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Faculty of Forest Sciences

Hitting the restoration target?

Decadal effects of ecological restoration in boreal forests

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Abstract

The continued decline of habitat and species in forest ecosystems highlights the urgent need for more effective conservation and restoration measures. The lack of improvement in biodiversity conditions suggests a disconnect between practical conservation, conservation science and conservation theory.

In this thesis, I investigate decadal, multi-taxon responses of wood-associated species communities to ecological restoration in boreal deciduous and pine forests.

Ecological restoration leads to divergent diversity patterns depending on the restoration method and taxonomic group studied. In deciduous forest restoration, beetle diversity patterns are clearly divergent both from a non-restored baseline and a restoration target, one to two decades post restoration. In pine forest restoration, deadwood substrate identity had a stronger influence on species communities of lichens, fungi and beetles than the specific restoration treatment. In addition, deadwood derived from restoration supported only a fraction of the species found on old, natural deadwood.

These findings demonstrate that species community responses to restoration are highly dependent on both time and taxon. Successful restoration must account for the varied ecological requirements of forest-dwelling species across space and time. The observed divergence in species-host relationships and the limited restoration target fulfilment underscore the need to diversify and improve conservation and restoration strategies. This thesis outlines the key lessons learned and discusses future perspectives for improving restoration of boreal forest biodiversity.

Keywords: Biodiversity, Conservation, Restoration, Deadwood, Multi-taxon, Community ecology

Uppnås restaureringsmålen? Effekter av ekologisk restaurering i boreala skogar

Sammanfattning

Fortsatta minskningar av habitat och artpopulationer i skogliga ekosystem belyser behovet av effektivare bevarande- och restaureringsåtgärder. Att många arter och livsmiljöer har dåliga förutsättningar att överleva på sikt tyder på ett glapp mellan forskning och praktik i bevarandet av biologisk mångfald.

Jag har undersökt effekten av ekologisk restaurering av boreala tall- och lövskogar på vedlevande artsamhällen tillhörande flera organismgrupper.

Ekologisk restaurering leder till avvikande effekter beroende på restaureringsmetod och vilken organismgrupp som studeras. I lövskogsrestaurering skiljde sig artsamhällena av skalbaggar både från icke-restaurerade och målhabitat, en till två decennier efter restaurering. I tallskogsrestaurering hade typen av död ved större påverkan på artsamhällen av lavar, svampar och skalbaggar än den specifika restaureringsmetoden. Den döda veden som skapades i restaureringen hyste dessutom endast en liten andel av de arter som fanns på gammal, naturlig död ved.

Resultaten från denna avhandling demonstrerar att effekten av restaurering skiljer sig över tid och mellan organismgrupper. Restaurering måste ta hänsyn till de varierande ekologiska behoven av skogslevande arter i både tid och rum. De avvikande förhållanden mellan arter och habitatstrukturer och den begränsade måluppfyllnaden understryker behovet att diversifiera och förbättra bevarande- och restaureringsstrategier. Denna avhandling belyser de viktigaste lärdomarna och diskuterar framtida behov för att förbättra restaurering av den biologiska mångfalden i boreala skogar.

Nyckelord: Biodiversitet, Bevarandebiologi, Restaurering, Naturvård, Död ved, Ekologi

Contents

List of publications

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

I. Larsson Ekström, Albin., Hjältén, Joakim., Löfroth, Therese (2024). A decadal study reveals that restoration guided by an umbrella species does not reach target levels. Journal of Applied Ecology, 61 (3), pp. 513-525. https://doi.org/10.1111/1365-2664.14586

II. Larsson Ekström, Albin., Hjältén, Joakim., Jones, Faith. A.M., Sjögren, Jörgen., Löfroth, Therese (2025). Ecological restoration alters functional-phylogenetic structure of saproxylic beetles. (submitted)

III. Larsson Ekström, Albin., Sjögren, Jörgen., Djupström, Line. B., Thor, Göran., Löfroth, Therese (2023). Reinventory of permanent plots show that kelo lichens face an extinction debt. Biological Conservation, 288, https://doi.org/10.1016/j.biocon.2023.110363

IV. Larsson Ekström, Albin., Djupström, Line. B., Hjältén, Joakim., Sjögren, Jörgen., Jönsson, Mari., Löfroth, Therese (2024). Deadwood manipulation and type determine species communities of saproxylic beetles and fungi after a decade. Journal of Environmental Management, 372, https://doi.org/10.1016/j.jenvman.2024.123416

V. Larsson Ekström, Albin., Gibb, Heloise., Jönsson, Mari., Djupström, Line. B., Löfroth, Therese (2025). Life-history traits and phylogeny structure taxon-specific species-host relationships in deadwood. (manuscript)

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The contribution of Albin Larsson Ekström to the papers included in this thesis was as follows:

I. Main author. Conceptualisation and planning of the study design, funding acquisition, data collection, formal analysis and led the writing of the manuscript.

II. Main author. Conceptualisation and planning of the study design, funding acquisition, data collection, formal analysis and led the writing of the manuscript.

III. Main author. Conceptualisation and planning of the study design, data collection of deadwood, formal analysis and led the writing of the manuscript.

IV. Main author. Conceptualisation and planning of the study design, funding acquisition, data collection, formal analysis and led the writing of the manuscript.

V. Main author. Conceptualisation and planning of the study design, funding acquisition, data collection, formal analysis and led the writing of the manuscript.

List of figures

1. Introduction

1.1 Biodiversity

Biodiversity describes the diversity and abundance of all living organisms (Wilson, 1988), encompassing the variability within and between species and of ecosystems (CBD, 2006). Land use and exploitation have led to global declines in biodiversity, the severity of which differ between geographic areas and biomes (Jaureguiberry et al., 2022; Newbold et al., 2015; Pimm et al., 2014). The threat is ongoing, with increasing pressures driven by human land-use (Tittensor et al., 2014). While some of the most threatened areas remain without protection (Pulido-Chadid et al., 2025), concerns have been raised that protection alone is not enough to conserve biodiversity, calling for restoration of lost or degraded habitat (Leclère et al., 2020; Strassburg et al., 2020).

As for biodiversity conservation efforts, most focus has been on charismatic taxa such as large mammals, birds or fish, while groups such as insects and fungi remain severely underrepresented in global conservation programmes (Chowdhury et al., 2023; Clark and May, 2002; Gonçalves et al., 2021; Heilmann-Clausen et al., 2015). As a result, conservation initiatives may disregard the majority of species in favour of a few more well-known species. For example, not until 2025 were the first 1000 species assessed in the IUCN red-list (iucnredlist.org). These shortcomings are concerning, as insects and fungi support much of terrestrial biodiversity, provide essential ecosystem functions, and face a high risk of extinction (Runnel et al., 2025; Seibold et al., 2021).

Biodiversity is a broad and multifaceted concept encompassing an array of different biodiversity indices which is essential to consider in order to efficiently conserve biodiversity. Common indices include species richness, evenness and dissimilarity indices (Magurran, 2021). Yet, these indices are not enough to describe the extent of biological diversity. Biodiversity can be broken down into different scales, describing the local diversity of a given site (α-diversity), the compositional change between sites (β-diversity) and the overall diversity in a wider landscape (*γ*-diversity) as proposed by Whittaker (1972), (Fig 1). For example, focusing solely on α-diversity may describe a sites unique biodiversity value, but says nothing about species identity or a sites complementary value in the broader landscape (β-diversity).

Just as biodiversity can be divided into different scales, it can also be described in terms of different facets. Historically, emphasis has been placed on taxonomic diversity, quantifying morphospecies (Magurran, 2021). Increasing recognition of the roles that species evolutionary and life-history traits play in shaping interactions with their environment has led to the development of functional and phylogenetic diversity concepts (Fig 1, Cadotte et al., 2012, 2011). Functional traits, including morphology, physiology and phenology, describe a species fitness (Violle et al., 2007), while ecological traits may describe a species habitat affinity such as saproxylic species utilizing deadwood under part of their life cycle (Speight, 1989). Larger-bodied species, for example, require more resources and exert greater influence on their environment (Peters, 1986; Pringle et al., 2023). At the same time, being large is often connected to slower reproduction rates, which can impact a species likelihood to go extinct, whereas smaller species may reproduce and disperse more easily (Gaston and Blackburn, 1997; McKinney, 1997). Just as the variety of morphospecies describes taxonomic diversity, the variety of traits in a species community describes functional diversity (Tilman, 2001).

Traits can also be phylogenetically structured due to evolutionary heritage, such that closely related species tend to share similar traits, whereas more distantly related species are less similar, a pattern referred to as niche conservatism (Wiens and Graham, 2005). The variety of evolutionary lineages is described as phylogenetic diversity (Faith, 1992). Functional trait ecology is an emerging field and has already improved our understanding of underlying processes to species assembly. Still, there are great knowledge gaps within trait ecology, not least in which traits are most informative and how they are related to phylogeny (de Bello et al., 2025; Guillerme et al., 2025).

While it is important to consider multiple scales and facets of biodiversity, so too are the variable habitat and niche requirements both within and between taxonomic groups. Focussing on a single taxonomic group may lead to biased decisions with contradictory outcomes for other taxa due to potentially diverging ecological requirements, not least in boreal forests (Fig 1, Koivula and Vanha-Majamaa, 2020). Instead, the needs of several groups of species are required for well-informed conservation decisions (Burrascano et al., 2023). Species communities can display great differences in both intra- and inter-taxon responses to. e.g., habitat restoration (Koivula and Vanha-Majamaa, 2020). In addition, species not only interact with their environment, but also across taxonomic borders. For example, beetles and fungi have developed a mutualistic relationship regarding their dispersal and resource requirement strategies (Birkemoe et al., 2018). Another cross-taxon relationship is seen in the relationship between woodpeckers and insects. where woodpeckers facilitate wood decomposition. but are in turn controlled by densities of beetle populations (Tuo et al., 2025). In other words, the manipulation of one species- or taxonomic group could have cascading effects across taxonomic borders.

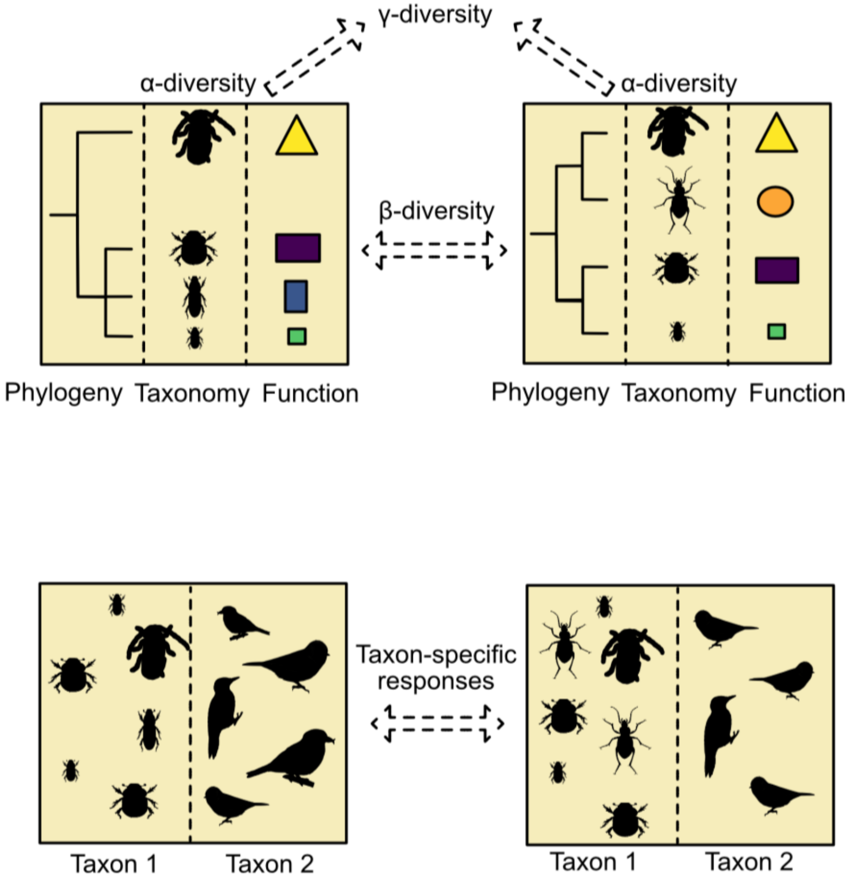

Figure 1. Conceptual figure visualising biodiversity scales (α, β and γ-diversity) and facets (phylogenetic, taxic and functional) in the upper panel and taxon-specific community responses in the lower panel. Each box represents a species community in a habitat.

1.1.1 Forest biodiversity

Forests make up one of the largest biomes and supports the majority of terrestrial biodiversity (Pimm et al., 2014; Watson et al., 2018). In addition, they provide and regulate functions that are essential for human life – ecosystem services such as climate- and water regulation, biomass production among others (Brockerhoff et al., 2017). There is increasing evidence that intact forests support both ecosystem functionality and services for human life – relative to degraded forests (Watson et al., 2018).

Despite their crucial role in supporting biodiversity and providing ecosystem services, forests are increasingly subject to destruction, degradation, and fragmentation (Aerts and Honnay, 2011). These pressures stem from a long history of unsustainable land use, which has already led to widespread habitat loss and numerous species extinctions. Human activity has also fundamentally altered landscapes by suppressing or eliminating key natural processes such as fire, natural succession and the presence of megaherbivores (Niklasson and Granström, 2000; Sandom et al., 2014). As a result, species communities have been reshaped - benefiting some species to the detriment of others that depend on these natural dynamics and structural features.

As an example, more than 80% of temperate forest plants are adapted to semi-open conditions, which is naturally maintained by large herbivores, a key disturbance component that is now lost (Czyżewski and Svenning, 2025). In boreal forests, many species are dependent on, or benefit from, natural disturbances such as fire (Goodman and McCravy, 2008; Olsson and Jonsson, 2010; Wikars, 2002), a process that has been greatly reduced due to fire prevention (Niklasson and Granström, 2000; Uotila et al., 2002; Zackrisson, 1977). Although the forest cover in Fennoscandia may remain unchanged or even increasing, the structural complexity of these forests have been heavily simplified compared to natural conditions. This is seen in the large reduction of key structures such as deadwood (Siitonen, 2001) or habitat such as unmanaged pine forests or deciduous forests rich in deadwood (Axelsson et al., 2002; de Jong, 2002; Engelmark, 1987). The principal threat to boreal forest biodiversity is forestry, which leads to destruction of habitat and hindering regeneration of new natural habitat (SLU Artdatabanken, 2020).

Deadwood is a key structure for forest biodiversity, serving as both a food and nesting resource for many forest species while also contributing to ecosystem functions (Löfroth et al., 2023). The utilisation of deadwood is an ancient habitat affinity spanning back at least ~370 million years ago for wood-decaying fungi (Stubblefield et al., 1985) and ~280 million years ago for the oldest beetle group, Protocoleoptera, which is thought to have utilized decaying wood (Ponomarenko, 2003; Stokland et al., 2012). This long evolutionary history has led to rich biodiversity, serving several key functions such as wood decomposition and nutrient turnover (Harmon, 2021; Müller et al., 2020). Beetles and fungi interact in a number of ways as a result of co-evolution, where fungi may provide nutrients while beetles facilitate fungal dispersal (Birkemoe et al., 2018). Forestry has greatly reduced this vital structure, threatening not only the species that depend on it but also the ecosystem functions it supports (Siitonen, 2001). For this reason, deadwood biodiversity is often a core focus of ecological restoration of forests (Hjältén et al., 2023; Löfroth et al., 2023). Beyond its conservation value, deadwood also provides a useful model system for studying ecological theory and community assembly.

1.2 Restoration ecology

Ecological restoration has emerged as a key priority in biodiversity initiatives, ranging in scale from the UN's *Decade on Ecosystem Restoration* (decadeonrestoration.org/about-un-decade) to the EU's Nature Restoration Law (European Union, 2024) and national conservation action programmes (see e.g., Swedish Environmental Protection Agency, 2025). Ecological restoration refers to "*the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed*" as defined by the Society for Ecological Restoration (2025). Although restoration is often seen through an interventionist lens (Hobbs and Cramer, 2008), it encompasses both passive, hands-off approaches and more direct interventions and should rather be seen as a more holistic approach aiding rather than doing harm to biodiversity (Chazdon et al., 2024). Still, restoration is a broad concept and can be implemented in a number of actions as well as deliberate inactions.

In destroyed habitats, restoration can be done by reinstating key structures such as the reforestation of former mining sites (Macdonald et al., 2015). In areas where trees still remain but lack important structures, i.e., degraded habitats, structural enhancement can be done such as deadwood enrichment (Hekkala et al., 2016). Restoration can also be implemented by reintroducing elements, such as species, that drive key ecological processes, through rewilding (Lorimer et al., 2015; Perino et al., 2019; Svenning et al., 2024). Species-focused rewilding has traditionally been done on large mammals, most famously in the Yellowstone National Park, where the reintroduction of wolves led to large cascading effects on the entire landscape (Ripple and Beschta, 2012). The notion that this led to full ecosystem recovery have however been challenged, see Hobbs et al., (2024). There are also good examples of reintroductions of the Eurasian beaver (*Castor fiber*) that improved conditions for biodiversity (Law et al., 2017, 2016). Reintroduction can also be done of certain species of conservation concern, in an attempt to repopulate declining species populations. This is seen in for example reintroducing the critically endangered White-backed woodpecker (*Dendrocopos leucotos*) in Sweden (Mild and Stighäll, 2005) or insects such as *Cerambyx cerdo* (Swedish Environmental Protection Agency, 2009). However, these approaches still lack substantial empirical evidence demonstrating its effectiveness at scale. Another novel rewilding approach is whole-of-community rewilding where the idea is that translocation of soil, litter or even deadwood will also translocate species communities that dwell within (Contos et al., 2021). This approach has some merit, shown in e.g., Australia where litter translocation benefitted decomposition rates (Contos et al., 2024). In an experiment from Swedish forests, translocating deadwood to a compensation area has shown to benefit saproxylic beetles and bryophytes in the short-term, but long-term evaluation is still required (Tranberg et al., 2025a, 2025b). In order to properly assess restoration success, clear targets based on ecological knowledge need to be set and monitored post restoration (Halme et al., 2013; Prach et al., 2019).

1.2.1 Restoration of boreal forest biodiversity

Small- and large-scale biotic and abiotic disturbances have shaped boreal forests and their inhabiting species. Such disturbances range from small gap dynamics caused by windthrows or localized insect and fungal outbreaks up to landscape-spanning wildfires and storms (Kuuluvainen and Aakala, 2011). Combined, these natural disturbances have in the past created a mosaic of ecological niches for forest-dwelling species (Berglund and

Kuuluvainen, 2021). However, these disturbances have been diminished and no longer drive ecological processes in large parts boreal forest. Instead, the main ecological process is now driven by anthropogenic pressure in the form of forestry, which has transformed the forested landscape into even-aged, monoculture tree plantations (Aakala et al., 2023; Ahlström et al., 2022; Axelsson and Östlund, 2001; Mönkkönen et al., 2022). This has led to poor conditions for many forest-dwelling species in Fennoscandia (Hyvärinen et al., 2019; SLU Artdatabanken, 2020).

As a way to reverse this trend, restoration in boreal forests builds upon the theory that it is efficient to mimic natural processes when restoring habitat (Halme et al., 2013; Lindenmayer et al., 2006). This has led to the emergence of several restoration methods attempting to mimic natural disturbances, Natural Disturbance Emulation (NDE) (Gauthier, 2009; Hjältén et al., 2023; Lindenmayer et al., 2006). NDE can take form in various ways but is most commonly implemented to restore habitat for the most threatened taxa, such as those connected to fire, deciduous forests and deadwood (Hjältén et al., 2023). Therefore, the most prominent restoration tools in boreal forests in Fennoscandia are prescribed burning as a means of mimicking wildfire, gap cutting and deadwood enrichment to mimic gap dynamics and the manipulation of tree species composition to favour early-successional habitat such as pioneer deciduous species (Hjältén et al., 2023). NDE has now been implemented for several decades in Fennoscandia, yet large gaps in knowledge remain related to taxa-specific responses, temporal longevity and certain habitat types such as deciduous forest (Hjältén et al., 2023).

1.2.2 Hypothetical assumptions of restoration

Despite these well-developed approaches, ecological restoration still rests on several assumptions regarding community assembly. These assumptions are often based on distribution patterns in areas without ecological barriers and with intact source populations able to colonize restored habitat (Hilderbrand et al., 2005). If the underlying assumptions of restoration are not dealt with, and the limitations recognized, there is great risk of over-applying flawed methods that do not achieve the goals we aim for. Some of these assumptions, proposed by Hilderbrand et al., (2005) and how they apply to forest settings, are outlined more in detail below (Fig 2).

Carbon copy

The carbon copy hypothesis relates to setting restoration targets and assumes that it is possible to achieve a replica of a previous ecosystem state, such as a pristine old-growth forest (Hilderbrand et al., 2005). This assumption is based on the idea that we 1) can identify a natural target state, 2) that it is possible to achieve this state through human intervention and 3) that nature eventually reaches a stable, equilibrium state sensu Clements (1936). In a forest setting, this implies that succession will reach a climax state of relatively little change. However, forests are inherently dynamic systems, shifting in both space and time, driven by natural processes such as succession and disturbances such as fire, gap dynamics and herbivory (Kuuluvainen and Aakala, 2011; Pringle et al., 2023). These ideas challenge the notion of a successional end-point, complicating the feasibility of the carbon copy hypothesis. In addition, the baseline conditions prior to restoration (i.e., the level of degradation) determine feasibility of restoration success. The greater the ecological distance between the baseline and the restoration target in terms of habitat quality, the more effort is needed, for example restoring a highly degraded forest to a pristine, old-growth forest, not least since species composition in managed and unmanaged or old-growth forests are highly divergent (Nirhamo et al., 2025; Paillet et al., 2010). Several factors may contribute to not achieving this state, including the field of dreams dilemma (see below).

Field of dreams

The field of dreams dilemma – “if you build it, they will come” - assumes self-assembly of species communities given that the suitable structures and habitats are present (Hilderbrand et al., 2005). In other words, if the physical properties of a habitat are in place, species communities will automatically colonize, preferably those species targeted with the intervention. This view, however, overlooks the extent to which human land use has transformed the natural landscape, fragmenting and degrading habitat while also creating ecological barriers, limiting species ability to colonize habitats (Berger-Tal and Saltz, 2019). In many cases, source populations may be lost, or species may be unable to disperse and colonize new habitat due to landscape fragmentation and degradation, e.g., Kouki et al., (2012). The field of dreams dilemma is closely tied to both the carbon copy assumption and the baseline conditions prior to restoration.

