Wood fungi in boreal forest patches of contrasting land use

- A long-term assessment of biodiversity

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Degree project in Biology, Master of Science • 30 credits
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Faculty of Natural Resources and Agricultural Sciences
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Uppsala 2024

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Credits:	30 credits
Level:	Master's level (A2E)
Course title:	Master's thesis in Biology, A2E - Ecology
Course code:	EX0953
Programme/education:	Master of Science
Course coordinating dept:	Department of Ecology
Place of publication:	Uppsala
Year of publication:	2024
Cover picture:	Mari Jönsson
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Keywords:	Wood fungi, saproxylic fungi, boreal forest, Picea abies, woodland key habitat (WKH), fungal conservation, fungal diversity, old-growth forest

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Abstract

Habitat loss and habitat degradation through land-use change continues to be the greatest challenge facing biodiversity worldwide. In Fennoscandia, boreal forests are becoming increasingly fragmented due to intensive management, and very little old-growth forest now remains in this area. Wood-inhabiting fungi have a key ecological role as decomposers of organic matter in forest ecosystems and it is important to ensure their continued survival and reverse the pattern of declining populations for wood fungal species of conservation concern. To create efficient conservation measures for wood fungi we need a better understanding of their ecology. Woodland Key Habitats (WKHs) are considered a cost-efficient conservation measure for many species groups. However, long-term changes in fungal diversity in WKHs are insufficiently studied, especially in relation to environmental factors and in comparison with natural old-growth forest fragments. It is crucial to bridge these knowledge gaps to understand if WKHs can function as an efficient tool for conservation of fungal diversity in managed forest landscapes. This study examines the long-term changes in abundance and species richness of wood fungi in boreal forest patches of contrasting land-use in northern Sweden, in relationship to four environmental variables, namely patch size, dead wood volume, basal area of living spruce and surrounding continuous cover forest. Data for this study was collected in year 2000, 2017 and 2022. WKH that are set-aside from management are compared with natural old-growth forest patches. I found that the abundance and species richness had decreased in the natural patches but remained relatively stable in the set-aside patches during the study period. Dead wood volume was the environmental variable most positively correlated with higher abundance and species richness in both natural and set-aside patches. The remaining environmental variables exhibited no clear trends in relation to the fungal diversity measures. My results can be utilized by forest managers and policy makes to guide conservation planning in favour of dead wood and fungal conservation.

Keywords: Wood fungi, saproxylic fungi, boreal forest, *Picea abies*, woodland key habitat (WKH), fungal conservation, fungal diversity, old-growth forest.

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1. Introduction

1.1 Fragmentation, habitat loss and species extinction

Habitat loss and degradation through land-use change continues to be the greatest challenge facing biodiversity worldwide (Newbold et al. 2016; IPBES 2019). Forest ecosystems are estimated to host 70 % of the Earth's terrestrial biodiversity (IUCN 2022), but much of this biodiversity is threatened by intensive forest management for forest resources, such as timber and pulp. For instance, extensive clearcutting forestry in Fennoscandia is known to cause habitat loss and habitat degradation in boreal forests (Esseen et al. 1997; Stokland & Larsson 2011; Svensson et al. 2019). Due to intensive management, forests are becoming increasingly fragmented and very little old-growth forest now remains in this area (Esseen et al. 1997; Linder & Östlund 1998; Rolstad et al. 2001; Kuuluvainen 2002; Stokland & Larsson 2011; Svensson & Dalen 2021). Furthermore, habitat fragmentation and loss of habitat leads to biodiversity decline (Haddad et al. 2015), and a large proportion of old-growth boreal forest species are now under threat of extinction (Tingstad et al. 2018; SLU Artdatabanken 2020). In Sweden, clear cutting forestry is considered a direct threat to at least 40 % (394 out of 999) of the red-listed boreal forest-dwelling species (Ottosson 2022), as well as being the second most important reason for red-listing of species (Eide 2020). Less than 10% of productive forests in Sweden are considered ‘old forest’ (>120-140 years old) today (Roberge et al. 2023), and only a few percent of the total forest area can be considered old-growth forest (Eriksson et al. 2023).

1.2 Conservation actions and Woodland Key Habitats

Much of Earths remaining old-growth forest and its associated biodiversity is now confined to small patches surrounded by matrices of managed forests (Haddad et al. 2015; Wintle et al. 2019). The state of biodiversity can be improved – or its decline at least slowed down – by a wide array of conservation actions, for instance protected areas, retention forestry and biodiversity-oriented management, according to a recent global synthesis by Langhammer et al. (2024). However, these conservation actions require radical upscaling to meet global diversity targets (Langhammer et al. 2024). Formally protected areas is probably the best-known conservation action and is considered the main policy tool for preventing biodiversity loss worldwide. However, additional measures, so-called ‘other effective area-based conservation measures’ (OECMs), are gaining recognition as tools highly important for reaching international goals (IUCN 2019; Maxwell et al. 2020), but also for local protection of biodiversity (Palfrey et al. 2022).

One type of OECM used in Sweden to preserve biodiversity in managed forest landscapes is to set aside areas of high conservation value, known as Woodland Key Habitats (hereafter WKHs), and exempt them from management. WKHs are small (median size 6.5 ha in Sweden) areas of semi-natural forest of high conservation value with a high, or likely high, occurrence of red-listed species (so called ‘biodiversity hotspots’) (Nitare & Norén 1992; Timonen et al. 2011b). The intention is for WKHs to host red-listed species and act as refuges and dispersal sources for the surrounding managed forest (Kärvemo et al. 2021). The concept of WKHs is used in the Fennoscandian (Sweden, Norway, Finland) and Baltic (Latvia, Estonia and Lithuania) countries and varies slightly between the countries, e.g. degree of formal protection and mean size of WKH patches (Timonen et al. 2010). In Sweden, WKHs are not formally protected and were appointed by the Swedish Forest Agency on private forest land for about 30 years (1990s to 2021), while larger companies were responsible for conducting their own inventories (Timonen et al. 2010; Skogsstyrelsen 2020). In addition, forest certifications such as Forest Stewardship Council (FSC) (FSC 2020) and the Programme for the Endorsement of Forest Certification (PEFC) (PEFC 2023) provide indirect protection for WKHs by excluding them from ordinary management practices and harvest in accordance with their certification commitments (Wikberg et al. 2009; Kyaschenko et al. 2022).

Many studies underline the importance of WKHs for preserving biodiversity (Timonen et al. 2011b; Gustafsson & Hannerz 2018; Häkkilä et al. 2021). However, further research is required to understand the impact of size and varying degrees of isolation over time on species occupying these habitats. A few individual studies add to the knowledge of the long-term conservation of biodiversity in WKHs (Jönsson et al. 2017; Dawson et al. 2020), as would national monitoring programs of WKHs. In Sweden, such monitoring has been carried out in slightly different forms during the past 20 years (Euler 2003; Wijk 2016; Skogsstyrelsen u.å.), but all has been discontinued or seen methodology changes before generating long-term results. Variables important for biodiversity in high conservation value forest fragments, such as WKHs, will be discussed in more detail below.

1.3 Patch ecology

In addition to WKHs in managed forest matrices, patches can also occur naturally as isolated forest fragments in a natural landscape, e.g. islands in a lake or a small, forested valley in an otherwise mountainous area. Both natural and anthropogenic patches often occur as small and isolated patches in the matrix and are thus affected by many aspects of the surrounding landscape, such as climate, connectivity, and disturbances.

Edge effect

The size and shape of both set-aside and natural patches can significantly impact their conservation effectiveness due to edge effects. Edge effects refer to gradient changes in microclimatic conditions that patch-edge areas experience, including variations in wind, light and moisture as well as disturbances from biotic factors (Hansen & DeFries 2007). These changes result in ecological differences between the patch edges and interiors, particularly when influenced by surrounding anthropogenically modified matrices of different qualities (Snäll & Jonsson 2001; Ruete et al. 2016). Small or narrow patches have a larger proportion of edge area relative to their size, resulting in less interior habitat than might be assumed based solely on size. Conversely, larger patches have a smaller proportion of edge area and thus include a larger amount of microclimatically more stable interior patch habitat. Studies suggests that negative long-term effects of clear-cutting could be mitigated by creating buffer zones with intact forests around set-asides when conducting harvest operations, effectively increasing the patch size (Ruete et al. 2017).

Species-area relationship and nestedness

Another factor related to patch size is the well-established species-area relationship, derived from the Island Biogeography theory, which suggests that larger areas can support a greater number of species compared to a smaller area of similar quality (Macarthur & Wilson 1967; Connor & McCoy 1979). Similarly, species in fragmented landscapes has been shown to exhibit nestedness, meaning that species found in smaller fragmented areas often are subsets of those found in larger areas (Berglund & Jonsson 2003). This nested pattern holds true for species in old-growth boreal forests as well (Berglund & Jonsson 2003). However, species are not evenly distributed across neither natural nor anthropogenically modified landscapes due to e.g. land-use and natural factors such as productivity and (micro)climatic variation, leading to hotspots of higher biodiversity (Fischer & Lindenmayer 2007; Howell et al. 2018; Svensson et al. 2019). Consequently, there are species not included in the low percentage of formally protected areas. Studies have shown that even small patches are important on a global scale to complement and preserve species that might be more scarce in larger, protected areas (Wintle et al. 2019). Furthermore, privately protected areas (PPAs), such as voluntary set-aside WKHs, contribute with 3.4% of protected land area globally (Palfrey et al. 2022).

Connectivity and meta population theory

Small and isolated anthropogenic old-growth forest patches are often poorly connected to other patches or areas of similar quality due to being located in a matrix with more ecological resistance in the landscape (Haddad et al. 2015; Howell et al. 2018; Svensson et al. 2019; Määttänen et al. 2022). Connectivity is also related to the amount of habitat available, on both local and landscape-scales. Larger patches generally tend to have higher connectivity due to a higher likelihood of adjacent habitat of suitable quality (Fahrig 2013). This provides more resources and habitat for a greater variety of species, thus supporting a higher biodiversity (Macarthur & Wilson 1967). Poor connectivity can, however, counteract generous amounts of habitat and result in low biodiversity nonetheless (Hanski 1994). Furthermore, poor connectivity causes dispersal difficulties for sessile organisms such as vascular plants and cryptogams (Norros et al. 2012; Auffret et al. 2017). Especially clear-cutting has been shown to create strong isolation between forest fragments in forest-dominated landscapes (Prugh et al. 2008; Paillet et al. 2010). Isolation affects meta-population dynamics by impeding (re)colonization of available patches of suitable habitat quality. This in turn, affects local meta-populations that are connected to each other by input (immigration) and output (emigration) of individuals and genetic exchange. Decreased connectivity between patches thus increases the risk of local extinctions, especially for smaller populations, leading to diminished local biodiversity (Hanski & Ovaskainen 2003).

