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Research article

Deadwood manipulation and type determine assemblage composition of saproxylic beetles and fungi after a decade

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ABSTRACT

The biodiversity crisis calls for immediate restoration of deteriorated and rare habitat. Due to fire suppression and intensive forest management, boreal pine forests of high conservation value are exceptionally rare. Despite decades of restoration research in boreal forests, relatively few studies have evaluated multi-taxon biodiversity response of restoration measures in pine forests. In a Scots pine experiment, we investigated biodiversity patterns of wood-inhabiting fungi and beetles a decade after restoration (prescribed burning and deadwood creation) and forest management (harvest with varying retention). We found that fungi and beetles develop differently and have distinct preferences in deadwood originating from restoration. Standing deadwood supported more species for beetles and lying deadwood for fungi and for both taxa, standing and lying deadwood harboured different species assemblages. Burned deadwood displayed less variable assemblages than unburned deadwood for both organism groups. We found that, after a decade, deadwood type and not harvest with different retention levels better explained diversity patterns of wood-inhabiting beetles and fungi in pine forests. Pine forests are naturally prone to recurring disturbances creating open light conditions. Pine-associated species are therefore likely resistant to disturbance as long as a variety of deadwood resources are present. To accommodate multiple taxa, a variety of substrate and environment types is required. Beetles benefit from standing deadwood while fungi benefit from lying deadwood. To support assemblages with both rapid and slow turnover rates, a combination of recurring restoration and leaving restored stands in the adjacent landscapes is required.

1. Introduction

Natural habitats have been used and modified by humans for a long time, resulting in the loss and degradation of species and habitats. In parallel with climate change, the global decline of biodiversity is one of the greatest challenges for humankind. During the last 40 years the global population of vertebrates has declined by 60 percent (Grooten and Almond, 2018) and the extinction rate is calculated to be 100 times faster than the background extinction rate (Ceballos et al., 2015). For insects, which represent extremely high diversity and provide essential ecosystem services, several studies suggest large global declines (Conrad et al., 2006; Hallmann et al., 2017, p. 75; Lister and Garcia, 2018; Sánchez-Bayo and Wyckhuys, 2019). For fungi, however, despite constituting most life on earth, few studies have evaluated global trends in fungal biodiversity and they are generally underrepresented in conservation goals (Gonçalves et al., 2021; Nic Lughadha et al., 2020). Against this background, the United Nations (UN) has declared the 2020′s as the Decade of Ecosystem restoration (United Nations Environment Agency, 2019). The UN thus pinpoint the need for ecosystem restoration to reach the sustainable development goals. Ecological restoration theory is generally based on the assumption that it is efficient to mimic natural processes and disturbances to support biodiversity (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 deadwood creation has profound positive effects on wood-living assemblages (Hjältén et al., 2017; Johansson et al., 2007, 2010; Olsson et al., 2011; Rudolphi et al., 2014), including both rare species (Hägglund et al., 2015; Hjältén et al., 2012) and functional diversity (Heikkala et al.,

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2016b), suggesting that burning and tree retention favor species associated with open habitat and fresh deadwood through environmental filteringHowever, burning has long lasting effects and might favor e.g., beetle predators and red-listed fungi to a larger extent than mere deadwood creation (Heikkala et al., 2016a; Olsson and Jonsson, 2010). In contrast, organism groups such as bryophytes may be disfavored by burning (Espinosa del Alba et al., 2021).

In Sweden, many species are directly or indirectly impacted by the loss and degradation of natural habitats as an effect of intensive land use, including forestry (SLU Artdatabanken, 2020). Swedish silviculture is among the most efficient and technically developed in the world, having a significant impact on the forest ecosystem. The implementation of even-aged forestry by clear-cutting has during a few decades transformed the forest landscape with consequences for biodiversity (Axelsson and Östlund, 2001). Many forest associated species are negatively affected by forestry, as a result of lack of natural disturbances, deadwood and old trees (Gibb et al., 2005; Paillet et al., 2010; Siitonen, 2001) and the dominance of dense, homogenous and relatively young stands (Hedwall and Brunet, 2016; Stokland et al., 2012). To counteract these negative effects, conservation measures have been intertwined into Swedish forest management since the mid 1990′s and a significant number of studies has evaluated the efforts (Felton et al., 2020; Johansson et al., 2013). However, there are still knowledge gaps, especially considering which amounts and qualities of considerations are needed, their spatial distribution and their long-term effects on biodiversity. In addition, most studies have been conducted in Norway spruce (*Picea abies* (L.) H. Karst) forest and pine forests remain in need of further studies.

Scots pine (*Pinus sylvestris* L.) forests have been especially heavily exploited for centuries through selective felling, tar production and collecting of fire wood (Östlund et al., 1997). During the last century, fire suppression and clear felling at moderate age has reduced the area of pine forest with high conservation values (Niklasson and Granström, 2000; Nitare, 2000). As a result of these structural changes, wood living species composition has changed and species that prefer deadwood of smaller diameter, earlier decay stages and species that are generalists, i.e. with wide habitat niches, benefit (Nordén et al., 2013; Seibold et al., 2015) while rare, specialised species associated with old or large diameter dead pines have been disfavored (Weslien et al., 2011). To maintain viable populations of these species, habitat restoration is necessary (Nitare, 2000). Old pine forests conservation values depend on management history, continuity and landscape context with many conservation values associated with forest fires (Kouki et al., 2012). Prescribed burning is used to reintroduce fire in the managed landscape but there is also a demand to develop alternative methods to restore natural values in large areas of pine forests where burning is hard to perform or where restoration for nature conservation and timber production occur in the same stand. The development and evaluation of such methods including various levels of tree retention are thus urgently needed. Trees of Scots pine can become hundreds of years old, dead pines can stand for centuries and burned wood, slowly grown trees and tar-impregnated wood are important substrates for biodiversity in old pine forest (Larsson Ekström et al., 2023; Nirhamo et al., 2024). Restoration of such substrates might include burning but also full or partial debarking or cutting of trees. Although some of these restoration measures have proven beneficial for red-listed species and both fire and green tree retention have positive effects on deadwood assemblages (Hägglund and Hjältén, 2018; Heikkala et al., 2016a) and functional diversity (Heikkala et al., 2016b), there is still a need to evaluate different ways of deadwood creation in combination with variable levels of retention, especially in relation to the performance of the most vulnerable species.

Wood-inhabiting beetles and fungi together provide essential ecosystem processes such as wood decomposition and nutrient cycling (Löfroth et al., 2023). Both groups are affected by forestry-induced deadwood deficits and are prominently featured on the national red-lists of Sweden and Finland (Hyvärinen et al., 2019; SLU Artdatabanken, 2020). Due to their sensitivity to environmental change, they are focal groups for conservation efforts although taxa-specific studies could lead to contradictory management implications. Increasingly, studies have shown that due to differing ecologies in terms of temporal turnover and habitat associations, there is a need to study several organism groups simultaneously (Kärvemo et al., 2021). Therefore, in this study, we have sampled wood-inhabiting beetles and fungi from the same substrates. Species communities of beetle and fungi may respond differently to disturbance such as fire, thus developing along different temporal trajectories. Fire leads to rapid changes to community composition and immediate increase to beetle richness, while fungi, may after an initial decrease, rebound and may take up to 10 years after fire before e.g., overall richness increases and more than 10 years before red-listed species are benefitted (Fredriksson, 2021; Hägglund et al., 2020; Penttilä et al., 2013; Suominen et al., 2015). Relatively few studies span more than a few years following deadwood enrichment and prescribed burning, but beetles and fungi clearly develop on different temporal scales. Fredriksson et al. (2020) found that the initially high beetle richness had decreased but that changes to beetle community composition could still be seen a decade after fire. Deadwood deficits in the landscape limits dispersal of species and local deadwood volumes have proven to be important dispersal sources for both beetles and fungi (Edman et al., 2004; Larsson Ekström et al., 2021; Olsson et al., 2011). The relative influence of local deadwood volumes is also mediated by the environment surrounding the substrate with canopy openness strongly influencing beetle diversity while e.g., less exposed logs typically support many fungal species (Johansson et al., 2017; Lindhe and Lindelöw, 2004; Seibold et al., 2016a, 2016b).

The aim of this study is to assess the effects of prescribed burning and harvest with varying levels of green tree retention, combined with deadwood creation, on successional pathways of wood-inhabiting beetles and fungi in pine forests after a decade. We use a large-scale field experiment and sample beetle and wood fungal assemblages in deadwood derived from the experiment and investigate α, β and γ-diversity of both taxa. We expect diversity patterns and assemblage composition to differ between substrate types after a decade, with beetles and fungi exhibiting different patterns. Additionally, we anticipate that surrounding stand treatments may mediate these substrate associations.

More specifically, at substrate level we expect that:

1) For fungi, we expect more species and different assemblage composition in burned compared to unburned substrates (Penttilä et al., 2013; Suominen et al., 2015). We expect logs to support more species and have a different assemblage composition compared to standing deadwood, due to the more stable and favourable microclimate near the ground (Boddy and Heilmann-Clausen, 2008; Lindhe et al., 2004).
2) For beetles, burned substrates are expected to support fewer species and have more similar assemblages compared to unburned substrates. This is due to drying out of the cambium, which leads to a homogenisation of deadwood at the later stages of decay (Wikars, 2002). We also expect richness to be similar between standing and lying deadwood, but that the assemblages will differ (Hjältén et al., 2010; Rothacher et al., 2023).

For stand level effects, we expect that:

3) For fungi, we expect that stand treatments producing large amounts of deadwood will support more species than treatments with lower deadwood amounts. This expectation arises from knowledge that stands with large deadwood amounts have been shown to support a more diverse local species pool, positively influencing local dispersal and colonization (Edman et al., 2004; Olsson et al., 2011). We also expect burned stands to support more species than unburned stands, due to the generally higher richness in burned substrates (Olsson and

Jonsson, 2010; Suominen et al., 2015). Lastly, we expect the assemblage composition will differ between burned and unburned stands, but not between retention levels in unburned stands (Berglund et al., 2011; Suominen et al., 2015).

4) For beetles, we expect similar richness patterns as for fungi regarding treatments producing large amounts of deadwood to positively influencing the local species pool and richness (Larsson Ekström et al., 2021). We expect that the assemblage composition to differ distinctly between burned and unburned stands, but to be similar between high and low retention levels.

2. Material and methods

2.1. Study design

This study was conducted in Effaråsen, Dalarna County (Fig. 1) in the southern boreal zone of Sweden (Ahti et al., 1968). The area is dominated by homogenous Scots pine (*Pinus sylvestris* L.) stands with occasional occurrences of Norway spruce (*Picea abies* (L.) H. Karst) and birches (*Betula pendula* Roth & *Betula Pubescens* Ehrh). Dwarf shrubs (*Vaccinium vitis-idaea* L. and *Vaccinium myrtillus* L.) and lichens (*Cladonia* spp.) dominate the ground vegetation. The forest stands are on dry-mesic soils broken off by small islands of Sphagnum peat mires and open water bodies. The forest stands are most likely regenerated following a wildfire in 1888, traces of which can be seen in the form of fire-scarred old living trees and old charred deadwood. The stands have since been managed for production through commercial thinning with almost all stands being fertilized approximately 30 years ago and have not been clear-cut. In the winter of 2012–2013, 24 forest stands amounting to 140 ha were randomly allocated subject to several experimental treatments. Altogether there were eight treatments including 1) a control with no treatment; 2) harvest with 3% retained trees; 3) harvest with 10% retained trees; 4) harvest with 30% retained trees; 5) harvest with 50% retained trees; 6) deadwood enrichment; 7) harvest with 50% retained trees followed by prescribed burning; 8) prescribed burning with no harvest (Table 1). Each treatment was replicated in three stands ranging from 2.3 to 13.8 ha in size. The retained trees in the harvested, unburned stands were then divided into four equal parts; 1) green tree retention of solitary trees or groups of trees; 2) creation of high-stumps of ca 3 m height; 3) tree-felling to create logs; 4) bark-peeling of trees with the purpose of creating fire scars, most trees since died. This means that a fourth of the retained trees were left as green tree retention, the rest was turned into deadwood so that e.g., 50% retention resulted in 12.5% green tree retention. Prescribed burning took place in May and September 2013 (Santaniello et al., 2016). Information on the number of substrates counted in 2012–2013 within square 1-ha plots in the centre of each stand to serve as background data can be found in Table A1.

2.2. Substrate and species inventory

We sought for pine deadwood, created at the time of the experimental treatment in each stand; therefore omitting the control treatments, since no deadwood was created there and the general volumes of pre-existing deadwood was very low. This resulted in 21 stands included in the study in each stand. We aimed to find five logs, five high-stumps of ~3 m height and five standing dead trees derived from the experiment. This means that we sampled substrates created by harvester in the unburned stands, hereafter created deadwood. In the burned stands, we sampled trees killed by fire, hereafter burned deadwood. This resulted in six substrate types: High-stump (created), n = 75, High-stump (burned), n = 30, Snag (created), n = 73, Snag (burned), n = 30, Log (created), n = 75 and Log (burned), n = 30 (Table 1). For high-stumps in the burned stands, we sought after snags with broken off tops to compare to the harvester-created high-stumps. In a few cases, we could not find five of each deadwood type in a stand, and then we sampled all substrates of that type. As the low retention stands had retention patches, we aimed for a clustered sampling in all stands, sampling substrates close to each other when possible. We prioritised substrates located at the centre of each stand when possible (on average 0–50 m between substrates), but in some stands with few substrates such as burned stands (distance between substrates 0–195 m) and 3 to 10 percent retention stands (distance between substrates 0–217 m), the sampling was more scattered.