Fast-forward

The fast-forwarding hypothesis assumes that natural processes that would otherwise take decades or centuries can be accelerated through ecological restoration (Hilderbrand et al., 2005). In a forest setting this is implemented in various ways such as damaging trees for the development of veteran trees (Fay, 2002), manipulation of tree species composition, enrichment of deadwood or plugging ditches to mimic flooding (Bernes et al., 2015; Hjältén et al., 2023). These measures are aiming to accelerate development of natural structures such as tree cavities and various types of deadwood that would otherwise take decades or centuries. If key components that are essential for species to thrive are neglected, such as restoring the physical structure but overlooking the ecosystems functionality, recovery may not fully occur (CHOI, 2004; Guerrero-Ramírez, 2021). In addition, focusing on active measures creating structures but neglecting to re-instate natural processes may provide rapid effects that declines over time (Pettorelli and Bullock, 2023).

Cookbook

The cookbook hypothesis refers to a standard implementation of restoration measures (Hilderbrand et al., 2005). This assumes that implementing the same measures or creating the same structures will have the same effect regardless of other factors. Although there is merit to the thought of standardised measures that can be implemented at large scale, just like the field of dreams, this line of thinking ignores context. In a forest setting this can express itself in over-application of standardised measures with limited value due to confounding factors and thus become costly and ineffective. As an example, it is assumed NDE, emulating natural disturbances, is an efficient way restore biodiversity (Lindenmayer et al., 2006). Therefore, restoration measures such as prescribed burning or gap-cutting are often implemented similarly across the forested landscape. This assumption also ties into the command and control hypothesis, explained next.

Command and control

The hypothesis of command and control refers to the idea that intervention and control of nature is the most efficient way to restore biodiversity (Holling and Meffe, 1996). This idea assumes that we have adequate knowledge of ecological processes such as speciation and drift (Vellend, 2016), that we can mimic natural processes, such as wildfires in a boreal forest setting, and that it is efficient to mimic natural processes (Lindenmayer et al., 2006). Boreal forest restoration is often performed with an interventionist mindset, either by creating specific substrates or manipulating tree species composition (Hjältén et al., 2023). Passive restoration on the other hand, by allowing natural processes to form the forest succession is the counterweight to the command and control hypothesis.

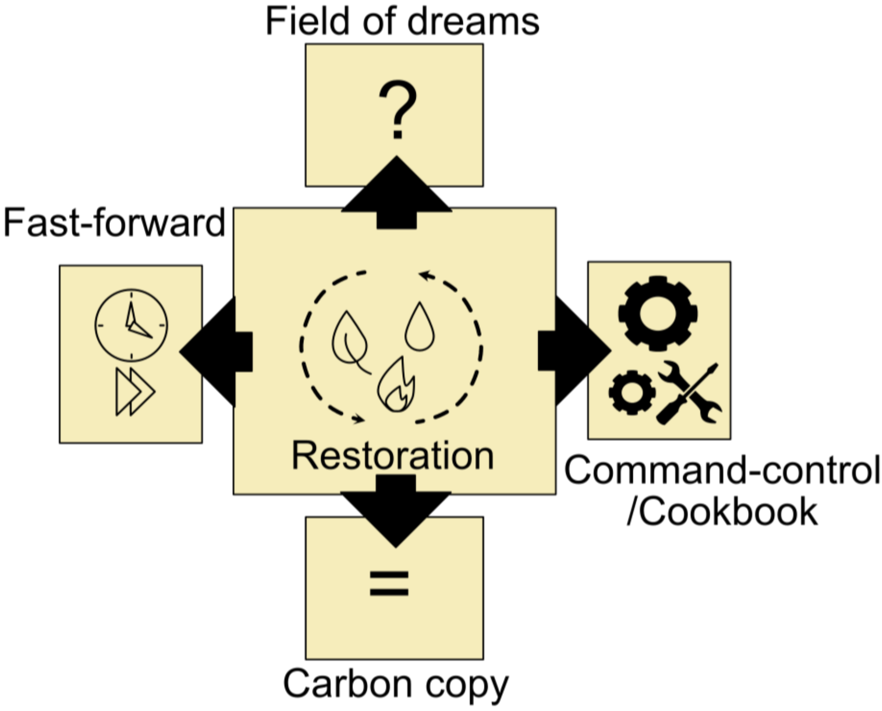

Figure 2. Conceptual figure visualising the underlying assumptions of restoration that: restoration can replicate target ecosystems (carbon copy), restored habitat will be colonized by targeted species (field of dreams), restoration can fast-forward slow, natural processes (fast-forward) and that restoration through intervention (command-control) in a standardised way (cookbook) is the most efficient way to assist recovery of biodiversity.

1.3 Aim of thesis

The studies in this thesis encompass multiple habitat types (pine & deciduous forest), spatial scales (stand & substrate), restoration methods (deadwood enrichment, prescribed burning, tree species manipulation), taxonomic groups (beetles, fungi, lichens) and time scales (2-21 years post restoration). The aim of this thesis was to evaluate multi-taxon responses of wood-associated species to ecological restoration in boreal forests. More specifically, I attempted to answer the following questions:

1) How are species communities structured by habitat restoration compared to negative- and positive references? (Papers I-III)
2) How are multi-taxon species communities structured by different restoration methods? (Papers III-V)
3) How do life-history traits and evolutionary history influence species community structure following habitat restoration? (Papers I,II,V)

In addition, I also relate my results to some of the main theories and underlying assumptions of habitat restoration to place them in a broader theoretical context.

2. Material and methods

Study sites

The data used in this thesis is derived from two study areas in the regions of Dalarna, Värmland and Dalsland in Central Sweden. The 23 forest stands in Papers I and II are situated in Värmland and Dalsland counties (Fig 3) representing a historical core area for the white-backed woodpecker's (*Dendrocops leucotos*) distribution range (Aulén, 1988). The stands were chosen to assess long-term outcomes of restoration aimed at the white-backed woodpecker on forest structure and associated saproxylic beetles.

These studies comprised eight stands that had undergone restoration (12-21 years ago) (henceforth restored), seven that remained unrestored representing the pre-restoration state (non-restored), and eight (target) stands with the highest potential to host breeding white-backed woodpecker pairs and serving as reference points. Non-restored stands were managed mixed deciduous-coniferous forests. Restoration activities involved the removal of Norway spruce (*Picea abies* (L.) H. Karst), girdling of certain deciduous trees, and the creation of high stumps to enhance habitat suitability for the target species. Target stands were characterized by large amounts of deciduous deadwood in different decay stages caused by small-scale disturbances such as gap dynamics and small-scale flooding.

The 24 forest stands in Papers III, IV and V are located in Effaråsen, Dalarna (Fig 3). This area is dominated by Scots pine (*Pinus sylvestris* L.) with sparse populations of Norway spruce and birches (*Betula pendula* Roth. & *Betula pubescens* Ehrh.). The area has a history of forest management in the form of single-tree felling, thinning and fertilization but has never been clear-cut prior to the experiment. In 1888, there was a wildfire in the area, which can be seen in traces in living trees with fire scars and charred old deadwood.

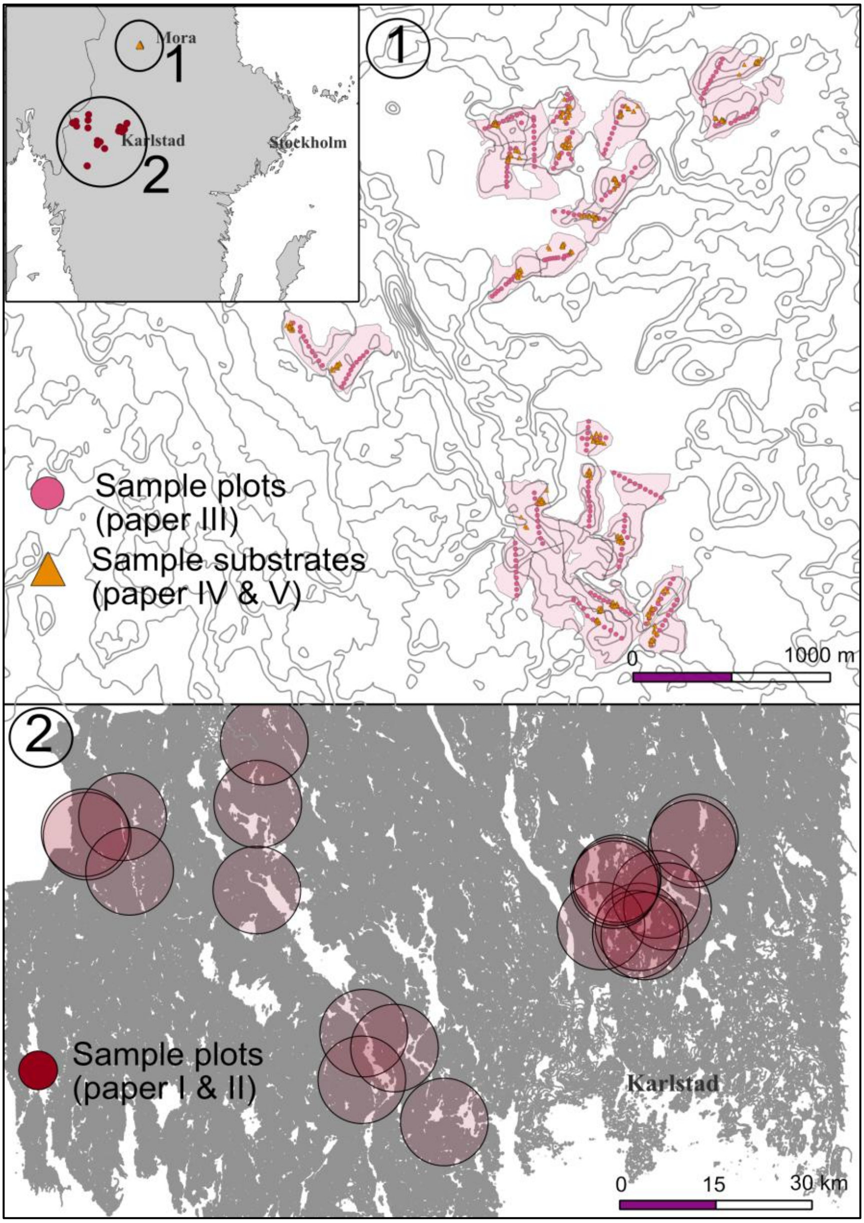

Figure 3. Map illustrating the location of the study sites and sampling design. Inset map illustrates the location of Effaråsen 1) papers III, IV and V and the sites for 2) papers I and II. 1) The stand borders outlined with transparent pink, the sample plot design for paper III (lichens) in pink circles and the sampled substrates for papers IV and V (beetles and fungi) in orange triangles. 2) The location of the stands used in papers I and II (beetles) in circles, masked to not disclose the exact location of the sites.

The Effaråsen experiment was initiated in 2012 with the goal of studying combined efforts of forest management and biodiversity conservation. Eight treatments were randomly allotted to 24 stands, resulting in three replicates of each treatment. The treatments were 1) Untreated control stands, 2) Felling with 3% retention, 3) Felling with 10% retention, 4) Felling with 30% retention, 5) Felling with 50% retention, 6) No felling, 100% retention, 7) Felling with 50% retention and subsequent prescribed burning and 8) No felling with subsequent prescribed burning. The retained trees in treatments 2-6 were subsequently divided into four equal parts (Fig 4): i) Green tree retention, where living trees are retained as single trees or groups of trees. ii) Bark-peeling, where a harvester peeled the bark as an attempt to damage and veteranize trees. Due to suboptimal implementation, most of these trees died as a result. iii) High-stump, trees cut by a harvester at 2-3 m height. iv) Felled trees, whole trees felled by a harvester.

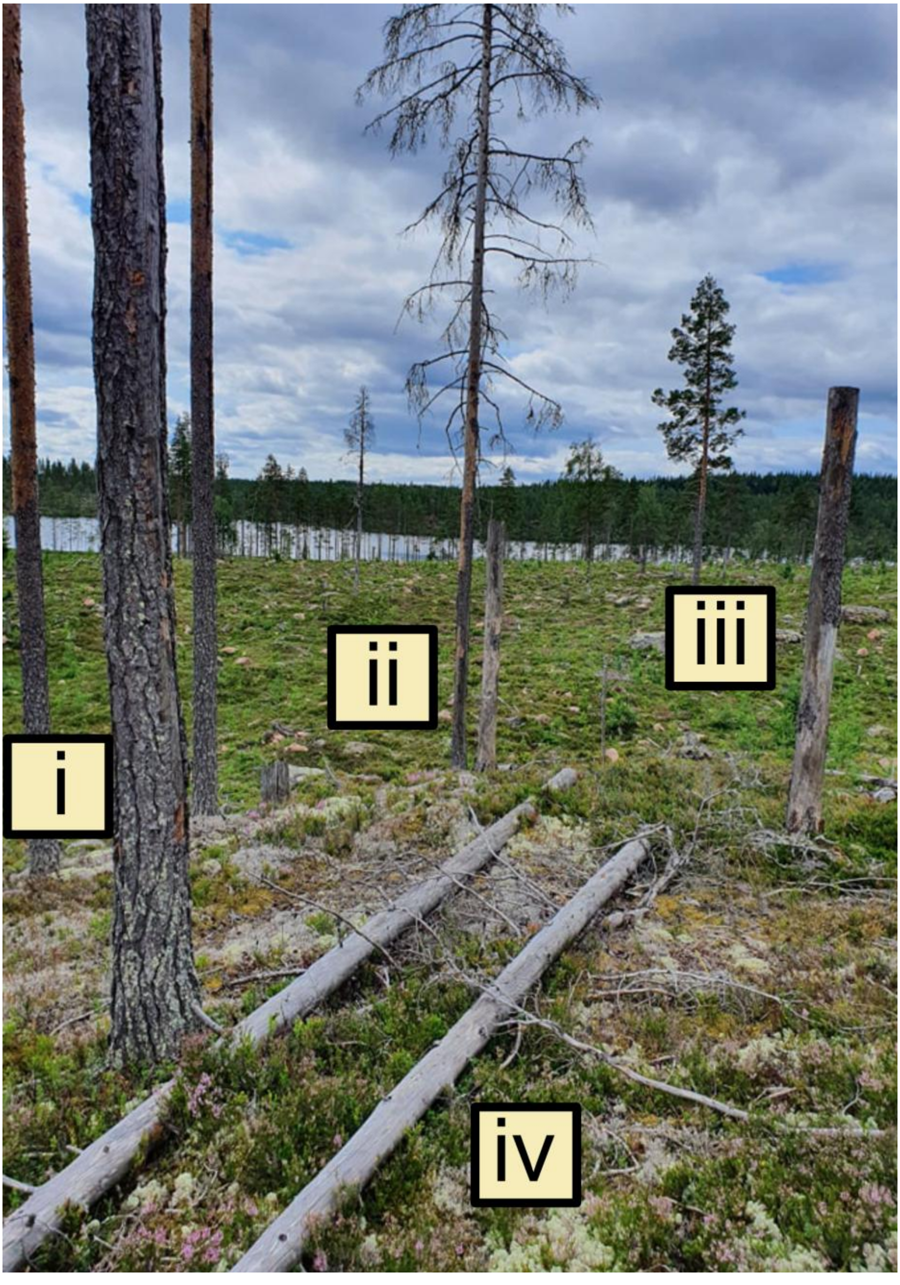

Figure 4. Pictures of retained trees divided into four parts: (i) living trees, (ii) snags -trees that were bark-peeled by harvester. (iii) high-stumps – trees that were cut at 2-3 m height with a harvester, (iv) logs – trees that were felled by harvester. Photo: Albin Larsson Ekström

Forest structure

Forest structure for Papers I & II was inventoried in 25- (deadwood) and 10- (living trees) m radius circular sample plots at the centre of each stand. Deadwood (diameter at 1.3 m height (DBH) >10 cm, length/height>1.3 m) within the 25-m plot was divided by type (logs or snags), tree species and decay stage following Gibb et al., (2005) for logs and Jung et al., (1999) for snags. Top- and bottom diameters and lengths were measured for logs and DBH and height assessments for snags. Logs and snags up to 6 m in height were calculated as cylinders, for snags taller than 6 m I used Brandel (1990) volume functions for southern Sweden for pine and spruce and the birch function for all deciduous tree species.

For living trees (DBH>5 cm, height >1.3 m), DBH and tree species was recorded.

Forest structure for Paper III was inventoried in 10 circular sample plots (5.64 m radius) along transects in each stand. Within each plot, all deadwood objects (≥ 25 cm^2 area of exposed wood) were measured. For standing deadwood, DBH and height was measured up to a maximum of two meters height. For downed deadwood, top- and bottom diameters and lengths were measured. Deadwood surface area was calculated based on the formula of cylinders. Estimated bark- and bryophyte cover was subtracted and for logs, 20 percent of the area was subtracted to account for parts that were in contact with the ground. For low-stumps and snags the bottom diameter was also subtracted since this was below ground. All deadwood was categorized according to substrate quality: Kelo (several centuries old, dead pine trees impregnated with tar and with a silvery surface), Old (decayed pine deadwood estimated to be around 80 years old, lacking kelo qualities), Young (machine-created deadwood originated from the experiment, 10 years old) and Burned (burned deadwood originated from the prescribed burning, 10 years old) (Fig 8). In addition, substrates were also categorized to type: low-stump (stump <50 cm height), high-stump (stumps or broken trees >50 cm height, summarised with snags for paper III but separated for papers IV and V), snag (intact, standing dead trees) and log (downed deadwood).

No environmental data except for the substrate categorisations was used for Papers IV & V.

Invertebrate sampling

For papers I & II, three IBL2 flight intercept traps were strung between trees with the trap centre approximately 1,3 metres above the ground in a North, South-east, South-west facing, approximately 30-70 m from each stand centre during June-October 2021. IBL2 traps are semi-transparent and shaped like downward facing triangles (Fig 5A). At the bottom of each trap was first placed a water-diverging module preventing rainwater and second, a bottle filled to one third with 70% propylene glycol and some detergent to contain trapped invertebrates. For papers IV & V, five logs, five high-stumps of ∼3 m height and five standing dead trees derived from the experiment were sampled in each stand. Emergence traps (0,5-1.5m from substrate base) were placed on each sampled substrate in October 2021-October 2022 (effective sampling time May-September). Emergence traps enclosed ~30 cm of the substrate with a polypropylene weed barrier cloth sealed with wire (Fig 5B). At the top of each trap, plastic bottles were filled to one third with 70 percent propylene glycol and detergent to conserve invertebrates. All saproxylic beetles were identified to species level by the same expert taxonomist (Hans-Erik Wanntorp) for papers I, II, IV and V following the Dyntaxa nomenclature (Dyntaxa, 2023).

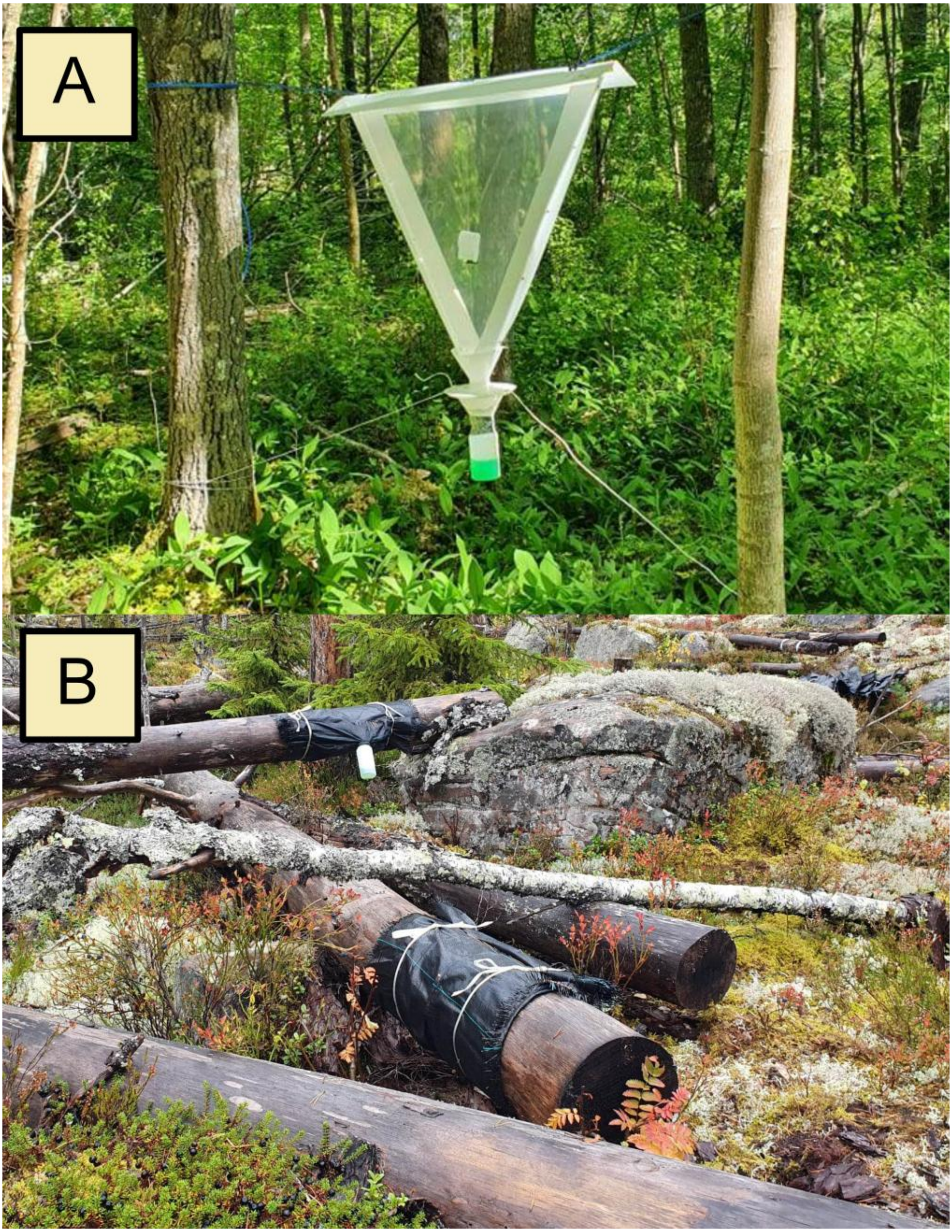

Figure 5. Pictures of IBL2-traps (A) and emergence traps (B) that were used to capture invertebrates. Photo: Albin Larsson Ekström

Fungal sampling

For papers IV, V, fungal samples were extracted by drilling ~10 cm into the wood at the same location as the emergence traps, two samples per substrate that were pooled in the field. First, I removed the bark and outer cambium with a knife and secondly, I extracted the wood samples into zip-lock bags. The knife and drill were sterilized with a gas burner between each sample. The samples were then freeze-dried for storage awaiting analysis.
The samples were then processed and DNA was extracted by the company Bioname. Reagent purity and cross-contamination levels were measured by adding a negative extraction control sample. Primers fITS7 and ITS4 were used for the construction of high-throughput amplicon sequencing (Ihrmark et al., 2012; White et al., 1990). 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 Operational Taxonomic Unit).