As a result of above ecological factors affecting patches, the size, shape, and geographic location are important considerations when setting aside high conservation value patches in managed forest landscapes.

1.4 Dead wood and associated organisms

1.4.1 Dead wood

Another aspect of biodiversity decline in boreal forest is the lack of dead wood (Stokland & Larsson 2011; Jonsson et al. 2016). Approximately 50% of red-listed forest-living species in Sweden are dependent on dead wood (SLU Artdatabanken 2020) and are declining due to lack of dead wood amounts and qualities (Eide 2020). As a result of to intensive forestry, Fennoscandian countries has seen a dramatic decrease in dead wood in managed forests over the last century. For example, boreal forests in Finland has lost 90-98% of their dead wood content since the mid-1900s, when management intensified (Östlund et al. 1997; Siitonen 2001). According to numbers from the early 2010s, Fennoscandian managed forests now has about 5-7 m^3/ha dead wood (Hekkala et al. 2016). In Sweden, dead wood volumes has slowly increased since the 1990s due to biodiversity-oriented forest policies, and now amounts to 8.4 m^3/ha on an average for all unprotected managed forests (Nilsson et al. 2020; Kyaschenko et al. 2022). However, this is still far from the natural volumes of dead wood, which ranges between 60-90 m^3/ha in the south and 20 m^3/ha in the (less productive) north, for old-growth forests in Fennoscandia (Siitonen 2001; Stokland et al. 2012).

Moreover, clear-cutting of previously less intensively manages forests is still ongoing in the north of Sweden, possibly contributing to the continued low volumes of dead wood in that region (Kyaschenko et al. 2022). A threshold of 20-40 m^3/ha of dead wood is considered a minimum in boreal forests to meet habitat requirements for many wood-dependent organisms (Müller & Bütler 2010; Ylisirniö et al. 2016; Hekkala et al. 2023). In Sweden only about 7% of the total forest area meet that requirement (Nilsson et al. 2020), while most WKHs do (Kyaschenko et al. 2022).

1.4.2 Wood-inhabiting fungi

Dead wood supports biodiversity by contributing with nutrition, shelter and reproduction possibilities for wood-inhabiting organisms (Siitonen 2001; Seibold et al. 2015). Some organisms live their whole lives inside the dead wood while some only use it occasionally (Stokland et al. 2012). For instance, the amount of dead wood has shown to be positively correlated to species richness in polyporous fungi (Junninen & Komonen 2011). Lack of dead wood will thus have a considerable impact on such wood-dependent organisms. Besides volume, wood-dependent organisms will also be affected by the quality of the dead wood. They are evolutionary adapted to dead wood of different qualities and the heterogeneity of substrate in terms of tree species, size, moisture level and decay stage (Stokland et al. 2012) result in different accessibility for wood-dependent species (Sandström et al. 2019). Anthropogenically created dead wood, such as felled logs and stumps, holds different properties compared to naturally produced dead wood. Wood-inhabiting (saproxylic) fungi constitutes one group of organisms completely dependent on dead wood, and there is a significant difference in fungal community composition between natural and felled logs (Saine et al. 2024). Felled logs exhibit a relatively high fungal diversity, but natural logs tend to harbor more species-rich and varied fungal communities.

Wood-inhabiting fungi have a key ecological role as decomposers of organic matter in forest ecosystems, as pathogens of trees, or as food and habitat for other organisms (Berglund et al. 2005; Stokland et al. 2012; Birkemoe et al. 2018). Of the over 10 000 known species of fungi in Fennoscandia, about 2500 are wood fungi who, one way or another, are dependent on the constant presence of dead wood (Stenlid et al. 2008; Stokland & Larsson 2011). Red-listed wood fungi are often habitat specialist and require a particular quality or type of dead wood as substrate, including e.g. large logs or late stages of decomposition (Nordén et al. 2013). Intensive forest management practices greatly reduce the volume of particularly large logs, resulting in difficulties for specialist wood fungi to persist in managed boreal forests (Stokland & Larsson 2011). As a matter of fact, approximately every fifth assessed wood-inhabiting fungi in Sweden is red-listed (SLU Artdatabanken 2020) with clear-cutting forestry listed as the factor with most negative impact (Eide 2020).

1.4.3 Conservation of wood fungi

As key ecological components of forest ecosystems, it is important to ensure the continued survival of wood fungi and reverse the pattern of declining populations for species of conservation concern (Heilmann-Clausen et al. 2015; SLU Artdatabanken 2020). The negative effect of forestry, e.g. fragmentation and habitat loss, creates a trade-off between the growing demand for forest products and the conservation of species and biodiversity (Paillet et al. 2010; Eggers et al. 2022). There is currently much research (Tikkanen et al. 2006; Blattert et al. 2023; Triviño et al. 2023) and ongoing debate on how to combine the goals (see e.g. the Flora and Fauna Conference 2024 (SLU Artdatabanken 2024) and Eggers et al. (2022)). The identification and set-aside of WKHs is considered a cost-efficient measure (Wikberg et al. 2009), and conservation measures are, as previously stated, crucial to mitigate the negative effect of anthropogenic land-use such as clear-cutting forestry (Majdanová et al. 2023; Langhammer et al. 2024). However, to create more efficient conservation measures for wood-inhabiting fungi we need a better understanding of their ecology. Insofar, we know that increasing the amount of dead wood on stand-level and the amount of old forests on landscape-level is associated to higher biodiversity of fungi of conservation concern in WKHs (Kärvemo et al. 2021). Insufficiently studied aspects are, however, long-term changes in fungal diversity in WKHs in relation to factors such as patch size, dead wood amount, and the amount of old forest in the surrounding landscape. These factors are important since they affect e.g. connectivity, edge effect exposure and meta population development of wood fungi. Also, comparisons of long-term changes in fungal diversity in naturally fragmented old-growth forest fragments and WKHs are needed. It is crucial to bridge these knowledge gaps to understand if WKHs can function as efficient tools for biodiversity conservation in managed forest landscapes.

1.5 Study objective

In this study I aim to examine the long-term changes in abundance and species richness of reproducing polyporous wood fungi and four corticoid species, in boreal forest patches in northern Sweden. For a deeper understanding of temporal trends for species of conservation concern, I aim to also analyze changes in abundance and species richness for red-listed fungi. My study utilize data from 53 isolated semi-natural to natural forest patches dominated by Norway spruce (*Picea abies*). The studied fungi inhabit spruce logs and were inventoried over a time period of 22 years with samples from year 2000, 2017 and 2022. The difference in fungal abundance and species richness is investigated over time and compared between 27 natural old-growth forest patches located in a naturally fragmented landscape (Granlandet Nature Reserve) and 26 set-aside patches classified as WKHs, located in managed forest landscapes. I further aim to examine if and how the four environmental variables *patch size*, *dead wood volume*, *basal area of living spruce* and two measures of the amount of *continuous cover forest* in the surrounding landscape are related to the abundance and species richness within each patch type (natural patches and set-aside patches).

Hence, my thesis aims to answer if, and under which environmental conditions, small and isolated WKHs and natural forest patches can function as efficient long-term conservation areas for wood fungal biodiversity, as such knowledge is currently lacking (Timonen et al. 2011b; Häkkilä et al. 2021). The natural forest patches in Granlandet Nature Reserve (28 000 ha) have been the focal subject for many previous studies (Kruys & Jonsson 1997; Berglund & Jonsson 2001, 2003, 2005, 2008; Moen & Jonsson 2003; Berglund et al. 2009; Dawson et al. 2020; Soler Kinnerbäck 2023), upon which my thesis provide a more long-term perspective, being the most recent study of the plots, spanning over the longest time period. The study by Dawson et al. (2020) might be the one most closely related to mine, where long-time changes in fungal community traits and diversity were examined between 2000 and 2017. However, it did not include all polyporous species and not inventories from year 2022.

1.6 Research question(s):

The overall aim of my study was to evaluate the long-term effectiveness of set-aside WKHs as a conservation tool for wood fungi. More specifically I aim to answer the following research questions:

How does species richness and abundance of wood fungi develop over time in isolated boreal forest patches of contrasting land use?

Which environmental variables are most strongly related to the observed temporal changes in fungal diversity?

Does set-aside WKHs conserve wood fungi similar to natural forest patches, and can they be considered an effective area-based conservation measure?

I hypothesize that:

- Natural patches will maintain their species richness and abundance over time due to having reached an equilibrium of natural dynamics (Berglund & Jonsson 2005) and containing large amounts of structures benefitting species diversity (Brūmelis et al. 2011).

- Set-aside patches will increase in species richness and abundance over time as they develop towards a more natural state and gain higher conservation values with greater structural values (Jönsson et al. 2009) and converging fungal trait assemblages (Dawson et al. 2020). I expect them to thus fulfill their intended conservation purpose as valuable complementary focal areas for conservation in relation to formally protected areas.

- Patch size will have a clear effect on changes over time, especially the smaller set-aside patches, since smaller patches can be expected to host fewer species according to the species-area relationship. Set-aside patches are also subject to relatively abrupt changes in microclimatic conditions and edge effects caused by clear-cutting of adjacent forests, which has a pronounced effect on smaller patches (Ruete et al. 2017). I expect natural patches to be less affected by patch size since natural edges of small forest fragments towards mires and water seem to be less related to wood fungal biodiversity declines (Ruete et al. 2017).

- Dead wood volumes will increase over time in WKHs as these patches have been set-aside under free development for several decades. Increasing dead wood volumes is positively correlated to fungal diversity in both patch types, as indicated by several previous studies (Bader et al. 1995; Junninen & Komonen 2011; Purhonen 2018; Hekkala et al. 2023).

- Basal area of living spruce will have increased over time in set-aside patches for the same reason as dead wood volumes, and I expect it to have a moderate, positive effect on fungal biodiversity due to increased canopy cover and beneficial humid microclimatic conditions (Komonen et al. 2021).

- Surrounding continuous cover forest (CC-forest) will have decreased over the past 22 years due to extensive clear-cutting of northern Swedish forests (Roberge et al. 2023). I expect a higher amount of remaining CC-forest to be positively correlated to fungal biodiversity in both patch types, based on previous studies indicating that a greater amount of old forest in the surrounding landscape is beneficial for fungal diversity in patches by i.e. acting as potential population sources and improving the connectivity between patches (Berglund et al. 2011; Junninen & Komonen 2011; Majdanová et al. 2023).