We captured beetles emerging from deadwood with emergence traps and retrieved information on wood-inhabiting fungi from DNA sequencing of wood samples. Emergence traps enclose a part of the substrate in polypropylene weed barrier cloth sealed with a wire (Hjältén et al., 2012). The traps covered ~30 cm and were placed around 0.5–1.5 m from the bottom of the substrate. At the top of each trap, a white (250 ml) plastic bottle was attached, filled to one third with 70 percent propylene glycol and a small amount of detergent to decrease surface tension. All beetles were then identified to species level by a taxonomic expert.

For fungi, we extracted samples by drilling ~10 cm into the wood of each substrate at two places around the substrate, at the same location as the emergence traps. We pooled the two samples from each substrate in the field. We first removed the bark and the outer cambium layer with a knife before drilling, sterilizing both the drill bit and the knife with a gas burner between each individual sample. The samples were then stored in a freezer at −20° °C before sample preparation. The samples were freeze dried and placed into Eppendorf tubes. The samples were then processed and DNA was extracted. A negative extraction control sample was added to measure reagent purity and cross-contamination levels. Primers fITS7 and ITS4 were used for the construction of high-throughput amplicon sequencing (Ihrmark et al., 2012; White et al., 1990). Low abundance taxa with less than two read counts were removed. Bioinformatics followed Kaunisto et al. (2020). Taxonomic assignment was done using the UNITE fungi database 9.0 with SINTAX in VSEARCH (Abarenkov et al., 2023; Edgar, 2016; Rognes et al., 2016). Unique reads were denoised and clustered into zOTU's (zero-radius OTU). The DNA analysis company Bioname carried out the molecular workflow as turnkey service from sample to the bioinformatics and final data.

2.3. Analysis

We performed all analyses in the statistical software R (R Core Team, 2021).

To investigate richness in individual substrates (α-diversity), we used GLMM's with Poisson distribution and stand ID as random factor, and for fungal zOTU's we included total sequencing depth as a second random factor, using the lme4 package (Bates et al., 2015). The models were then evaluated using diagnostic plots. For pairwise comparisons we used emmeans with sidak adjusted p-values (Lenth et al., 2019). We calculated conditional and marginal coefficients of determination to quantify the variation explained by the models using the MuMIn package (Barton and Barton, 2015).

For β-diversity, we pooled data for each substrate type per stand performed BETADISPER on a Jaccard distance matrix for fungal zOTU's and a Bray–Curtis distance matrix for beetles followed by an ANOVA to compare median distances to the species community centroid. We used permutest with 99 permutations for pairwise comparisons.

We also investigated differences in assemblage composition among deadwood types and stand treatment with PERMANOVA, visualised by NMDS with 999 permutations. For PERMANOVA, BETADISPER and NMDS we used the vegan package, pooling data to each substrate type per stand for convergence (Oksanen et al., 2022). For the identification of indicator species for substrate types and stand treatments, we used the multipatt function in the indicspecies package with 999 permutations (De Caceres et al., 2016).

For γ-diversity, we produced sample-based species accumulation curves using the iNEXT package

with trap and wood-core as samples (Hsieh et al., 2016).

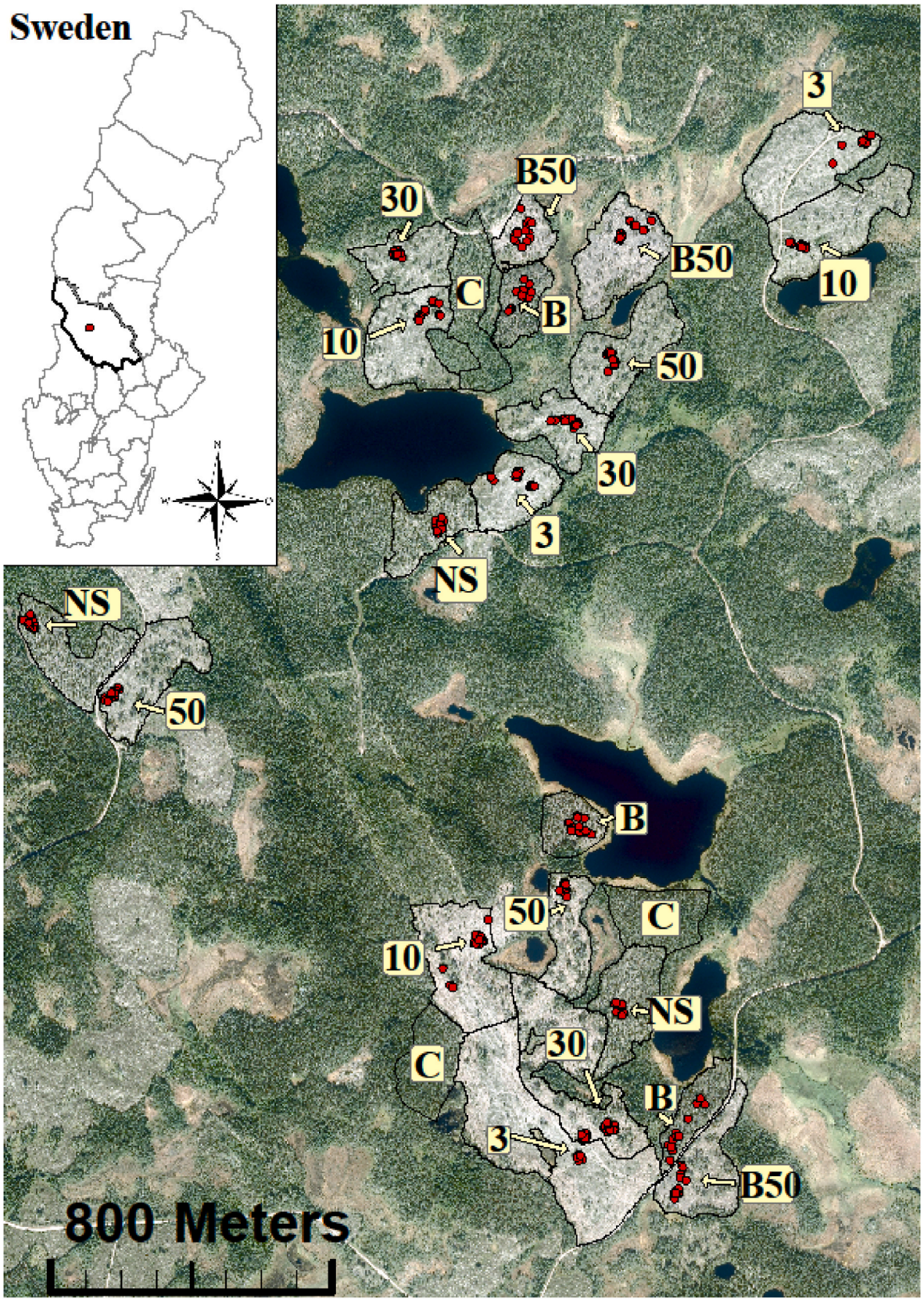

Fig. 1. Location of the study area in the inset map (red dot) in Dalarna (highlighted county border), central Sweden. Highlighted areas in map are stand borders and red dots are substrate positions. Orthophoto in the background from Lantmäteriet (2021).

Table 1
Description of stand treatments and substrate types including stand sizes.

Name	Stand size (ha)	Treatment	Substrate types
1) C	4.1 & 4.2 & 5.6	Untreated control	None (Not part of study)
2) Ret3	5.3 & 6.6 & 13.8	Felling with 3% retention and deadwood enrichment	High-stump (created, **n = 14**) = High-stumps cut at 3 m height by harvester & Snag (created, **n = 13**) = Standing trees killed by bark-peeling from harvester & Log (created, **n = 15**) = Whole trees felled by harvester
3) Ret10	6.2 & 7.4 & 7.7	Felling with 10% retention and deadwood enrichment	High-stump (created, **n = 15**) = High-stumps cut at 3 m height by harvester & Snag (created, **n = 15**) = Standing trees killed by bark-peeling from harvester & Log (created, **n = 15**) = Whole trees felled by harvester
4) Ret30	5.8 & 5.8 & 10.1	Felling with 30% retention and deadwood enrichment	High-stump (created, **n = 15**) = High-stumps cut at 3 m height by harvester & Snag (created, **n = 15**) = Standing trees killed by bark-peeling from harvester & Log (created, **n = 15**) = Whole trees felled by harvester
5) Ret50	3.9 & 5.6 & 8.5	Felling with 50% retention and deadwood enrichment	High-stump (created, **n = 15**) = High-stumps cut at 3 m height by harvester & Snag (created, **n = 15**) = Standing trees killed by bark-peeling from harvester & Log (created, **n = 15**) = Whole trees felled by harvester
6) NS	4.5 & 4.8 & 6.2	No felling with 100% retention and deadwood enrichment	High-stump (created, **n = 15**) = High-stumps cut at 3 m height by harvester & Snag (created, **n = 13**) = Standing trees killed by bark-peeling from harvester & Log (created, **n = 15**) = Whole trees felled by harvester
7) Burn50	3 & 5.5 & 5.6	Prescribed burning following 50% felling	High-stump (burned, **n = 15**) = Broken trees killed by fire, usually 3–5 m & Snag (burned, **n = 14**) = Standing trees killed by fire & Log (burned, **n = 15**) = Trees killed by fire then fallen
8) Burn100	2.3 & 2.8 & 3.2	Prescribed burning with no felling	High-stump (burned, **n = 15**) = Broken trees killed by fire, usually 3–5 m & Snag (burned, **n = 13**) = Standing trees killed by fire & Log (burned, **n = 15**) = Trees killed by fire then fallen

3. Results

In total, we sampled 314 substrates, but because some traps broke we only have species information on beetles from 256 of the substrates. Fungal sampling resulted in 1272 zOTU's, out of which 208 were determined to species level. From the emergence traps, we caught 1423 individuals and 102 species of saproxylic beetles. For beetles, five species and twelve individuals were categorised as red-listed according to the national red-list of Sweden (SLU Artdatabanken, 2020).

3.1. Deadwood type

3.1.1. α-diversity

For fungal zOTU's, richness per substrate did not differ significantly

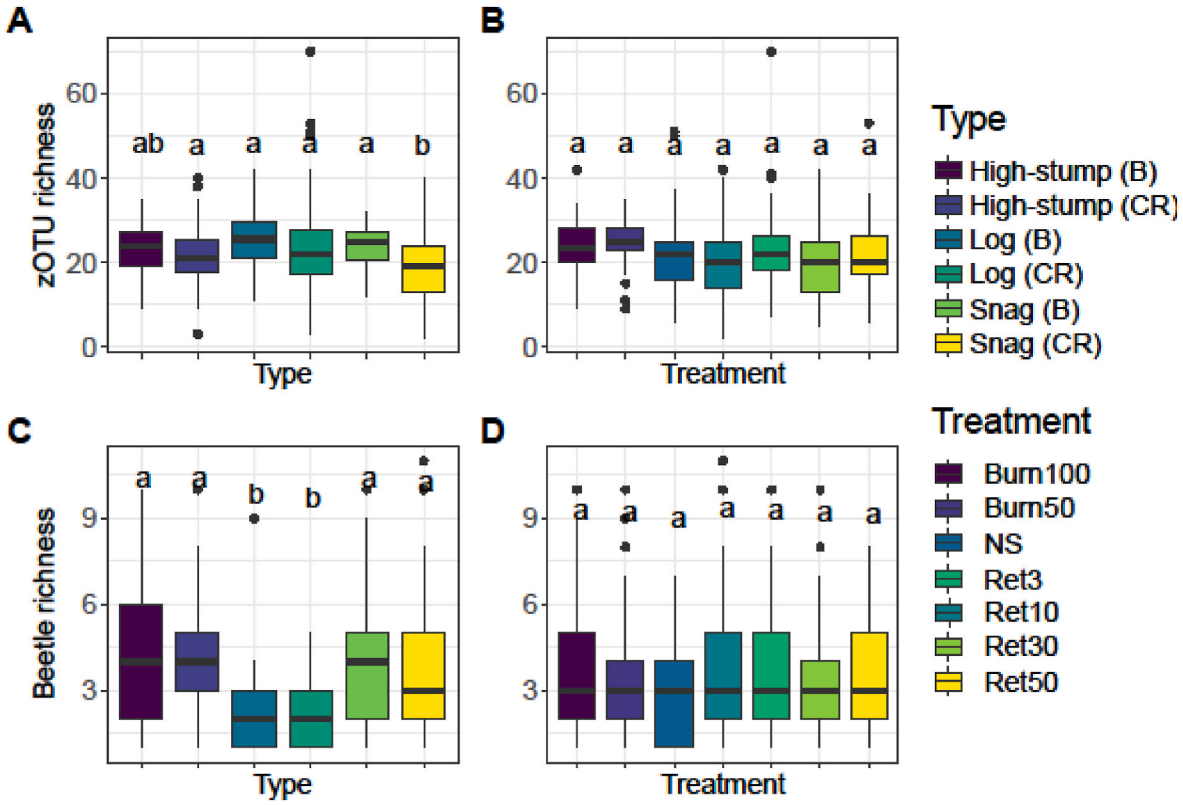

Fig. 2. Boxplots of species richness (α-diversity) between substrates of fungal zOTU's A) and beetles C) and between treatments of fungal zOTU's B) and beetles D). (B) = Trees died from prescribed burning. (CR) = Trees died from harvester head. High-stump = ~3m high-stumps. Snag = Standing dead trees. Log = Lying dead trees. Burn100 = Prescribed burning with no harvest. Burn50 = Prescribed burning with harvest, 50% retention. NS = Deadwood enrichment. Ret3 = Final harvest with 3% retention. Ret10 = Final harvest with 10% retention. Ret30 = Final harvest with 30% retention. Ret50 = Final harvest with 50% retention. Letters indicate significantly similar or dissimilar estimated marginal means based on compact letter display.