Lichen sampling

For paper III, detailed species inventories of lignicolous lichens (Spribille et al., 2008) were performed in the 5.64 m circular sample plots on all decorticated deadwood as described under forest structure. The species inventories were done in 15 (excluding non-treated controls and prescribed burned) stands in 2013-2014 and then including all 24 stands in Effaråsen in 2021. Both inventories were done by Göran Thor using the same methodology.

Life-history traits and phylogeny

Life-history traits of beetles and fungi were based on available literature, databases and expert opinions, details of which can be found in each individual paper. Phylogeny was retrieved from Dyntaxa (Dyntaxa, 2023), based on taxonomic hierarchy (i.e., Order-Family-Genus).

Statistical analysis

All statistical analysis was done using R, versions 4.0.2 to 4.3.2 (R Core Team, 2023).

For taxonomic α-diversity, I calculated trap-or-substrate level (papers I, II, III, IV) taxonomic richness, evenness and abundance. For functional α-diversity (paper II) I calculated trap-level functional richness, evenness and divergence, package FD (Laliberté et al., 2014). For phylogenetic α-diversity (Paper II) I calculated trap-level phylogenetic richness, evenness and variability, package picante (Kembel et al., 2010). I analysed the taxonomic, functional and phylogenetic α-diversity using generalized linear mixed effects models, lme4 (Bates et al., 2014) and GLMMTMB (Magnusson et al., 2017) packages for papers I, II, IV and Kruskal-Wallis tests for paper III. For pairwise comparisons of α-diversity between groups I used emmeans (Lenth et al., 2019) for papers I, II, IV and Wilcoxon pairwise tests for paper III.

For taxonomic β-diversity, I computed Bray-Curtis or Jaccard dissimilarity indices and tested the homogeneity of dispersal (betadisper) between samples and the difference in community composition (PERMANOVA), papers (I, III, IV) using the vegan package (Oksanen et al., 2017). In addition, I performed a metacommunity analysis between substrate quality types in paper III to disentangle the two components of β-diversity, turnover and nestedness, using the metacomm package (Dallas, 2014). In order to identify species that were influential on potential community composition differences, I identified indicator species using the indicspec package (De Caceres et al., 2016).

For taxonomic *γ*-diversity, I produced inter- and extrapolated species accumulation curves (papers I, III, IV) based on sampling effort (number of individuals, samples or inventoried wood cm^2) using the iNEXT package (Hsieh et al., 2016). In addition, to compare *γ*-diversity between deadwood types for papers III and IV (Fig 7), I computed estimated *γ*-diversity, standardised to twice the sample amount of the sample with the lowest sample coverage for each taxonomic group using the function estimated, iNEXT package (Hsieh et al., 2016).

In order to test for the influence of life-history traits and phylogeny on species-host relationships (paper V), I applied Hierarchical Modelling of Species Communities (HMSC) which is a Bayesian Joint species distribution model (Ovaskainen et al., 2017). HMSC integrates species occurrences (Y) with environmental variables (X), species traits (T) and phylogeny (C) (Ovaskainen et al., 2017). The Y matrix consisted of presence-absence of beetles and fungi in each substrate. I tested for species-host (substrate type) relationships rather than species-habitat (stand treatment) relationships due to null results in paper IV. The X matrix consisted of substrate type (Burned or Machine-created high-stump, snag or log) and occurrence of emergence holes of *T.depsarium*, *M. sutor* and *T. minor* (only for subset models on logs) on substrate scale. I included species traits (T) and phylogenetic signal (C) to relate X and Y. The T matrix consisted of: Body size (mm) and feeding guild for beetles and primary lifestyle for fungi. I produced a C matrix based on taxonomic hierarchy from order to species level for beetles and kingdom to zOTU for fungi treating each fungal zOTU as an individual species as is also described above, assuming equal branch lengths between each level.

Substrate ID was included as random effect in all models and using default priors with a posterior distribution of 150 000 MCMC iterations of which 50 000 where burn-in. I used 2 MCMC chains thinned by 100 and a sample size of 1000 per chain. Model convergence was evaluated by the potential scale reduction factors visualized through beta, gamma and omega plots considering good convergence for models that fell within 1 (+-0.10) (Gelman and Rubin, 1992). For explanatory power, I evaluated species-specific AUC-values that were then averaged and Tjurs R2-value. I considered differences to have strong support if the mean posterior was greater or lower with at least 95% posterior probability.

3. Results

3.1 Ecological restoration of deciduous forests (I, II)

Forest structure

In restored and non-restored stands, 60 and 48 percent of trees with a DBH smaller than 20 cm respectively, were coniferous (Fig A1). All trees with a DBH of <20 cm were deciduous in target stands (Fig A1). Deciduous deadwood volumes were lower in restored than in target stands ($p=0.03$) but higher than in non-restored stands ($p=0.006$, Fig A1). The deadwood in restored stands was dominated by logs in late decay stages ($p<0.001$, Fig A1). In target stands, the intermediate decay stages were most common ($p=0.02$, Fig A1).

Saproxylic beetles

In total, 16320 individuals and 339 species of saproxylic beetles were caught for papers I and II. The most abundant species were *Enicmus rugosus* (12% of the total abundance), *Triplax russica* (8%), *Enicmus testaceus* (5%) and *Pteryx suturalis* (5%).

Target stands displayed greater taxonomic, functional and phylogenetic α-diversity (richness) than restored stands with non-restored stands displaying intermediate functional and phylogenetic α-diversity (Fig 6). When comparing community weighted means (CWM) between stand types, body size was lower in restored stands compared to the non-restored ($p=0.043$) and target ($p=0.007$) stands (Fig 6). The proportion of deciduous-specialised beetle species was greater ($p=<0.001$) in target stands and the proportion of coniferous-specialised beetle species was lower ($p=0.001$) compared to the other stand types (Fig 6).

Beetle assemblage composition differed among all stand types (PERMANOVA, Fig 6). Target stands had higher β-diversity (betadisper) of species of conservation concern ($p=0.01$). For deciduous species, β-diversity was highest in restored stands, followed by non-restored and target stands.

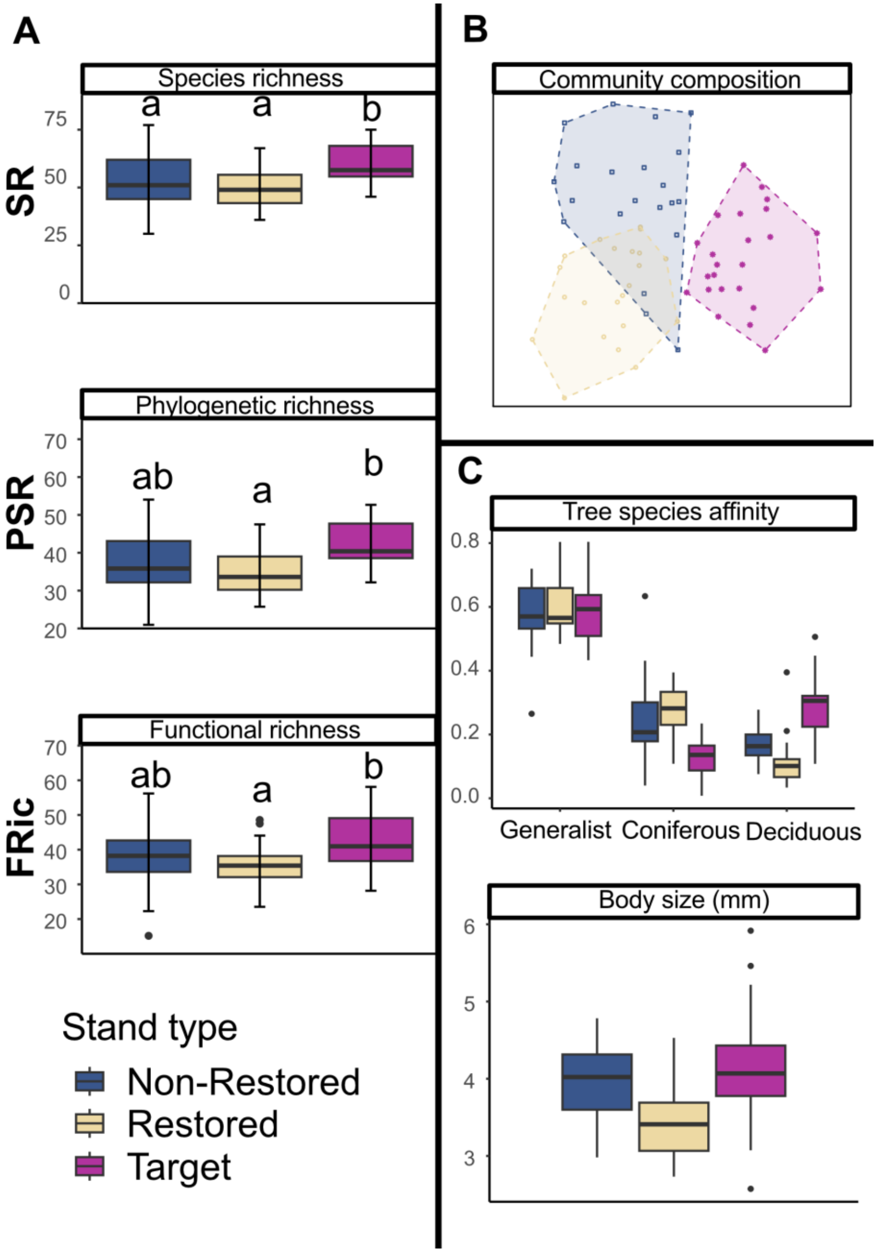

Figure 6. A) Species, phylogenetic and functional richness between stand types. B) Community composition visualised in an NMDS between stand types. C) Trait composition between stand types based on community-weighted means.

3.2 Restored deadwood structures taxa-specific community patterns (III, IV, V)

Species richness and community composition

In Paper III, I found that kelo wood supported similar α-diversity of lichens as young and burned deadwood qualities. However, rarefaction curves indicated greater γ-diversity on kelo and old wood compared to young and burned substrates (see paper III). Notably, all red-listed lichen species detected in 2021 occurred on kelo substrates.

For deadwood type α-diversity, lichen richness and abundance were similar between snags and logs, while low-stumps displayed higher species richness when controlled for sampled volume. Rarefaction curves also showed that low-stumps had a higher potential γ-diversity, despite their smaller sample size (Fig 7).

Lichen assemblages showed significant variation among deadwood types and quality classes. Eight years post-treatment, species composition differed clearly among low-stumps, snags, and logs within all deadwood quality categories. Deadwood type explained 28% of the variation in young, 20% in old, and 12% in kelo substrates ($p = 0.001$). Assemblage composition was more homogeneous (lower β-diversity) in young and burned wood than in kelo and old wood. This corresponded with high total richness despite lower richness on individual plots. Metacommunity analyses revealed nested lichen assemblages with clumped species loss between substrate types, as indicated by significant coherence, low turnover, and high species clumping (all $p \leq 0.001$, Fig 8).

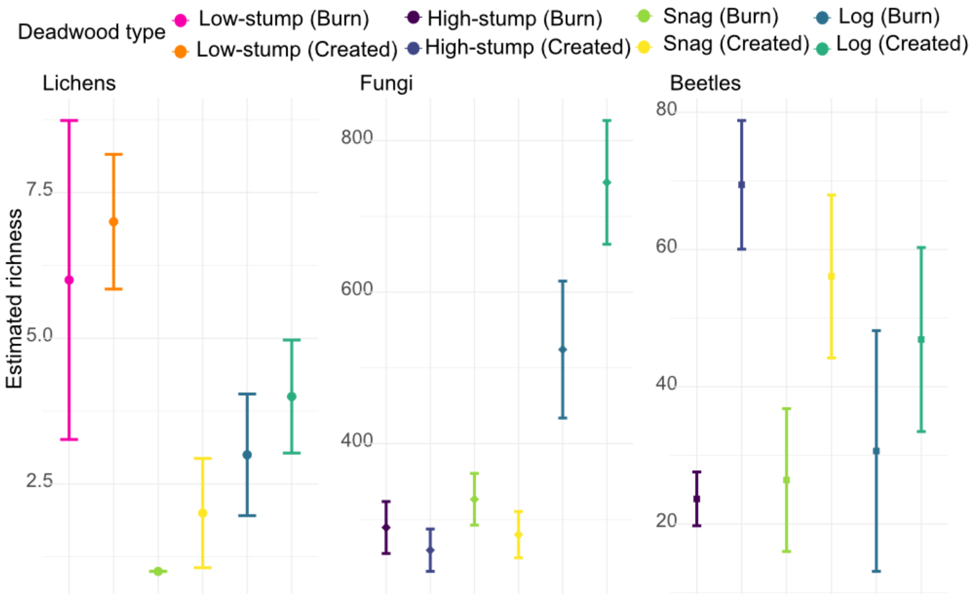

Figure 7. Estimated species richness of lichens, fungi and beetles on different deadwood types. Estimates are standardised to twice the sample amount of the sample with the lowest sample coverage for each taxonomic group using estimateD in the iNEXT package. Dots are the estimates and error bars represent a 95% CI. Burn = Burned substrates, Created = Machine-created substrates, Low-Stump = Low-stumps < 2 m, (lichens only), High-Stumps = High-stumps >2 m, (collated with snags for lichens due to few samples), Log = lying deadwood, Snag = Standing dead trees.

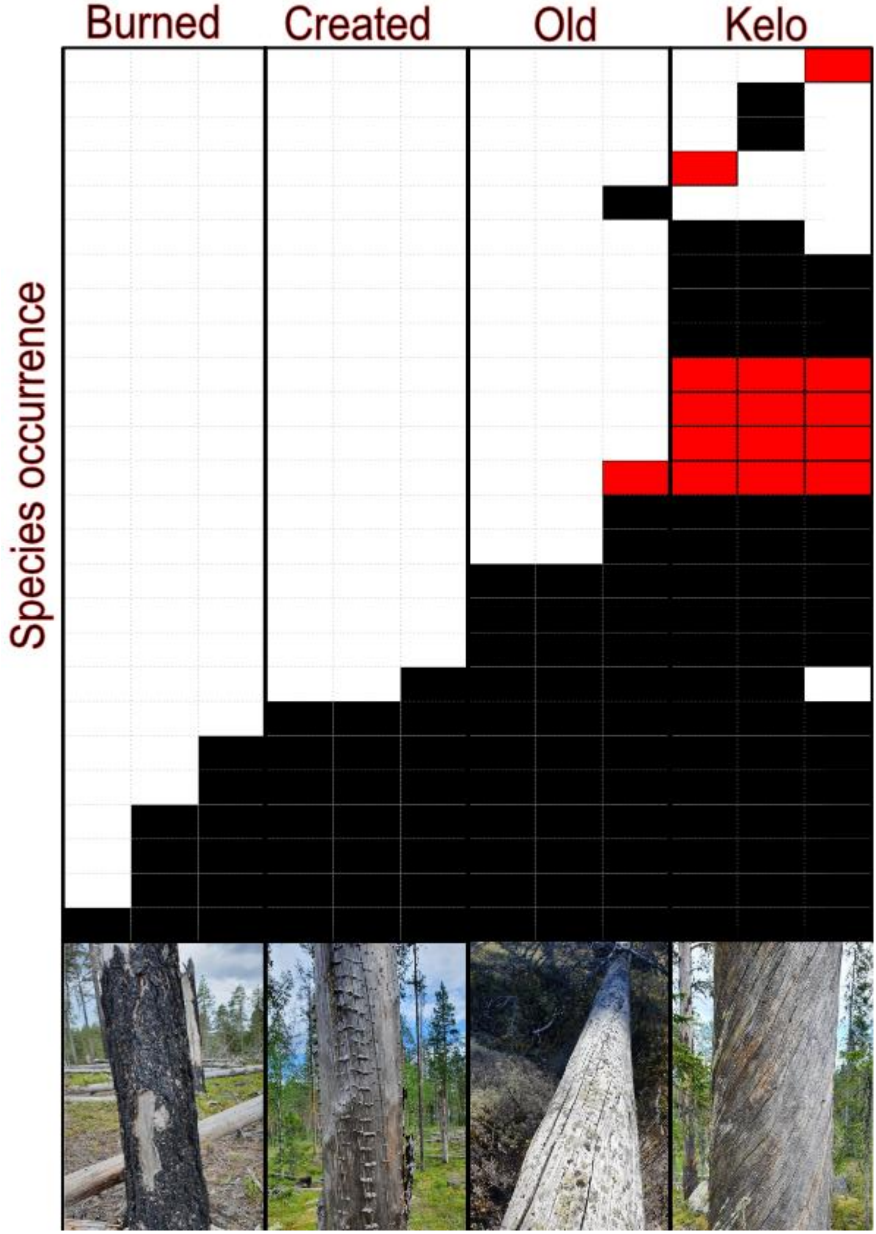

Figure 8. Binary matrix visualizing lichen species occurrence (rows represents species) by deadwood qualities (columns) with black boxes indicating occurrence of a species, white absence and red boxes being occurrence of red-listed species.

In Paper IV, fungal zOTU richness per substrate did not significantly differ among deadwood types, with the exception of slightly lower richness on machine-created snags. In contrast, beetle richness was lower in logs than in snags and high-stumps, and no consistent differences emerged between burned and machine-created deadwood (see paper IV). Rarefaction analysis showed that fungal zOTU curves did not reach an asymptote, making total richness comparisons uncertain. However, the highest total fungal richness was observed in both burned and machine-created logs, while the lowest was found in machine-created snags and high-stumps (Fig 7).

Beetle rarefaction curves approached a plateau, indicating more complete sampling. Machine-created substrates hosted more beetle species than burned ones, with the highest richness found in machine-created high-stumps and the lowest in burned high-stumps (Fig 7).

Assemblage composition of both fungi and beetles differed significantly between substrate types (Fig 9). For fungi, deadwood type explained 17% of the variation in assemblage structure (PERMANOVA, p=0.001). Assemblages in machine-created substrates were distinct, while burned snags and high-stumps overlapped (Fig 9). β-diversity for fungal zOTUs varied by substrate (p=0.01), with burned substrates exhibiting lower β-diversity than their machine-created counterparts. Machine-created logs supported the greatest β-diversity, while burned high-stumps had the lowest.

For beetles, deadwood type explained 27% of the variation in assemblage composition (PERMANOVA, p=0.001). Assemblage differences were driven more by deadwood type (snag, log, high-stump) than by whether substrates were burned or machine-created (Fig 9). β-diversity was significantly different between substrate types (betadisper, p = 0.01), with logs having greater β-diversity than both snags and high-stumps, which did not differ from each other.

Trait composition and phylogenetic signal

For paper V, 256 substrates were sampled in total. When including only species that occurred on ten or more substrates, 24 beetle species and 1172 individuals and 136 fungal zOTUs remained.

Species-host associations

Traits explained 43% of the overall variation of beetle species occurrences and 37-77% of the variance of beetle species response to substrate type. For fungi, traits explained 12% of the overall variation of species occurrences and 11-14% of fungal species response to machine-created substrates and 39-53% to burned substrates.

Beetles occurring on logs were smaller in body size compared to standing substrate but similar in size between burned and machine-created substrate with a posterior probability of >0.95 (Fig 9). Most beetles belonged to the feeding guilds fungivores and omnivores. Fungivore beetles were occurring more frequently in logs compared to snags and on machine-created logs more than in burned logs, posterior probability >0.95 (Fig 9). In contrast, omnivorous beetles tended to occur less frequently in logs compared to snags although with large variation and a posterior probability of >0.8 (Fig 9).

For fungi, the proportion of occurrences within traits were distributed among all of the substrate types with animal parasites and saprotrophs accounting for the highest proportion. For lichenized fungi, lichen parasites and mycoparasites, the proportion were higher on machine-created high-stumps compared to their burned counterparts. Machine-created logs were characterized by greater proportion of plant pathogens than burned logs. Animal parasites were negatively correlated to machine-created logs and nectar/tap- and litter saprotrophs were positively correlated to burned snags.

For beetles, there was no phylogenetic signal (posterior mean 0.22, posterior probability 0.5) but for fungi, there was a strong phylogenetic signal (posterior mean 0.78, posterior probability 1) (Fig 9).