2. Materials and methods

2.1 Study area

This study investigates the presence of wood fungi within boreal forest patches situated in the northern boreal zone of Norrbotten County, Sweden (figure 1a). Forest tree layers in all surveyed forests were dominated by Norway spruce (*Picea abies)* with bilberry (*Vaccinium myrtillus*) dominating the ground vegetation. Ground moisture levels ranged from moist to mesic and there were no visible indications of previous forest fires within the patches. A total of 53 forest patches were examined, of which 27 were categorized as 'natural patches' located within Granlandet Nature Reserve, and 26 were categorized as 'set-aside patches' (designated as WKH) more widely distributed around Norrbotten County (figure 1b) (Berglund & Jonsson 2003; Berglund et al. 2005).

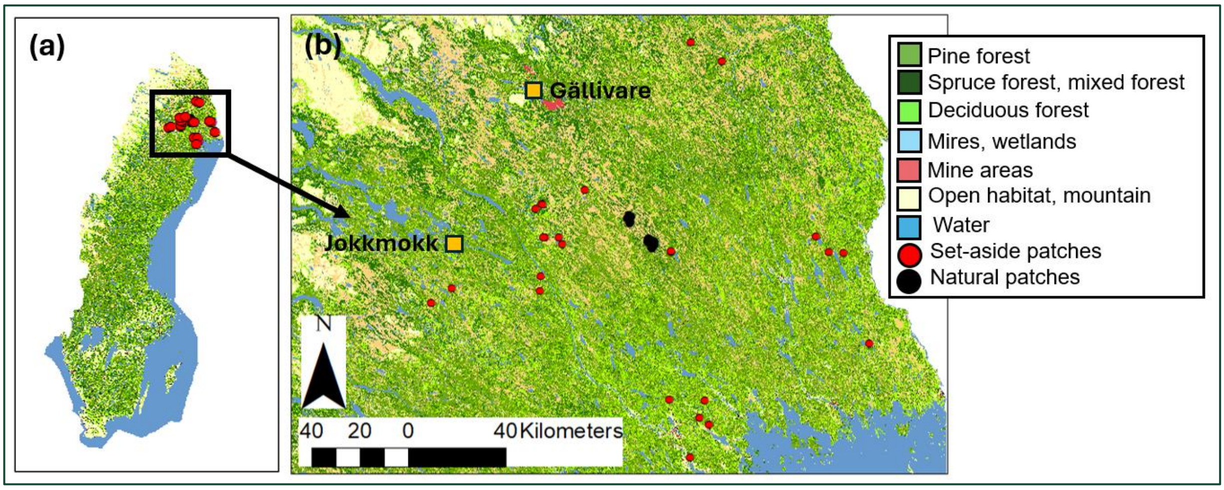


Figure 1 (a) Location of study area in northern Sweden and (b) layout of the 26 set-aside study forest patches (red circles) across Norrbotten County and 27 natural study forest patches (black circles) in Granlandet Nature Reserve (circles overlap due to resolution). Maps were derived from the Swedish National Land Cover Database (2018) provided by (Naturvårdsverket 2023). Figures created by Mari Jönsson, 2024.

2.1.1 Granlandet Nature Reserve:

The area is located approximately 70 km east of Jokkmokk in Norrbotten County, right on the Arctic Circle at latitude 66°. Granlandet is one of the largest Norway spruce forests reserves in Sweden, covering 28 000 ha. The 27 inventoried forest patches are naturally isolated “forest islands” situated in a Sphagnum wetland matrix. The natural patches consist of low moraine hills with spruce forest growing on top. Unaffected by human interventions and regenerated mainly by internal gap-phase dynamic they represent natural old-growth forest (Berglund & Jonsson 2005). The reserve contains approximately 1000 forest islands with a variety of shapes and sizes. The 27 natural patches were randomly selected to encompass patch sizes ranging from very small (0.2 ha) to medium (9.9 ha) size. The natural patches in Granlandet are considered to be in a natural state, having reached an equilibrium of natural dynamics due to long periods of undisturbed continuity (Berglund & Jonsson 2003; Berglund et al. 2005). The area is primarily protected for research purposes (Länsstyrelsen i Norrbottens län 1997) and serves as a reference landscape for this study. Henceforth, patches within it are referred to as “natural patches”.

2.1.2 Set-aside patches:

Anthropogenic patches in this study consisted of areas that are set-aside from forestry, henceforth called “set-aside” patches. They were randomly selected and were constituted by semi-natural forest fragments designated as Woodland Key Habitats (WKHs), situated in intensively managed forest matrices across Norrbotten County. WKH are small forest areas with high natural values and of high conservation concern due to presence of old-growth forest indicator species and/or structures (Gustafsson & Hannerz 2018; Kärvemo et al. 2021). The set-aside patches were exempt from management in the late 1990s but have historically been selectively cut to varying degrees at different points in time (Berglund & Jonsson 2005). The set-aside patches are situated throughout various locations surrounding Granlandet Nature Reserve, with distances between 5 and 120 km from Granlandet (figure 1b). Comparable to the natural patches, the randomly selected set-aside patches were dominated by Norway spruce trees, with bilberry (*Vaccinium myrtillus*) understory vegetation and of moist to mesic moraine ground conditions. The 26 inventoried sites varied in size from 0,1 – 6,7 ha, a range similar to that of natural patches.

2.2 Fungal inventories

In this Master’s Thesis, I compile data on abundance and species richness of wood fungi as well as four environmental factors, sourced from three different fungal inventories conducted in 2000, 2017, and 2022. I did not collect any additional data for this study. The initial inventory was conducted and published by Berglund and Jonsson (2003, 2005). The second one was conducted by Dawson et al. (2020), and the third by Soler Kinnerbäck (2023). Notably, abundance data was not collected for set-aside patches in the year 2000.

All fungal inventories used a consistent methodology across the three sampling periods. Dead wood and fungi were inventoried within circular sample plots with a 20 m radius, each plot permanently marked by a numbered central stick. Within the plots, all lying dead wood ≥1.3 m in length and with base diameter ≥10 cm originating within the plot, was measured and investigated for the presence of sporocarps (fruit bodies) of the focal species. Focal species included 52 polyporous fungi and four corticoid old-growth indicator species (Asterodon ferruginosus, Cystostereum murrai, Laurilia sulcata, and Phlebia centrifuga). Sporocarp investigation is the most common method used when surveying fungal occurrence (Stenlid et al. 2008). Sporocarps indicates high fungal fitness, as the presence of sporocarps suggests adequate resources for reproduction, spore production and dispersal (Moore et al. 2008). Sporocarp occurrence was recorded only once per log in all inventories, with the abundance measure representing the number of logs inhabited by a fungal species within the plot. DNA-based sampling techniques can also be used for this type of study, but while they produce more extensive fungal data per sample, they are constrained by limited coverage due to smaller sample volumes of dead wood. They are thus less effective in detecting rarer species, as discussed in Rajala et al. (2015) and Purhonen (2018). Furthermore, a study by Ovaskainen et al. (2013) supports that there is a high correlation between observation of sporocarps and mycelia detected by DNA-based techniques in Norway spruce wood, further supporting sporocarp investigation as a useful method for this study.

Data of all fungal species as well as environmental variables measured within each sample plot were compiled from all surveys. A complete list of all inventoried fungal species can be found in Appendix 1.

2.3 Environmental variables

The analysis included a total of six explanatory environmental variables, all considered important to fungal development within patches: (I) **patch type** (natural vs. set-aside), (II) **survey year** (2000, 2017 or 2022), (III) **patch size** (ha), (IV) mean **dead wood volume** per hectare (m^3/ha), (V) **basal area** of living Norway spruce trees (m^2/ha) and (VI) areal cover of **continuous cover forest** (km^2), within a 1 or 5 km radius around each plot.

Patch type and **survey year** were treated as categorical variables, with non-changing values.

Patch size varied from very small patches (<1 ha) to medium sized ones (5-10 ha), within each patch type. One circular sample plot (20 m radius) was located in the middle of each patch. Patch size can be viewed as a proxy for edge effect, since smaller patches tend to exhibit a higher edge-to-interior ratio, potentially making them more susceptible to edge effects caused by sun and wind exposure (Ruete et al. 2016). Consequently, small-patch sample plots will include a greater proportion of edge environment compared to plots centered within larger patches. This is however also connected to patch shape, which further affects the edge-to-interior ratio as an elongated patch will have proportionally less interior habitat compared to a circular patch of equal size. Since patch shape is not included in my study, the patch size measure has to be regarded as a simplified proxy for edge effect.

Dead wood volume was calculated from dead wood inventories of all logs within plots from each survey year. Detailed size measurements of lengths, base and top diameters were used along with the conic–paraboloid volume formula by Fraver et al. (2007) to obtain the volumes of dead wood per hectare.

Basal area of living spruce served as a proxy for canopy closure and microhabitat shading. The values were derived from relascope measurements taken from the center of each survey plot in 2000 and 2017. No new measurements were undertaken in 2022, but basal area variation within plots was assumed to be minimal over the five-year period and the basal area value was hence assumed to have remained consistent between 2017 and 2022.

Continuous cover forest (CC-forest) in the surrounding landscape served as a proxy for potential high-quality habitats and dispersal sources to the patches. This measure, alongside patch area, was computed for 2000 and 2017 using geospatial analyses and aerial imagery as outlined in Dawson et al. (2020). Similar to basal area, the 2017 data was also used for 2022.

2.4 Statistical analyses

All data analyses were performed in the program R, version 4.4.3. A complete list of packages used can be found in Appendix 1. Code used for the analyses included in Appendix 2.

Response variables

Response data included counts of abundance and species richness of all the focal species. To facilitate a more detailed investigation of species of conservation concern, the data was further divided into a subset including only red-listed species, resulting in four response variables: **Total Abundance** (TotAbun), **Red-listed Abundance** (RLAbun), **Total Species Richness** (TotSR) and **Red-listed Species Richness** (RLSR). However, both Total and Red-listed abundance were excluded from the analyses of set-aside patches due to missing abundance values from year 2000 for that patch type.

Data distribution

Response variable data was not normally distributed, but strongly skewed towards lower numbers for most of the variables (Appendix 1), as expected for count data. This pattern was consistent for the two patch types also when regarded separately. The exception was Total Species Richness where counts were somewhat closer to a normal distribution.

2.4.1 Diversity changes over time in natural and set-aside patches

Data was analyzed in two steps. Initially, I investigated temporal changes in abundance and species richness for all species as well as the subset of red-listed species, and the difference in diversity between natural and set-aside patches. This was achieved by developing four generalized linear models (GLMs) (package MASS and base R (Venables & Ripley 2002; R Core Team 2024)), one for each response variable. GLMs are useful for modelling count data, such as species occurrences. The error structure was assumed to be Poisson distributed, but since models exhibited overdispersion when fitted with Poisson, I used negative binomial distribution instead, with an associated log-link function (code in Appendix 2). In these models I included two categorical explanatory variables, namely patch type (natural or set-aside) and survey year (2000, 2017 or 2022). Furthermore, I analyzed diversity changes in natural and set-aside patches separately to confirm the difference between the two patch types, with values pooled across all three survey years and with patch type as the only explanatory variable.