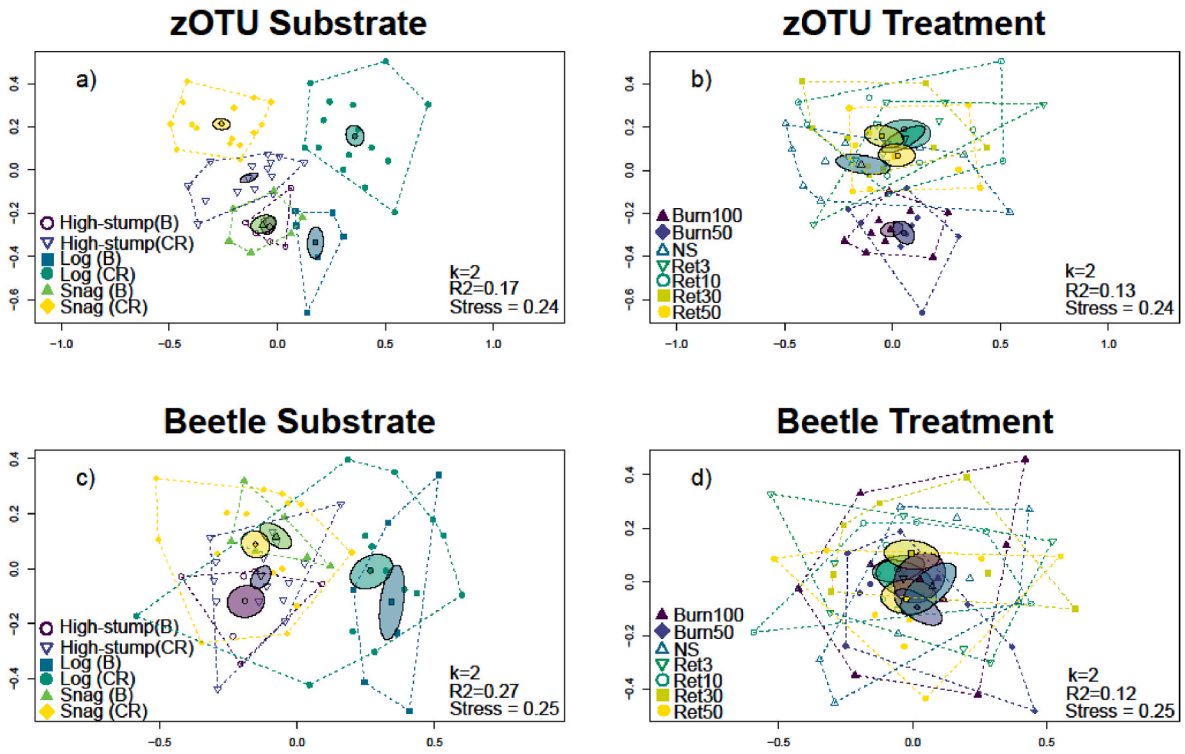

Fig. 3. NMDS plot visualising assemblage composition of fungi and beetles between deadwood and treatment types. Filled ellipsoids visualize the assemblage centroid, 95% CI, and dashed polygons the assemblage edges. Symbols highlighted with black at the centre of the ellipsoid visualize the symbols related to the ellipsoid and are not data points. a) Fungal zOTU and substrate types, b) fungal zOTU and treatment type, c) beetle and substrate types, d) beetle and treatment types. (B) = Trees died from prescribed burning. (CR) = Trees died from harvester head. High-stump = ~3m high-stumps. Snag = Standing dead trees. Log = Lying dead trees. Burn100 = Prescribed burning with no harvest. Burn50 = Prescribed burning with harvest, 50% retention. NS = Deadwood enrichment. Ret3 = Final harvest with 3% retention. Ret10 = Final harvest with 10% retention. Ret30 = Final harvest with 30% retention. Ret50 = Final harvest with 50% retention.

between substrate types except for created snags that displayed slightly lower richness than the other substrate types (Table A2, Fig. 2a). For beetles, logs displayed a lower local richness than snags and high-stumps, although with no differences between burned and unburned substrates (Table A2, Fig. 2c).

3.1.2. *β-diversity and assemblage composition*

Assemblage composition of fungal zOTU's differed significantly between most deadwood types according to the PERMANOVA, with deadwood type explaining 17% of the variation ($p = 0.001$) and assemblage centroids only overlapped between burned snags and high-stumps (Fig. 3a). zOTU's in different created deadwood types displayed highly distinct assemblages while the burned deadwood types were more similar (Fig. 3a). We also found differences in β-diversity between substrate types for fungal zOTU's ($p = 0.01$, Table A3, Fig A1). Pairwise comparisons revealed that burned substrates were characterized by a lower β-diversity than their unburned, created counterparts for fungi (Table A3, Fig A1). Created logs had the greatest β-diversity and burned high-stumps the lowest (Table A3, Fig A1). For beetles, deadwood type explained 27% of the variation in assemblage composition in the (PERMANOVA, $p = 0.001$) (Fig. 3c). Upon visual inspection of the NMDS-plot, deadwood manipulation (burned or created) did not seem to influence assemblages, but the types (high-stumps, snags and logs) displayed distinct assemblages for beetles (Fig. 3c). Also for beetles, β-diversity differed between substrates ($p = 0.01$, Table A3, Fig A1). There was no difference in β-diversity between burned and unburned substrates (Table A3, A1). Instead, logs had a greater β-diversity than high-stumps and snags, but the two latter were similar in β-diversity (Table A3, Fig A1).

In total, 123 fungal zOTU's and 11 beetle species were identified as indicator species for substrate types with a 0.05 significance level (Table A4).

For burned substrates, including combinations of the three types, we identified 55 zOTU's for fungi and the following species for beetles: *Sericus brunneus*, *Megatoma undata, Phloeonomus punctipennis* and *Anisotoma glabra* (Table A4).

Our analysis shows that 28 fungal zOTU's were identified for the created deadwood types and there were no beetle indicator species for created high-stumps, snags and logs (Table A4).

We found 49 fungal zOTU's to be associated to standing deadwood and for beetles, the following species: *Sericus brunneus*, *Megatoma undata*. *Anisotoma glabra*, *Xylita laevigata*, *Ampedus balteatus*, *Ampedus nigrinus*, *Arhopalus rusticus* and *Melanotus castanipes* (Table A4).

For lying deadwood, we found 29 fungal zOTU's as indicator species and for beetles, one indicator species, *Phloeonomus punctipennis* (Table A4).

3.1.3. *γ-diversity*

We found that the overall number of fungal zOTU's was greatest in both burned and created logs (Fig. 4a). Created snags and high-stumps had the lowest number of zOTU's and overlapped with burned high-stumps (Fig. 4a). None of the rarefaction curves for fungal zOTU's showed signs of reaching an asymptote, why comparisons between overlapping trajectories may be uncertain (Fig. 4a & b).

Contrary to the fungal zOTU's, the trajectories of beetles showed signs of reaching a plateau, indicating a more complete sample, especially for created deadwood (Fig. 4c & d). Created deadwood had higher amounts of species than the burned deadwood with created high-stumps supporting the highest number of species and created logs lower number of species (Fig. 4c).

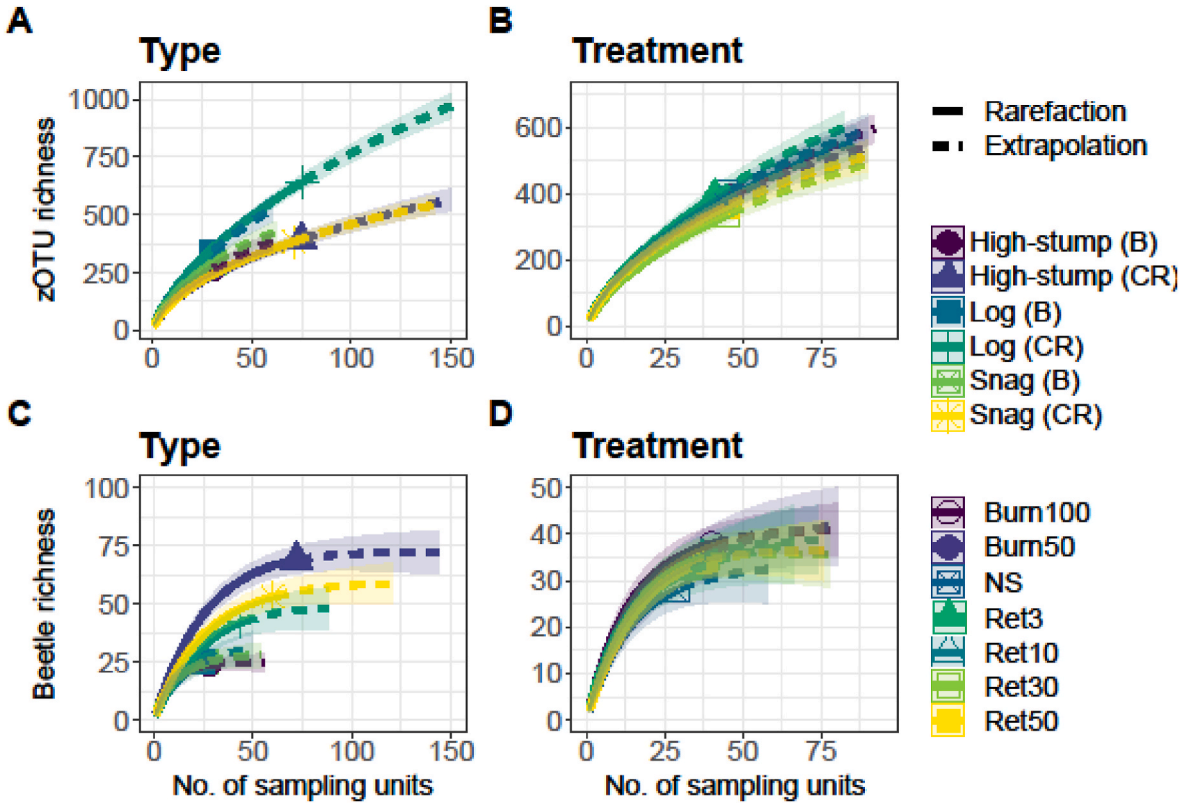

Fig. 4. Sample-based rarefaction curves displaying fungal zOTU and beetle richness in deadwood and treatment types. The Y-axis represents observed (full line) and extrapolated (dashed line) richness to twice the observed sampling effort. X-axis represents the number of sampling units, which is number of DNA-samples for fungi and emergence traps for beetles. Error bars are at 95% CI. (B) = trees killed by prescribed burning. (CR) = trees killed by harvester. High-stump = ~3 m high-stumps. Snag = standing dead trees. Log = Lying dead trees. Burn100 = Prescribed burning with no harvest. Burn50 = Prescribed burning with harvest, 50% retention. NS = Deadwood enrichment. Ret3 = Final harvest with 3% retention. Ret10 = Final harvest with 10% retention. Ret30 = Final harvest with 30% retention. Ret50 = Final harvest with 50% retention.

3.2. Stand treatment

3.2.1. α-diversity

We found no initial difference in substrate-level richness between stand level treatments for neither organism groups (Table A2, Fig. 2b & d).

3.2.2. β-diversity and assemblage composition

Differences in fungal assemblage composition was explained to 13% by stand treatment (PERMANOVA, $p = 0.001$) with overlapping assemblages in retention felling treatments and NS stands slightly separating from the lower retention treatments (Fig. 3b). In addition, both burned treatments displayed distinct assemblage composition compared with retention felling and deadwood enrichment, but assemblages were similar between burn treatments (Fig. 3b). There was no significant relationship between stand treatment and β-diversity for fungal zOTU's, $p = 0.15$ (Table A3, Fig. 3b).

Stand treatment explained 12% of the difference in beetle assemblage composition but was non-significant (PERMANOVA, $p = 0.08$), with assemblage centroids overlapping between treatments (Fig. 3d). Stand treatment did not have a significant effect on β-diversity for beetles ($p = 0.96$, Table A3, Fig. 3d).

For fungi, 25 zOTU's but no beetle species were identified as indicator species for burned stands (Table A5). For unburned stands, six zOTU's and one beetle species (*Holobus apicatus*) were identified as indicator species (Table A4).

3.2.3. γ-diversity

Overall, richness overlapped between stand level treatments for both fungi and beetles (Fig. 4).

4. Discussion

This study provides novel insight into decadal effects of forest management and restoration on deadwood biodiversity. Due to the large quantity of short-term studies and the relatively few studies on long-term, including decadal, effects, management decisions may be biased towards short-term effects (Koivula and Vanha-Majamaa, 2020). However, forest management and restoration may have decadal if not centennial effects on biodiversity (Bader et al., 1995; Dynesius et al., 2021; Fredriksson, 2021; Larsson Ekström et al., 2024; Ramberg et al., 2023). In addition, taxa-specific studies may also lead to decisions that favor one taxonomic group and disfavours another (Bunnell and Huggard, 1999). Our main findings show that there are taxa-specific responses to deadwood position and manipulation. This strongly suggests that forest management and restoration need to diversify its implementation by creating and maintaining various types and positions of deadwood to support multiple taxa.

4.1. Deadwood type

For fungi, we expected that, firstly, burned substrate would support more species and different assemblages than unburned substrate and secondly, that lying deadwood would support more species and different assemblages than standing deadwood. We found support for these predictions in most cases except for species richness between burned and unburned substrates and α-diversity between standing and lying deadwood, which did not differ.