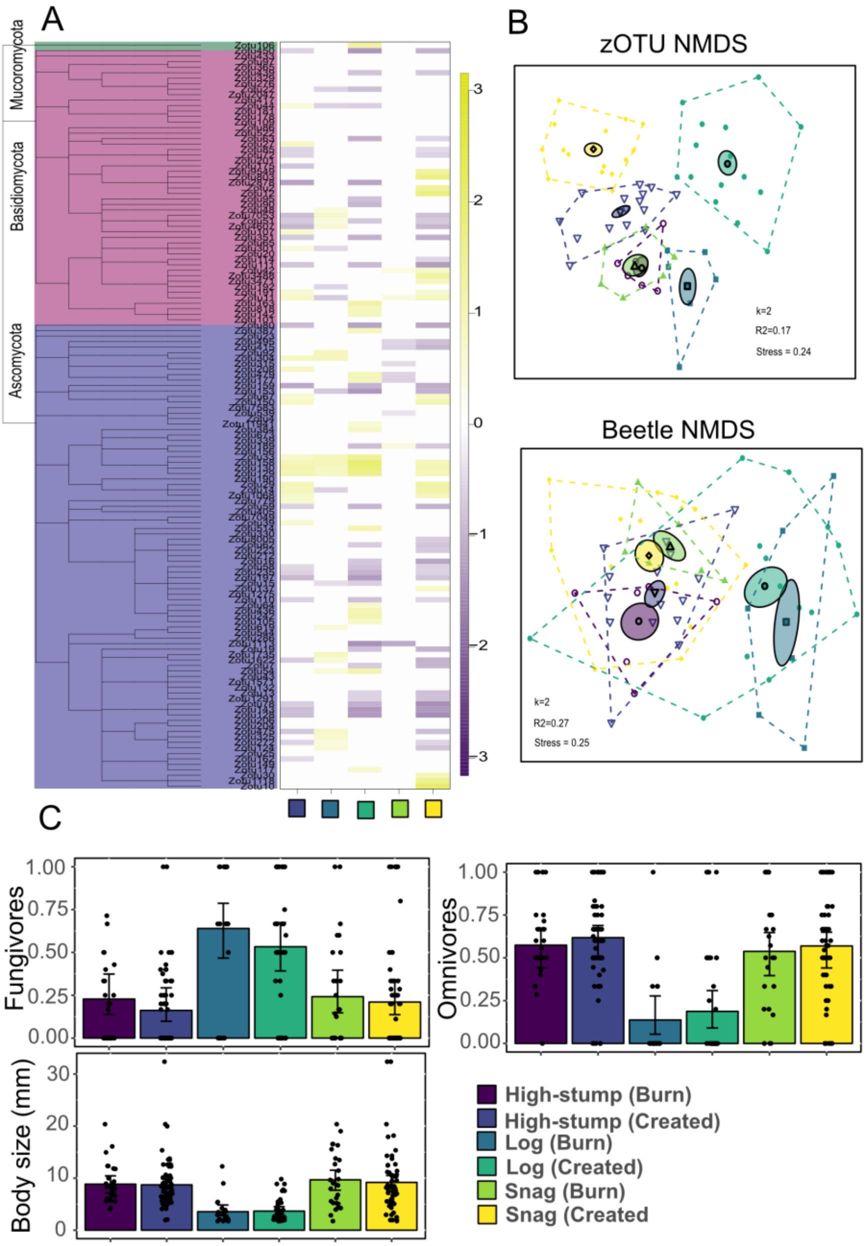

Figure 9. A) zOTU species-host associations and phylogenetic signal. B) NMDS illustrating species assemblages in deadwood types for zOTU's and beetles. C) Community-weighted means of beetle fungivores, omnivores and for body size.

4. Discussion

The main objectives of this thesis were to evaluate community assembly following ecological restoration with respect to: 1) negative and positive references, 2) multiple taxa and 3) the influence of life-history traits and phylogeny.

The results show that 1) ecological restoration benefits several taxa decades after restoration compared to negative references but fails to reach positive target references (papers I and III), see 4.1 for further discussion of these limitations.

Community responses to restoration are 2) highly divergent depending on taxonomic group (papers III and IV).

Finally, community responses are 3) shaped by both life history traits and phylogeny, offering insight into the mechanisms underlying species assembly in restored habitats (papers I, II and V).

In relation to objective 1, Papers I, II and III investigate the impact of ecological restoration on species diversity in relation to both negative and positive references. Together, papers I and II show that, while ecological restoration can affect beetle community composition and forest structure after 12-21 years, restored habitats fall short of matching target reference conditions (see 4.1 for theoretical implications). Figure 10 (top panel) illustrates how biodiversity benefits over time depend on whether resource accumulation (trajectory A) exceeds resource loss (trajectory B). In Figure 10 (bottom panel), the trajectory observed in Paper I corresponds to line 3 — a divergence from the expected recovery path (line 2) — indicating that repeated or enhanced restoration efforts (line 4) may be necessary to reach target conditions. These results show that in in boreal Fennoscandia, where long-term studies on deciduous forest restoration are rare, restoration can shift communities and partially recover elements of target conditions, but the restored habitats remain structurally, functionally and phylogenetically distinct after one to two decades. In addition, paper III demonstrates that deadwood derived from restoration treatments supports fewer lichen species, especially red-listed. This limitation contributes to an extinction debt for habitat specialists - a phenomenon illustrated by line 1 in Figure 10 (bottom panel), where species loss lags behind habitat loss. These studies highlight the importance of selecting appropriate reference habitats to serve as both positive and negative references to better assess the outcome of restoration.

For objective 2, Papers III and IV investigate multi-taxon responses to habitat restoration along a management-conservation gradient in pine forests. Together, these papers show that substrate origin and type is highly influential on deadwood taxa, but that these responses are taxon-dependent. In order to support multiple taxa, a variety of deadwood substrate types (e.g., logs and snags both burned and unburned) are required as they all support distinct communities. Conservation strategies need to implement a long-term, multi-taxon approach to not limit themselves to short-lived effects that benefit only a portion of species in order to ensure the sustained conservation of biodiversity (see 4.1 “Cookbook” theory for implications for adaptive management).

The vast majority of restoration studies focus on taxonomic diversity, often overlooking evolutionary and functional dimensions of biodiversity. For objective 3, Papers II and V investigate community patterns and restoration of biodiversity in a broader sense, also accounting for evolutionary and functional aspects. Paper II shows that lower species richness can be related to a narrower phylogenetic and functional trait space. The contrasting patterns of substrate affinity of saproxylic beetles and fungi can be partially attributed to life-history traits and phylogeny, investigated in paper V. This relationship diverges between taxa, with fungal communities being structured more by phylogeny and beetles more by their feeding strategy and body size (see 4.1 for broader implications for restoration planning).

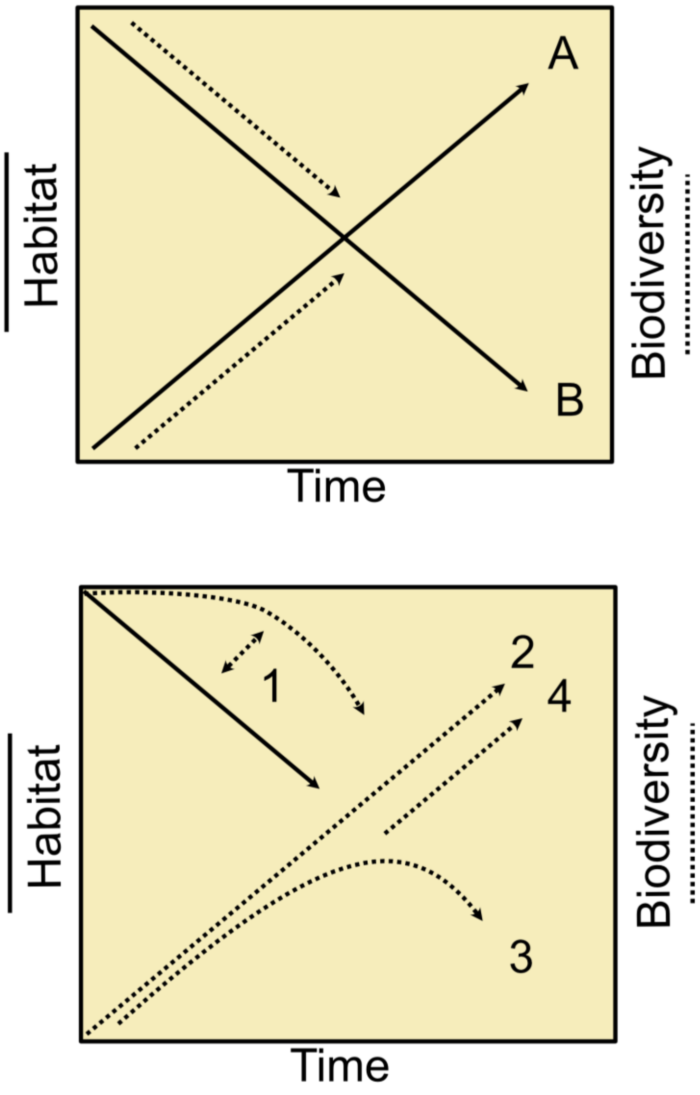

Figure 10. Conceptual figure visualising the relationship between habitat availability and biodiversity over time. The top panel conceptualises restoration trajectories when A) resource gain exceeds resource loss, benefitting biodiversity over time and B) when resource loss exceeds resource gain with declining biodiversity benefits. The bottom panel visualises 1) the relaxation time between habitat loss and biodiversity loss, 2) the expected trajectory following restoration, 3) the observed trajectory from paper I and 4) the expected outcome if repeated or enhanced restoration efforts are undertaken to reach the restoration target.

4.1 Reconnecting ecological restoration to ecological theory

Restoring pristine forests – carbon copy

The idea that restoration can recreate pristine, pre-disturbance forests — a “carbon copy” of the past — is increasingly challenged. This assumption is often unrealistic, especially in boreal Fennoscandia, where remnants of natural forests are both rare and fragmented, complicating dispersal between these remnants and restored habitat (Axelsson and Östlund, 2001; Östlund et al., 1997; Svensson et al., 2020). These fragments are additionally affected by the hinderance of natural processes such as fire dynamics, which in turn leads to darker, denser stands (Hedwall and Mikusiński, 2016). Even where old-growth remnants remain, they may not represent broader forest conditions. For example, low-productive, mountain-near forests may differ fundamentally from historically productive lowland sites. As such, defining appropriate reference conditions remains a major challenge for ecological restoration.

The results in this thesis question the assumption that restoration approximates natural forest conditions. In Paper III, the comparison between restored deadwood and ancient kelo wood highlights this issue: restored substrates did not replicate the unique ecological role of kelo wood, a structure absent from managed landscapes (Hämäläinen et al., 2021; Nirhamo et al., 2024). Similar mismatches between restored and natural deadwood communities have been observed for other taxa as well (Pasanen et al., 2018; Saine et al., 2024). In Papers I and II, forest stands restored for the white-backed woodpecker exhibited altered forest structure and beetle communities but still fell short of target reference conditions (See section 4., Figure 10, for discussion on trajectory).

Most restoration evaluations compare restored habitats to degraded or unmanaged states, which often displays positive results of increased species richness or changes to community composition. However, comparisons to target reference conditions may reveal a less complete recovery (Atkinson et al., 2022). This thesis reinforces that restoration outcomes depend on the quality of the baseline, pre-restoration conditions and the feasibility of the target. If targets are set unrealistically high and baselines are severely degraded, even well-designed restoration may fall short. However, targets that are set too low will ensure target fulfilment but have limited real-world impact. This means that 1) restoration does not manage to mimic natural conditions and requires further development based in ecological knowledge and 2) the few remnants of natural conditions that still remain must be conserved and safeguarded from exploitation such as forestry.

The results from papers I & II suggest that assisted recovery may not just fall short of targets, but may actively generate new, distinct community structures. This emerging pattern aligns with the concept of novel ecosystems in restoration ecology (Hobbs et al., 2009; Kerr et al., 2025; Svenning et al., 2024). With ongoing landscape transformation and climate-driven shifts in species distributions, understanding and managing these novel systems will be increasingly important.

In cases where historical reference conditions are absent or unattainable, some have proposed shifting focus toward enhancing structural complexity and habitat heterogeneity (Bullock et al., 2022). While potentially beneficial, this approach is not inherently equivalent to restoring natural conditions. Increasing habitat heterogeneity at the cost of habitat area may reduce local abundance, due to dilution effects (Ben-Hur and Kadmon, 2020). Structural enhancement must therefore be grounded in ecological understanding and focused on features of known conservation importance.

Restoring for the field of dreams

Several factors challenge the validity of the "carbon copy" theory and suggest that restoration may not achieve target conditions. The so-called "field of dreams" dilemma suggests that self-assembly will occur once habitat structures have been restored. However, restoration extends beyond the mere recreation of habitat; it also involves the assembly of species following successful colonization, sensu the "field of dreams" hypothesis. In the highly degraded and fragmented forest landscape of boreal Fennoscandia (Ahlström et al., 2022), it is unlikely that viable source populations capable of colonizing novel habitat persist. The targeted species, i.e., threatened species, remain only in small scattered patches and are potentially subject to habitat and dispersal limitation (Edman et al., 2004; Gustafsson et al., 2025). This could partially explain why restoration such as the restoration of deciduous forest in papers I & II does not perform as expected.

The challenge of self-assembly from restoration, or the “field of dreams” dilemma, is not confined to boreal forest restoration but extends across ecosystems. In a stream restoration experiment, restoration failed to produce clear improvements in stream metabolism and nitrate uptake, leaving the “field of dreams” hypothesis unresolved (Sudduth et al., 2011). Restoration of former mining sites did lead to the recovery of bird pollination, yet the species composition differed markedly from that of remnant habitats, offering only partial support for the hypothesis (Frick et al., 2014). In restored prairies, soil invertebrate communities gradually became more similar to those in remnant prairies over time, but high variability among remnants prevented a full match, underscoring the difficulty of defining variable reference targets (Wodika and Baer, 2015). Likewise, tropical forest restoration in Brazil demonstrated partial recovery of species communities, but poor dispersers failed to colonize restored areas without assisted migration (Suganuma and Durigan, 2022).

Ecological connectivity and closeness to source populations in biodiversity hotspots should thus be considered in restoration of boreal forests (Edman et al., 2004; Hämäläinen et al., 2023; Kouki et al., 2012; Lachat et al., 2025; Ramberg et al., 2025). This is also likely highly species- or taxon-specific where highly mobile species may be more successful (e.g., saproxylic beetles) whereas dispersal limited species (e.g., lichens) may require shorter distances from source- to novel habitat (Hilmo and Såstad, 2001; Ranius, 2006). Although lacking in empirical evidence, assisted migration and translocation of species should also be considered, especially for those that are limited by dispersal ability (Bellis et al., 2019; Seddon and Redford, 2025).

Space-for time & Quantity-for quality – Fast forward theory

Area-based conservation has become a dominant strategy in global biodiversity efforts (Maxwell et al., 2020). However, a critical issue arises when large areas set aside for conservation offer low ecological quality or lack critical habitat features, resulting in limited conservation value. This connects to ongoing debates like the SLOSS dilemma (Single Large or Several Small), where empirical support suggests that a number of smaller, diverse reserves support more species than single large (Fahrig, 2020; Huber et al., 2025). Yet, these discussions often emphasize spatial extent while neglecting the temporal dimension.

Forests, and many ecosystems, are not static. They are dynamic systems that evolve over time through natural succession, disturbances, and species turnover (Berglund and Kuuluvainen, 2021). This temporal complexity introduces challenges for restoration: not only is it difficult to define clear targets (e.g., which successional stage to aim for), but even when targets are set, ecosystems may develop along unintended trajectories, eventually diverging from conservation goals.

An illustrative case from Paper I demonstrates this: a large-scale input of deadwood created an immediate pulse of resources beneficial to saproxylic beetles (see Bell et al., (2015)). However, the benefit was ephemeral, deadwood decayed over time, and the resulting beetle communities diverged from those expected in the target reference conditions, indicating a temporal mismatch between restoration inputs and ecological needs.

Long-term restoration goals, such as re-establishing viable populations of species like the white-backed woodpecker, require resources not just across space (~500 hectares of suitable habitat) but also sustained over time. For example, birch deadwood can become highly decayed in 10–20 years. And even though many fungal species may benefit from this resource, the targeted effect is gone. Thus, successful restoration must anticipate and plan for the timing, continuity, and decay of resources (Butterworth et al., 2023).

Additional evidence from Papers III and IV reveals how different taxa respond to restoration actions like prescribed burning across different time scales. Pyrophilous insects often respond rapidly, within the first few post-burn years, while red-listed fungi and lichens (e.g., *Carbonicola* spp.) may require decades to centuries to establish on burned substrates (Esseen et al., 1992; Goodman and McCravy, 2008; Ramberg et al., 2023). These contrasting temporal responses highlight the space-for-time dilemma and expose the limits of short-term, one-size-fits-all restoration strategies (see “Cookbook” theory further down).

This temporal disconnect also relates to the “carbon-copy” theory, the mistaken assumption that restoration can recreate reference ecosystems simply by mimicking structural elements. Many restored habitats may never reach the functional quality of natural reference systems. As shown in Paper I, restoration may entirely fail to develop the intended community structures.

Paper III further illustrates that some key structures take centuries to form and are therefore not quickly recoverable through restoration.

Ultimately, this points to a fundamental trade-off between habitat quantity and quality. While increasing area is essential, restoration success depends on the quality of ecological functions and the timeframes over which they emerge.

Effective restoration planning must explicitly incorporate spatio-temporal dynamics. This involves not only ensuring restoration is implemented at sufficient spatial scales, but also acknowledging the long timelines required for ecosystems to recover key structures, processes, and community assemblages. Attempts to fast-forward ecological processes are often unrealistic and may result in the failure to meet long-term biodiversity goals.

Moreover, habitat quantity cannot substitute for quality. Restoration efforts must consider which taxa and ecological functions are being targeted, how long those targets take to materialize, and whether management interventions can realistically replicate or accelerate those processes. In cases where natural disturbances are absent, the effects of restoration may be ephemeral, requiring repeated interventions to maintain key habitat features or resources over time. This highlights a broader need to move beyond one-off restoration efforts and toward strategies that support ongoing ecological dynamics.

Ultimately, the goal of restoration should be to reestablish natural processes and disturbance regimes that can sustain biodiversity without continual human input. However, further research is needed to understand how best to reinstate such processes across different ecosystems and contexts (Pettorelli et al., 2019; Plumanns-Pouton et al., 2025). When this is not possible due to e.g., small and fragmented habitats, conservation planning must ensure a continuous input of habitat. Moving forward, both conservation practice and research must confront these complexities directly, abandoning simplistic assumptions of rapid recovery and embracing adaptive, long-term, and process-based restoration frameworks.

The Cookbook and Command-and-Control theories in Restoration

To be implemented at scale, restoration often requires a certain degree of standardisation to ensure feasibility and consistency. However, overly rigid or prescriptive approaches risk falling into the cookbook and command-and-control theories, the belief that ecosystems can be restored through fixed recipes or tightly managed interventions with predictable outcomes.

Restoration must be adaptive, context-specific, and ecologically dynamic. The findings from this thesis reinforce this complexity: no single restoration measure benefits all taxa, and instead, a diversity of habitats, niches, and successional stages is required to support biodiversity across multiple temporal scales.

For example, in boreal forests, prescribed burns differ significantly from natural wildfires in their ecological outcomes. Research has shown that beetle and wood fungi communities vary between these disturbance types (Fredriksson, 2021) and although increasing fire severity in prescribed burns may benefit certain saproxylic beetles, it can simultaneously harm other taxa by destroying existing high-quality deadwood, which may host rare lichens (Paper III). This highlights a key limitation of standardised interventions: targeting one ecological function (e.g., deadwood for beetles) without accounting for unintended trade-offs.

Similarly, Paper I illustrates how aiming to support the white-backed woodpecker by increasing food availability (i.e., beetles in deadwood) is insufficient if nesting resources such as standing dead trees that can form cavities are missing. This disconnect shows that restoration cannot succeed through isolated actions—it requires a holistic approach that supports several ecological niches.

Although not explored in depth in this thesis, another critical dimension is the spatial planning of restoration. Landscape-level restoration must consider habitat connectivity, distribution of resources, and heterogeneity, further challenging the idea that restoration can be standardized or tightly controlled.

To summarise, while some level of standardisation is necessary for scaling up restoration efforts, this should not come at the cost of ecological adaptability. And to repeat. effective restoration must embrace complexity, avoid one-size-fits-all approaches, and be grounded in adaptive management that is responsive to local conditions and ecological feedbacks.

Additional aspects

In addition to the main findings, this thesis highlights three broader considerations for ecological restoration.

First, as discussed under the “Cookbook” theory, no single restoration measure benefits all taxa. Different organism groups respond to different habitat attributes, meaning that a single action may benefit some species while leaving others unaffected or even disadvantaged. The results from Section 4.1 (Papers III and IV) illustrate this clearly: varying deadwood types and origins each support distinct communities. Long-term biodiversity conservation therefore requires a deliberate combination of habitat features rather than reliance on a narrow set of structures.

Second, restoration research has historically placed greater emphasis on taxonomic diversity than on evolutionary and functional dimensions of biodiversity. This narrow focus can overlook important mechanisms shaping community assembly. As shown in Section 4.1 (Papers II and V), phylogenetic relatedness and life-history traits influence restoration outcomes differently across taxa, revealing patterns invisible when considering species richness alone. Integrating these dimensions into restoration planning can improve both predictive accuracy and the ecological relevance of management targets.

Finally, a persistent gap between research and implementation remains. Restoration interventions are often designed to benefit specific threatened species, yet empirical studies tend to focus on entire communities. Threatened species are rarely abundant or influential in community-level analyses, making it difficult to assess the effectiveness of restoration for conservation priorities. Improved integration between research and applied management is needed to ensure that restoration efforts align with conservation goals and deliver measurable benefits for target species.

Conclusion

Ecological restoration in boreal forests cannot be evaluated by its ability to recreate a carbon copy of the past. The results of this thesis show that restored habitats often diverge from target reference conditions, either because key structures (such as kelo wood) are irreplaceable within current timeframes or because community assembly follows novel trajectories. Restoration outcomes are therefore dependent not only on the actions implemented, but also on the ecological context in which they occur – including baseline conditions, landscape connectivity, dispersal limitations and the time required for habitat features to develop. This means that restoration must move beyond static targets and one-time interventions.

Instead, conservation planning should set adaptive goals that fulfil the ecological requirements of several taxa, account for spatio-temporal dynamics and prioritize continuity of ecological processes. In highly fragmented boreal forest landscapes, safeguarding the few remaining remnants of natural forests is crucial, while restoration should focus on creating heterogenous forests and connectivity to those remnants. For dispersal-limited species, assisted migration or translocation should also be considered.

An important step forward is aligning practical restoration with ecological theory. Monitoring should implement functional and phylogenetic dimensions, which offers a wider picture of biodiversity, identify clear goals and make sure that these goals are met (Monsarrat et al., 2022). Restoration strategies must also be adaptive, since no single restoration measure will benefit all taxa but will inevitably lead to trade-offs between taxa and cost-benefits. Recognising and implementing this complexity into conservation planning is essential.