2.4.2 Relationships with environmental variables within patch types

In the second step I investigated if and how the temporal changes observed in the first step related to variation in the explanatory environmental variables, for natural and set-aside patches separately. I constructed GLMs with all response variables available for each patch type, resulting in four models for natural patches and two models for set-aside patches, due to missing abundance values for the latter one. Similar to the previous GLMs, these models were fitted with a Poisson distribution, or a negative binomial regression in cases of overdispersion (TotAbun and RLAbun). The models were compared in effect size plots (package dotwhisker (Solt & Hu 2024)).

The models included five of the above-mentioned explanatory environmental variables: (I) survey year (2000, 2017 or 2022), (II) patch size (ha), (III) dead wood volume (m^3/ha), (IV) basal area (BA) of living spruce (m^2/ha), and (V) surrounding continuous cover forest (CC-forest) within 1 or 5 km from each plot (km^2). When examined for correlations (package GGally (Schloerke et al. 2024)) most explanatory variables were not highly correlated (Pearsons correlation coefficient <0.7, Appendix 1). As expected, the two measures of surrounding CC-forest (1 and 5 km) exhibited higher correlation (r >0.7). Both measures were therefor tested in separate models to avoid collinearity and inaccurate attribution of effect. To get comparable estimates of effect sizes, the three variables dead wood volume, basal area of living spruce and CC-forest (1 and 5 km) were scaled before analysis.

2.4.3 Changes in environmental variables

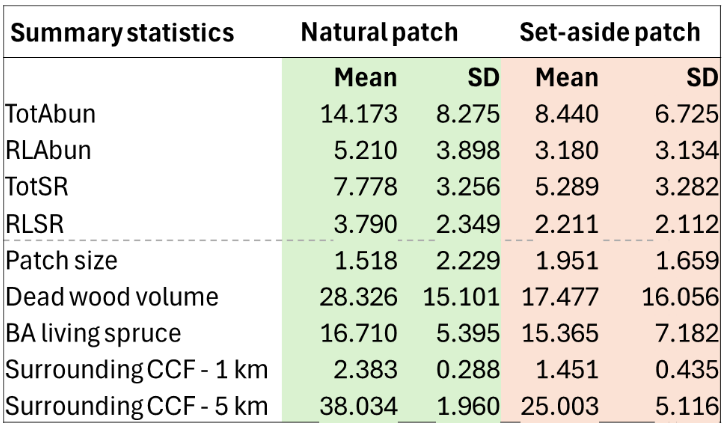
The environmental variables were tested individually to distinguish any temporal changes potentially affecting the diversity measures. I created linear regression models (base R (R Core Team 2024)) to test for long-term changes in dead wood volume, basal area of living spruce, and CC-forest (1 and 5 km). Patch size remained constant throughout the study period and did not require further investigation. To determine if these variables had changed over time, I used survey year (2000, 2017 or 2022) as a categorical explanatory variable in the models. Values for 2022 were assumed to have remained stable and were thus replicates of 2017.

3. Results

3.1 Descriptive statistics

A total of 1564 occurrences of 56 species of wood fungi were observed in the study, of which 25 species (45%) were red-listed. Mean and standard deviation (SD) of the studied diversity measurements and environmental variables are summarized for each patch type, pooled across all three years in table 1.

Table 1 Summary statistics of the diversity measures (total abundance, red-listed abundance, total species richness and red-listed species richness) and four studied environmental variables for natural and set-aside patches. Values pooled across all three years (2000, 2017 and 2022).



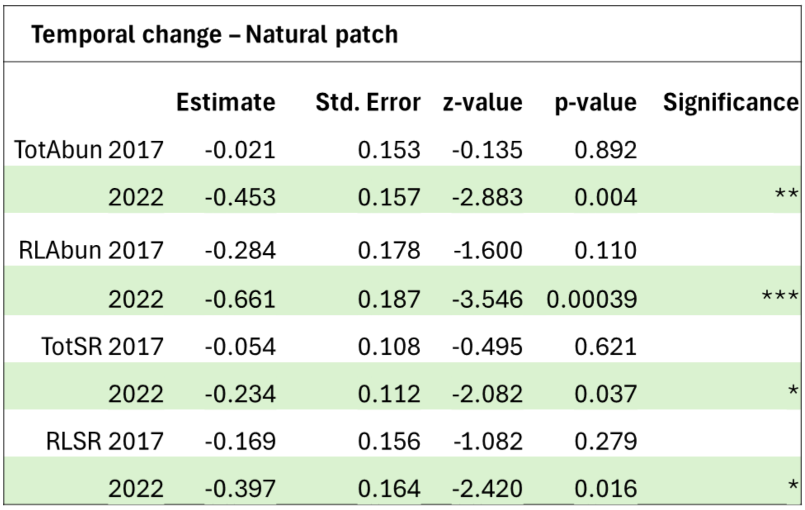
Summary statistics	**Natural patch**		**Set-aside patch**	
	Mean	**SD**	**Mean**	**SD**
TotAbun	14.173	8.275	8.440	6.725
RLAbun	5.210	3.898	3.180	3.134
TotSR	7.778	3.256	5.289	3.282
RLSR	3.790	2.349	2.211	2.112
Patch size	1.518	2.229	1.951	1.659
Dead wood volume	28.326	15.101	17.477	16.056
BA living spruce	16.710	5.395	15.365	7.182
Surrounding CCF - 1 km	2.383	0.288	1.451	0.435
Surrounding CCF - 5 km	38.034	1.960	25.003	5.116

3.2 Diversity changes over time in natural and set-aside patches

3.2.1 Temporal change

In natural patches, both abundance and species richness of total species, as well as red-listed species, decreased between the years 2000 and 2022 (figure 2, table 2). The earlier time period between years 2000 and 2017 showed a negative but not significant trend for natural patches. Species richness in set-aside patches remained stable over time, both total and red-listed species (figure 2, table 3). Abundance data was not available from year 2000 in set-aside patches and therefore not analyzed.

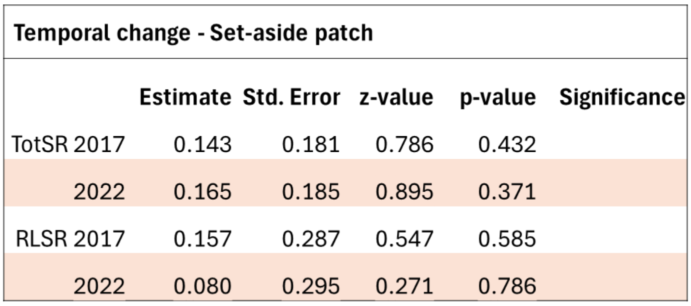
Table 2 Temporal diversity changes in natural patches. Table presents regression results from 4 different GLMs, one for each response variable; total abundance, red-listed abundance, total species richness and red-listed species richness. Year 2000 serves as the reference to year 2017 and 2022. All measures of diversity are decreasing over time, but only changes in year 2022 are significant (p<0.05).
*Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.'*



Temporal change – Natural patch

	Estimate	Std. Error	z-value	p-value	Significance
TotAbun 2017	-0.021	0.153	-0.135	0.892	
2022	-0.453	0.157	-2.883	0.004	**
RLAbun 2017	-0.284	0.178	-1.600	0.110	
2022	-0.661	0.187	-3.546	0.00039	***
TotSR 2017	-0.054	0.108	-0.495	0.621	
2022	-0.234	0.112	-2.082	0.037	*
RLSR 2017	-0.169	0.156	-1.082	0.279	
2022	-0.397	0.164	-2.420	0.016	*

Table 3 Temporal diversity changes in set-aside patches. Table presents regression results from 2 different GLMs, one for each response variable; total species richness and red-listed species richness (abundance was not analysed for set-aside patches due to missing data). Year 2000 serves as the reference to year 2017 and 2022. All measures of diversity are decreasing over time, but only changes in year 2022 are significant (p<0.05).
*Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.'*



Temporal change - Set-aside patch

	Estimate	Std. Error	z-value	p-value	Significance
TotSR 2017	0.143	0.181	0.786	0.432	
2022	0.165	0.185	0.895	0.371	
RLSR 2017	0.157	0.287	0.547	0.585	
2022	0.080	0.295	0.271	0.786	

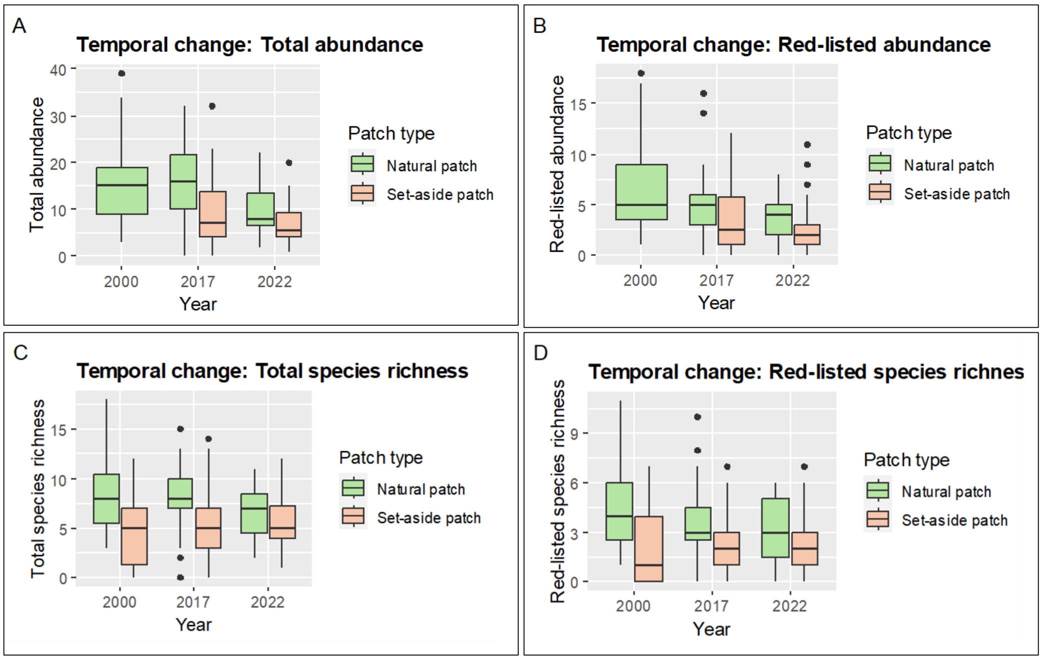


Figure 2 Boxplots describing temporal changes in (A) Total abundance, (B) Red-listed abundance, (C) Total species richness and (D) Red-listed species richness in natural and set-aside patches. Boxes represent the second and third quartiles with a line marking the median. Error bars show minimum and maximum values, with outliers marked as dots. The changes are significantly different ($p<0.05$) from the reference (year 2000) only for year 2022 in natural patches, where all diversity measures decreased. Species richness was stable over time in set-aside patches (abundance was not analysed for set-aside patches due to missing data for year 2000). Model output values described in table 2 and 3.