Prescribed burning led to a homogenisation of fungal assemblage composition between deadwood positions (logs and snags), compared to unburned deadwood types that displayed more distinct assemblages and greater β-diversity. For burned deadwood we had fewer samples which could also contribute to the lower β-diversity. However, the assemblage composition in burned deadwood still differed from unburned wood, complementing species assemblages found in unburned wood. Interestingly, we also found that burned deadwood displayed more indicator species for both taxa compared to created deadwood. This could be due to burned substrate assemblages being less variable, thus frequently occurring species are more likely to be strong indicators. This further strengthens that burned deadwood contributes with complementary diversity. Burning alters the physical properties and chemical composition of deadwood, which in turn alters competitive outcomes in fungal species communities, filtering out fire-sensitive and favouring fire-resistant species (Carlsson et al., 2012; Edman and Eriksson, 2016). Burned deadwood serves as unique substrates that host many specialist species, some of which are red-listed due to current day's general lack of wildfires. Red-listed species in particular respond positively to fire (Olsson and Jonsson, 2010; Ramberg et al., 2023) and although most of the zOTU's in this study are not determined to species level and several species and genera in the study lack general ecological information, the clearly distinct assemblages between burned and unburned substrate indicate a clear specialisation of species. The fungal assemblages on the experimental deadwood of this study will most likely continue to develop for several decades (Penttilä et al., 2013; Ramberg et al., 2023).

Lying deadwood hosted more fungal species overall and distinct assemblages from standing deadwood types although standing deadwood displayed more indicator species. Microclimatic conditions determine initial species colonization and subsequent community succession for wood-inhabiting fungi (Boddy and Heilmann-Clausen, 2008). Deadwood microclimate is more stable close to the ground, e.g., around logs, leading to lower environmental stress for many fungal species. This would explain the higher richness and different species assemblages of fungi in logs compared to standing deadwood, as is seen in several other studies (Boddy and Heilmann-Clausen, 2008; Lindhe et al., 2004; Uhl et al., 2022). The greater species pool found in deadwood logs as well as variation in soil moisture would also lend the opportunity for a greater variability between substrate, as shown in the greater β-diversity and fewer distinct indicator species of created logs.

We expected beetle assemblage composition on burned deadwood to be more homogenized in terms of β-diversity and depauperate in terms of species richness and that standing deadwood would support species communities that differ from lying deadwood. We found strong support for these predictions in lower γ-diversity and β-diversity of burned substrates compared to their unburned counterparts although the assemblage composition was similar. Even though we sampled fewer burned substrates the rarefaction curves trajectory suggests that this would hold true even for greater sampling.

Earlier studies have shown clearly distinct assemblages between burned and unburned sites early in succession but that assemblages become more similar with time although not on substrate level (Fredriksson et al., 2020). As we investigate species assemblages after a decade, potential differences e.g., between burned and unburned wood have disappeared or gone undetected, although differences in richness may remain and certain species may favor burned substrates as seen in the indicator species. Fresh deadwood offers resources to a great number of early successional cambium feeders. By burning the deadwood however, this resource is highly ephemeral and may lead to depauperate assemblages due to a more rapid turnover of specialised species with assemblages between burned and unburned substrate becoming less distinct with time (Gutowski et al., 2020; Hekkala et al., 2014; Toivanen and Kotiaho, 2007). Our results should be seen in the light of earlier studies investigating also early responses. Thus, in order to support early successional species and specialised species, it is essential to ensure the availability of fresh deadwood, both burned and unburned, in adequate volumes across the landscape (Hekkala et al., 2014).

The main differences in assemblage composition were shown between deadwood position for beetles, with standing deadwood types also hosting more indicator species and species overall than lying deadwood, contrary to fungal richness patterns and according to our expectation. Where fungal species may thrive in low-stress environments, disturbance-favoured saproxylic beetles thrive in exposed microclimates with warm temperatures (Hägglund et al., 2020; Seibold

et al., 2016b). Standing deadwood is less affected by ground moisture and is more exposed to sunlight, creating a warmer and drier climate, favouring many beetle species. While standing deadwood supports more species overall for beetles and logs for fungi, different deadwood types display distinct assemblages. Therefore, a variety of substrates is required to support the full species pool in our study.

Our results show that burning led to a homogenisation of species assemblages overall, but in different ways for the two taxa. For fungi, the variability between assemblages in burned deadwood was smaller than in cut wood, but assemblage composition differed also between burned substrates (logs and snags). For beetles, assemblage composition did not differ between burned and unburned deadwood after a decade, although we know that there are initial differences between burned and unburned substrates at least for spruce (Hägglund and Hjältén, 2018; Wikars, 2002). We confirm that saproxylic beetles respond positively to snags that provide sun-exposure and warm conditions whereas wood-inhabiting fungi thrive in logs with a more damp and protected microclimate closer to the ground. Created logs displayed more variable species communities for both taxa. This could be because the more variable microclimate supports a greater range of species whereas standing deadwood is closer to the limit of microclimatic stressors, filtering out potential variability. Thus, a variety of burned and unburned substrates at different positions are required to fulfil the needs of deadwood inhabiting beetle and fungi biodiversity.

4.2. Stand-level treatment

Stand level-treatment did not seem to influence the number of species for either organism group although the greater amount of deadwood derived from high-retention stands would affect species densities. Treatment also had a much lower explanatory power for assemblage composition than substrate type, especially for beetles, although burned stands clearly differed from unburned stands for fungi. This may come as a surprising result given that the significant effects retention has been shown to have on microclimate (Zhang et al., 2024). A potential explanation could be that pine forests are typically much lighter and sun-exposed than, for example spruce forests. The relative difference in climatic conditions between a standing forest and a clearcut may thus be smaller in pine forests than spruce forests. This could partially explain the lack of stand-level treatment differences we see in our results. In addition, species associated to pine forests are typically adapted to various types of disturbance, rendering them well adapted to stand-level disturbances (Stokland and Larsson, 2011). It seems that in the short-term, a variety of resources is more important to local production of beetles and the occurrence of wood-fungi than the local surrounding environment in pine forests. Earlier studies have shown the importance of land-use history and composition of the surrounding landscapes for a range of organisms (Bergmark et al., 2024; Hämäläinen et al., 2023; Kouki et al., 2012; Nordén et al., 2013), a highly important factor that we do not address in this study. The majority of retained trees was also turned into deadwood, resulting in only a fourth of the trees retained being alive as described in the Methods section. This means that the treatments all created somewhat open light conditions. The experimental setup with stand treatments being adjacent in a fairly small landscape (~140 ha) might also saturate potential differences between stands due to pine forests and those species associated with pine being prone to disturbance, resulting in spillover effects.

For fungi, there is slight separations of species assemblage centroids from low to high retention levels. In addition, the species accumulation curves were steep; indicating that addition of more samples (substrates) would increase the number of species. This suggests that the stand-level deadwood amount would influence species assemblages to a small degree, but the number of species to a large degree. Even if we do not find that stand-level treatment has an immediate effect on substrate-level species richness for fungi, substrates (samples) have an additive effect, i.e., stands with large amounts of deadwood substrates support more species overall. This is seen in the steep rarefaction curves, meaning that adding more samples will lead to the discovery of new species, why we suggest that local sources of dispersal are highly important for wood fungi (Edman et al., 2004; Olsson et al., 2011). We thus find partial support for our expectation 3. Contradicting our 3) expectations however, there is slight separation in assemblage centroids between high and low retention levels and no difference in fungal species richness between burned and unburned stands.

We do not find support for our expectation 4. For beetles, there was large overlaps in both species richness and assemblage composition for stand-level treatments, and we found a saturation of sample-based species accumulation curves. This suggests that as long as the specific deadwood type is present, the immediate addition of deadwood in the stand does not affect number of species or the assemblage composition. However, although the species richness and assemblage were unaffected by stand treatment, the fact that more substrates are generated in high retention levels, would have a positive effect on the overall species density (Hjältén et al., 2012).

5. Conclusion

Our results clearly show that artificially created deadwood types differ in diversity patterns between deadwood-inhabiting fungi and beetles proving to be more influential to our results than stand-level treatment, 9–10 years after tree death. Beetles and fungi that rely upon deadwood have successional pathways that operate on different temporal scales for the two organism groups. Deadwood of varying manipulation (burned or created) and position (standing or lying) have complementary effects for several organism groups and all deadwood types are essential in order to support deadwood biodiversity. The effect of disturbance-induced light conditions from the stand-level treatments does not seem to affect pine-associated species as long as a variety of substrate remain. For fungi especially, the local amount of substrate has an additive effect to species richness. Forest management needs to provide a wide array of substrate types in restoration action in adequate densities. The implementation of varied retention and restoration efforts in form of creation of different deadwood types is long overdue. Planning of restoration needs to address spatiotemporal aspects that differ between organism groups. For many beetle species with rapid turnover, re-occurring intervals of disturbance such as fire is required in the adjacent landscape (Hekkala et al., 2014). For fungi with a slower development as well as specialist beetle species requiring long-lasting substrate, restored stands rich in deadwood need to be exempt from re-occurring disturbance for some time (Lindman et al., 2022; Penttilä et al., 2013; Wikars, 2004). This places high demands on the spatiotemporal planning of stand allocated to restoration action in the forest landscape.

CRediT authorship contribution statement

Albin Larsson Ekström: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Line Boberg Djupström:** Writing – review & editing, Methodology, Conceptualization. **Joakim Hjältén:** Writing – review & editing, Conceptualization. **Jörgen Sjögren:** Writing – review & editing, Conceptualization. **Mari Jönsson:** Writing – review & editing, Conceptualization. **Therese Löfroth:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

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 1

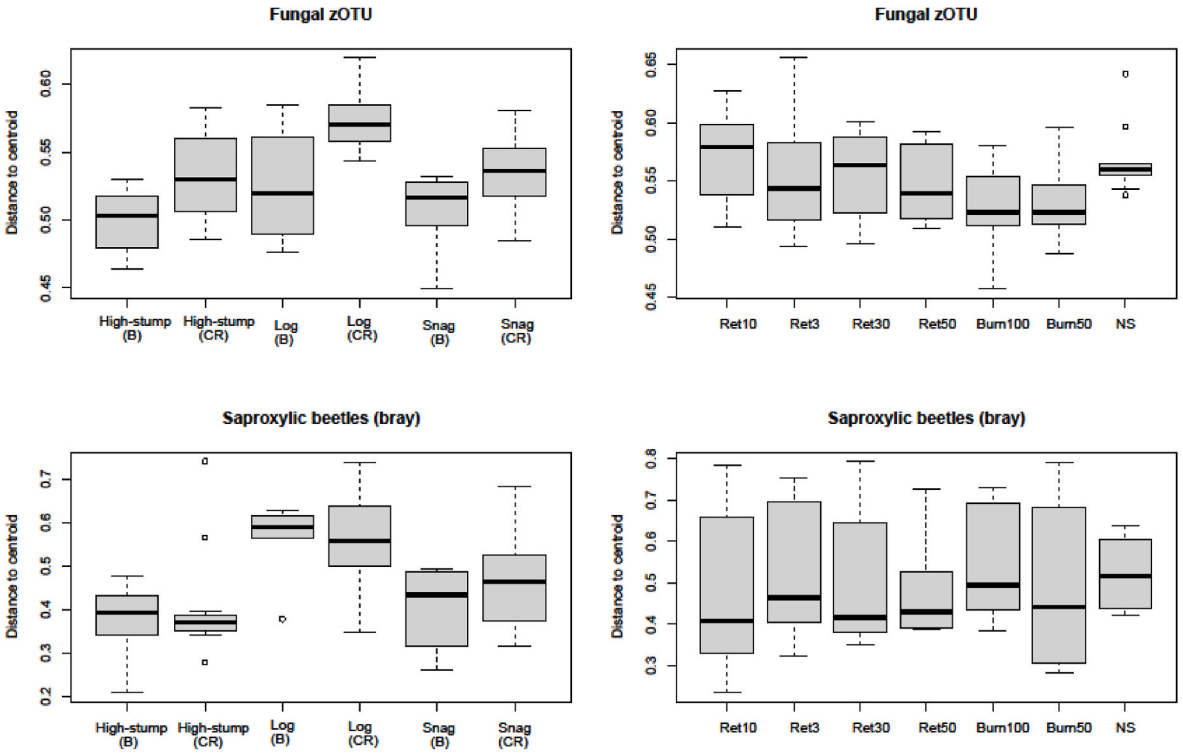

Fig. A1. Boxplots visualising distance to the community centroid (results from betadisper, vegan package) between substrate types and treatment types for both taxonomic groups.

Table A1
Number of substrates per hectare following the experimental treatments in 2012–2013. These substrates were counted within square 1-ha plots in the centre of each stand to serve as background-data and was not part of any analysis of this study. Cut high-stumps and felled logs are substrates created by harvester in the experiment. Bark-peeling of trees was done by harvester and were alive in 2012–2013 but has since died. Green trees are retained living trees. Snags were dead standing trees already present.