The ultimate task of ecological restoration of boreal forests is to sustain and enhance biodiversity in the future. This requires the abandonment of simplistic assumptions of rapid recovery and embracing adaptive, long-term and process-based restoration frameworks. By combining conservation of existing areas of conservation concern with dynamic restoration informed by ecological research, the fulfilment of restoration targets and the overarching goal of biodiversity conservation can be achieved.

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Popular science summary

Forests are home to a rich variety of life, or biodiversity, but many of their species are declining. Despite ongoing conservation work, conditions are still declining for many species. This gap suggests that our current efforts to restore forests do not match the species actual needs.

In this thesis, I studied how different groups of forest-dwelling species, such as beetles, fungi and lichens, respond to restoration efforts in boreal deciduous and pine forests. The results show that there is no single method that will benefit the rich variety of life in forests.

In restored deciduous forests, beetle communities developed in ways that did not match either the pre-restoration baseline or the intended restoration targets, even after two decades. In restored pine forests, beetles, fungi and lichens all preferred different types of deadwood, whether standing or lying, burnt or unburnt. Additionally, newly created deadwood from restoration hosted far fewer species than ancient, naturally formed deadwood.

The main message is that restoration outcomes vary widely depending on the species group and the timescale. In order to halt biodiversity loss, restoration strategies need to better reflect the varying ecological requirements of species across both space and time.

This work highlights the complexity of restoring forest biodiversity and calls for more flexible and diversified approaches to biodiversity conservation.

Populärvetenskaplig sammanfattning

Skogar hyser en oerhört rik biologisk mångfald. Trots satsningar på att bevara den biologiska mångfalden så är läget allvarligt för en mängd arters överlevnad. Det här tyder på att de satsningar som görs inte når upp till arternas behov.

I denna avhandling undersöker jag hur olika grupper av skogslevande arter, såsom svampar, lavar och skalbaggar, påverkas av naturvårdsåtgärder, så kallad restaurering, i tall- och lövskogar. Resultaten visar att det inte finns en enskild metod som gynnar alla olika arter. I restaurerade lövskogar så påverkades skalbaggar på ett sätt som varken liknade miljön innan restaurering eller i miljöer som använts som restaureringsmål även efter tio till tjugo år. I restaurerade tallskogar föredrog svampar, lavar och skalbaggar olika typer av död ved, till exempel stående eller liggande, bränd eller obränd död ved. Död ved som skapades under restaureringen hyste dessutom färre arter än ved som dog för länge sedan.

Den viktigaste lärdomen är att effekten av naturvårdsåtgärder varierar beroende på vilken artgrupp eller tidsskala som studerats. För läget för den biologiska mångfalden ska förbättras måste naturvårdsstrategier bättre anpassas till de varierande ekologiska behov som flera arter har över tid och rum. Denna avhandling belyser komplexiteten i att restaurera för biologisk mångfald och uppmanar till en mer flexibel och varierad naturvård.

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Thank you to Stora Enso, Skogforsk, Naturskyddsföreningen and the County Administration boards of Värmland and Dalsland for land-hosting and collaboration.

Thank you to my family for being one of few stable aspects of my life during this time.

And last but certainly not least, thank you, lady K, for being the best!

Appendix

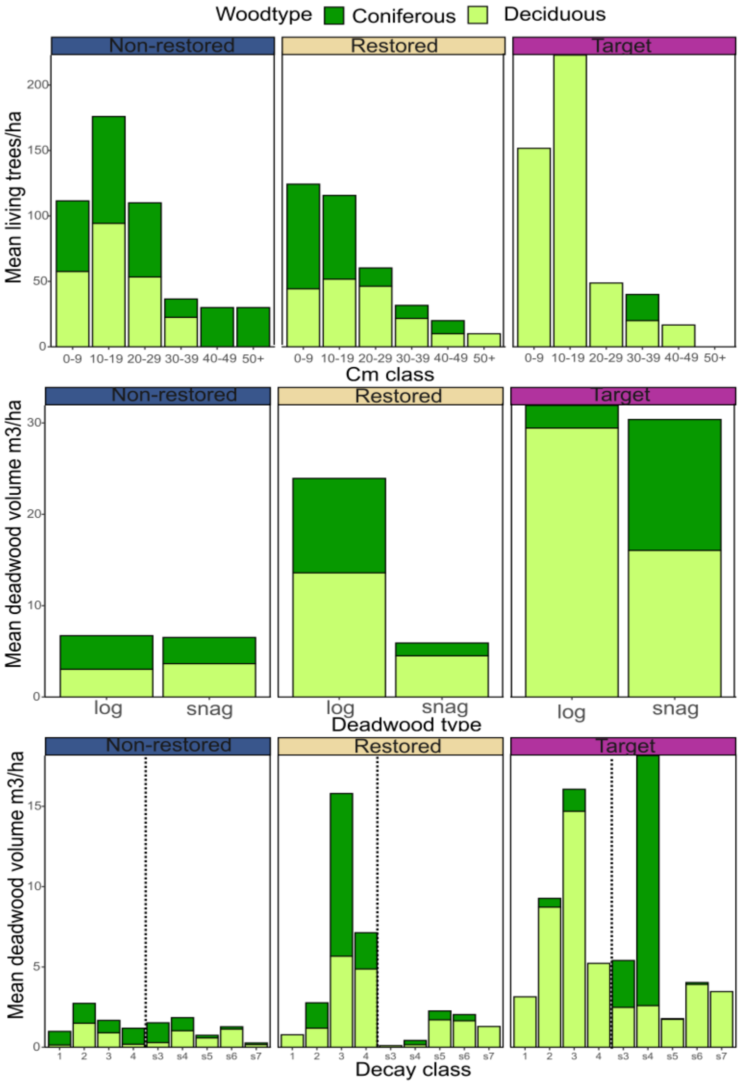

Figure A1. Mean values for forest structure in paper I. Decay classes 1-4 are for logs (Gibb et al., 2005) and s3-s7 for snags (Jung et al., 1999).

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RESEARCH ARTICLE

A decadal study reveals that restoration guided by an umbrella species does not reach target levels

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Abstract

1. Maintaining structural and functional elements of ecosystems are essential in order to preserve biodiversity and ecosystem function. As a means of guiding conservation work, the umbrella species concept was developed. In Sweden, one putative umbrella species, the white-backed woodpecker, has guided conservation and restoration of deciduous forests for two decades.
2. Here, we evaluate the decadal effects of restoration aimed at the white-backed woodpecker on biodiversity of saproxylic beetles. We compare stands that were restored 12 to 21 years ago to non-restored stands and historical white-backed woodpecker habitats acting as restoration target stands.
3. Restored stands contained higher deciduous deadwood volumes than non-restored stands but lower volumes than restoration target stands. The deadwood in restored stands was concentrated in later decay stages, whereas target stand deadwood was more evenly distributed across decay stages.
4. Restored stands had similar species richness and abundance of most groups of saproxylic beetles compared with non-restored stands while not reaching the levels of restoration target stands. Species assemblages differed among all stand types with restored stands supporting late decay stage and generalist species while target stands supported more deciduous associated and threatened species.
5. *Synthesis and applications*: We conclude that after one to two decades, restoration improve stand structure and benefit beetle diversity but that target levels are not yet reached. Thus, only partial restoration is achieved. Our results stress that for restoration to be successful both continuous and repeated restoration efforts are needed and that it is important to identify target levels of important habitat characteristics when assessing restoration outcome.

KEYWORDS
beetle, biodiversity, community ecology, conservation, deadwood, deciduous, focal species, forest

1 | INTRODUCTION

Maintaining biodiversity is essential to ensure stable and functional ecosystems (Díaz et al., 2013; Oliver et al., 2015). Human land use, including degradation and habitat loss (Betts et al., 2017; Newbold et al., 2015), has led to worldwide biodiversity declines (Jaureguiberry et al., 2022), which in turn calls for large-scale conservation and restoration (Aronson & Alexander, 2013; Benayas et al., 2009). The process of natural ecosystem recovery can be very slow, spanning decades or even centuries (Dobson et al., 1997). Thus, restoration is often needed (Gann et al., 2019) especially for rare or remnant habitat types and if source populations are lacking (Brederveld et al., 2011).

Internationally, forest restoration research is generally focussed on replanting or reseeding of severely degraded habitats. In boreal forests of Fennoscandia, restoration is focussed on restoring structural elements, for example, deadwood, in degraded forests. Common methods are to mimic natural processes such as fire and gap dynamics, so-called natural-disturbance-emulation (NDE) (Gauthier et al., 2009; Hjältén et al., 2023). However, for some habitats, NDE does not provide suitable habitats in short term. One example is natural regeneration of deciduous forest, which might take decades. To generate deciduous dominated stands and deciduous deadwood immediately, direct management of the tree species composition is needed.

Biodiversity conservation is often resource demanding why the development of cost-efficient methods is crucial. The umbrella species concept is based on the idea that conservation focussed on focal species with particularly high demands on habitat quality or size, will also benefit co-occurring species (Fleishman et al., 2000; Lambeck, 1997). When selected using appropriate criteria, umbrella species can be a useful concept in guiding restoration work (Branton & Richardson, 2014; Hurme et al., 2008; Roberge & Angelstam, 2004). Birds are widely used as umbrella species since many species have high demands on both habitat size and quality. In addition, many birds are charismatic, which increase engagement from the public and possibilities of funding (Branton & Richardson, 2011; Roberge et al., 2008; Smith & Sutton, 2008). The high demand of habitat quality and size makes the white-backed woodpecker (*Dendrocopos leucotos*) a putative umbrella species (Roberge et al., 2008). Once widespread throughout Sweden (Aulén, 1988), this critically endangered species has guided restoration of deciduous forest for two decades (Mild & Stighäll, 2005). The white-backed woodpecker demands deciduous forest with large amounts of deadwood, a habitat type almost lost from the Swedish landscape (Axelsson et al., 2002; de Jong, 2002).

Restoration aimed to provide food and nesting possibilities for the white-backed woodpecker, in total, spans tens of thousands of hectares in Sweden. The most commonly used method is to remove spruce in stands where deciduous trees are abundant and thus provide adequate levels of deciduous dominated forest rich in deadwood. A previous study found that restoration of habitat for the white-backed woodpecker supports many deciduous associated beetle species and species of conservation concern in short term, 2–12 years of postrestoration (Bell et al., 2015). However, our knowledge of the long-term effect of restoration for the white-backed woodpecker is limited and thus urgently needed.

Saproxylic beetles are highly represented among forest biodiversity, including species of conservation concern and provide the main food source for the white-backed woodpecker (Hjältén et al., 2023). In addition, saproxylic beetles respond quickly to change in their surrounding environment, making them an appropriate organism group to study in assessing ecological restoration effects on biodiversity.

Biodiversity patterns are scale-dependent (Chase et al., 2019) and a hierarchical approach is often used in biodiversity studies (Gran, 2022; Rubene et al., 2015) going from landscape (γ-diversity) to local (α-diversity) scale while also describing the variation of communities (β-diversity). For example, although α-diversity may be low in a certain habitat type, the overall γ-diversity may be great due to a greater among habitat variability (β-diversity) (Vellend, 2016). This hierarchical approach is thus useful to discern diversity patterns following, for example, ecological restoration.

With the umbrella species concept as a guiding framework, we aim to investigate the decadal effects of ecological restoration on forest stand structures and α-, β-, and γ-diversity of saproxylic beetles by re-visiting the restored stands in Bell et al. (2015), 12–21 years after restoration.

Even though a focal species is not currently inhabiting a site, it may still serve a high value for biodiversity and could thus under the wider umbrella species concept serve as a restoration target (Lõhmus et al., 2021). We therefore define deciduous forest habitat with recent occurrence of breeding white-backed woodpeckers as a restoration target habitat. We define stands that have potential for restoration but are non-restored as reference stands. With the forest landscapes of Sweden being highly degraded and fragmented, hindering dispersal and colonisation of many species, for example, (Edman et al., 2004) and with restoration typically resulting in novel ecosystems supporting different species and structures than, for example, target ecosystems (Aerts & Honnay, 2011), we predict only partial rather than full restoration (Gann et al., 2019). This study is unique as it addresses two major gaps in previous research; we investigate restoration in the context of both negative and positive reference stands and we evaluate decadal effects of restoration. We predict that:

1. Structures of importance to beetle diversity, such as canopy layering and deadwood, will continuously be generated in target stands, whereas restoration stands had a one-time pulse of created structures. Therefore, we expect that living trees in target stands will be distributed in a j-shape of mainly deciduous trees whereas restored stands will have a large proportion of coniferous trees in smaller diameter classes.
2. Deadwood volumes in restored stands will be greater than in non-restored stands but lower than in target stands and concentrated

in later decay stages since deadwood created from restoration was a one-time addition, whereas target stands will have a more even distribution of deadwood among decay stages as a result of continuous supply.

3. We expect the α-diversity of saproxylic beetles, including species of conservation concern, main prey species of the white-backed woodpecker and species preferring deciduous deadwood to be greater in restored than non-restored and similar to target stands. Due to high amounts of late decay deadwood in restored stands, we expect α-diversity of late decay stage species to be greater in restored than non-restored and target stands.
4. Given that that non-restored and restored stands have a management history, which usually results in homogenous stands, we expect overall saproxylic beetle β-diversity to be lower in these stands compared with target stands, which we expect to be more structurally heterogeneous. Responses may be trait-specific, with, for example, coniferous and deciduous specialists responding differently based on variation in forest structures.
5. We expect the overall γ-diversity to be greatest in target stands and restored stands to display intermediate γ-diversity between non-restored and target stands.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was conducted in the central boreal zone in Värmland and Dalsland counties, Sweden (Ahti et al., 1968) between latitudes 59.1–59.9° N and longitudes 12.0–13.7° E (Figure S1). In total, 23 stands were included in the study: eight stands restored in 2000–2010, seven commercially managed mixed stands targeted for restoration that had not been restored and eight stands consisting of historical breeding habitat for the white-backed woodpecker, hereafter target stands, these stands hosted breeding white-backed woodpeckers up until 2005–2016. The target stands are considered to have the highest potential to host breeding pairs of the white-backed woodpecker in their respective region, and extensive restoration work has been done in the landscape surrounding these stands for more than 20 years. The average stand size was 11.4, 5.7 and 9 hectares for non-restored, restored and target stands, respectively. Prior to restoration, restored and non-restored stands were deemed similar regarding environmental variables based on stand data and field visits. Non-restored stands are production stands that have undergone conventional forest management, but where the proportion of deciduous trees is higher than average, making them suitable for restoration. In 2000–2010, spruce trees were removed from the restored stands. Some deciduous trees were girdled or made into high-stumps (Bell et al., 2015). The field studies conducted in protected areas had permission granted by the County Administration Board of Värmland [525-4458-2021]. The study did not require ethical approval.

2.2 | Environmental data

Tree species and diameter at breast height (DBH, 1.3 m) were recorded for all living trees higher than 1.3 m and >5 cm in DBH within a 10-m circular sample plot at the centre of each stand. Coarse woody debris (DBH >10 cm, length/height >1.3 m) was measured within one 25-m circular sample plot, at the centre of each stand. We divided all deadwood by type (logs and snags), tree species and decay stage following Gibb et al. (2005) for logs and Jung et al. (1999) for snags. Top and bottom diameter and length was measured for logs. For snags, we measured diameter in breast height and assessed height. Deadwood volumes for logs and snags up to 6-m height (as these snags were usually broken) were calculated as cylinders. For taller snags (>6 m), we used Brandel's (1990) southern Sweden volume functions for pine and spruce with birch being used for all deciduous tree species.

2.3 | Beetle sampling

Three IBL2, flight-intercept traps were strung between trees at breast height in a North, South-east, South-west pattern based on the centre of each stand, approximately 30–70 m from the stand centre. IBL2 traps are large (base 1 m, height 1 m, intercept area 0.3 m^3); semi-transparent flight-intercept traps shaped like downward facing triangles (Bell et al., 2015). All flying invertebrates were contained in bottles, filled to one-third with 70% propylene glycol and some detergent, at the bottom of the traps. The traps were equipped with water-diverging modules that prevent rainwater from entering and flooding the bottles. The traps were set out in the first week of June 2021 and collected in mid-October 2021. An expert taxonomist identified all saproxylic beetles to species level. We then categorised beetles based on their affiliation to deadwood, decay stage, tree species, their conservation status and if they were recorded as prey species for the white-backed woodpecker. This resulted in the following categories: (a) Saproxylics, (b) Saproxylic species of conservation concern, meaning that they have had the conservation status of NT or higher during the last three Swedish red lists (Gärdenfors, 2010; Swedish Species Information Centre, 2015, 2020), (c) WBW prey species, species pointed out as especially attractive as food for the white-backed woodpecker according to Aulén (1988), (d) Coniferous preferring, (e) Deciduous preferring, (f) Generalist, with no tree species preference, (g) Early, species occurring at early stages of deadwood decay, (h) Middle, middle decay species, (i) Late, late decay species and (j) decay stage generalists, with no known preferences of decay stage. The same species can occur in several groups. Classifications of ecological preferences were based on available literature (Hagge et al., 2019; Koch, 1992; Seibold et al., 2015) and personal communication with taxonomic experts; nomenclature following the Swedish Dyntaxa system (Dyntaxa, 2023).

2.4 | Statistical analysis

All analysis was performed in the statistical software program R vers. 4.0.2. (R Core Team, 2020). We used LM's to test for differences in forest structure variables. We tested the effect of stand type on α-diversity (species richness and abundance) of saproxylic beetles with LMM's on log-transformed beetle abundance data, between stand types, package lme4 (Bates et al., 2015) and GLMMs for richness with trap as a random effect and negative binomial or Poisson distribution; package GlmmTMB (Magnusson et al., 2017). As model diagnostics, we used residual plots and tested for overdispersion in the DHARMa package (Hartig & Hartig, 2017). We performed pairwise comparisons of the stand types with estimated marginal means in the package emmeans (Lenth et al., 2019). In case of missing traps, we produced a third 'dummy' trap based on the mean values of the two existing traps to get GLMM models to converge.

To calculate β-diversity, we performed BETADISPER on a Bray–Curtis distance matrix followed by an ANOVA to compare distances to the community centroid. For pairwise comparisons, we used permutest with 999 permutations. We investigated differences in species composition among stand types with PERMANOVA and visualised by NMDS with 999 permutations and Bray–Curtis dissimilarity measure, in the vegan package (Oksanen et al., 2007). In order to identify indicator species for the different stand types, we used the function multipatt with 999 permutations in the Indicspecies package (De Caceres et al., 2016). Finally, for γ-diversity analyses, we performed species accumulation curves using the iNEXT package with 95% confidence intervals (Hsieh et al., 2016).

3 | RESULTS

3.1 | Structures

Of the living trees, 56, 49 and 99 per cent were deciduous in restored stands, non-restored and target stands, respectively (Figure 1).

In restored stands, 60 per cent of trees smaller than 20 centimetres were coniferous. For non-restored stands, corresponding numbers were 48 per cent of trees smaller than 20 centimetres being coniferous and in target stands, 100 per cent of trees smaller than 20 centimetres being deciduous (Figure 1).

The deadwood volumes in restored stands was non-significantly lower than target stands ($p = 0.15$) and near significantly greater than in non-restored stands ($p = 0.075$) (Figure 1). Volumes of logs were similar between restored and target stands ($p = 0.34$) but greater in restored and target than in non-restored stands ($p = 0.024$). Coniferous deadwood volumes did not differ between stand types but volumes of deciduous deadwood was lower in restored compared with target stands ($p = 0.03$) and greater in restored compared with non-restored ($p = 0.006$). Restored stands were characterised by large proportions of deadwood logs in the later decay stages ($p = <0.001$), whereas logs in non-restored stands was more evenly spread among decay classes ($p = 0.1494$) and for target stands, intermediate decay stages were greatest ($p = 0.02$; Figure 1).

3.2 | Beetles

We caught 16,324 individuals and 322 species of saproxylic beetles with 58, 38 and 28 species unique for target, restored and non-restored stands, respectively, and 119 species occurred in all stand types (Figure S2).

3.2.1 | α-Diversity

We found greater α-diversity in terms of both species richness and abundance in target stands than the other stand types for saproxylic, conservation concern, white-backed woodpecker prey, deciduous and generalist species but lower α-diversity of coniferous species (Table S1, Figures 2 and 3). Restored stands displayed similar levels of α-diversity as non-restored stands for all saproxylic, white-backed woodpecker prey, deciduous and generalist species. Coniferous and early decay stage species was less abundant and species of conservation concern species was more abundant in restored compared with non-restored stands (Tables S1 and S2, Figures 2 and 3).

3.2.2 | β-Diversity

Assemblage composition differed significantly among all stand types for all beetle groups (Table S3, Figure 4). We found differences in β-diversity for species of conservation concern ($p = 0.043$), WBW prey ($p = 0.01$) and deciduous species ($p = 0.001$; Table S3, Figure 4). Pairwise comparisons revealed a greater β-diversity in target stands compared with restored stands for species of conservation concern ($p = 0.01$) and lower in target stands than in restored stands for WBW prey species ($p = 0.02$; Figure 4). For deciduous species, β-diversity was highest in restored stands, followed by non-restored and target stands (Table S3, Figure 4). For late decay stage species, β-diversity was lower in target stands compared with non-restored and restored stands (Table S3, Figure 4). We also found less overlap among stand types for early decay stage species compared with species associated with mid and late decay stages (Figure 4).