3.2.2 Patch type difference

The abundance and species richness of both total and red-listed species were significantly higher in natural patches compared to set-aside patches (table 4). The greatest difference was found in red-listed species richness.

Table 4 Regression results from 4 different GLMs, one for each response variable; total abundance, red-listed abundance, total species richness and red-listed species richness, describing how much set-aside patches differ from the natural patches reference. Values pooled across all three years (2000, 2017 and 2022). Negative estimate means lower species diversity in set-aside patches compared to natural patches. All measures of diversity are significantly ($p<0.05$) lower in set-aside patches compared to natural patches.
*Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.'*

Set-aside patches in relation to natural patches

	Estimate	Std. Error	z-value	p-value	Significance
TotAbun	-0.433	0.129	-3.363	0.0008	***
RLAbun	-0.318	0.158	-2.017	0.0437	*
TotSR	-0.385	0.083	-4.641	3.47E-06	***
RLSR	-0.537	0.124	-4.339	1.43E-05	***

3.3 Relationships with environmental variables within patch types

In natural patches, the abundance and species richness of total as well as red-listed species increased significantly with dead wood volume (table 5A, figure 3). The effect size for dead wood volume was largest for the total abundance of species in natural patches, compared to the other three diversity measurements. Dead wood volume was also significantly positively related to the species richness of both total and red-listed species in set-aside patches (table 5B, figure 4). The effect size for dead wood was larger for the red-listed species richness than total species richness in set-aside patches.

The abundance and richness of wood fungi also generally increased with basal area of living spruce in natural patches, whilst the opposite pattern was observed for richness in set-aside patches. The effect size of basal area was strongest for red-listed species in both patch types, although in diverging directions.

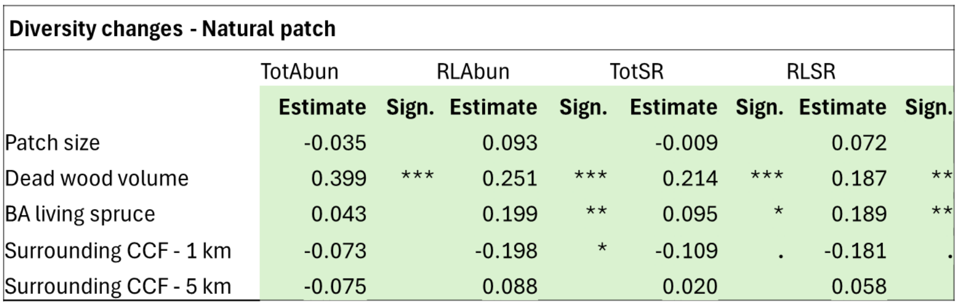
Other than dead wood volume and basal area of living spruce, only vague, non-significant relationships between environmental variables the abundance and richness of wood fungi could be distinguished within the two patch types. Increasing area of surrounding CC-forest (1 km) was weakly significant, and negatively related to red-listed species abundance in natural patches, albeit with smaller effect size than that of dead wood volume and the temporal changes (year 2022) (figure 3).

As described in materials and methods, section 2.4.2, the two measurements of surrounding CC-forest (1 and 5 km) were tested in separate models due to their high correlation. However, since no substantial difference in results were found when tested individually, both measures were included in the model outputs plotted in figures 3 and 4.

Table 5 Regression results from 4 + 2 different GLMs, one for each response variable; total abundance, red-listed abundance, total species richness and red-listed species richness, for (A) natural patches and (B) set-aside patches (abundance was not analysed for set-aside patches due to missing data). Values pooled across all three years (2000, 2017 and 2022). The results describe relationships between environmental variables and diversity measures. The most prominent variable was dead wood volume that exhibited a positive, significant (p<0.05) relationship to all measures of diversity, in both set-aside and natural patches. Effect sizes are visualized in figure 3 and 4.

*Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.'*

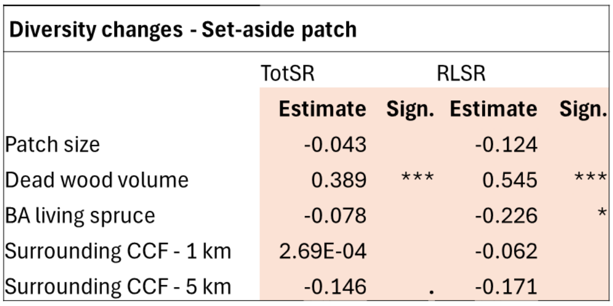
A



Diversity changes - Natural patch

	TotAbun		RLAbun		TotSR		RLSR	
	Estimate	**Sign.**	**Estimate**	**Sign.**	**Estimate**	**Sign.**	**Estimate**	**Sign.**
Patch size	-0.035		0.093		-0.009		0.072	
Dead wood volume	0.399	***	0.251	***	0.214	***	0.187	**
BA living spruce	0.043		0.199	**	0.095	*	0.189	**
Surrounding CCF - 1 km	-0.073		-0.198	*	-0.109	.	-0.181	.
Surrounding CCF - 5 km	-0.075		0.088		0.020		0.058	

B



Diversity changes - Set-aside patch

	TotSR		RLSR	
	Estimate	**Sign.**	**Estimate**	**Sign.**
Patch size	-0.043		-0.124	
Dead wood volume	0.389	***	0.545	***
BA living spruce	-0.078		-0.226	*
Surrounding CCF - 1 km	2.69E-04		-0.062	
Surrounding CCF - 5 km	-0.146	.	-0.171	

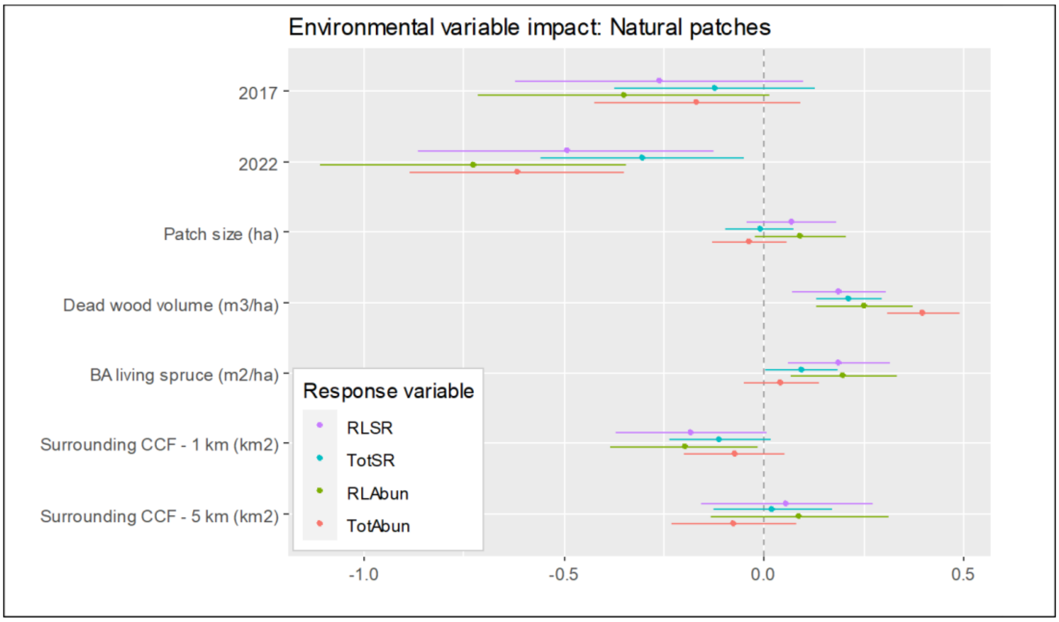


Figure 3 Comparison of model estimates of the relationship between environmental variables and diversity measures (total abundance, red-listed abundance, total species richness and red-listed species richness) in natural patches. The x-axis represents coefficient estimates, values detailed in table 5A. The dashed vertical line (zero) represents no difference, meaning that if the error bars (95% confidence interval) intersect the line, the effect is not significant. Effect sizes on the right side of zero mean that the environmental variable has a positive effect on the analysed diversity measure. Environmental variables are scaled for comparison (by calculating the mean and standard deviation of the variable and then subtracting the mean and dividing it by the standard deviation). Survey years are categorical measures that cannot be scaled.
Dead wood volume exhibits the most significant ($p<0.05$) positive relationship with all measures of species diversity.

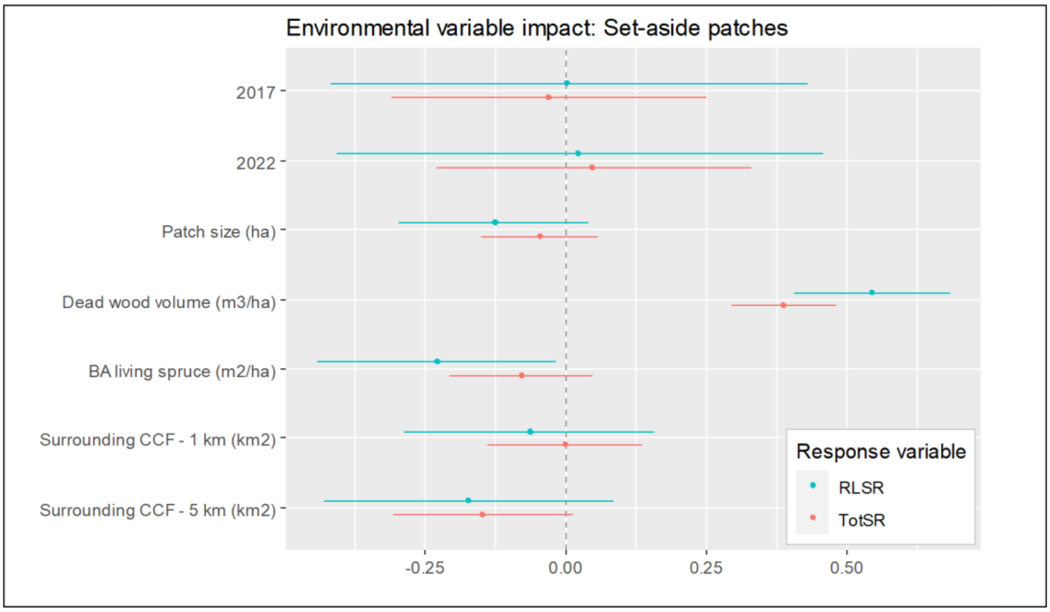


Figure 4 Comparison of model estimates of the relationship between environmental variables and diversity measures (total species richness and red-listed species richness) in set-aside patches. The x-axis represents coefficient estimates, values detailed in table 5B. The dashed vertical line (zero)

represents no difference, meaning that if the error bars (95% confidence interval) intersect the line, the effect is not significant. Effect sizes on the right side of zero mean that the environmental variable has a positive effect on the analysed diversity measure. Environmental variables are scaled for comparison (by calculating the mean and standard deviation of the variable and then subtracting the mean and dividing it by the standard deviation). Survey years are categorical measures that cannot be scaled.
Dead wood volume exhibits the most significant ($p<0.05$) positive relationship with all measures of species diversity.