Stand name	Treatment	Cut high-stump	Bark-peeled tree	Log	Green tree	Felled log	Snag
DS-3p	Felling with 3% retention and deadwood enrichment	13	8	51	11	7	9
ETO-3p	Felling with 3% retention and deadwood enrichment	9	8	21	17	7	3
TM-3p	Felling with 3% retention and deadwood enrichment	5	2	21	5	2	7
ETV-10p	Felling with 10% retention and deadwood enrichment	9	6	22	17	12	5
KS-10p	Felling with 10% retention and deadwood enrichment	10	7	43	32	17	24
TM-10p	Felling with 10% retention and deadwood enrichment	15	11	10	26	17	10
DS-30p	Felling with 30% retention and deadwood enrichment	31	23	16	48	24	1
ETO-30p	Felling with 30% retention and deadwood enrichment	20	24	12	61	35	7
ETV-30p	Felling with 30% retention and deadwood enrichment	17	26	11	37	32	4
Eff-50p	Felling with 50% retention and deadwood enrichment	32	46	5	93	46	5
ETO-50p	Felling with 50% retention and deadwood enrichment	37	38	19	74	46	13
KS-50p	Felling with 50% retention and deadwood enrichment	54	67	22	135	107	9
ds-ns	No felling with 100% retention and deadwood enrichment	117	126	110	249	361	33
Eff-NS	No felling with 100% retention and deadwood enrichment	86	95	11	135	208	6
eto-ns	No felling with 100% retention and deadwood enrichment	101	101	18	208	244	10
ds-b50p	Prescribed burning with 50% felling	0	0	25	180	11	7
eto-b50p	Prescribed burning with 50% felling	1	0	29	153	0	7
ETV-B50p	Prescribed burning with 50% felling	6	1	11	113	8	4

(*continued on next page*)

Table A1 (*continued*)

Stand name	Treatment	Cut high-stump	Bark-peeled tree	Log	Green tree	Felled log	Snag
DS-B	Prescribed burning with no felling	0	0	17	464	19	6
etv-b	Prescribed burning with no felling	0	0	20	570	0	8
ks-b	Prescribed burning with no felling	0	0	24	315	0	29
ds-k	Untreated control	0	0	88	648	0	44
etv-k	Untreated control	0	0	15	269	0	12
ks-k	Untreated control	0	0	51	714	0	113

Table A2
Output tables from GLMM's with fungal zOTU and beetle richness as response variables and deadwood type or stand treatment as explanatory variables. For deadwood type, high-stump (burned) is the intercept and for stand treatment Burn100. Results from emmeans pairwise comparisons are presented in Fig. 2.

glmer(Richness(zOTU) ~ Deadwood type+(1|Stand)+(1|Sequencing depth), poisson)				
Predictors	Estimates	SE	z-value	p-value
Intercept	3.1028	0.07733	40.125	<2e-16
High-stump (created)	−0.07405	0.09236	−0.802	0.4227
Log (burned)	0.09142	0.09454	0.967	0.3336
Log (created)	−0.01631	0.09158	−0.178	0.8586
Snag (burned)	0.06271	0.09399	0.667	0.5046
Snag (created)	−0.23317	0.09265	−2.517	0.0118
Random effects	Variance	SD		
Sequencing depth	0.091514	0.30251		
Stand	0.008646	0.09298		
Observations	No of obs: 310	Groups: 21		
Marginal R2	0.074			
Conditional R2	0.712			
glmer(Richness(beetle) ~ Deadwood type+(1|Stand), poisson)				
Predictors	Estimates	SE	z-value	p-value
Intercept	1.421124	0.09396	15.125	<2e-16
High-stump (created)	0.008419	0.110664	0.076	0.939355
Log (burned)	−0.563299	0.159959	−3.522	0.0004
Log (created)	−0.684502	0.140742	−4.864	1.15E-06
Snag (burned)	−0.008232	0.132855	−0.062	0.950593
Snag (created)	−0.109276	0.115837	−0.943	0.345497
Random effects	Variance	SD		
Stand	0.00122	0.03492		
Observations	No of obs: 256	Groups: 21		
Marginal R2	0.21			
Conditional R2	0.214			
glmer(Richness(zOTU) ~ Treatment+(1|Stand)+(1|Sequencing depth), poisson)				
Predictors	Estimates	SE	z-value	p-value
Intercept	3.14724	0.07069	44.524	<2e-16
B50	0.01346	0.10021	0.134	0.8932
NS	−0.12582	0.10094	−1.246	0.2126
Ret10	−0.19814	0.10222	−1.938	0.0526
Ret3	−0.06277	0.10231	−0.614	0.5395
Ret30	−0.24961	0.10166	−2.455	0.0141
Ret50	−0.12089	0.1009	−1.198	0.2309
Random effects	Variance	SD		
Sequencing depth	0.09859	0.31399		
Stand	0.00577	0.07596		
Observations	No of obs: 310	Groups: 21		
Marginal R2	0.052			
Conditional R2	0.714			
glmer(Richness(beetle) ~ Treatment+(1|Stand), poisson)				
Predictors	Estimates	SE	z-value	p-value
Intercept	1.29473	0.08276	15.644	<2e-16
B50	−0.04196	0.11829	−0.355	0.7228
NS	−0.23121	0.13695	−1.688	0.0914
Ret10	0.05018	0.11786	0.426	0.6703
Ret3	0.04505	0.1216	0.37	0.711
Ret30	−0.03104	0.11873	−0.261	0.7938
Ret50	−0.09603	0.1216	−0.79	0.4297
Random effects	Variance	SD		
Stand	0	0		
Observations	No of obs: 256	Groups: 21		
Marginal R2	0.024			
Conditional R2	0.024			

Table A3
Result output from PERMANOVA and BETADISPER with subsequent Permutest for fungal zOTU's and beetles for deadwood type and stand treatment.

PERMANOVA zOTU Deadwood type							
	Df	SumOfSqs	R2	F value	p-value		
Substrate type	5	3.786	0.17214	2.3704	0.001		
Residual	57	18.209	0.82786				
Total	62	21.995	1				
Betadisper							
	Df	Sum Sq	Mean Sq	F value	p-value		
Groups	5	0.037402	0.0074805	8.7958	0.01		
Residuals	57	0.048476	0.0008505				
Permutest (observed diagonal, permuted above diagonal)							
	High-stump (burned)	High-stump (created)	Log (burned)	Log (created)	Snag (burned)	Snag (created)	
High-stump (burned)		8.00E-02	2.70E-01	1.00E-02	6.60E-01	0.02	
High-stump (created)	3.75E-02		6.90E-01	1.00E-02	9.00E-02	1	
Log (burned)	2.28E-01	6.72E-01		1.00E-02	3.80E-01	0.59	
Log (created)	2.03E-06	2.16E-04	1.92E-03		1.00E-02	0.01	
Snag (burned)	6.85E-01	1.05E-01	3.95E-01	1.68E-05		0.06	
Snag (created)	1.85E-02	9.59E-01	6.17E-01	7.67E-05	6.66E-02		
PERMANOVA beetle Deadwood type type							
	Df	SumOfSqs	R2	F value	p-value		
Substrate type	5	5.1871	0.26837	4.1082	0.001		
Residual	56	14.1415	0.73163				
Total	61	19.3286	1				
Betadisper							
	Df	Sum Sq	Mean Sq	F value	p-value		
Groups	5	0.31546	0.063092	5.9332	0.01		
Residuals	56	0.59549	0.010634				
Permutest (observed diagonal, permuted above diagonal)							
	High-stump (burned)	High-stump (created)	Log (burned)	Log (created)	Snag (burned)	Snag (created)	
High-stump (burned)		0.63	0.01	0.02	0.66	0.08	
High-stump (created)	0.64355632		0.01	0.01	0.95	0.14	
Log (burned)	0.00592908	0.00550224		0.96	0.03	0.05	
Log (created)	0.00205763	0.00060368	0.95635142		0.01	0.02	
Snag (burned)	0.60447312	0.92658339	0.01639557	0.0076812		0.29	
Snag (created)	0.07728769	0.11533817	0.04357855	0.01694218	0.2355925		
PERMANOVA zOTU Treatment type							
	Df	SumOfSqs	R2	F value	p-value		
Treatment	6	2.8571	0.1299	1.3934	0.001		
Residual	56	19.1375	0.8701				
Total	62	21.9946	1				
Betadisper							
	Df	Sum Sq	Mean Sq	F value	p-value		
Groups	6	0.016159	0.0026932	1.7991	0.15		
Residuals	56	0.08383	0.001497				
Permutest (observed diagonal, permuted above diagonal)							
	Ret10	Ret3	Ret30	Ret50	B100	B50	NS
Ret10		0.49	0.42	0.19	0.05	0.02	0.92
Ret3	0.433229		1	0.76	0.25	0.24	0.41
Ret30	0.371286	0.988716		0.66	0.16	0.17	0.42
Ret50	0.187473	0.76181	0.705179		0.26	0.32	0.18
B100	0.035274	0.23742	0.172555	0.260763		0.91	0.03
B50	0.023461	0.230181	0.151314	0.237933	0.90517		0.01
NS	0.887507	0.474323	0.404852	0.19229	0.032483	0.019018	
PERMANOVA beetle Treatment type							
	Df	SumOfSqs	R2	F value	p-value		
Treatment	6	2.3734	0.12279	1.2832	0.078		
Residual	55	16.9552	0.87721				
Total	61	19.3286	1				
Betadisper							
	Df	Sum Sq	Mean Sq	F value	p-value		
Groups	6	0.04028	0.0067134	0.254	1		
Residuals	55	1.45361	0.0264293				
Permutest (observed diagonal, permuted above diagonal)							
	Ret10	Ret3	Ret30	Ret50	B100	B50	NS
Ret10		0.58	0.75	0.79	0.51	0.9	0.54
Ret3	0.46071		0.65	0.6	0.98	0.67	0.87
Ret30	0.75648	0.61664		0.97	0.52	0.88	0.65
Ret50	0.76756	0.5527	0.96369		0.5	0.91	0.56
B100	0.39808	0.94544	0.53832	0.46057		0.54	0.87
B50	0.8835	0.56959	0.88699	0.90851	0.50714		0.66
NS	0.4976	0.85407	0.6764	0.58096	0.7652	0.62689	

Table A4
Indicator species for each deadwood type including combinations. Only significant (p = 0.05) species displayed. A = Sample estimate of probability of species belonging to the deadwood type. B = Sample estimate of the probability of finding the species in the deadwood type. For fungi, the assigned name is displayed which is either species level (full name) or genus level (spp.).