Restored stands displayed seven indicator species of which five had no tree species association. Target stands had 23 indicator species of which 12 preferred deciduous trees and non-restored

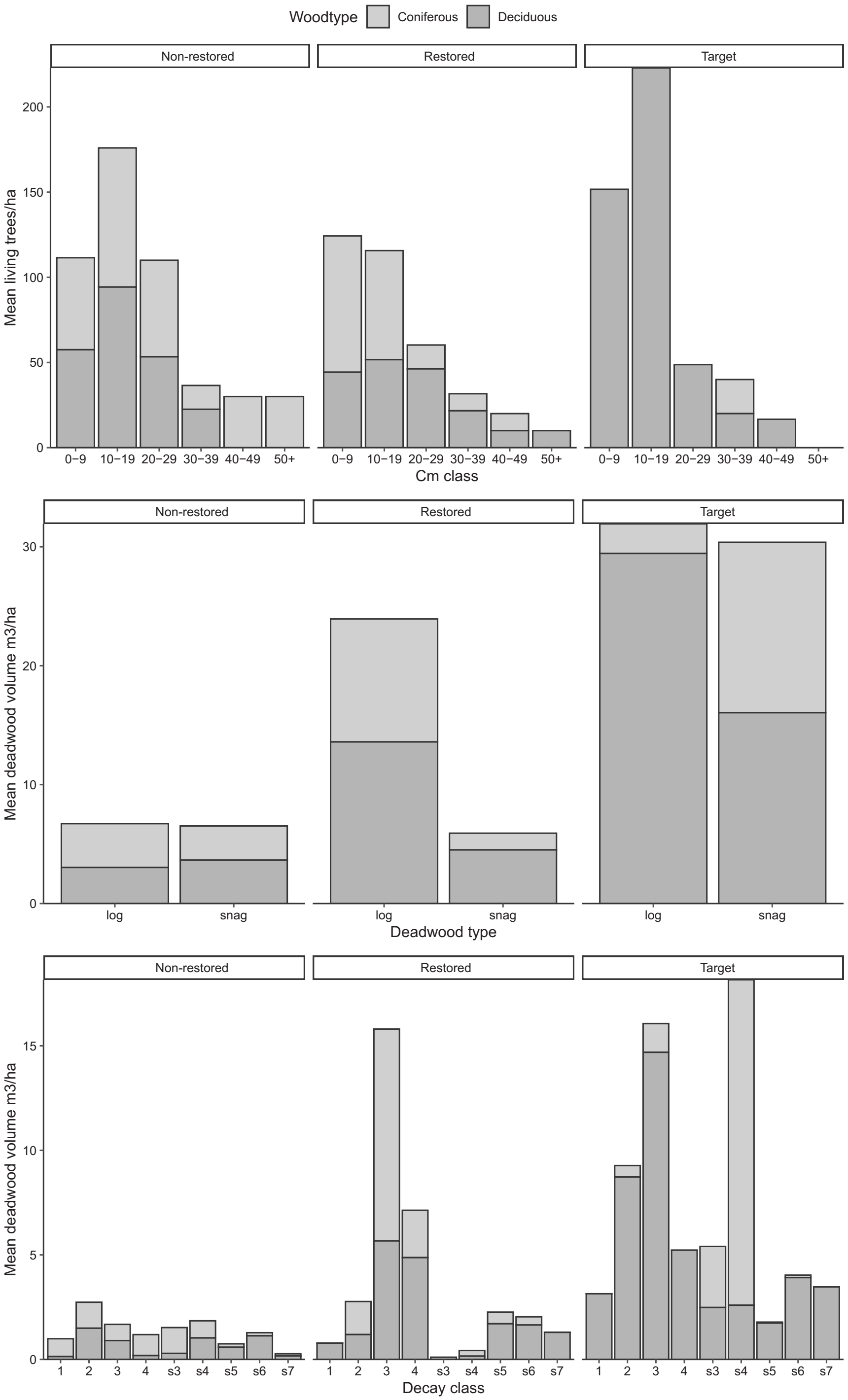


FIGURE 1 Mean values of environmental variables per stand type. Decay classes 1–4 (Gibb et al., 2005) are for logs and s3–s7 is for snags (Jung et al., 1999) with higher decay classes indicating higher decay.

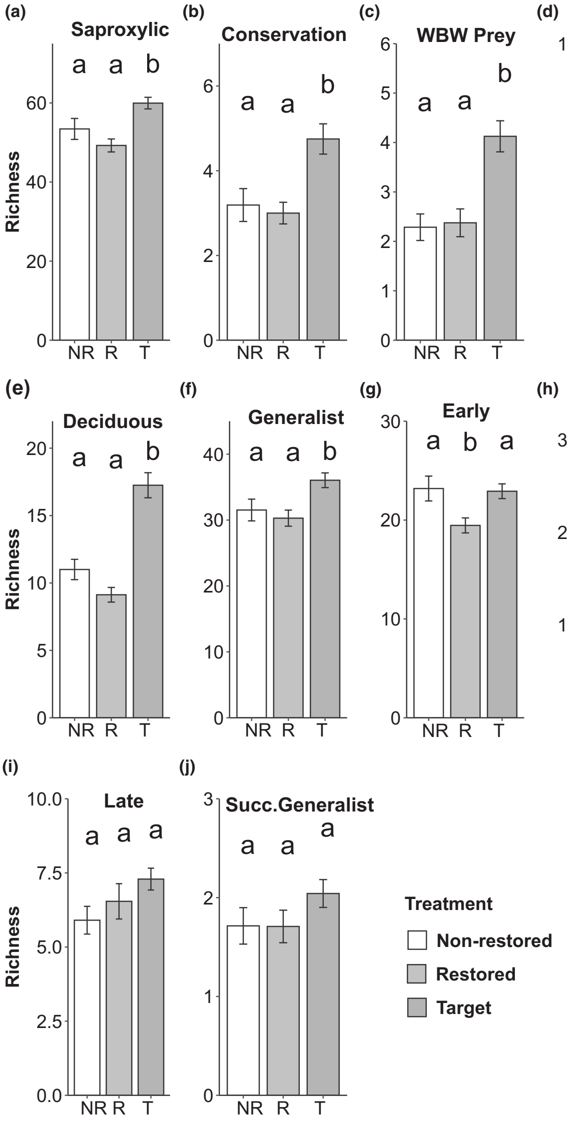


FIGURE 2 Mean ± SE species richness of saproxylic beetle groups in the different stand types. Unique letters indicate significant differences and shared letters indicate non-significance from emmeans results. (a) Saproxylic beetles, (b) species of conservation concern, (c) white-backed woodpecker prey species, (d) coniferous preferring species, (e) deciduous preferring species, (f) tree generalist species without tree species preference, (g) early decay stage species, (h) middle decay stage species, (i) late decay stage species, and (j) secay stage generalists.

stands 18 indicator species with nine preferring coniferous trees (Table S4).

3.2.3 | γ-Diversity

Rarefaction curves displayed generally overlapping trajectories between stand types (Figure 5). Extrapolated trajectories show that the γ-diversity of saproxylic, conservation concern and deciduous species is greater in target than non-restored stands and that late decay stage γ-diversity is greater in restored than non-restored stands (Figure 5).

4 | DISCUSSION

Studies on deciduous forest restoration and its impact on saproxylic beetles or other taxa are rare in boreal Fennoscandia. In fact, most studies are conducted in coniferous forests, where the use of negative references are common, while positive references are sparse (e.g. Hägglund et al., 2020). We do acknowledge that the restoration target habitats in our study are not 'natural' per se. Given the purpose of the restoration studied, we still consider these recent breeding habitats for the white-backed woodpecker suitable target stands. We emphasise the importance

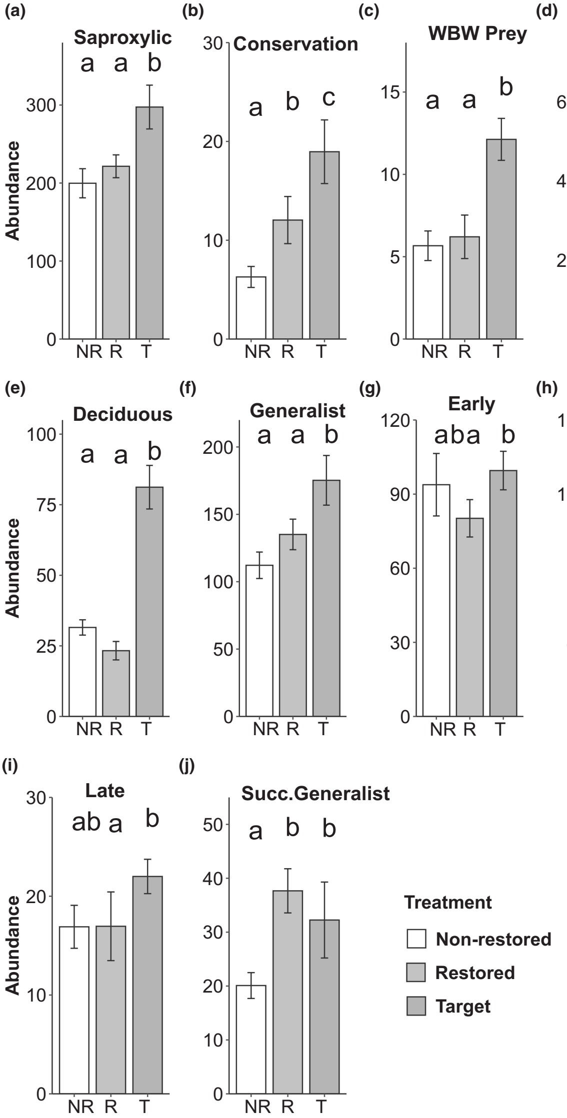


FIGURE 3 Mean ± SE species abundance of saproxylic beetle groups in the different stand types. Unique letters indicate significant differences and shared letters indicate non-significance from emmeans results. (a) Saproxylic beetles, (b) species of conservation concern, (c) white-backed woodpecker prey species, (d) coniferous preferring species, (e) deciduous preferring species, (f) tree generalist species without tree species preference, (g) early decay stage species, (h) middle decay stage species, (i) late decay stage species, and (j) decay stage generalists.

of using appropriate references when assessing restoration, as only using one of negative or positive references greatly limits the potential of assessment. Our study provides novel insights into decadal effects of deciduous forest restoration in a managed landscape dominated by conifer forest plantations. As one of very few studies, we compared restored stands in relation to both ends of a restoration gradient including non-restored stands and target habitats. We show that after 12–21 years, restoration impacts both stand structure and beetle diversity. However, the restored stands display lower deciduous deadwood volumes and α-diversity (measured as species richness and abundance) and different assemblage composition compared with the target stands. This means that restored stands now differ from both target and non-restored stands. Our results show that deciduous forest restoration guided by an umbrella species achieves partial restoration of local stand structure and beetle diversity after two decades, although the qualities of target stands are not reached.

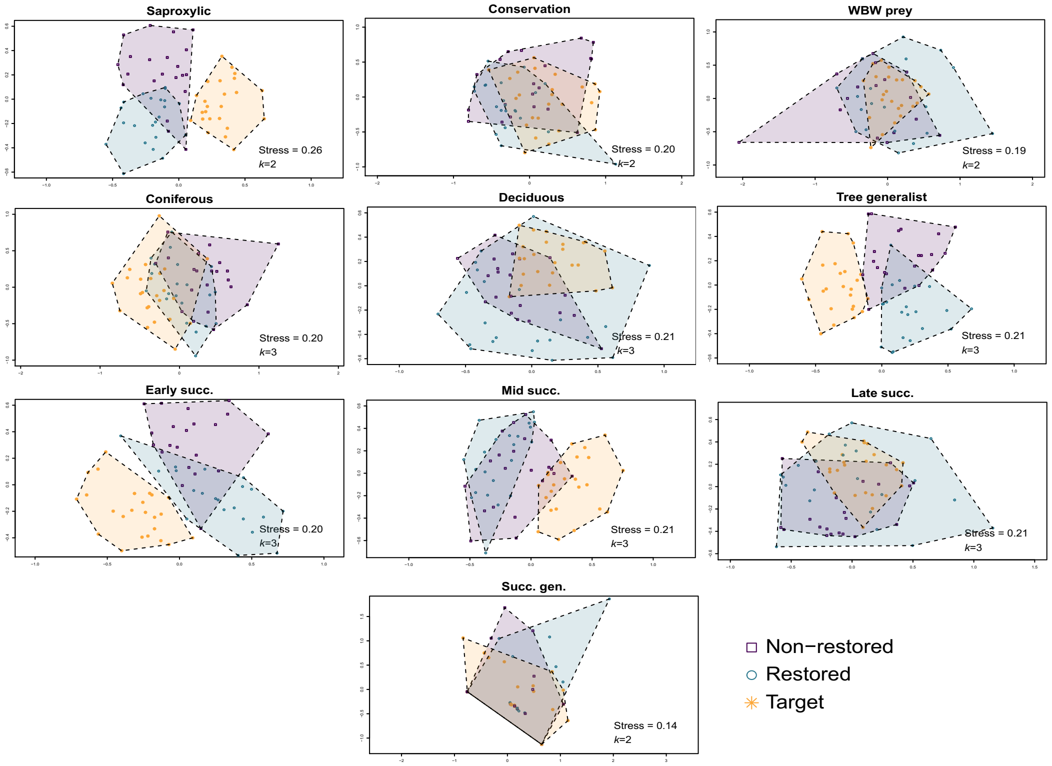


FIGURE 4 NMDS plot visualising differences in assemblage composition of saproxylic beetle groups in the different stand types.

4.1 | Structures

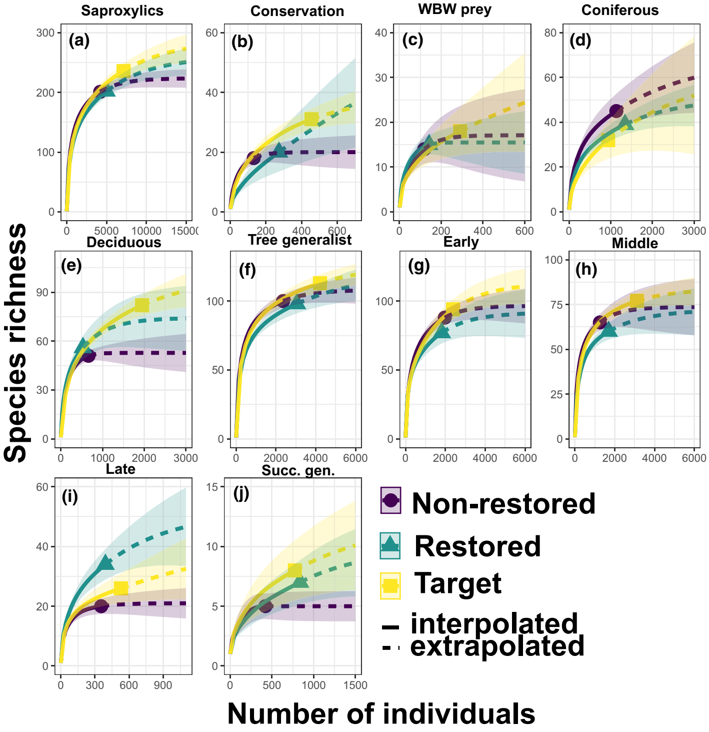
In line with Prediction 1, we found that forest structure differed between target stands and restored stands. Coniferous trees dominated tree regeneration in restored stands while deciduous trees dominated in target stands. This suggest that target stands will continue to be deciduous dominated without further interventions but that the restored stands will need repeated spruce removal. Hämäläinen et al. (2020) showed that spruce removal in white-backed woodpecker restoration could successfully benefit establishment of aspen but not birch saplings. In order to ensure successful establishment of deciduous seedlings, removing encroaching spruce and creating gaps large enough to increase light is needed (Götmark, 2007). Further measures such as site preparation and direct seeding of deciduous tree species might also be necessary (Castro et al., 2021). Tree size stratification is needed in order to ensure a future supply of deadwood in varying decay stages and tree species such as those found in target stands.

Aligning with Prediction 2, volumes of mainly deciduous deadwood in restored stands were greater than in non-restored stands but lower than in target stands. Deadwood in the restored stands was also allocated in the later decay stages while the target habitat had a more even spread among decay classes. The levels reached threshold levels of ~20–30 m^3/ha suggested in (Hekkala et al., 2023; Müller & Bütler, 2010) showing that the restorations have potential to benefit biodiversity. The deadwood created in our restoration stands consisted of fresh deadwood created at one occasion in even aged stands. This deadwood is now highly decayed and has fulfilled much of its initial purpose, at least for early decay stage saproxylic beetles. The structure of the initial forest stand determines the extent of how much deadwood can be created from living trees without depleting the future supply of deadwood or making the restored stand too sparse. These results implies an intermediate restoration effect, rather than complete restoration regarding tree species composition, layering and deadwood amount and quality.

4.2 | Beetles

We predicted the α-diversity of restored stands to be greater than non-restored and similar to target stands (Prediction 3). Instead, we found that both restored and non-restored stands displayed lower α-diversity than that of target stands and α-diversity of species

FIGURE 5 Rarefaction curves with 95% confidence intervals comparing γ-diversity of saproxylic beetle groups in the different stand types. (a) Saproxylic beetles, (b) species of conservation concern, (c) white-backed woodpecker prey species, (d) coniferous preferring species, (e) deciduous preferring species, (f) tree generalist species without tree species preference, (g) early decay stage species, (h) middle decay stage species, (i) late decay stage species, and (j) decay stage generalists.



associated with deadwood in late decay stages did not differ among stand types. After another 10 years, differences in species richness and abundance of deciduous associated and species of conservation concern between restored and non-restored stands, shown in Bell et al. (2015), could not be detected. Nor did restored stands reach levels of α-diversity similar to that of target stands. Fresh deadwood benefits many early decay stage beetle species causing an immediate increase in α-diversity at least in conifer dominated forest (Hägglund et al., 2020), an effect that may decrease to background levels as the deadwood decays (Jonsell et al., 2019). Target stands probably maintain higher levels of saproxylic beetle diversity due to the continuous supply of deadwood in various decay stages contrasting the one-time addition of deadwood in restored stands. Tree removal opens up the canopy and creates a warmer and drier microclimate, which may affect fungi negatively (Müller et al., 2010). As many deciduous-associated species are fungivores, this could explain the lack of difference in deciduous species between non-restored and restored stands.

We found partial support for our-fourth prediction that target stands would support greater β-diversity, but for species of conservation concern. For white-backed woodpecker prey species, deciduous and late decay stage species we found the opposite, with target stands displaying a lower β-diversity. This could be due to a variation in the baseline of forest structures in non-restored stands, a variation that is also realised after restoration through, for example, varying size and number of deciduous trees. In target stands, the overall quality may be high, resulting in higher species richness, whereas the variation between stands may not be as high, resulting in a comparatively lower β-diversity. For the overall saproxylic assemblage composition and the beetle sub-groups, we found distinct species assemblages in each stand type, with restored and non-restored stands more similar to each other than to target stands. We found relatively small overlaps among stand types for early decay stage species and more overlap for later decay stage species. This could be due to different colonisation patterns of deciduous and coniferous deadwood (Saint-Germain et al., 2007), where non-restored stands may favour early stage coniferous species, target stands mid and late deciduous species with an intermediate pattern in restored stands. This is further strengthened by the pattern we see in indicator species, with most coniferous specialists in non-restored stands being early decay stage specialists while deciduous specialists in target stands are represented among several decay stages with few indicator species overall in restored stands. However, assemblage composition in restored stands still differed from non-restored stands after more than 10 years, suggesting that restoration has managed to alter species composition into a new trajectory. The difference in stand structure and deadwood composition suggest however that the restored stands will not become more similar to the target stands with time. The majority of indicator species in target stands preferred deciduous deadwood, in non-restored stands indicator species were associated with coniferous deadwood while restored stands only had one deciduous indicator species. One of the strongest indicator species for target stands, *Sinodendron cylindricum*, is not only a deciduous specialist, but also considered an important prey species for the white-backed woodpecker, which further strengthens the position of these stands as restoration targets.

Although γ-diversity trajectories overlap between stands, extrapolation suggest greater γ-diversity in target compared to non-restored stands regarding saproxylics, conservation concern and deciduous species. However, predictions may be unreliable when extrapolated further than twice the reference sample (Chao et al., 2016). We did not find that restored stands had a greater α-diversity of late decay stage species as expected in Prediction 3; instead, we found this was the case for γ-diversity. This aligns well with structural elements as the majority of deadwood in restored stands belonged to later decay stages. Greater γ- and not α-diversity of late decay stage species indicates that only some restoration stands support these species. Once deadwood resources are depleted, late decay stage species may thus be lost, supporting the need for provisioning multiple decay stages in restored stands.

4.3 | Implications for restoration

We suggest that management strategies for restoration of habitat for the white-backed woodpecker need re-evaluation. In order to provide fresh deadwood to maintain high levels of saproxylic beetle diversity, restoration needs to be repeated every 10–20 years. Further action is also needed to ensure regeneration of deciduous trees and to prevent spruce encroachment (Hämäläinen et al., 2020). Since the initial number of large deciduous trees in stands subjected to restoration was low, repeated restoration may deplete the supply of large, old trees and the future supply of deadwood. We recommend restoration to be planned in adjacent stands in the landscape to make sure that stands are continuously restored every 10–20 years. Woodland key habitats and voluntary set-asides are usually small in size and fragmented in the forest landscape (Hof & Hjältén, 2018); hence, conventional forest management needs to contribute to the landscape supply of habitat for disturbance-dependent species including deciduous trees and deadwood (Tälle et al., 2023). Future supplies of deciduous trees should therefore be a priority across all stages of forest management, from regeneration of clear-cuts, promoting deciduous trees in pre-commercial and commercial thinning, to leaving deciduous trees as retention at final felling (Mild & Stighäll, 2005).

Previous research have shown that in order to maintain a rich beetle diversity, deadwood of varying species and decay stages in both shaded and sun-exposed conditions is needed (Hjältén et al., 2012; Seibold et al., 2016). Furthermore, planning for a continuous supply of snags in different decay stages is also important for cavity-nesting birds such as the white-backed woodpecker (Drapeau et al., 2009; Edworthy & Martin, 2013). For beetle assemblages associated with birch deadwood, the amount of deciduous deadwood within 100 m as well as the landscape-level amount of deciduous stands was important for providing rich assemblages (Johansson et al., 2017). To boost populations of deciduous-associated species in the landscape, it is likely important to complement spruce removal in deciduous rich stands with other disturbance emulating management such as prescribed burning and rewetting of wetlands.

We conclude that decades after restoration, restored stands do not produce more species or individuals than non-restored stands but support other species assemblages, mainly of generalist and late decay stage species, although dissimilar to target stands. More effort is thus needed to achieve restoration targets and the forest structure and tree species composition before restoration will surely determine restoration success. Additionally, future assessment of restoration success would also benefit from more precise host-use sampling of larvae and emerging adults such as wood dissection and rearing (Saint-Germain et al., 2006). Target stands are able to produce a continuous supply, whereas restoration manages to create a pulse but no continuous supply of deadwood. This suggests that several restoration stands are needed to fill the same function as a single target stand.