3.4 Changes in environmental variables

Of the five environmental variables included in the study, four could be investigated for temporal change, namely dead wood volume, BA living spruce and surrounding continuous cover forest (1 + 5 km). Dead wood exhibited no significant change in volume over time in neither natural (figure 5A) nor set-aside patches (figure 6A). BA spruce increased slightly but significantly in both natural (15 to 17 m2/ha, figure 5B) and set-aside patches (11 to 16 m2/ha, figure 6B). Both measures of surrounding forest decreased over time in both patch types (figures 5A+B and 6A+B). The decrease was weak and not significant on a 1 km-scale, but strong and significant on a 5 km-scale.

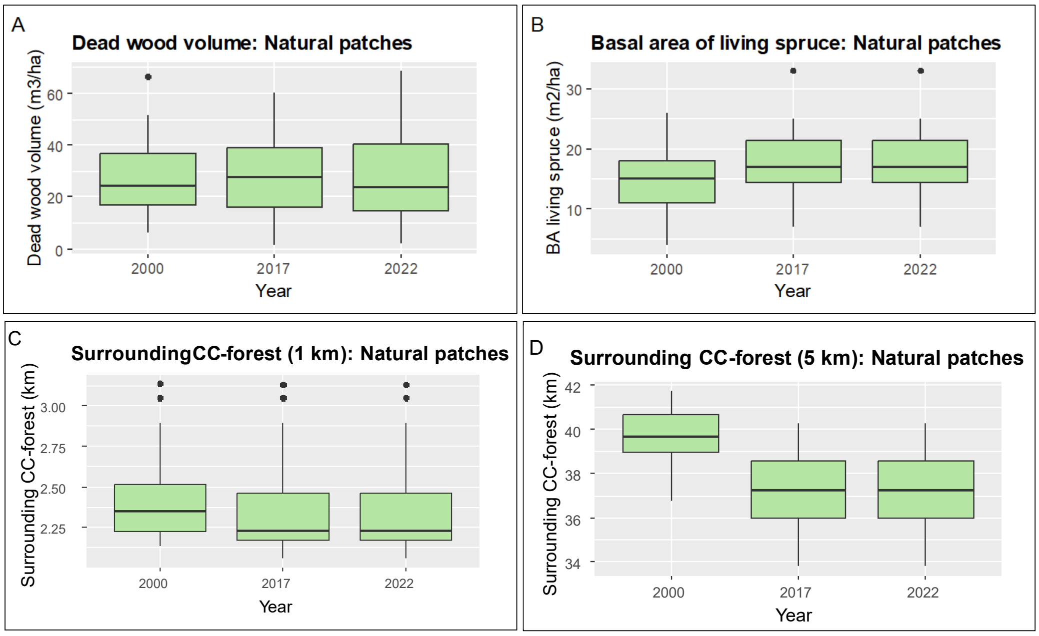


Figure 5 Boxplots describing temporal changes in environmental variables in natural patches. (A) Dead wood volume, (B) basal area of living spruce, (C) surrounding continuous cover-forest 1 km, (D) surrounding continuous cover-forest 5 km. Boxes represent the second and third quartiles with a line marking the median. Error bars show minimum and maximum values, with outliers marked as dots. BA living spruce exhibited a significant ($p<0.05$) increase and surrounding continuous cover-forest (5 km) a significant decrease between year 2000 and 2017. No other changes were significant (linear model estimates can be found in Appendix 1). Note that data from year 2022 only was available for dead wood volume. Values for the remaining three variables were assumed to have remained stable between 2017 and 2022.

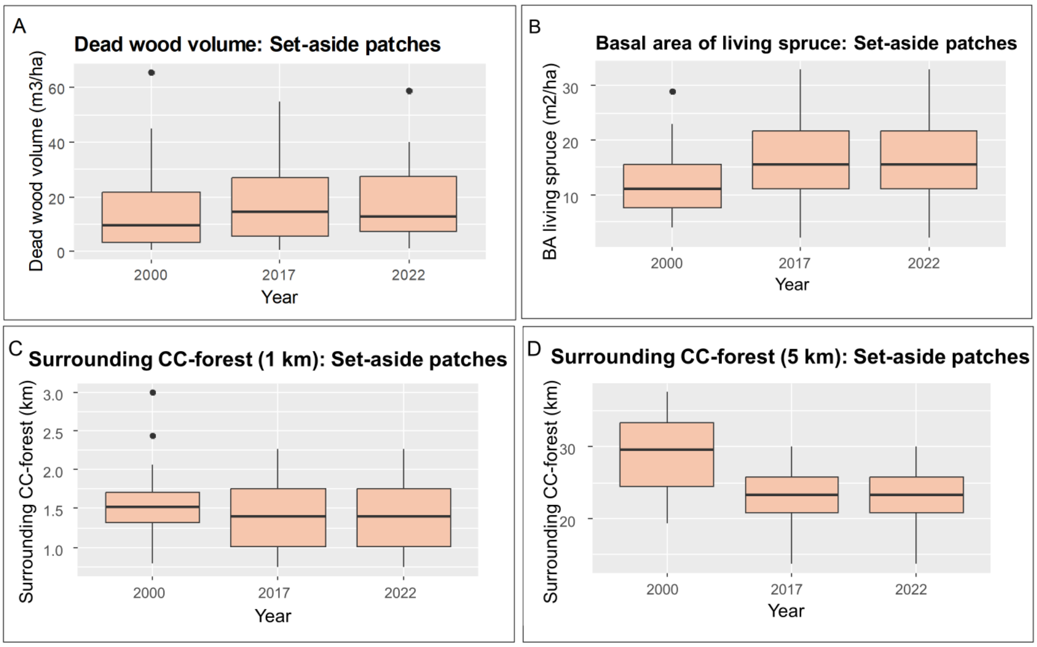


Figure 6 Boxplots describing temporal changes in environmental variables in set-aside patches. (A) Dead wood volume, (B) basal area of living spruce, (C) surrounding continuous cover-forest 1 km, (D) surrounding continuous cover-forest 5 km. Boxes represent the second and third quartiles with a line marking the median. Error bars show minimum and maximum values, with outliers marked as dots. BA living spruce exhibited a significant ($p<0.05$) increase and surrounding continuous cover-forest (5 km) a significant decrease between year 2000 and 2017. No other changes were significant (linear model estimates can be found in Appendix 1). Note that data from year 2022 only was available for dead wood volume. Values for the remaining three variables were assumed to have remained stable between 2017 and 2022.

4. Discussion

4.1 Fungal diversity

The overall results showed that the abundance and species richness had decreased in natural patches but remained relatively stable in set-aside patches during the study period. The results thus contradict my hypotheses for both patch types, that the abundance and species richness in natural patches would remain stable as a result of having reached an equilibrium of natural dynamics, while the abundance and species richness in set-aside patches would increase over time, along with increasing conservation values. The result that natural patches in a large nature reserve are performing below expectations is worth further investigation. My study cannot clearly explain these findings, since none of the four environmental variables I examined showed any significant change that corresponded with the changes observed in abundance and richness. My results are in line with the results of Dawson et al. (2020) that are based on partially overlapping data from the same patches in years 2000 and 2017. They did not find any clear relationships between individual species occurrences and various environmental variables in their study either, except for in dead wood volume.

Rising temperatures and increasing precipitation due to global warming (IPCC 2023) has a large impact on boreal forest ecosystems (UNECE 2023) and could possibly have affected the richness of fruiting fungi in the patches during the 22 years of ongoing study. Fruit body production of wood fungi is influenced by temperature and moisture (Moore et al. 2008; Sakamoto 2018) and changes in micro and macro climate on both yearly and long-term basis can thus impact the perceived fungal species diversity, since fruiting can exhibit a lot of variation between years. Particularly when the sample is relatively small, as in this study of three years, one year of climatic conditions favorable or unfavorable for wood fungi could have a quite large impact on the results. To avoid the issue of sample errors due to between-year variation, Berglund et al. (2005) suggests that wood fungal studies, if possible, should be based on species with perennial fruit bodies, based on an 8-year study of wood fungal diversity in Granlandet Nature Reserve. Perennials are more robust and exhibit less variation than annual species. For example, the spruce specialist polypore species *Phellinus nigrolimitatus* has a tough texture and low mean annual mortality rates (Jönsson et al. 2008), making it suitable for long-term surveillance of diversity trends. In my study, proportions of annual and perennial species were relatively stable between sample years and could thus not explain the temporal diversity changes. Both annual and perennial species decreased only slightly in natural patches in 2022, just like the total species count, with annual species exhibiting some more variation than perennial. Trends in set-aside patches were similar, but with less variation. Further studies of individual species development and natural dynamics (i.e. colonizations and extinctions) in natural patches in Granlandet could add to the still limited knowledge on wood fungal survival in natural old-growth forest fragments, which requires further attention.

In terms of set-aside patches, the results indicate no clear temporal change in abundance and species richness, and they were less diverse than natural patches. Relatively stable dead wood volumes could be one explanation for the stable species diversity levels, but I had expected the set-aside patches to exhibit greater temporal changes due their exposure to edge effects, fragmentation, and habitat loss in the surrounding landscape. The set-aside WKH patches did, however, fulfill their purpose in conserving species diversity and red-listed species over time.

My results can be utilized by forest managers and policy makes to guide conservation planning in favor of dead wood and fungal conservation, as has been requested by others (Brondizio et al. 2019). Moreover, these results carry important value for evaluating the effectiveness of so-called ‘other effective area-based conservation measures’ (OECM) for reaching international goals (IUCN 2019; Maxwell et al. 2020).

I discuss the relationship between fungal diversity and the studied environmental variables in more detail below.