A	B	stat	p-value	Indicator	Organism group	Assigned name
0.7442	0.6667	0.704	0.002	High-stump (burned)	Fungi	Athelia_decipiens
0.8824	0.5	0.664	0.009	High-stump (burned)	Fungi	Cryptodiscus_pini
0.8421	0.3333	0.53	0.02	High-stump (burned)	Fungi	Femsjonia_peziziformis
0.8421	0.3333	0.53	0.027	High-stump (burned)	Fungi	Infundichalara spp.
1	0.3333	0.577	0.023	High-stump (burned)	Fungi	Mariannaea_camptospora
1	0.3333	0.577	0.023	High-stump (burned)	Fungi	Oidiodendron spp.
1	0.3333	0.577	0.024	High-stump (burned)	Fungi	Phialocephala spp.
1	0.5	0.707	0.001	High-stump (burned)	Fungi	Piskurozyma spp.
0.7143	0.3333	0.488	0.049	High-stump (burned)	Beetle	Megatoma undata
0.6383	1	0.799	0.001	High-stump (burned)	Beetle	Sericus brunneus
1	0.3182	0.564	0.022	High-stump (burned) & High-stump (created)	Fungi	Sistotrema_brinkmannii
1	0.2727	0.522	0.044	High-stump (burned) & high-stump (created)	Fungi	Umbilicaria spp.
0.8826	0.7442	0.81	0.008	High-stump (burned) & High-stump (created) & Log (burned) & Log (created)	Fungi	Carcinomyces spp.
0.8785	0.5814	0.715	0.027	High-stump (burned) & High-stump (created) & Log (burned) & Log (created)	Fungi	Umbilicaria spp.
0.9302	0.8367	0.882	0.008	High-stump (burned) & High-stump (created) & Log (burned) & Log (created) & Snag (burned)	Fungi	Phialocephala spp.
0.9594	0.8367	0.896	0.001	High-stump (burned) & High-stump (created) & Log (burned) & Log (created) & Snag (burned)	Fungi	Phialocephala spp.
0.9272	0.4706	0.661	0.012	High-stump (burned) & High-stump (created) & Log (burned) & Snag (burned)	Fungi	Colacogloea spp.
0.8678	0.7647	0.815	0.003	High-stump (burned) & High-stump (created) & Log (burned) & Snag (burned)	Fungi	Vexillomyces_verruculosus
0.8485	0.7059	0.774	0.006	High-stump (burned) & High-stump (created) & Log (burned) & Snag (burned)	Fungi	Rhinocladiella spp.
0.9	0.5	0.671	0.02	High-stump (burned) & High-stump (created) & Log (burned) & Snag (burned)	Fungi	Oidiodendron spp.
0.9237	0.898	0.911	0.013	High-stump (burned) & High-stump (created) & Log (burned) & Snag (burned) & Snag (created)	Fungi	Exophiala spp.
0.9246	0.9592	0.942	0.001	High-stump (burned) & High-stump (created) & Log (burned) & Snag (burned) & Snag (created)	Fungi	Hamamotoa_lignophila
1	0.5306	0.728	0.003	High-stump (burned) & High-stump (created) & Log (burned) & Snag (burned) & Snag (created)	Fungi	Capturomyces_luteus
0.8871	0.7907	0.838	0.011	High-stump (burned) & High-stump (created) & Log (created) & Snag (burned)	Fungi	Infundichalara spp.
0.7553	0.5714	0.657	0.019	High-stump (burned) & High-stump (created) & Snag (burned)	Fungi	Phaeotremella_foliacea
0.9902	0.9762	0.983	0.001	High-stump (burned) & High-stump (created) & Snag (burned) & High-stump (created)	Beetle	Xylita laevigata
0.9838	0.881	0.931	0.001	High-stump (burned) & High-stump (created) & Snag (burned) & High-stump (created)	Beetle	Ampedus balteatus
0.9506	0.881	0.915	0.001	High-stump (burned) & High-stump (created) & Snag (burned) & High-stump (created)	Beetle	Ampedus nigrinus
1	0.7857	0.886	0.001	High-stump (burned) & High-stump (created) & Snag (burned) & High-stump (created)	Beetle	Arhopalus rusticus
1	0.5952	0.772	0.001	High-stump (burned) & High-stump (created) & Snag (burned) & High-stump (created)	Beetle	Melanotus castanipes
0.8962	0.9302	0.913	0.001	High-stump (burned) & High-stump (created) & Snag (burned) & Snag (created)	Fungi	Tremella_encephala
0.9012	0.5814	0.724	0.027	High-stump (burned) & High-stump (created) & Snag (burned) & Snag (created)	Fungi	Sydowia_polyspora
0.8861	0.75	0.815	0.001	High-stump (burned) & Log (burned)	Fungi	Coniochaeta spp.
0.8609	0.4231	0.604	0.034	High-stump (burned) & Log (burned) & Log (created)	Beetle	Scaphisoma agaricinum
0.8743	0.7576	0.814	0.001	High-stump (burned) & Log (burned) & Log (created) & Snag (burned)	Fungi	Carcinomyces spp.
0.8938	0.4545	0.637	0.036	High-stump (burned) & Log (burned) & Log (created) & Snag (burned)	Fungi	Peniophorella_praetermissa
0.8615	0.6364	0.74	0.017	High-stump (burned) & Log (burned) & Log (created) & Snag (burned)	Fungi	Peniophorella_praetermissa
1	0.5	0.707	0.002	High-stump (burned) & Log (burned) & Log (created) & Snag (created)	Fungi	Ascocoryne_albida
0.9551	0.6111	0.764	0.001	High-stump (burned) & Log (burned) & Snag (burned)	Fungi	Crumenulopsis_pinicola
0.9524	0.2778	0.514	0.038	High-stump (burned) & Log (burned) & Snag (burned)	Fungi	Crumenulopsis_pinicola
0.9375	0.2778	0.51	0.039	High-stump (burned) & Log (burned) & Snag (burned)	Fungi	Crumenulopsis_pinicola
0.7692	0.5556	0.654	0.01	High-stump (burned) & Log (burned) & Snag (burned)	Fungi	Exidia_saccharina
0.8134	0.6111	0.705	0.003	High-stump (burned) & Log (burned) & Snag (burned)	Fungi	Exophiala spp.
0.7355	0.7778	0.756	0.02	High-stump (burned) & Log (burned) & Snag (burned)	Fungi	Exophiala spp.
0.7288	0.8889	0.805	0.001	High-stump (burned) & Log (burned) & Snag (burned)	Fungi	Fomitopsis spp.
0.8848	0.7222	0.799	0.001	High-stump (burned) & Log (burned) & Snag (burned)	Fungi	Gyromitra_tianshanensis
0.8558	0.8889	0.872	0.001	High-stump (burned) & Log (burned) & Snag (burned)	Fungi	Oidiodendron_griseum
0.8989	0.7222	0.806	0.001	High-stump (burned) & Log (burned) & Snag (burned)	Fungi	Stereum_sanguinolentum
0.7634	0.8889	0.824	0.001	High-stump (burned) & Log (burned) & Snag (burned)	Fungi	Talaromyces_rademirici
0.9492	0.3889	0.608	0.009	High-stump (burned) & Log (burned) & Snag (burned)	Fungi	Talaromyces_rademirici
0.9047	0.8485	0.876	0.001	High-stump (burned) & Log (burned) & Snag (burned) & Snag (created)	Fungi	Exophiala spp.
0.793	0.4762	0.615	0.014	High-stump (burned) & Log (created)	Fungi	Hypogymnia_physodes
1	0.2857	0.535	0.03	High-stump (burned) & Log (created)	Fungi	Cerinomyces spp.
0.9231	0.3333	0.555	0.033	High-stump (burned) & Log (created) & Snag (burned)	Fungi	Ascocoryne spp.
0.9608	0.5962	0.757	0.008	High-stump (burned) & Log (created) & Snag (created)	Fungi	Phaeotheca spp.
0.7282	0.5833	0.652	0.009	High-stump (burned) & Snag (burned)	Fungi	Cladosporium spp.
0.7579	0.5833	0.665	0.001	High-stump (burned) & Snag (burned)	Fungi	Cosmospora spp.
0.8658	0.3333	0.537	0.024	High-stump (burned) & Snag (burned)	Fungi	Dacrymyces_lacrymalis
0.7843	0.5833	0.676	0.002	High-stump (burned) & Snag (burned)	Fungi	Genolevuria spp.
1	0.3333	0.577	0.009	High-stump (burned) & Snag (burned)	Fungi	Infundichalara spp.
0.7767	0.3333	0.509	0.05	High-stump (burned) & Snag (burned)	Fungi	Infundichalara_microchona

(*continued on next page*)

Table A4 (*continued*)

A	B	stat	p-value	Indicator	Organism group	Assigned name
0.7692	0.75	0.76	0.001	High-stump (burned) & Snag (burned)	Fungi	Paratritirachium spp.
0.7663	0.4167	0.565	0.024	High-stump (burned) & Snag (burned)	Fungi	Unilacryma_bispora
0.7971	0.5	0.631	0.005	High-stump (burned) & Snag (burned)	Beetle	Anisotoma glabra
0.8516	0.4286	0.604	0.02	High-stump (burned) & Snag (created)	Fungi	Leuconeurospora spp.
1	0.3333	0.577	0.012	High-stump (burned) & Snag (created)	Fungi	Capturomyces_luteus
0.6352	0.5625	0.598	0.023	High-stump (created)	Fungi	Phlebiopsis_gigantea
0.6522	0.625	0.638	0.007	High-stump (created)	Fungi	Sistotrema_brinkmannii
1	0.25	0.5	0.049	High-stump (created)	Fungi	Dacrymyces spp.
0.8491	0.3125	0.515	0.046	High-stump (created)	Fungi	Vexillomyces_palatinus
0.8745	0.6486	0.753	0.004	High-stump (created) & Log (burned) & Snag (created)	Fungi	Exophiala_abietophila
1	0.4565	0.676	0.011	High-stump (created) & Log (created) & Snag (created)	Fungi	Phaeotheca spp.
1	0.5217	0.722	0.005	High-stump (created) & Log (created) & Snag (created)	Fungi	Vexillomyces_palatinus
0.976	0.6216	0.779	0.001	High-stump (created) & Snag (burned) & Snag (created)	Fungi	Sydowia_polyspora
1	0.3333	0.577	0.026	Log (burned)	Fungi	Archaeorhizomyces spp.
0.8333	0.5	0.645	0.008	Log (burned)	Fungi	Coniochaeta spp.
1	0.5	0.707	0.002	Log (burned)	Fungi	Coniochaeta spp.
0.8	0.5	0.632	0.008	Log (burned)	Fungi	Coniochaeta spp.
0.7299	0.8333	0.78	0.001	Log (burned)	Fungi	Crumenulopsis_pinicola
0.5797	0.5	0.538	0.029	Log (burned)	Fungi	Ditiola spp.
0.75	0.5	0.612	0.006	Log (burned)	Fungi	Ditiola_haasii
0.7273	0.8333	0.778	0.001	Log (burned)	Fungi	Fomitopsis spp.
0.7692	0.8333	0.801	0.001	Log (burned)	Fungi	Fomitopsis spp.
0.6667	0.6667	0.667	0.003	Log (burned)	Fungi	Fomitopsis spp.
0.6667	0.6667	0.667	0.003	Log (burned)	Fungi	Fomitopsis spp.
0.8333	0.3333	0.527	0.045	Log (burned)	Fungi	Trichaptum_fuscoviolaceum
1	0.3333	0.577	0.026	Log (burned)	Fungi	Trichaptum_fuscoviolaceum
1	0.3333	0.577	0.027	Log (burned)	Fungi	Trichoderma spp.
1	0.3333	0.577	0.027	Log (burned)	Beetle	Phloeonomus punctipennis
0.9372	0.4286	0.634	0.005	Log (burned) & Log (created)	Fungi	Hypogymnia spp.
0.7379	0.6667	0.701	0.004	Log (burned) & Log (created)	Fungi	Amyloporia_sinuosa
0.871	0.381	0.576	0.021	Log (burned) & Log (created)	Fungi	Cladophialophora spp.
1	0.2381	0.488	0.046	Log (burned) & Log (created)	Fungi	Sugiyamaella spp.
0.8669	0.3704	0.567	0.046	Log (burned) & Log (created) & Snag (burned)	Fungi	Hyaloscypha spp.
0.8027	0.4815	0.622	0.042	Log (burned) & Log (created) & Snag (burned)	Fungi	Hyaloscypha spp.
0.9207	0.3333	0.554	0.047	Log (burned) & Log (created) & Snag (burned)	Fungi	Hyaloscypha spp.
0.8871	0.4615	0.64	0.018	Log (burned) & Log (created) & Snag (burned)	Beetle	Atomaria umbrina
0.8392	0.3333	0.529	0.029	Log (burned) & Snag (burned)	Fungi	Hypochnicium_albostramineum
1	0.5	0.707	0.002	Log (burned) & Snag (burned)	Fungi	Taphrina spp.
0.7033	0.5	0.593	0.026	Log (burned) & Snag (burned)	Fungi	Tympanis_pini
0.8635	0.6296	0.737	0.001	Log (burned) & Snag (burned) & Snag (created)	Fungi	Pichia_holstii
1	0.4286	0.655	0.004	Log (burned) & Snag (created)	Fungi	Stereum_sanguinolentum
0.9091	0.5333	0.696	0.002	Log (created)	Fungi	Umbelopsis spp.
1	0.3333	0.577	0.007	Log (created)	Fungi	Helicogloea_dryina
0.7138	0.4667	0.577	0.031	Log (created)	Fungi	Phaeotheca spp.
0.8649	0.3333	0.537	0.03	Log (created)	Fungi	Phialocephala spp.
0.6358	0.6	0.618	0.017	Log (created)	Fungi	Phaeococcomyces spp.
1	0.2667	0.516	0.021	Log (created)	Fungi	Tubulicrinis_borealis
0.6431	0.9333	0.775	0.001	Log (created)	Fungi	Phialocephala_melitaea
1	0.3333	0.577	0.016	Log (created)	Fungi	Skeletocutis_kuehneri
1	0.2667	0.516	0.014	Log (created)	Fungi	Phialocephala spp.
1	0.2667	0.516	0.014	Log (created)	Fungi	Phaeotremella spp.
1	0.2667	0.516	0.012	Log (created)	Fungi	Skeletocutis_kuehneri
0.613	0.6667	0.639	0.007	Snag (burned)	Fungi	Colacogloea spp.
1	0.3333	0.577	0.022	Snag (burned)	Fungi	Cryptococcus spp.
0.8333	0.3333	0.527	0.042	Snag (burned)	Fungi	Exidia_saccharina
1	0.3333	0.577	0.016	Snag (burned)	Fungi	Exidia_saccharina
1	0.3333	0.577	0.019	Snag (burned)	Fungi	Graphilbum_fragrans
1	0.3333	0.577	0.021	Snag (burned)	Fungi	Pycnora spp.
1	0.3333	0.577	0.017	Snag (burned)	Fungi	Umbelopsis spp.
1	0.3333	0.577	0.017	Snag (burned)	Fungi	Umbelopsis spp.
1	0.3333	0.577	0.017	Snag (burned)	Fungi	Umbelopsis spp.
0.7983	0.619	0.703	0.004	Snag (burned) & Snag (created)	Fungi	Lachnellula spp.
0.9655	1	0.983	0.001	Snag (created)	Fungi	Lachnellula spp.
1	0.2667	0.516	0.019	Snag (created)	Fungi	Rhinocladiella spp.
1	0.6	0.775	0.001	Snag (created)	Fungi	Lachnellula spp.
0.9	0.7333	0.812	0.001	Snag (created)	Fungi	Stereum_sanguinolentum
1	0.3333	0.577	0.017	Snag (created)	Fungi	Collophora spp.
0.8372	0.7333	0.784	0.001	Snag (created)	Fungi	Stereum_sanguinolentum
0.8387	0.7333	0.784	0.001	Snag (created)	Fungi	Tremella_encephala
0.9057	0.4667	0.65	0.002	Snag (created)	Fungi	Heterophaeomoniella_pinifoliorum
1	0.4	0.632	0.002	Snag (created)	Fungi	Lachnellula spp.
0.8283	0.8	0.814	0.001	Snag (created)	Fungi	Stereum_sanguinolentum
1	0.2667	0.516	0.011	Snag (created)	Fungi	Kurtzmanomyces spp.

Table A5
Indicator species for each stand treatment type including combinations. Only significant (p = 0.05) species displayed. A = Sample estimate of propability of species belonging to the treatment type. B = Sample estimate of the probability of finding the species in the treatment type. For fungi, the assigned name is displayed which is either species level (full name) or genus level (spp.).