AUTHOR CONTRIBUTIONS

All authors (Albin Larsson Ekström, Joakim Hjältén and Therese Löfroth) were part of conceptualisation and planning of the study design. Albin Larsson Ekström was responsible for the collection of data and formal analysis and led the writing of the manuscript. All authors contributed to writing of the manuscript and have given their approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.c2fqz61gv (Larsson Ekström et al., 2024).

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SUPPORTING INFORMATION

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

Figure S1. Map showing the location of the forest stands, sampling of environmental variables and an image of the IBL2-flight intercept traps used to sample invertebrates.

Figure S2. Venn-diagram displaying number of unique and shared species between stand types (percentage % of total species).

Table S1. GLMM and LMM results for Saproxylic (Sx), Conservation concern (Cons.), White-backed woodpecker prey (WBW), Coniferous (Con.), Deciduous (Dec.) and Generalist (Gen.) beetles. Non-restored stands (NR) is the intercept level.

Table S2. GLMM and LMM results for Early decay stage (Early), Middle decay stage (Middle), Late decay stage (Late) and Generalist (Gen.) beetles. Non-restored stands (C) is the intercept level. Significant results highlighted in bold.

Table S3. Result output from BETADISPER and Permutest given significance and PERMANOVA divided by beetle group.

Table S4. Indicator species for each stand type.

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Reinventory of permanent plots show that kelo lichens face an extinction debt

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Conservation

ABSTRACT

Intensive forestry has led to landscape level deficits of important substrates such as deadwood and its associated biodiversity. Several taxa face extinction debts due to continuous declines and lack of regeneration of important habitats. Deadwood-dependent lichens are of great conservation concern due to a general lack of deadwood and due to their slow establishment, especially of rare species. In a field restoration experiment in central Sweden, we studied deadwood-dependent lichens for eight years, their association to different types of deadwood and their response to environmental change caused by variable retention forestry, deadwood enrichment and prescribed burning. Prescribed burning and site preparation caused depauperate lichen species assemblages throughout the study period but retention felling did not majorly affect lichen species assemblages. We found that lichen species were nested along deadwood qualities and deadwood created in the experiment only hosted a subset of lichen species found on kelo wood. Despite large reductions of kelo wood with lichen occurrences over the study period, overall species richness did not decrease. The fact that a large part of the lichen community occur only on kelo wood and that kelo wood is not regenerated implies that lichens associated with kelo wood face an extinction debt. In order to avoid local extinctions of deadwood-dependent lichens, site preparation and prescribed burning should be avoided in areas rich in high quality deadwood. There is urgent need to start creating new kelo wood through reoccurring fires in order to halt the impending extinction debt.

1. Introduction

Human land use and subsequent loss of habitat are considered important drivers of biodiversity loss globally (Sánchez-Bayo and Wyckhuys, 2019; Almond et al., 2020; Jaureguiberry et al., 2022). The majority of global, terrestrial biodiversity is found in forests (Thompson et al., 2009), yet forests are continually being degraded and fragmented (Haddad et al., 2015; Venter et al., 2016; Potapov et al., 2017). This is also true for the boreal forest ecosystems of northern Europe and America where forest management has transformed natural habitats into monocultures lacking in natural dynamics and structures (Esseen et al., 1992; Cyr et al., 2009; Shorohova et al., 2011). In Fennoscandia, natural and semi-natural forests now only remain in small and fragmented patches with larger areas being confined to the mountain region (Svensson et al., 2020). Despite a more conservation-oriented management (Kruys et al., 2013; Kyaschenko et al., 2022), many forest and deadwood-dependent species are on the national and European Red List (Hyvärinen et al., 2019; Swedish Species Information Centre, 2020; IUCN, 2022). Late seral Scots pine (*Pinus sylvestris*) forests in particular have become rare both due to direct harvesting of living and dead trees but also due to fire suppression resulting in lack of regeneration of structures such as fire scars and burned wood. Consequently, unique properties found in such forests are lost from the forest landscape. Kelo wood is the unique deadwood legacy of several centuries' old pine trees characterized by tar-impregnated wood and a silvery-coloured surface. Kelo wood is resistant to decay and can endure for many centuries (Sirén, 1961; Niemelä et al., 2002). The unique properties of kelo wood are formed when slow-growing trees are injured by disturbances such as fire. As a response, the trees impregnate the wood with decay-resistant chemicals (Venugopal et al., 2016a, 2016b). Kelo wood is known to occur across the Palearctic boreal forests throughout Europe and Russia but due to a long period of intensive logging, it has disappeared from

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large parts of Europe and is increasingly rare in Fennoscandia (Niemelä et al., 2002; Kuuluvainen et al., 2017). A few studies have examined the importance of kelo wood for biodiversity, and the findings indicate that kelo trees support specialised lichen and fungal species. Moreover, kelo wood may act as sources of species dispersal during succession in disturbed forests (Niemelä et al., 2002; Santaniello et al., 2017).

Several studies on short-lived and mobile organisms suggest that different deadwood substrates complement each other and that a diversity of substrates is needed to support intact species assemblages (Thorn et al., 2020; Löfroth et al., 2023). For sessile organisms, assemblages are often nested, i.e., species-rich substrates or sites contain the complete assemblage while more species poor sites contain only a subset of the species from the richer sites (Wright et al., 1997; Zhao et al., 2015). If deadwood derived from restoration displays species assemblages that are distinct from natural deadwood, the complementary effect of restoration is greater than if species assemblages are nested, with created deadwood only supporting a subset of species found on natural deadwood.

Lichens are an important part of forest biodiversity and can be found on a range of substrates (Boch et al., 2013), although some species such as deadwood-dependent lichens are often overlooked (Spribille et al., 2008). Substrate type and quality has proven to be important to deadwood-dependent lichens and therefore retaining deadwood legacies in felling operations is instrumental in maintaining lichen diversity (Svensson et al., 2016; Santaniello et al., 2017). Disturbances including fire generally have a direct negative effect on lichens. Furthermore, species that are rare in managed forests recolonize at a slow rate (Johansson, 2008; Hämäläinen et al., 2014; Lõhmus et al., 2018). Lichen response to disturbance might however be trait-specific, with for example, pine associated species responding positively to increased sun-exposure (Johansson et al., 2006; Benítez et al., 2018; Ranlund et al., 2018). Due to lack of deadwood, specialised lichen species face a forestry-induced extinction debt (Berglund and Jonsson, 2005; Öckinger and Nilsson, 2010), one that can take a long time to realise due to slow extinction rates (Johansson et al., 2013, 2018). In order to halt species loss, the colonisation credit, through restoration, needs to be greater than the extinction debt (Watts et al., 2020), occur at a faster rate and needs to include rare and threatened species. Kelo-associated lichen species especially risk extinction debt due to the scarcity and isolation of kelo wood, making them highly sensitive to anthropogenic and stochastic extinction.

We investigated the effects of forest management and the importance of substrate type and quality for deadwood-dependent lichens. We revisited a large-scale experiment with permanent plots in pine forests subjected to felling, mechanical site preparation and restoration treatments to follow up on a study conducted by Santaniello et al. (2017). We also included untreated and burned stands in order to address forest management in a broader sense. Although large-scale experimental monitoring of biodiversity responses to forestry and restoration has been studied in other parts of the world (Wiersma, 2022), in Fennoscandia, studies usually spans a few years and long-term studies are rare (Koivula and Vanha-Majamaa, 2020). Our experiment provides a unique opportunity to follow the response of lichen diversity to forest management and restoration in the initial phases of lichen regeneration and recolonization while simultaneously providing opportunity to follow the future development in more long term.

More specifically we:

I) Examine changes in diversity patterns of lichens over time for different deadwood qualities.
II) Investigate how site preparation, prescribed burning and tree retention affect lichen species richness, abundance and composition over time.
III) Analyse the lichen diversity patterns in relation to substrate quality and type.

We expected both site preparation and prescribed burning to result in lower species richness and abundance of lichens due to substrate destruction while tree retention will maintain lichen species richness and abundance due to a maintained microclimate and deadwood legacies. Moreover, we expected that harvested areas outside of the retention would be affected by increased sun exposure that may have mixed or intermediate effects on lichen diversity. We expected lichen species richness to benefit from deadwood enrichment. We also expected kelo wood to host more red-listed species than old wood without kelo-qualities and deadwood generated during restoration, but that different deadwood qualities would host distinct, non-overlapping species assemblages.

2. Methods

2.1. Study design and field survey

The study was conducted in Effaråsen (60°58′29″N, 14°01′55″E), Dalarna county, in the southern boreal vegetation zone of Sweden (Ahti et al., 1968). The study area comprises 24 stands with a mean size of ~5 ha and the entire study area comprise around 140 ha. Scots pine (*Pinus sylvestris* L.) dominated the stands with an age of around 120–140 years. Norway spruce (*Picea abies* (L.) H. Karst) and birches (*Betula pendula* Roth. & *Betula pubescens* Ehrh.) occurred in sparse populations. The area has a history of forest management but has not previously been clear-felled. In 1888, there was a wildfire in the area, remnants of which is seen in form of living trees and kelo wood with fire scars.

In 2012–2013, the 24 stands were randomly allotted and subjected to harvest treatments with varying levels of tree retention (3–100 %), deadwood enrichment and prescribed burning. Mechanical site preparation was performed in felled areas in 2014, after the first lichen inventory. Retained trees were further divided in all stands, except the burned and unharvested, into: 1) Green tree retention of single trees or groups of trees, 2) high-stump creation at ~3 m height, 3) log creation by felling trees and 4) damaging of trees by bark-peeling by the harvester head. For further details, see Santaniello et al. (2016).

In 2014, ten circular permanent sampling plots (5.64 m radius) along transects were laid out in each stand covering the longest possible distance within the stand. In cases where ten plots did not fit within the transect, a second transect was laid out covering the second longest distance. In 2014, 15 stands were surveyed (i.e., deadwood and lichen inventory), excluding the prescribed burned and the control stands. In 2021, prescribed burned and control stands were surveyed additionally, and the plots from 2014 were resampled (due to an error, only nine plots were established in one of the stands in 2014), resulting in 239 plots. Based on the stand-level treatments, we categorized five plot types: 1) Closed; plots within retention patches with a closed canopy, varying in size depending on the felling intensity, 2) Open with no site preparation; plots in felling areas without retained canopy/open canopy, 3) Open with site preparation; plots in felling areas that were subjected to site preparation, 4) Untreated; plots within control stands with no treatment, and 5) Burned; plots within stands subjected to prescribed burning. Due to large variation among and within stands, these plot types occur across several stand and treatment types.

2.1.1. Deadwood inventory

Within each plot, we registered and measured all deadwood objects with an overall area of exposed wood $\geq$25 cm^2, excluding parts outside of the plots. Deadwood was classified into different types: low-stump (stump <50 cm height), snag (dead, standing tree >50 cm height) and log (downed deadwood). Deadwood quality was classified according to a combination of age and characteristics being: Kelo (since before or during the wildfire of 1888, 130+ years, with kelo-quality), Old (after the wildfire but before treatment, usually around 70–80 years, lacking kelo-quality), Young (created during or after treatments, <10 years), and Burned (created in the prescribed burning, <10 years). For standing deadwood, diameter was measured at breast height (DBH) and height was measured up to a maximum of two meters, as this was the limit for surveying lichens without using a ladder. For downed deadwood, top and bottom diameter and length was measured. We calculated deadwood surface area based on the formula of a cylinder and high-cut stumps were given a height of two meters since lichens were only inventoried to this height. The estimated bark and bryophyte cover was subtracted from all substrates and for logs by subtracting 20 % of the area as we estimated this area to be in contact with the ground and thus not surveyed. For low-stumps and snags, we also subtracted the bottom diameter since the bottom part is below ground. Deadwood types were analysed separately per deadwood quality: Young, Old and Kelo. Burned deadwood was left out of this part of the analysis due to too few replicates when separated into different types.

2.1.2. *Lichen inventory*

Deadwood-dependent lichens according to Spribille et al. (2008) were surveyed in 2013–2014 (here referred to as before treatment, as the response to the treatment one to two years prior likely had little effect in that time) and again in 2021 (post treatment) in order to examine the development over time. Both inventories were performed by the same person (G. Thor) using the same methodology (see Santaniello et al. (2017)). All deadwood-dependent lichens were surveyed on objects with an area available for colonisation of at least 25 cm^2 (decorticated wood), up to two meters on standing objects.

The facultatively lignicolous species *Cladonia botrytes* was searched for on the ground along all transects but was only found lignicolous in this area and was thus treated as lignicolous.

Trapeliopsis sp. is a distinct species that has not yet been described. Classification of the genus *Xylographa* follow Spribille et al. (2014).

We recorded all species of lichens and calculated species richness as the number of unique species divided by the sampled decorticated deadwood (m^2) per plot or per deadwood category per plot to account for differences in deadwood amount. Species abundance was calculated as the number of discrete species records on each substrate, divided by the sampled decorticated deadwood (m^2), then summarised per plot or by deadwood category per plot. The total number of plots used for each analysis can be found in Table A.2.

2.1.3. *Canopy cover*

We photographed the canopy using a phone camera with a fisheye lens, at the centre of each plot, from approximately 1 m above ground. The photos where then analysed in ImageJ (Schneider et al., 2012) using the Hemispherical 2.0 plugin (Beckschäfer, 2015) in order to achieve data on the canopy gap fraction. Gap fraction data was then divided into 2 classes, open or closed canopy ranging from 0.45 to 0.8 for closed canopy and 0.8–1 for open canopy.

2.2. *Data analysis*

All statistical analyses were performed using the open source programme R (R Core Team, 2020).

Due to non-normality in the data, we used Kruskal-Wallis tests followed by Wilcoxon pairwise tests to analyse relationships between lichen richness and abundance with deadwood type and quality, year and treatment effects on plot level. When testing for deadwood types and qualities, analysis were performed on deadwood type per plot and only for plots containing species abundance on that specific type of deadwood. Fine woody debris (<10 cm) was included in analysis of treatment but excluded from comparisons between deadwood types. Rarefaction curves were produced using the package iNEXT (Hsieh et al., 2016) to relate species richness to the accumulated sample effort. We rescaled the x-axis of the rarefaction curves to represent the cumulative wood surface area.

We produced a Jaccard distance matrix, followed by BETADISPER and subsequent ANOVA to test for differences in mean distance to the community centroid, which we treat as beta diversity. With non-significant results in BETADISPER, we performed a PERMANOVA to test for differences in species composition, with Jaccard distance, 999 permutations. We visualised species assemblages with NMDS, with 999 permutations and Jaccard distance except for young deadwood where Bray-Curtis distance was used. We used the vegan package to perform the BETADISPER, PERMANOVA and NMDS functions which were all done on stand level (Oksanen et al., 2017).

To identify indicator species, we used package indicspecies, with 999 permutations (Cáceres and Legendre, 2009). To test whether or not lichen species assemblages were nested within deadwood types, we followed Leibold and Mikkelson (2002), summarising species abundances by deadwood type and quality, using a binary matrix and the metacom package (Dallas, 2014).

3. Results

In total, we surveyed 787.7 m^2 decorticated deadwood with potential lichen occurrences; 451.3 in 2014 and 336.4 in 2021, resulting in a total of 27 deadwood-dependent lichen species. The species with the highest abundances were *Mycocalicium subtile* (21 % total abundance), *Micarea denigrata/nowakii* (14 %) and *Xylographa parallella/pallens* (13 %). Six of the species found were categorized as NT in the 2020 Red List of Sweden (Swedish Species Information Centre, 2020); *Calicium denigratum*, *Carbonicola anthracophila*, *C. myrmecina*, *Cladonia parasitica*, *Elixia flexella* and *Hertelidea botryosa* that together make up 11 % of the total abundance (Table A.1).

3.1. *Deadwood quality — time and treatment effects*

Our results show that lichen species richness increased slightly on kelo wood in the permanent plots between 2014 and 2021 but remained the same for red-listed species, when correcting for the sampled deadwood amount (Table A.2). Rarefaction curves revealed similar total species richness on kelo wood, despite an 80 % reduction in sampled wood surface area (from 26 m^2 to 4.9 m^2) with lichen occurrences between 2014 and 2021 (Fig. 1). The total species richness increased slightly on old deadwood between 2014 and 2021 (Fig. 1c). Assemblage composition on kelo- and old deadwood differed between years but not among treatments (PERMANOVA, $p = 0.001$, $R^2 = 0.03$).

3.2. *Treatment effect on lichens*

Untreated control plots, closed canopy and open canopy plots displayed similar total species richness while site prepared and burned plots, displayed lower species richness (Fig. 2). Species richness did not decrease between 2014 and 2021 on plot level (Table A.2). Rarefaction curves were overlapping between year and treatment but with a significant decrease of species richness in site prepared plots between 2014 and 2021 (Fig. 1b). Species assemblages differed between plot types (PERMANOVA, $p = 0.02$, $R^2 = 0.16$) with partial overlaps between closed canopy, open canopy and site prepared plots while control plots displayed assemblages not overlapping with any plot type. Assemblages in burned areas overlapped with open canopy and areas affected by site preparation (Fig. 2). PERMANOVA results of year * treatment were non-significant ($p = 0.185$), although visual interpretation of NMDS plots suggest that site preparation caused a shift in species assemblage between 2014 and 2021 while the assemblages in the other plot types did not change (Fig. 2).

3.3. *Deadwood quality and type*

Kelo wood had similar species richness as young and burned deadwood on plot level while rarefaction curves revealed a greater total species richness on old and kelo wood compared with young and burned deadwood (Fig. 1c, Table A.2). All red-listed species in 2021 were found

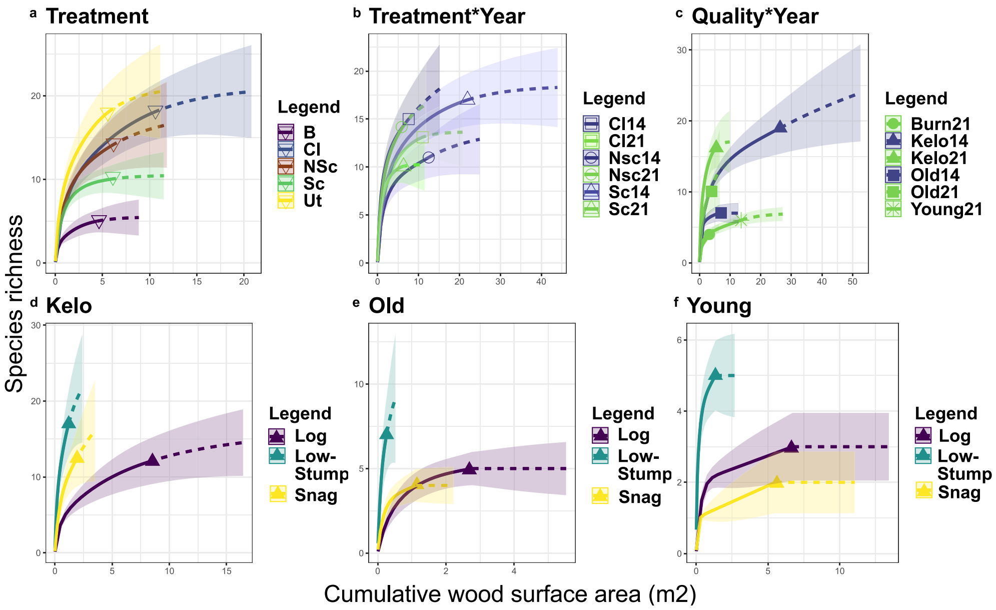

Fig. 1. Rarefaction curves displaying species richness of different treatments and deadwood types and qualities. Y-axis represents observed (full lines) and extrapolated (dashed) species richness. X-axis may differ between panels and represents the sample effort in cumulative wood surface area (m^2). Error bars show 95 % S.E. a) Treatment types sampled in 2021. b) Treatment types sampled both 2014 and 2021, untouched and burned not included since they were only sampled in 2021, legend indicates treatment * year of sampling. c) Deadwood qualities and sampling year. d) Kelo deadwood by type, snags, logs and low-stumps. e) Old deadwood by type, snags, logs and low-stumps. f) Young deadwood by type, snags, logs and low-stumps.
Abbreviations: B = burned plots. Cl = retention plots. Nsc = harvested plots with no site preparation. Sc = harvested plots with site preparation. Ut = untreated control.

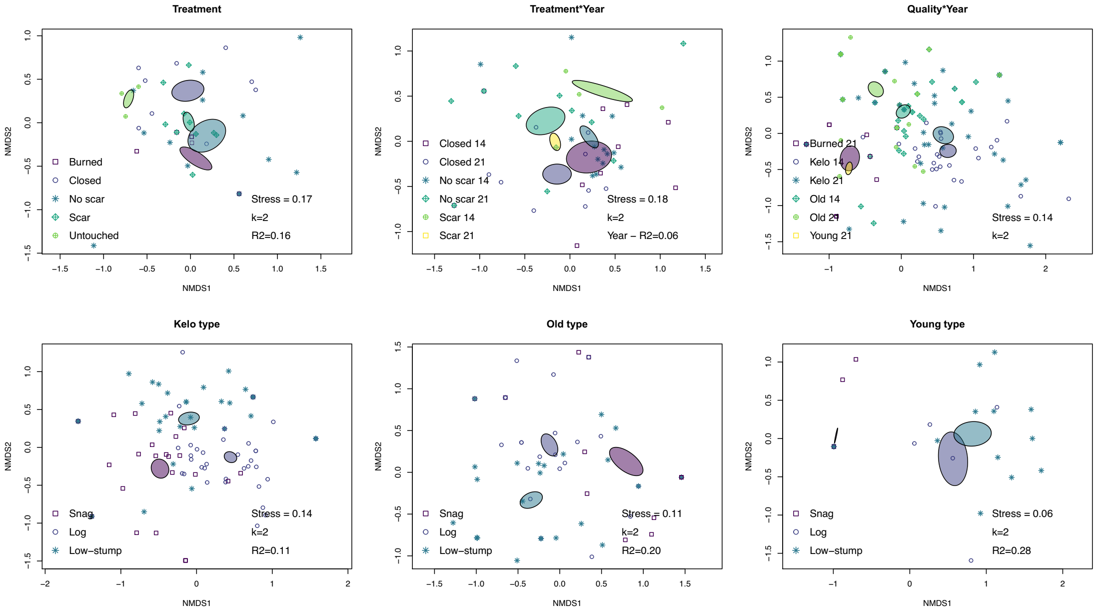

Fig. 2. NMDS plot visualising species assemblages between deadwood quality, type and treatments. Ellipsoids visualize the centroids with standard error, conf = 0.95.

on kelo wood substrates. Beta diversity was similar between kelo and old deadwood types within stands but lower on young and burned deadwood types (BETADISPER, $p \leq 0.001$), which would explain the low species richness on plot level and the high total richness of those qualities (Figs. 2 & A.1, Table A.2). Lichen assemblages were nested with clumped species loss among deadwood qualities (metacommunity analysis with positive coherence ($p \leq 0.001$), negative turnover ($p \leq 0.001$) and positive species clumping ($p \leq 0.001$)) (Fig. A.1). Indicator species analysis revealed the following species as indicators of kelo wood: *Hertelidea botryosa* (NT), *Cladonia parasitica* (NT), *Carbonicola anthracophila* (NT) and *Xylopsora friesii*. Notably *Elixia flexella* (NT), *Carbonicola myrmecina* (NT) and *Calicium denigratum* (NT) were only found on kelo wood but in such low numbers that they had no indicator value (Fig. A.1).

