix of clear-cuts, young forest and patches of older mature forests. This type of landscape dominates the Swedish productive forest landscape and generally has very low amounts of deadwood due to forestry (Felton et al., 2020). However, the unburned control in Bodträskfors included some sites in set asides rich in deadwood which contributed to richer polypore and beetle assemblages. Our results suggest that larger amounts of deadwood are generated at wildfires than in unburnt forests and prescribed burns, hence the potential to contribute to biodiversity over a long period of time is considerably higher for wildfires than for the prescribed burns, especially for polypores. For beetles burned areas host fire associated species for a shorter period of time and for these species a continuous supply of new burned areas is of outmost importance. However, burning consumes existing deadwood so burning of areas that already contain high numbers of saproxylic species might result in destruction of habitats that is hard to regenerate (Larsson Ekström et al., 2023). In such areas, prescribed burning should be avoided, or valuable deadwood substrates need to be protected from the fire.

4.4. Limitations of the study

The absence of baseline data limits our possibilities to directly assign the post-fire differences to the fires *per se*. The limitations are mainly associated with the lack of estimations on deadwood quality and quantity before the fires and thus also the lack of measure on how much and which qualities of deadwood that was consumed by the fires. Furthermore, lack of baseline data for beetles and polypores limit the possibilities to direct measures of the shift in assemblage composition following fire.

The fact that some deadwood sampling plots were only partially sampled add some uncertainty to our data. However, because these plots only comprise a small share of the total sampling plots and deadwood were evenly distributed in these plots we judge that our results are representative.

Our sampling methods included IBL-traps for beetles and occurrences of sporocarps for polypores. Flight intercept traps only capture beetles that are flying and thus miss species that only move on the ground or potentially species that can avoid the traps. However, the type of flight intercept trap used is a commonly used model which have been shown to effectively catch saproxylic beetles and fire associated beetles. We thus consider our catch to represent true differences between the different habitats included and to be representative for the saproxylic beetle assemblages in the area. Sporocarp inventories have limiations as they overlook species and individuals only occurring as mycelium. We only recorded presence-absence, as (1) the correlation between sporocarp numbers and amount or activity of mycelia in wood is context dependent and varies among species, and (2) the relationship between sporocarp number and mycelial individuals also is context dependent and varies among species.

4.5. Management implications

Our results implies that there is a large potential to improve the amount and qualities of habitats and substrates created at prescribed burns to better emulate wildfire and improve biodiversity goals. The prescribed burns in the current study, from 2005 to 2008, were performed quite soon after the implementation of Forest certification schemes that demand prescribed burning. Although it could be expected that the practice may have developed and more recent prescribed burns might have more desired effects on fire associated biodiversity a recent study show that also more recent prescribed burns often fail to create structures and processes that benefit biodiversity (Ramberg, 2025). Prescribed forest burns in Sweden aims to mimic wildfire in terms of its effects on biodiversity in general and specifically to form appropriate habitat and substrate for fire associated threatened species (Anonymous, 2021b). Our results suggest that, considering polypores, the five prescribed fires in this study did not reach these goals but that the wildfire areas provided high quality habitat. The fact that there were few differences between wildfires and prescribed burns for beetles after 12 years suggest that beetle population have to a large extent recovered. To better mimic wildfires and to form habitat for fire associated species, prescribed burns need to aim for higher tree mortality and thus higher deadwood production than was achieved by the prescribed burns in this study. Relevant deadwood volumes should be based on species habitat demands, for example an aim for at least 20 m^3*ha^{-1} would increase the chance for red-listed species to establish (Hekkala et al., 2023). The mortality rate needed to generate these deadwood volumes depend on the standing volume in the burned stand before burning and might also be a trade-off between the aim of developing old trees with fire scars and the aim to generate deadwood. To better mimic wildfires it would also be beneficial to burn larger areas so that a variation of habitats, including trees of different ages in sites with different soil moisture, slope and aspect, can be included. Further improvements could be to burn at dryer conditions and to combine burning with the creation of deadwood. The high volumes of deadwood in the wildfire will provide habitat for saproxylic species for many years to come. This implies that it is probably cost-efficient to set aside parts of naturally burned areas for conservation, when such opportunities arise.

5. Conclusions

Our study demonstrates that wildfire and prescribed burning differ in their long-term effects on deadwood dynamics and on the diversity and assemblage structure of polypores and saproxylic beetles in boreal forests.

Consistent with our first hypothesis, wildfires generated substantially higher volumes of logs and snags than prescribed burns and present in unburned controls, thereby providing a broader range of substrates for saproxylic species. Prescribed burns produced lower overall deadwood volumes, in particular low amounts of deciduous logs, reflecting their generally lower fire intensity and more limited ecological impact.

Hypothesis 2 was only partly supported. For polypores, abundance, richness and diversity were clearly higher in wildfires than in prescribed burns, reflecting the larger volumes and variety of deadwood substrates. By contrast, beetle abundance, richness and diversity showed little difference between fire types, and in some cases higher abundance was found in unburned controls, suggesting that beetle responses to fire were weaker or more transient than those of polypores.

With respect to assemblage composition (Hypothesis 3), both polypores and beetles differed among wildfires, prescribed burns, and unburned forests. Polypore communities in prescribed burns overlapped with wildfires and unburnt forests but exhibited lower beta-diversity, indicating less within-site variation. Beetle assemblages showed substantial overlap among treatments but still retained higher beta-diversity in burned areas, suggesting that both wildfire and prescribed burning contribute to heterogeneity over time.

Finally, indicator species analyses (Hypothesis 4) largely confirmed our expectations: pioneer and fire-associated polypores such as *Amyloporia* spp. and *Daldinia loculata* were strongly associated with wildfires, while fungivorous beetles were linked to burned habitats and bark beetles to unburned controls. However, prescribed burns supported very few indicator species, underlining their weaker role in sustaining fire-favoured taxa.

Taken together, these results show that while prescribed burning contributes to structural diversity and can support some fire-associated species, its ecological effects remain more limited than those of wildfires, especially for polypores. Wildfires continue to play a disproportionate role in generating high volumes and diversity of deadwood and in sustaining early successional, fire-dependent species. For long-term biodiversity conservation in boreal forests, prescribed burning may function as a complementary tool, but cannot fully substitute for the ecological functions of natural wildfire.

CRediT authorship contribution statement

Emelie Fredriksson: Writing – original draft, Visualization, Supervision, Methodology, Formal analysis, Data curation, Conceptualization. **Isak Vahlström:** Writing – review & editing, Methodology. **Anders Dahlberg:** Writing – review & editing, Supervision, Conceptualization. **Magnus Magnusson:** Writing – review & editing, Conceptualization. **Therese Löfroth:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work the author(s) used Elicit in order to compile literature. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.127956.

Data availability

Data will be made available on request.

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