A	B	stat	p-value	Indicator	Organism group	Assigned name
1	0.3333	0.577	0.012	B100	Fungi	Infundichalara spp.
0.5625	0.5556	0.559	0.027	B100	Fungi	Oidiodendron spp.
0.5333	0.7778	0.644	0.002	B100	Fungi	Cosmospora spp.
1	0.4444	0.667	0.003	B100	Fungi	Cladosporium spp.
0.5385	0.7778	0.647	0.013	B100	Fungi	Cladosporium spp.
0.75	0.3333	0.5	0.047	B100	Fungi	Phialocephala spp.
0.8	0.3333	0.516	0.045	B100	Fungi	Infundichalara spp.
0.75	0.3333	0.5	0.043	B100	Fungi	Acrodontium spp.
0.697	0.8889	0.787	0.001	B100 & B50	Fungi	Oidiodendron_griseum
0.8824	0.5556	0.7	0.002	B100 & B50	Fungi	Coniochaeta spp.
0.7805	0.7222	0.751	0.001	B100 & B50	Fungi	Stereum_sanguinolentum
0.8571	0.4444	0.617	0.003	B100 & B50	Fungi	Genolevuria spp.
1	0.4444	0.667	0.001	B100 & B50	Fungi	Fomitopsis spp.
1	0.3333	0.577	0.016	B100 & B50	Fungi	Taphrina spp.
0.9091	0.3889	0.595	0.012	B100 & B50	Fungi	Fomitopsis spp.
0.75	0.7222	0.736	0.002	B100 & B50	Fungi	Gyromitra_tianshanensis
0.8	0.4815	0.621	0.027	B100 & B50 & NS	Fungi	Ascocoryne_albida
0.8824	0.4815	0.652	0.005	B100 & B50 & NS	Fungi	Paratritirachium spp.
0.9	0.3333	0.548	0.043	B100 & B50 & NS	Fungi	Hypochnicium spp.
1	0.3333	0.577	0.019	B50	Fungi	Stereum spp.
0.7368	0.8889	0.809	0.001	B50	Fungi	Crumenulopsis_pinicola
0.7	0.5556	0.624	0.003	B50	Fungi	Peniophora_pini
0.8889	0.5556	0.703	0.001	B50	Fungi	Crumenulopsis_pinicola
0.8571	0.5556	0.69	0.001	B50	Fungi	Crumenulopsis_pinicola
0.8182	0.5556	0.674	0.003	B50	Fungi	Trapeliopsis spp.
0.625	0.5556	0.589	0.005	B50	Fungi	Talaromyces_rademirici
0.8333	0.5556	0.68	0.001	B50	Fungi	Fomitopsis spp.
0.8333	0.5556	0.68	0.001	B50	Fungi	Fomitopsis spp.
0.8333	0.5	0.645	0.003	B50 & NS	Fungi	Crumenulopsis_pinicola
0.8	0.3333	0.516	0.047	NS	Fungi	Crumenulopsis_pinicola
0.7778	0.5556	0.657	0.024	Ret10 & B100 & B50	Fungi	Exophiala spp.
0.9831	0.5926	0.763	0.039	Ret10 & Ret3 & Ret30 & B100 & B50 & NS	Fungi	Carcinomyces spp.
0.9467	0.7037	0.816	0.045	Ret10 & Ret3 & Ret30 & B100 & B50 & NS	Fungi	Exophiala spp.
1	0.3056	0.553	0.045	Ret10 & Ret3 & Ret30 & B50	Fungi	Dacrymyces_capitatus
0.9444	0.7778	0.857	0.041	Ret10 & Ret3 & Ret30 & Ret50 & B100 & B50	Fungi	Phialocephala spp.
1	0.5	0.707	0.039	Ret10 & Ret3 & Ret30 & Ret50 & B100 & NS	Fungi	Hyphodiscus_hymeniophilus
1	0.4444	0.667	0.014	Ret10 & Ret3 & Ret30 & Ret50 & NS	Fungi	Phaeotheca spp.
0.925	0.5556	0.717	0.046	Ret10 & Ret3 & Ret30 & Ret50 & NS	Fungi	Exophiala_abietophila
0.8333	0.5185	0.657	0.005	Ret10 & Ret30 & B100	Fungi	Rhinocladiella spp.
0.9565	0.4167	0.631	0.017	Ret10 & Ret30 & B100 & B50	Beetle	Sericus brunneus
0.9706	0.7111	0.831	0.001	Ret10 & Ret50 & B100 &B50 & NS	Fungi	Fomitopsis spp.
1	0.4444	0.667	0.001	Ret3	Beetle	Holobus apicatus
1	0.2778	0.527	0.019	Ret3 & Ret30	Fungi	Vexillomyces_palatinus
0.9697	0.6389	0.787	0.001	Ret3 & Ret30 & Ret50 & NS	Fungi	Vexillomyces_palatinus
0.8	0.5556	0.667	0.008	Ret30 & B100 & B50	Fungi	Colacogloea spp.
1	0.3333	0.577	0.021	Ret50	Fungi	Exophiala spp.

Data availability

Data will be made available on request.

References

Abarenkov, K., Zirk, A., Piirmann, T., Pöhönen, R., Ivanov, F., Nilsson, R.H., Kõljalg, U., 2023. UNITE USEARCH/UTAX release for Fungi. https://doi.org/10.15156/BIO/2938083.

Ahti, T., Hämet-Ahti, L., Jalas, J., 1968. Vegetation zones and their sections in northwestern Europe. Ann. Bot. Fenn. 5, 169–211.

Axelsson, A.-L., Östlund, L., 2001. Retrospective gap analysis in a Swedish boreal forest landscape using historical data. For. Ecol. Manag. 147, 109–122. https://doi.org/10.1016/S0378-1127(00)00470-9.

Bader, P., Jansson, S., Jonsson, B.G., 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biol. Conserv. 72, 355–362. https://doi.org/10.1016/0006-3207(94)00029.

Barton, K., Barton, M.K., 2015. Package 'mumin.', vol. 1, p. 439.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Statis. Software 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.

Berglund, H., Jönsson, M.T., Penttilä, R., Vanha-Majamaa, I., 2011. The effects of burning and dead-wood creation on the diversity of pioneer wood-inhabiting fungi in managed boreal spruce forests. For. Ecol. Manag. 261, 1293–1305. https://doi.org/10.1016/j.foreco.2011.01.008.

Bergmark, P., Hjältén, J., Svensson, J., Neumann, W., Hekkala, A.-M., 2024. Trait-environment interactions of saproxylic beetles as a guide to biodiversity conservation strategies. J. Environ. Manag. 360, 121080. https://doi.org/10.1016/j.jenvman.2024.121080.

Boddy, L., Heilmann-Clausen, J., 2008. Chapter 12 Basidiomycete community development in temperate angiosperm wood. In: Boddy, L., Frankland, J.C., van West, P. (Eds.), British Mycological Society Symposia Series, Ecology of Saprotrophic Basidiomycetes. Academic Press, pp. 211–237. https://doi.org/10.1016/S0275-0287(08)80014-8.

Bunnell, F.L., Huggard, D.J., 1999. Biodiversity across spatial and temporal scales: problems and opportunities. For. Ecol. Manag. 115, 113–126. https://doi.org/10.1016/S0378-1127(98)00392-2.

Carlsson, F., Edman, M., Holm, S., Eriksson, A.-M., Jonsson, B.G., 2012. Increased heat resistance in mycelia from wood fungi prevalent in forests characterized by fire: a possible adaptation to forest fire. Fungal Biol. 116, 1025–1031. https://doi.org/10.1016/j.funbio.2012.07.005.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human–induced species losses: entering the sixth mass extinction. Sci. Adv. https://doi.org/10.1126/sciadv.1400253.

Conrad, K.F., Warren, M.S., Fox, R., Parsons, M.S., Woiwod, I.P., 2006. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. Biol. Conserv. 132, 279–291. https://doi.org/10.1016/j.biocon.2006.04.020.

De Caceres, M., Jansen, F., De Caceres, M.M., 2016. Package 'indicspecies.'. indicators 8.