On plot level, there were only small differences in lichen species richness and abundance between snags and logs while low-stumps displayed a higher richness when controlled for the sampled deadwood amount (Table A.2) which was also seen rarefaction curves, revealing a higher potential total richness on low-stumps although low-stumps comprised a smaller sample (Fig. 1d, e, f). Eight years after treatment, low-stumps, snags, and logs displayed distinct species assemblages in all quality classes. Deadwood type explained 28 %, 20 % and 12 % of the differences in young, old- and kelo wood qualities, respectively ($p = 0.001$) (Fig. 2).

4. Discussion

Our data show that kelo wood is a key feature for deadwood-dependent lichen conservation in boreal pine forests and retained kelo wood after felling hosts unique lichen assemblages. However, the kelo-associated lichen assemblages face an extinction debt. The amount of kelo wood with lichen occurrence decreased by >80 % between 2014 and 2021 (Fig. 1). This is in large part caused by substrate destruction. However, this did not affect overall species richness (Fig. 1c) and composition (Fig. 2c) on kelo wood, which we, together with the greater beta diversity, interpret as a potential extinction debt. Our results also show that deadwood-dependent lichen species assemblages are seemingly resilient to low severity disturbance through changes in light exposure by retention felling, with similar diversity patterns in closed and open canopy plots. High severity disturbance, such as site preparation and high severity burning caused depauperate deadwood-dependent lichen species assemblages, as a direct effect of substrate destruction. Our results also clearly suggest that species assemblages of deadwood-dependent lichens confined to both old deadwood and newly generated deadwood are a subset of those occurring on kelo wood. This limits the potential of restoration and suggest that for lichens species specialised on kelo wood, conservation of existing substrate is of major importance. Thus, deadwood enrichment benefits common deadwood-dependent lichen species, but rare species risk extinction without future recruitment of kelo wood.

4.1. Disturbance emulation, forest management and lichen diversity

Our results are consistent with previous studies showing that lichen response to disturbances is highly dependent on severity and whether or not substrate legacies remain in disturbed forests (Johansson, 2008; Hämäläinen et al., 2014; Rudolphi et al., 2014). We found that increased sun-exposure from retention felling had no effect on the deadwood-dependent lichen diversity. However, our results clearly show that direct and highly destructive measures such as prescribed burning and site preparation diminished the lichen diversity through reductions in species richness and abundance. Disturbance and sun-exposure are natural elements in pine forests resulting in open forests rich in deadwood (Nilsson et al., 2002). Organisms associated with pine deadwood are therefore adapted to such conditions, explaining why a more open canopy due to felling does not influence lichens in our study. Eight years may also be a relatively short time to study indirect effects on persistence of deadwood-dependent lichens, meaning that the effect of such factors as indirect sun-exposure may be lagging behind. Thus, to reveal long-term responses to restoration monitoring over several decades is needed.

Heavy disturbance such as fire typically alters the species composition, favouring certain lichen species and disfavouring others (Lõhmus et al., 2018). That fire does not always have a positive effect on species has also been shown for other taxonomic groups such as bryophytes (Espinosa del Alba et al., 2021; Rudolphi et al., 2011). The significance of stand replacing fires has lately been questioned with studies showing that non-stand-replacing disturbance play a much larger role in pine dominated boreal forest than previously thought (Kuuluvainen and Aakala, 2011; Berglund and Kuuluvainen, 2021). Repeated low severity fires are also what creates kelo wood along with other important structures (Niemelä et al., 2002). Furthermore, without heavy landscape alteration, natural borders such as lakes, wetlands or other topographical factors would release certain areas from the most severe fires (Zackrisson, 1977; Hellberg et al., 2004). In our study, the changed species assemblage is mainly a result of species loss, with limited recolonization during the time span of 8 years. This is in contrast with, e. g., (Lõhmus et al., 2018) who showed partial recolonization after 9 years in pine dominated stands. However, they studied a wider range of lichens, while we only studied deadwood-dependent species. Species such as *Carbonicola anthracophila* and *C. myrmecina* grow exclusively on charred wood, indicating a fire dependency (Bendiksby and Timdal, 2013), although their colonisation could potentially take centuries (Esseen et al., 1992; Hämäläinen et al., 2014). Wildfires or prescribed burning is most likely a prerequisite for the establishment of such species. The destructive effect of fire shown in this study suggest that our burned stands are in the initial stages of recovery. During the coming decade we expect partial recolonizations of generated deadwood structures, as shown in Motiejūnaitė et al. (2014), Lõhmus et al. (2018) and Salo et al. (2019). Burned stands could therefore be subject to a colonisation credit, that may be fulfilled if studied over a longer time-span (Cristofoli et al., 2010; Jackson and Sax, 2010; Gjerde et al., 2012) and under the condition that source populations are available in the surrounding landscape (Hämäläinen et al., 2023). Lichens on intact kelo trees could potentially survive fires better than the kelo remnants in our study. Our results suggest that the extinction rate is greater than the colonisation rates, that kelo wood is not generated and that dispersal sources are disappearing. Repeated prescribed burning and conservation of existing deadwood is needed to reverse this trajectory, a slow process that may be possible due to the apparent longevity of lichens.

4.2. Deadwood type

Our results show that kelo wood supports a large proportion of the total lichen diversity and a number of red-listed, deadwood-dependent lichens are exclusively found on kelo wood which was also seen in Santaniello et al. (2017). In addition, we show that lichens on this substrate show a high beta diversity and that there is a nested pattern among deadwood qualities. This means that individual kelo wood substrates host unique species making them sensitive to anthropogenic and stochastic extinction (Hanski and Ovaskainen, 2002) and that deadwood lacking kelo-qualities only supports a subset of the deadwood-dependent lichen diversity found on kelo wood. Because we did not include natural forest in this study, we cannot evaluate if the higher beta diversity of kelo wood also occur in old-growth forests rich in natural structural elements or if this is a result of a continuous decrease of kelo wood in the landscape. Kelo qualities are formed during the trees' life and cannot be formed after tree death. Therefore, we do not expect lichen diversity on young deadwood to reach up to the levels of kelo wood as it is lacking the unique qualities found on kelo wood. Our findings show that for conservation of lichen diversity, it is of outmost importance to retain existing kelo wood, and that restoration through deadwood enrichment is not sufficient for conservation of deadwood-dependent lichens. It is possible that the remaining trees that survived the prescribed burning, as well as the partially bark-peeled trees will develop suitable kelo-characteristics in the future. However, this is a slow process that probably demands repeated restoration measures, such as repeated prescribed burnings and bark peelings. As the already rare kelo wood is not recreated in the managed forest landscape (nor in old-growth reserves), a bottleneck situation is evident for kelo-associated species. If kelo wood volumes continue to decrease in the landscape, kelo wood may symbolise an extinction debt yet to be paid.

In addition to deadwood quality, a variety of substrate types is needed to support lichen diversity, though some previous studies have investigated epiphytic lichens on deadwood while we investigated obligate lignicolous lichen species (Caruso and Rudolphi, 2009; Svensson et al., 2016). We show that different species assemblages on deadwood types (logs, snags and low-stumps) are maintained over time and that this pattern is evident across different deadwood qualities. This means that deadwood types complement each other and contribute to the full assemblage. On kelo wood, snags and low-stumps supported more red-listed species than logs. Snags may provide a favourable microclimate for lichens due to their sun-exposure and lack of ground contact, as is shown in Lõhmus and Lõhmus (2001) and Svensson et al. (2016). In addition, low-stumps have shown to support high number of species, probably because they provide both vertical and horizontal surfaces and support terricolous species (Caruso and Rudolphi, 2009). We observe that low-stumps support high species numbers also for lignicolous lichen species. Young snags supported the least species and seems to be of relatively low importance for lichens in the short-term, something that may change with increasing deadwood age (Hämäläinen et al., 2021). We only inventoried lichens up to 2 m in this study, which means that we might have missed species occurring higher up and on vertical surfaces higher up. This could possibly explain observed differences between low-stumps and snags, although previous studies have shown that 2 m is enough to capture a significant part of the overall species assemblage (Caruso and Thor, 2007; Svensson et al., 2014).

4.3. Conclusions

This study provides novel information on deadwood-dependent lichen ecology related to deadwood types and response to varying disturbances. We show that deadwood quality and type are important to explain diversity patterns of deadwood-dependent lichens. We also show that the creation of new deadwood has limited effect, in the short-term regardless of volume created.

In order to conserve a rich lichen diversity, a variety of substrates is needed although we can likely not substitute naturally developed deadwood with deadwood generated at restoration operations. Thus, the conservation of kelo wood is a prerequisite for deadwood-dependent lichen conservation. As many lichens are poor at dispersal (Hilmo and Såstad, 2001), and rich source populations are scarce and fragmented (Berglund and Jonsson, 2005), assisted colonisation through transplantation may be needed. Site preparation and high-severity prescribed burning is detrimental for deadwood-dependent lichens. Such actions should therefore be planned carefully to avoid the destruction of high-quality deadwood. We suggest that prescribed burning should be performed in close affinity to, but not within, hotspot areas for lichen diversity to avoid local extinctions. This could potentially also promote colonisation at the same time as it would improve conditions for future recruitment of kelo wood. Felling-induced light exposure seems to have small effects on deadwood-dependent lichens as long as deadwood legacies are maintained and continuously added. We can therefore conclude that direct (site preparation & burning) but not indirect effects (retention logging) of forest management result in a decrease in deadwood-dependent lichen diversity. Although studies show that landscape connectivity increase lichen species richness (see, e.g., Kärvemo et al. (2021)), studies that directly investigate dispersal and colonisation of deadwood-dependent lichens are scarce (but see Caruso et al. (2010)). Studies on both natural and assisted dispersal and colonisation are thus urgently needed (Mallen-Cooper and Cornwell, 2020). By all accounts, lichens on kelo wood face an extinction debt that is continuously realised through substrate destruction. There is no indication that current measures like tree retention and creation of high stumps constitute a colonisation credit, as these measures will not contribute to the generation of kelo wood. To halt this extinction debt there is urgent need to start creating new kelo wood by reoccurring prescribed fires or other methods such as bark-peeling to induce tar production.

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CRediT authorship contribution statement

All authors contributed to the conceptualization of the study. TL initiated the project and obtained funding, GT collected field data on lichens and ALE on deadwood. ALE performed the formal analysis and wrote the original draft. All authors contributed to reviewing and editing of the manuscript.

Declaration of competing interest

The authors have no competing interests to declare.

Data availability

Data will be made available on request.

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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).

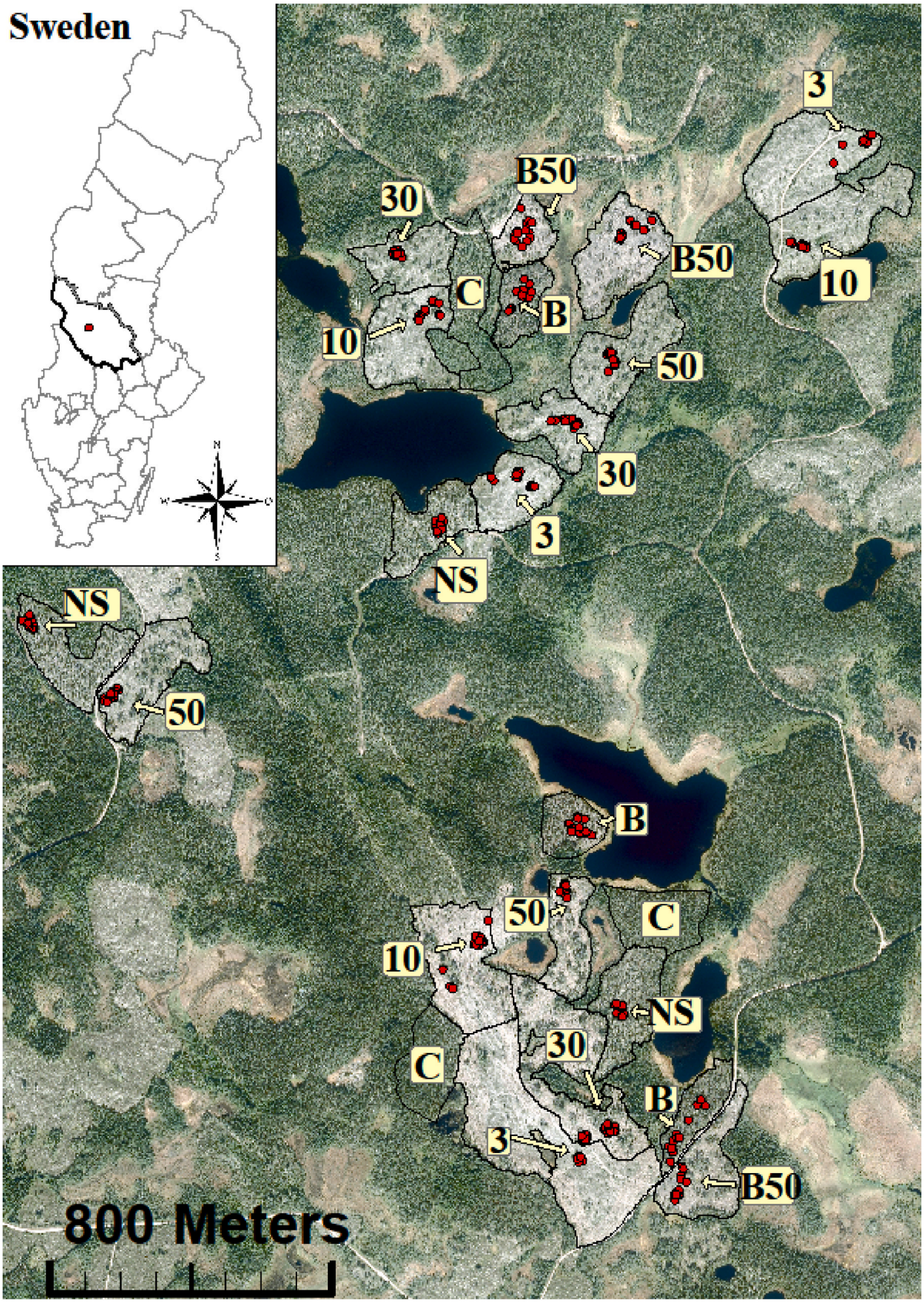

Fig. 1. Location of the study area in the inset map (red dot) in Dalarna (highlighted county border), central Sweden. Highlighted areas in map are stand borders and red dots are substrate positions. Orthophoto in the background from Lantmäteriet (2021).

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

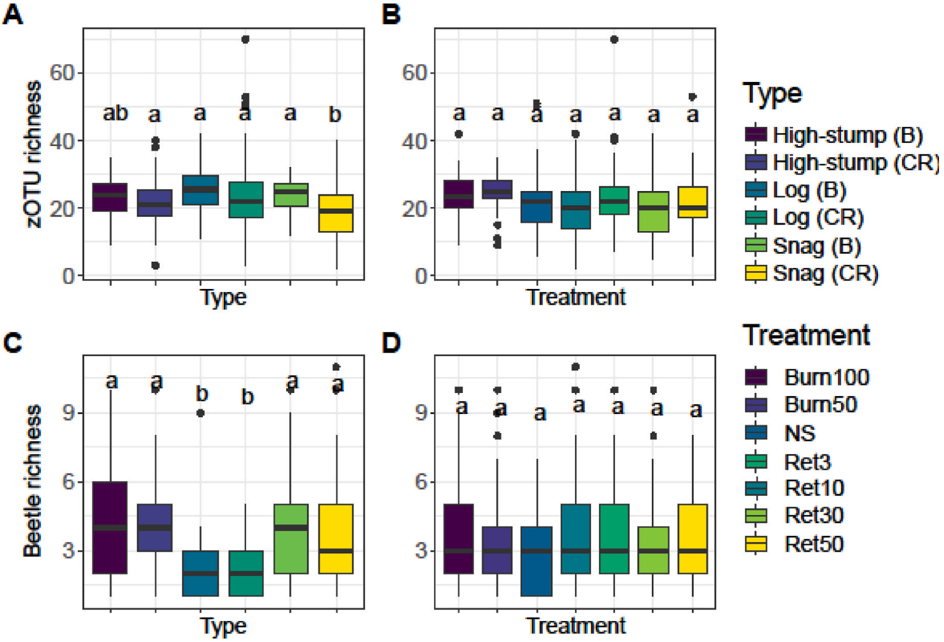

Fig. 2. Boxplots of species richness (α-diversity) between substrates of fungal zOTU's A) and beetles C) and between treatments of fungal zOTU's B) and beetles D). (B) = Trees died from prescribed burning. (CR) = Trees died from harvester head. High-stump = ~3m high-stumps. Snag = Standing dead trees. 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.

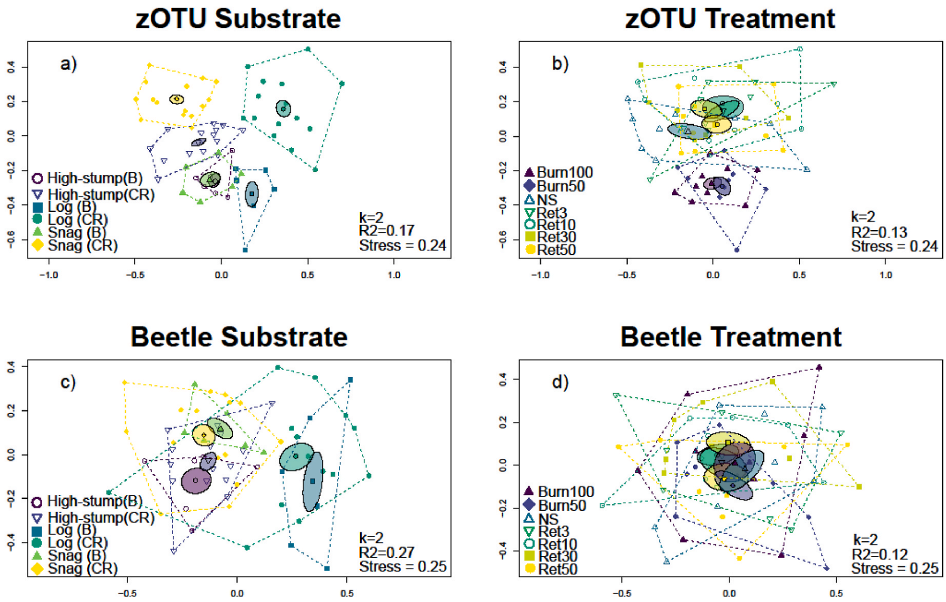

Fig. 3. NMDS plot visualising assemblage composition of fungi and beetles between deadwood and treatment types. Filled ellipsoids visualize the assemblage centroid, 95% CI, and dashed polygons the assemblage edges. Symbols highlighted with black at the centre of the ellipsoid visualize the symbols related 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).

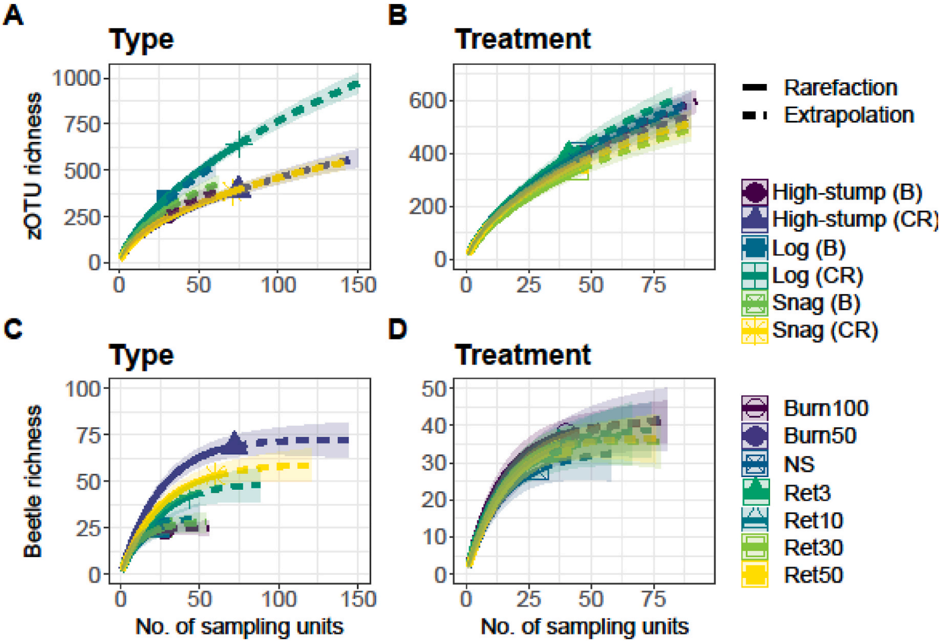

Fig. 4. Sample-based rarefaction curves displaying fungal zOTU and beetle richness in deadwood and treatment types. The Y-axis represents observed (full line) and extrapolated (dashed line) richness to twice the observed sampling effort. X-axis represents the number of sampling units, which is number 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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Data availability

Data will be made available on request.

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Habitat and species declines highlight the need for effective conservation and restoration efforts. In this thesis, I investigate decadal, multi-taxon responses of wood-associated species to ecological restoration of boreal forests. The results show that 1) restoration does not succeed in mimicking target conditions, 2) taxonomic groups (beetles, fungi and lichens) respond differently to different methods and 3) community responses are shaped by life history traits and phylogeny. The results are also discussed in relation to restoration theory.

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