4.2 Environmental variables

4.2.1 Dead wood volume

Dead wood volume was highly positively correlated with abundance and species richness in both natural and set-aside patches, consistent with the vast majority of previous studies (Bader et al. 1995; Junninen & Komonen 2011; Lassauce et al. 2011; Ylisirniö et al. 2016; Purhonen 2018; Tomao et al. 2020), as well as the most recent study of the overlapping data from Granlandet Nature Reserve (Dawson et al. 2020). Similar to my study, their study found dead wood volume to have the highest explanatory power of individual species occurrences. Consequently, one would expect the changes in the volume of dead wood to correspond to the diversity patterns found in the study plots. Indeed, the richness in set-aside patches did follow the patterns of dead wood volume, with no significant temporal changes in neither species richness (abundance was not examined) nor dead wood. This result indicates stable levels of both dead wood volumes and species richness in set-aside patches over the last decades. However, based on available research (Timonen et al. 2011b; Jönsson et al. 2017; Gustafsson & Hannerz 2018; Dawson et al.

2020) I had assumed that 30 years of non-management would have contributed to increasing volumes of dead wood in set-aside patches.

The natural patches, contrastingly, are surrounded by a matrix of wetland and protected forests, assumed to having reached an equilibrium state of natural dynamics, unaffected by anthropogenic forest disturbances (Berglund & Jonsson 2005). Hence, I expected both species diversity and environmental variables to be relatively stable in this environment. Dead wood volumes were stable over time, as expected, yet abundance and species richness decreased.

Changes in wood fungal richness may also be related to the quality of the dead wood. Since dead wood volume did not correspond to and thus did not seem to explain the diversity decrease, I briefly investigated stages of decomposition of logs (early, mid, late decay classes, see Berglund & Jonsson (2001) for details) in each examined plot, to see if I could detect any patterns worth further exploration. I found a slight increase in the number of logs in early stages of decomposition along with a subsequent decrease in late stages in 2022. Otherwise, proportions remained relatively stable over time and between patch types (Appendix 1), indicating a temporal balance in the decomposition-stage distribution, with balance between creation and decomposition of dead wood. Evidently, temporal changes in the representation of decomposition stages did not seem to be the driver of the temporal change in diversity. Worth noting, however, is the risk of greater detection errors among surveyors when locating and inventorying logs in late decomposition stages. Such logs are often more sunken into the ground or covered with moss and thus more difficult to detect, measure and inventory (personal communication, Mari Jönsson, 2024). They can be a potential source of bias between surveyors and years, requiring calibration between survey years and sites.

Furthermore, volumes of dead wood were higher in the natural patches of old-growth forest, compared to lower volumes in set-aside patches, consistent with the aforementioned earlier research on the subject (Berglund & Jonsson 2008; Dawson et al. 2020). Hence, the set-aside WKHs clearly have the potential to develop greater volumes of dead wood over time, towards the levels found in the natural patches. This may, however, take longer time than the decades studied here.

4.2.2 Patch size

Patch size did not have any distinct effect on species abundance and richness in neither natural nor set-aside patches, contrary to my hypothesis. The hypothesis was based on previous studies on patches suggesting that smaller patches are subject to larger edge effects which affect species with higher habitat requirements negatively (Snäll & Jonsson 2001; Moen & Jonsson 2003; Ruete et al. 2016; Wintle et al. 2019), and that small patches have lower polypore species richness than larger patches (Ylisirniö et al. 2016). Yet, similar relationships were not visible in my study. One explanation for my unexpected result could be that the patch edges were too old, since the magnitude of edge effects will be reduced with time (Harper et al. 2005; Ruete et al. 2016) and the edge-related impact on humidity in patches might only apply if edges are newly created (> 4 years) (Ylisirniö et al. 2016).

Furthermore, because edge effects are estimated to reach 50-100 m into the patch (Esseen 2006; Ruete et al. 2016; Ylisirniö et al. 2016), small patches (>1 ha) might be so small that they have no functional interior habitat, equating the whole patch to edge habitat. This effect is further pronounced in patches with a higher edge-to-interior ratio (Ruete et al. 2016), such as elongated patches. As a matter of fact, based on WKH size (median 1.4 ha), only 30% of the total WKH area in Sweden can be considered interior habitat (Aune et al. 2005). Many patches included in this study are indeed smaller than 1 ha and thus presumably highly exposed to edge effects such as solar radiation and desiccating wind from the surrounding open environment. Those patches might in fact not have any interior habitat and are thus not suitable for this comparison.

Still, unknown factors regarding patch size and edge effects remain. For example, no one have yet studied the effects of the extreme summer drought in 2018 on the microclimate and fungal diversity in the natural patches in Granlandet or the surrounding WKHs.

4.2.3 Basal area of living spruce

Regarding the basal area of living spruce, this variable exhibited a curious and unexpected pattern. The basal area measurement showed a significant relationship with the red-listed abundance and richness, both in natural and set-aside patches. However, while the relationship was positive in natural patches, it was negative in set-aside patches. Furthermore, the basal area of living spruce increased significantly over time in both patch types. This result is curious since basal area of living trees can be viewed as a proxy for canopy cover and thus, shade and humidity. Shade and humidity can impact the fungal community (Krah et al. 2018), and positive relationships between fungal diversity and basal area of living trees and increased canopy cover has been reported (Tomao et al. 2020), as a more humid microclimate affects fungal fruit body production. Increased shade and a more humid microclimate should be important especially for smaller patches that due to a large proportion of edge compared to interior patch habitat are more susceptible to desiccation (Snäll & Jonsson 2001; Ylisirniö et al. 2016). I therefore expected my species diversity measures to react positively to a higher basal area of living trees, as was the case in natural patches. However, basal area of living spruce was found to have no significant effect on diversity in one of the earliest studies of Granlandet (Berglund & Jonsson 2001), and Kärvemo et al. (2021) found basal area to be negatively related to fungal species richness in WKHs. Similar to my negative results for set-aside patches, Kärvemo et al. also studied species richness in WKHs and thus our results are generally in agreement. They discuss if a negative relationship with basal area could be misleadingly obtained if measures are taken in production forest, where relatively young stands can have high BA but generally low diversity (ibid.).

One other possible explanation for the negative relationship with spruce basal area in my study is that set-aside patches might be more dependent on dispersal from outside the patch because they have lower local amounts of dead wood substrate and lower abundance of spore-producing fruit bodies (table 1). Lower abundance could result in dispersal limitations for fungal species with spores that does not spread so far and are highly specialized on certain types of dead wood, which require mass deposition of spores for successful establishment (Jönsson et al. 2008; Moor et al. 2020). Too dense forests could thus possibly make it difficult for spores to reach the more sparse dead wood located within these isolated patches, since fungal dispersal can be restricted even in relatively short distances (Jönsson et al. 2008; Norros et al. 2012). The pattern might look different if the analysis had been made with regard to species composition, since it has been shown that generalist and specialist species has different life strategies in relation to e.g. dispersal (Nordén et al. 2013). Indeed, red-listed species, that tends to be specialists, exhibited a stronger, significant relationship to BA for both patch types.

In contrast, the larger amount of dispersal source habitat and open environment surrounding natural patches, likely result in a greater background spore deposition in these patches and overall positive relationships with increased humidity from greater basal area and canopy cover. However, these patterns require further study, and the survey data would be interesting to combine with new spore deposition data in the different landscapes, to disentangle potential patterns.

Furthermore, there may be interactions between the basal area (affecting microclimate), surrounding landscape, and the local dead wood, that I do not study that could better explain my results. Long-term increasing basal area across patches could be the result of changing climate, but also need to be tested for potential survey year inventory bias.

In summary, the effect of basal area of dead wood on fungal diversity seems to differ between patch types and landscapes. Krah et al. (2018) observed that previous studies on the matter seem to be inconsistent, an observation further demonstrated by my study results. Further research is thus required to better understand the mechanisms involved. This could also include studies of substrate level dynamics on dead wood, with colonizations and extinctions, which could be done partly with data from the same data set as studied here (sensu Jönsson et al. (2008) and Moor et al. (2020)).

4.2.4 Surrounding forest

Forests that have never been clear cut often contain more dead wood and holds higher conservation quality than managed forests (Svensson et al. 2019, 2023; Tomao et al. 2020). In this study, I assumed the continuous cover forests surrounding the patches to be good dispersal sources for fungi to and from the patches, in line with studies that have found mature forest in the surrounding landscape to be positive for fungal richness (Timonen et al. 2011b; Tomao et al. 2020; Kärvemo et al. 2021). Higher volumes and more diverse dead wood in mature forests facilitates habitat connectivity and dispersal (Norros et al. 2012; Nordén et al. 2018). Consequently, I hypothesized that the surrounding forest variables would be positively correlated with species abundance and richness. Contrary to this expectation, none of the measures of surrounding forest (1 or 5 km radius) exhibited a positive correlation to fungal diversity in this study. In fact, few diversity measures were even significantly related to the amount of surrounding CC-forest. Only the abundance of red-listed fungi in natural patches decreased significantly with increasing amount of CC-forest within 1 km. There was a tendency for similar negative results also for the other measures of species richness in natural patches, but they were not significant. The negative correlation could possibly be related to the biased distribution of set-aside areas and WKHs towards low productive land, which could be negative for biodiversity, however not necessarily for wood fungi (Kärvemo et al. 2021). Adding to the complexity, the most influential forest measure differed between patch types. While for natural patches the 1 km measure was significant, the 5 km measure exhibited the more prominent relationship with richness in set-aside patches. These results are difficult to explain, but perhaps much larger scales or other measures are needed to be able to study the role of landscape amount and connectivity for wood fungi in forest patches.

The higher mean values of surrounding CC-forest in natural patches were, however, expected, since they are located within a very large nature reserve (28 000 ha) with vast areas of untouched forest surrounding them. This was also confirmed by Dawson et al. (2020), who is responsible for compiling the data on landscapes surrounding the patches in this data set. Greater between-patch variation for set-aside patches was also expected, as a result of set-aside patches being scattered over a much larger geographical area than natural patches, in landscapes with different proportions of clear-cut and older forest. Furthermore, the area of CC-forest decreased over the course of the study period, with a strongly significant decrease for the 5 km measure in both patches. This likely reflects the intensive forest management currently ongoing in all of Sweden, with more old forests being cut in the north (Ahlström et al. 2022).

In total, the surrounding CC-forest measures that I used is too vague to draw strong conclusions from. Despite that this study implies a negative correlation, I would be careful with drawing that conclusion since it contradicts so many other studies (Edman et al. 2004; Hansen & DeFries 2007; Abrego et al. 2015; Kärvemo et al. 2021), that has studied such relationships in more detail.