Dynesius, M., Olsson, J., Hjältén, J., Löfroth, T., Roberge, J.-M., 2021. Bryophyte species composition at the stand scale (1 ha) – differences between secondary stands half a century after clear-cutting and older semi-natural boreal forests. For. Ecol. Manag. 482, 118883. https://doi.org/10.1016/j.foreco.2020.118883.
Edgar, R.C., 2016. SINTAX: a simple non-Bayesian taxonomy classifier for 16S and ITS sequences. https://doi.org/10.1101/074161.
Edman, M., Eriksson, A.-M., 2016. Competitive outcomes between wood-decaying fungi are altered in burnt wood. FEMS (Fed. Eur. Microbiol. Soc.) Microbiol. Ecol. 92, fiw068. https://doi.org/10.1093/femsec/fiw068.
Edman, M., Kruys, N., Jonsson, B.G., 2004. Local dispersal sources strongly affect colonization patterns of wood-decaying fungi on spruce logs. Ecol. Appl. 14, 893–901. https://doi.org/10.1890/03-5103.
Espinosa del Alba, C., Hjältén, J., Sjögren, J., 2021. Restoration strategies in boreal forests: differing field and ground layer response to ecological restoration by burning and gap cutting. For. Ecol. Manag. 494, 119357. https://doi.org/10.1016/j.foreco.2021.119357.
Felton, A., Löfroth, T., Angelstam, P., Gustafsson, L., Hjältén, J., Felton, A.M., Simonsson, P., Dahlberg, A., Lindbladh, M., Svensson, J., Nilsson, U., Lodin, I., Hedwall, P.O., Sténs, A., Lämås, T., Brunet, J., Kalén, C., Kriström, B., Gemmel, P., Ranius, T., 2020. Keeping pace with forestry: multi-scale conservation in a changing production forest matrix. Ambio 49, 1050–1064. https://doi.org/10.1007/s13280-019-01248-0.
Fredriksson, E., 2021. Decadal effects of forest fire on biodiversity and browsing : a comparison between wildfire and prescribed burning [WWW Document]. URL. https://pub.epsilon.slu.se/26120/. accessed 12.23.21.
Fredriksson, E., Mugerwa Pettersson, R., Naalisvaara, J., Löfroth, T., 2020. Wildfire yields a distinct turnover of the beetle community in a semi-natural pine forest in northern Sweden. Ecological Processes 9, 44. https://doi.org/10.1186/s13717-020-00246-5.
Gibb, H., Ball, J.P., Johansson, T., Atlegrim, O., Hjältén, J., Danell, K., 2005. Effects of management on coarse woody debris volume and composition in boreal forests in northern Sweden. Scand. J. For. Res. 20, 213–222. https://doi.org/10.1080/02827580510008392.
Gonçalves, S.C., Haelewaters, D., Furci, G., Mueller, G.M., 2021. Include all fungi in biodiversity goals. Science 373. https://doi.org/10.1126/science.abk1312, 403–403.
Grooten, M., Almond, R.E., 2018. Living Planet Report-2018: Aiming Higher. WWF international.
Gutowski, J.M., Sućko, K., Borowski, J., Kubisz, D., Mazur, M.A., Melke, A., Mokrzycki, T., Plewa, R., Żmihorski, M., 2020. Post-fire beetle succession in a biodiversity hotspot: białowieża Primeval Forest. For. Ecol. Manag. 461, 117893. https://doi.org/10.1016/j.foreco.2020.117893.
Hägglund, R., Dynesius, M., Löfroth, T., Olsson, J., Roberge, J.-M., Hjältén, J., 2020. Restoration measures emulating natural disturbances alter beetle assemblages in boreal forest. For. Ecol. Manag. 462, 117934. https://doi.org/10.1016/j.foreco.2020.117934.
Hägglund, R., Hekkala, A.-M., Hjältén, J., Tolvanen, A., 2015. Positive effects of ecological restoration on rare and threatened flat bugs (Heteroptera: aradidae). J. Insect Conserv. 19, 1089–1099. https://doi.org/10.1007/s10841-015-9824-z.
Hägglund, R., Hjältén, J., 2018. Substrate specific restoration promotes saproxylic beetle diversity in boreal forest set-asides. For. Ecol. Manag. 425, 45–58. https://doi.org/10.1016/j.foreco.2018.05.019.
Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., Kroon, H. de, 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS One 12, e0185809. https://doi.org/10.1371/journal.pone.0185809.
Hämäläinen, A., Fahrig, L., Strengbom, J., Ranius, T., 2023. Effective management for deadwood-dependent lichen diversity requires landscape-scale habitat protection. Journal of Applied Ecology n/a. https://doi.org/10.1111/1365-2664.14429.
Hedwall, P.-O., Brunet, J., 2016. Trait variations of ground flora species disentangle the effects of global change and altered land-use in Swedish forests during 20 years. Global Change Biol. 22, 4038–4047. https://doi.org/10.1111/gcb.13329.
Heikkala, O., Martikainen, P., Kouki, J., 2016a. Decadal effects of emulating natural disturbances in forest management on saproxylic beetle assemblages. Biol. Conserv. 194, 39–47. https://doi.org/10.1016/j.biocon.2015.12.002.
Heikkala, O., Seibold, S., Koivula, M., Martikainen, P., Müller, J., Thorn, S., Kouki, J., 2016b. Retention forestry and prescribed burning result in functionally different saproxylic beetle assemblages than clear-cutting. Forest Ecology and Management, Special Section: forests. Roots and Soil Carbon 359, 51–58. https://doi.org/10.1016/j.foreco.2015.09.043.
Hekkala, A.-M., Päätalo, M.-L., Tarvainen, O., Tolvanen, A., 2014. Restoration of young forests in eastern Finland: benefits for saproxylic beetles (Coleoptera). Restor. Ecol. 22, 151–159. https://doi.org/10.1111/rec.12050.
Hjältén, J., Hägglund, R., Löfroth, T., Roberge, J.-M., Dynesius, M., Olsson, J., 2017. Forest restoration by burning and gap cutting of voluntary set-asides yield distinct immediate effects on saproxylic beetles. Biodivers. Conserv. 26, 1623–1640. https://doi.org/10.1007/s10531-017-1321-0.
Hjältén, J., Stenbacka, F., Andersson, J., 2010. Saproxylic beetle assemblages on low stumps, high stumps and logs: implications for environmental effects of stump harvesting. For. Ecol. Manag. 260, 1149–1155. https://doi.org/10.1016/j.foreco.2010.07.003.
Hjältén, J., Stenbacka, F., Pettersson, R.B., Gibb, H., Johansson, T., Danell, K., Ball, J.P., Hilszczański, J., 2012. Micro and macro-habitat associations in saproxylic beetles: implications for biodiversity management. PLoS One 7. https://doi.org/10.1371/journal.pone.0041100.
Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol. Evol. 7, 1451–1456. https://doi.org/10.1111/2041-210X.12613.
Hyvärinen, E., Juslén, A., Kemppainen, E., Uddström, A., Liukko, U., 2019. Suomen lajien uhanalaisuus–Punainen kirja 2019. Ympäristöministeriö & Suomen Ympäristökeskus.
Ihrmark, K., Bödeker, I.T.M., Cruz-Martinez, K., Friberg, H., Kubartova, A., Schenck, J., Strid, Y., Stenlid, J., Brandström-Durling, M., Clemmensen, K.E., Lindahl, B.D., 2012. New primers to amplify the fungal ITS2 region – evaluation by 454-sequencing of artificial and natural communities. FEMS (Fed. Eur. Microbiol. Soc.) Microbiol. Ecol. 82, 666–677. https://doi.org/10.1111/j.1574-6941.2012.01437.x.
Johansson, T., Andersson, J., Hjältén, J., Dynesius, M., Ecke, F., 2010. Short-term responses of beetle assemblages to wildfire in a region with more than 100 years of fire suppression. Insect Conservation and Diversity 4, 142–151. https://doi.org/10.1111/j.1752-4598.2010.00114.x.
Johansson, T., Gibb, H., Hjältén, J., Dynesius, M., 2017. Soil humidity, potential solar radiation and altitude affect boreal beetle assemblages in dead wood. Biol. Conserv. 209, 107–118. https://doi.org/10.1016/j.biocon.2017.02.004.
Johansson, T., Gibb, H., Hjältén, J., Pettersson, R.B., Hilszczański, J., Alinvi, O., Ball, J. P., Danell, K., 2007. The effects of substrate manipulations and forest management on predators of saproxylic beetles. For. Ecol. Manag. 242, 518–529. https://doi.org/10.1016/j.foreco.2007.01.064.
Johansson, T., Hjältén, J., de Jong, J., von Stedingk, H., 2013. Environmental considerations from legislation and certification in managed forest stands: a review of their importance for biodiversity. For. Ecol. Manag. 303, 98–112. https://doi.org/10.1016/j.foreco.2013.04.012.
Kärvemo, S., Jönsson, M., Hekkala, A.-M., Sjögren, J., Strengbom, J., 2021. Multi-taxon conservation in northern forest hot-spots: the role of forest characteristics and spatial scales. Landscape Ecol 36, 989–1002. https://doi.org/10.1007/s10980-021-01205-x.
Kaunisto, K.M., Roslin, T., Forbes, M.R., Morrill, A., Sääksjärvi, I.E., Puisto, A.I.E., Lilley, T.M., Vesterinen, E.J., 2020. Threats from the air: damselfly predation on diverse prey taxa. J. Anim. Ecol. 89, 1365–1374. https://doi.org/10.1111/1365-2656.13184.
Koivula, M., Vanha-Majamaa, I., 2020. Experimental evidence on biodiversity impacts of variable retention forestry, prescribed burning, and deadwood manipulation in Fennoscandia. Ecol Process 9, 11. https://doi.org/10.1186/s13717-019-0209-1.
Kouki, J., Hyvärinen, E., Lappalainen, H., Martikainen, P., Similä, M., 2012. Landscape context affects the success of habitat restoration: large-scale colonization patterns of saproxylic and fire-associated species in boreal forests. Divers. Distrib. 18, 348–355. https://doi.org/10.1111/j.1472-4642.2011.00839.x.
Lantmäteriet, 2021. Orthophoto. https://www.lantmateriet.se/sv/geodata/vara-produkter/produktlista/ortofoto-nedladdning/ (Accessed 15 March 2021).
Larsson Ekström, A., Bergmark, P., Hekkala, A.-M., 2021. Can multifunctional forest landscapes sustain a high diversity of saproxylic beetles? For. Ecol. Manag. 490, 119107. https://doi.org/10.1016/j.foreco.2021.119107.
Larsson Ekström, A., Hjältén, J., Löfroth, T., 2024. A decadal study reveals that restoration guided by an umbrella species does not reach target levels. J. Appl. Ecol. 61, 513–525. https://doi.org/10.1111/1365-2664.14586.
Larsson Ekström, A., Sjögren, J., Djupström, L.B., Thor, G., Löfroth, T., 2023. Reinventory of permanent plots show that kelo lichens face an extinction debt. Biol. Conserv. 288, 110363. https://doi.org/10.1016/j.biocon.2023.110363.
Lenth, R., Singmann, H., Love, J., Buerkner, P., Herve, M., 2019. Package 'emmeans.'.
Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biol. Conserv. 131, 433–445. https://doi.org/10.1016/j.biocon.2006.02.019.
Lindhe, A., Åsenblad, N., Toresson, H.-G., 2004. Cut logs and high stumps of spruce, birch, aspen and oak – nine years of saproxylic fungi succession. Biol. Conserv. 119, 443–454. https://doi.org/10.1016/j.biocon.2004.01.005.
Lindhe, A., Lindelöw, Å., 2004. Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. For. Ecol. Manag. 203, 1–20. https://doi.org/10.1016/j.foreco.2004.07.047.
Lindman, L., Öckinger, E., Ranius, T., 2022. Microclimatic conditions mediate the effect of deadwood and forest characteristics on a threatened beetle species, Tragosoma depsarium. Oecologia 199, 737–752. https://doi.org/10.1007/s00442-022-05212-w.
Lister, B.C., Garcia, A., 2018. Climate-driven declines in arthropod abundance restructure a rainforest food web. Proc. Natl. Acad. Sci. USA 115, E10397–E10406. https://doi.org/10.1073/pnas.1722477115.
Löfroth, T., Birkemoe, T., Shorohova, E., Dynesius, M., Fenton, N.J., Drapeau, P., Tremblay, J.A., 2023. Deadwood biodiversity. In: Girona, M.M., Morin, H., Gauthier, S., Bergeron, Y. (Eds.), Boreal Forests in the Face of Climate Change: Sustainable Management, Advances in Global Change Research. Springer International Publishing, Cham, pp. 167–189. https://doi.org/10.1007/978-3-031-15988-6_6.
Nic Lughadha, E., Bachman, S.P., Leão, T.C.C., Forest, F., Halley, J.M., Moat, J., Acedo, C., Bacon, K.L., Brewer, R.F.A., Gâteblé, G., Gonçalves, S.C., Govaerts, R., Hollingsworth, P.M., Krisai-Greilhuber, I., de Lirio, E.J., Moore, P.G.P., Negrão, R., Onana, J.M., Rajaovelona, L.R., Razanajatovo, H., Reich, P.B., Richards, S.L., Rivers, M.C., Cooper, A., Iganci, J., Lewis, G.P., Smidt, E.C., Antonelli, A., Mueller, G. M., Walker, B.E., 2020. Extinction risk and threats to plants and fungi. PLANTS, PEOPLE, PLANET 2, 389–408. https://doi.org/10.1002/ppp3.10146.
Niklasson, M., Granström, A., 2000. Numbers and sizes of fires: long-term spatially explicit fire history in a Swedish boreal landscape. Ecology 81, 1484–1499. https://doi.org/10.1890/0012-9658(2000)081[1484:NASOFL]2.0.CO;2.

Nirhamo, A., Hämäläinen, A., Hämäläinen, K., Kouki, J., 2024. Retention forestry can maintain epiphytic lichens on living pine trees, but provides impoverished habitat for deadwood-associated lichens. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.14772.

Nitare, J.S., 2000. Indikatorer på skyddsvärd skog. Flora över kryptogamer. Jönköping: Skogsstyrelsen. ISBN: 9789188462688.

Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E., Ovaskainen, O., 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. J. Ecol. 101, 701–712. https://doi.org/10.1111/1365-2745.12085.

Oksanen, J., Simpson, G., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P., O'hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouelette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J. vegan: community ecology package. R package. https://CRAN.R-project.org/package=vegan.

Olsson, J., Jonsson, B.G., 2010. Restoration fire and wood-inhabiting fungi in a Swedish Pinus sylvestris forest. For. Ecol. Manag. 259, 1971–1980. https://doi.org/10.1016/j.foreco.2010.02.008.

Olsson, J., Jonsson, B.G., Hjältén, J., Ericson, L., 2011. Addition of coarse woody debris – the early fungal succession on Picea abies logs in managed forests and reserves. Biological Conservation, The New Conservation Debate: Beyond Parks vs. People 144, 1100–1110. https://doi.org/10.1016/j.biocon.2010.12.029.

Östlund, L., Zackrisson, O., Axelsson, A.-L., 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. Can. J. For. Res. 27, 1198–1206. https://doi.org/10.1139/x97-070.

Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., Bruyn, L.D., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.-T., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K., Virtanen, R., 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in europe. Conserv. Biol. 24, 101–112. https://doi.org/10.1111/j.1523-1739.2009.01399.x.

Penttilä, R., Junninen, K., Punttila, P., Siitonen, J., 2013. Effects of forest restoration by fire on polypores depend strongly on time since disturbance – a case study from Finland based on a 23-year monitoring period. For. Ecol. Manag. 310, 508–516. https://doi.org/10.1016/j.foreco.2013.08.061.

R Core Team, 2021. R: A Language and Environment for Statistical Computing.

Ramberg, E., Berglund, H., Penttilä, R., Strengbom, J., Jönsson, M., 2023. Prescribed fire is an effective restoration measure for increasing boreal fungal diversity. Ecol. Appl. 33, e2892. https://doi.org/10.1002/eap.2892.

Rognes, T., Flouri, T., Nichols, B., Quince, C., Mahé, F., 2016. VSEARCH: a versatile open source tool for metagenomics. PeerJ 4, e2584. https://doi.org/10.7717/peerj.2584.

Rothacher, J., Hagge, J., Bässler, C., Brandl, R., Gruppe, A., Müller, J., 2023. Logging operations creating snags, logs, and stumps under open and closed canopies promote stand-scale beetle diversity. For. Ecol. Manag. 540, 121022. https://doi.org/10.1016/j.foreco.2023.121022.

Rudolphi, J., Jönsson, M.T., Gustafsson, L., 2014. Biological legacies buffer local species extinction after logging. J. Appl. Ecol. 51, 53–62. https://doi.org/10.1111/1365-2664.12187.

Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: a review of its drivers. Biol. Conserv. 232, 8–27. https://doi.org/10.1016/j.biocon.2019.01.020.

Santaniello, F., Line, D.B., Ranius, T., Rudolphi, J., Widenfalk, O., Weslien, J., 2016. Effects of partial cutting on logging productivity, economic returns and dead wood in boreal pine forest. For. Ecol. Manag. 365, 152–158. https://doi.org/10.1016/j.foreco.2016.01.033.

Seibold, S., Bässler, C., Baldrian, P., Reinhard, L., Thorn, S., Ulyshen, M.D., Weiß, I., Müller, J., 2016a. Dead-wood addition promotes non-saproxylic epigeal arthropods but effects are mediated by canopy openness. Biol. Conserv. 204, 181–188. https://doi.org/10.1016/j.biocon.2016.09.031.

Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M.D., Müller, J., 2016b. Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. J. Appl. Ecol. 53, 934–943. https://doi.org/10.1111/1365-2664.12607.

Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S., Müller, J., 2015. Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. Conserv. Biol. 29, 382–390. https://doi.org/10.1111/cobi.12427.

Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: fennoscandian boreal forests as an example. Ecol. Bull. 11–41.

SLU Artdatabanken, 2020. Rödlistade Arter I Sverige. Artdatabanken, SLU, Uppsala.

Stokland, J.N., Larsson, K.-H., 2011. Legacies from natural forest dynamics: different effects of forest management on wood-inhabiting fungi in pine and spruce forests. For. Ecol. Manag. 261, 1707–1721. https://doi.org/10.1016/j.foreco.2011.01.003.

Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in Dead Wood. Cambridge University Press.

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

Toivanen, T., Kotiaho, J.S., 2007. Burning of logged sites to protect beetles in managed boreal forests. Conserv. Biol. 21, 1562–1572. https://doi.org/10.1111/j.1523-1739.2007.00808.x.

Uhl, B., Krah, F.-S., Baldrian, P., Brandl, R., Hagge, J., Müller, J., Thorn, S., Vojtech, T., Bässler, C., 2022. Snags, logs, stumps, and microclimate as tools optimizing deadwood enrichment for forest biodiversity. Biol. Conserv. 270, 109569. https://doi.org/10.1016/j.biocon.2022.109569.

United Nations Environment Agency, 2019. Resolution 73/284: United Nations Decade on Ecosystem Restoration (2021–2030).

Weslien, J., Djupström, L.B., Schroeder, M., Widenfalk, O., 2011. Long-term priority effects among insects and fungi colonizing decaying wood. J. Anim. Ecol. 80, 1155–1162. https://doi.org/10.1111/j.1365-2656.2011.01860.x.

White, T.J., Bruns, T., Lee, S., Taylor, J., 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. PCR protocols: a guide to methods and applications 18, 315–322.

Wikars, L.-O., 2002. Dependence on fire in wood-living insects: an experiment with burned and unburned spruce and birch logs. J. Insect Conserv. 6, 1–12. https://doi.org/10.1023/A:1015734630309.

Wikars, L.-O., 2004. Habitat requirements of the pine wood-living beetle tragosoma depsarium (Coleoptera: cerambycidae) at log, stand, and landscape scale. Ecol. Bull. 287–294. https://doi.org/10.2307/20113317.

Zhang, S., Sjögren, J., Jönsson, M., 2024. Retention forestry amplifies microclimate buffering in boreal forests. Agric. For. Meteorol. 350, 109973. https://doi.org/10.1016/j.agrformet.2024.109973.