4.3 About WKHs as a conservation tool:

The results of my study show that WKHs in boreal spruce forest have lower abundance and species richness of wood fungi than comparable natural patches of old-growth spruce forest. Nonetheless, contrary to the declining levels in natural patches, the examined WKHs maintained their fungal diversity levels over time, indicating conservation value in terms of sufficient habitat resources. My observation-based result, however, contradicts two previous studies (Berglund & Jonsson 2005, 2008) conducted on the very same WKHs, where fungal and lichen diversity levels were predicted to decrease over time. They suggest that long-term degradation of habitat quality causes an extinction debt in WKHs, which might be to blame for their seemingly good conservation ability, resulting in an over-confidence in WKHs as a conservation tool. On the contrary, other studies have found that WKHs conservation values may improve over time, for example in terms of high and/or increasing levels of dead wood, making them important for biodiversity (Timonen et al. 2011b; Gustafsson & Hannerz 2018; Häkkilä et al. 2021; Kyaschenko et al. 2022). Supported by previous studies, my results suggest that WKHs in boral spruce forest can be utilized as functional conservation tools for wood fungi since they maintain fungal diversity, at least over two decades. However, with diversity levels below those found in natural old-growth forest patches, WKHs should be regarded as a complement to nature reserves and other formally protected areas rather than a substitute (Laita et al. 2010; Häkkilä et al. 2021), especially since it is also not yet clear if an extinction debt affects fungal diversity within WKHs (Berglund & Jonsson 2005).

4.4 Study limitations and future perspectives

One main issue with this study, and the many previous ones based on the same plots in Granlandet Nature Reserve and WKHs in the surrounding area, is (in my opinion) the assumption that Granlandet can function as a comparable reference area for the WKHs. Admittedly, patches are similar in terms of vegetation, size and broader geographic region. However, where the natural old-growth patches in Granlandet are surrounded by permanent “soft edges” towards sphagnum wetland, the WKHs are more often surrounded by abrupt but regenerating “hard edges” towards production forest or clear-cuts (Harper et al. 2005; Ruete et al. 2016). Furthermore, all natural patches are rather homogenous, located in a relatively small area (28 000 ha = 280 km^2) with more similar environmental conditions and microclimatic properties, while the WKHs are spread out over a 45 000 km^2 large area with varying immediate surroundings and microclimatic properties. The WKHs thus naturally have more between-patch variation than the natural patches. Between-patch variation in WKHs could be a suitable subject of a future study, perhaps with the assistance of microclimatic logger data to further examine macro- and microclimatic variation in relation to landscape variables. Similar attempts have been made by e.g. Timonen et al. (2011a), who sought to perform a meta-analysis of WKHs surrounded by old-growth respective production forest but did not find enough studies to draw any conclusions. Moreover, Jönsson et al. (2009) analyzed old-growth forest structural characteristics in WKHs and Jönsson et al. (2011) investigated differences in temporal dead wood input in WKHs, as a result of historical forest management and natural disturbances. Their result shows that WKHs can exhibit great between-stand variation also within a smaller landscape than the one I studied. An understanding of whether and how detailed landscape factor differences impact results in my study would require additional long-time environmental and landscape data. However, despite the differences between patch types, I acknowledge the fact that it would be difficult to find more suitable reference forest patches than those in Granlandet, where environmental variation is kept to a minimum.

Apart from my study, and related ones from the same area and data set, there is relatively little knowledge about wood fungi development over time in boreal forest. However, based on my relatively small sample size (three years with 53 plots for each year, divided in two patch type categories) this data might not be comprehensive enough to draw solid general conclusions. Due to the lack of similar previous research, my results cannot be easily compared to others, and there is a general need for long-term monitoring programs of wood fungi to improve the knowledge on this area. Furthermore, this study is based on data compiled from three earlier inventories, conducted by several different persons on infrequent, far spread occasions (year 2000, 2017 and 2022). Data acquired in this way entails elevated risk of detection errors, especially with regards to the different knowledge of the inventory personnel. Future studies building on the current data set would benefit from thorough communication of methodology to future surveyors.

From a statistical perspective, the models included in this study would benefit from including patch identities, to account for the fact that each site has been measured three times and avoid the pseudo-replication in the current models. This could be done with a nested model, where you define patch identity as a random effect and where year is a variable nested under patch identity. This was not done in this study partly due to statistical inexperience on my part, and partly due to the limited time and scope of this Master's Thesis. Any further development of this study should however consider nested models for a possibly more accurate temporal analysis.

Finally, the data set from Granlandet and the surrounding WKHs includes counts of separate species occurrences on substrate-level in each plot. Although not used in my study, such data could be further utilized to examine species communities in each plot, particularly with regard to red-listed species. Dawson et al. (2020) investigate species composition in the same patches for years 2000 and 2017, and similar studies have been conducted on species composition by Komonen et al. (2021) and to some degree Jönsson et al. (2008) and Moor et al. (2020), which might serve as valuable comparisons. Additionally, drawing on the findings by Berglund et al. (2005), counts and long-time comparison of species with annual and perennial fruit bodies could further improve recommendations on wood fungal survey methodology.

4.5 Implications for conservation:

As demonstrated in this study, and along with the vast majority of the previous research examining dead wood, these studies conclude that higher volumes and diversity of dead wood favor wood-inhabiting species in general, and wood fungi particularly. I found that dead wood volume was the environmental variable most positively related to both abundance and species richness of wood fungi in both patch types. Hence, conservation actions targeting wood fungal diversity should safeguard sufficient volumes and diversity of dead wood in both managed and set-aside forests. It has been suggested that a minimum for maintaining polypore diversity in boreal Europe is a 20 ha stand with an average of 20 m^3/ha of dead wood, with a large proportion of logs >20 cm (Junninen & Komonen 2011). This is confirmed also by Ylisirniö et al. (2016) who found the polypore diversity to level out at about 20-30 m^3/ha of dead wood. My results agree with these findings, insofar that the dead wood volume in natural patches, which had higher abundance and species richness, was above 20 m^3/ha (mean 28 m^3/ha) while set-aside patches exhibited lower abundance and species richness and dead wood volumes below 20 m^3/ha (mean 17 m^3/ha). I thus support the 20/20/20 concept as a guideline for conservation of wood fungi in boreal forests.

Additionally, my study also supports previous research reporting that set-aside WKHs in northern Fennoscandian boreal forest contain lower volumes of dead wood compared to old-growth boreal forest (Siitonen 2001; Rouvinen & Kouki 2002; Timonen et al. 2011b; Hekkala et al. 2016; Ylisirniö et al. 2016). To reach the suggested 20 m^3 dead wood per hectare I would therefor recommend that fungal conservation management include some means of dead wood enrichment, in agreement with other authors (Olsson et al. 2011; Uhl et al. 2022). Prescribed burning seems to be a method particularly beneficial for red-listed polypores (Ramberg et al. 2023), but see relevant research on the topic for a more thorough understanding.

Furthermore, to develop conservation practices that are more efficient in preserving wood fungal diversity, more knowledge about their ecology is required. From this study we learn that even a large nature reserve does not necessarily preserve wood fungal abundance and diversity as well as one might assume. It is thus crucial that investigation of wood fungi continues, in a variety of environments, and preferably over long time. Their role as key ecological components highlights the importance of protecting wood fungal diversity.

Finally, I want to add that I wholeheartedly agree with the many voices urging both forest industry and policy makers to exempt all remaining old-growth forests from management (e.g. Linder & Östlund 1998; Nordén et al. 2013; Komonen et al. 2021). Today, only fractions of the old-growth forest remains in Fennoscandia (Esseen et al. 1997; Linder & Östlund 1998; Rolstad et al. 2001; Kuuluvainen 2002; Svensson & Dalen 2021), and what is left is disappearing in an alarming rate (Ahlström et al. 2022). Large amounts of old-growth forest has been demonstrated to be the most beneficial factor for a wide array of species (Kärvemo et al. 2021), and seeing the high abundance and species richness of wood fungi and other species groups demonstrated in this study and others, as well as diversity-supporting structures like dead wood, it becomes evident that old forest is a crucial habitat for boreal ecosystems.

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Populärvetenskaplig sammanfattning

Popular science summary

Att livsmiljöer förstörs och försvinner är det största hotet mot biologisk mångfald globalt. I de nordiska länderna pågår det ett intensivt skogsbruk och det finns nu bara ytterst små ytor kvar av den naturliga granskogen som historiskt sett har täckt större delen av Sverige, Norge och Finland. I granskogen lever många olika svamparter på både levande och död ved, så kallade vedsvampar. Vedsvamparna har en nyckelroll i skogen eftersom de bryter ner trä som så småningom blir till jord igen, en förutsättning för att växter och andra organismer ska kunna leva. Många arter av vedsvampar har svårt att klara sig i skog där det bedrivs skogsbruk och riskerar därför att dö ut på lång sikt. På grund av deras viktiga roll som nedbrytare behöver vi se till att de kan överleva långsiktigt, eftersom de har stor påverka på både djur, växter och människor. Men för att kunna bevara vedsvampsarterna behöver vi känna till mer om hur de lever. Många av de små, kvarvarande ytorna av naturlig (ej planterad) granskog är hem åt ett stort antal arter som inte trivs bra i den planterade skogen. Dessa ytor kallas nyckelbiotoper och anses vara ett bra sätt att bevara arter. Genom att undersöka om antalet arter av vedsvampar förändras över tid i nyckelbiotoper kan man ta reda på om de är en effektiv metod för att hjälpa vedsvamparna överleva. I den här studien undersöks hur många arter av vedsvampar som hittas och på hur många liggande trädstammar de förekommer i små ytor med äldre granskog, under åren 2000, 2017 och 2022. Hälften av granskogsytorna är nyckelbiotoper som är utspridda runt den andra hälften av ytorna, som består av urskog och finns i naturreservatet Granlandet i Norrbotten. Antalet arter och vedsvampar jämförs mellan nyckelbiotoperna och naturreservatet för att se om det är någon skillnad. Studien undersöker också om miljöfaktorerna ytstorlek, volym död ved, mängd levande granar och mängd gammal skog i landskapet runt omkring ytan har någon påverkan på antalet arter av vedsvampar eller hur ofta de förekommer. Resultaten visar att både antalet och förekomsten av vedsvampar hade minskat över tid i naturreservatet, men varit i stort sett oförändrat i nyckelbiotoperna. Större volym av död ved var positivt för vedsvamparna i båda områdena, men ingen av de övriga miljöfaktorerna hade någon tydlig effekt på vedsvamparna. Den nya kunskapen om vedsvampar från den här studien kan användas för att fatta beslut och planera hur skogsbrukare och naturvårdare ska jobba för att vedsvampar ska överleva i framtiden.

Acknowledgements

First, I want to thank my supervisor Mari Jönsson for excellent support and many new insights regarding the ecology of wood fungi. I have sincerely enjoyed working with someone so knowledgeable and enthusiastic about the subject!

Without everyone who has been collecting data over the years I could not have written this thesis, so I owe them a debt of gratitude as well. Many people have been involved in Granlandet the past 30 years, but most frequently reoccurring in this work has been Håkan Berglund, Samantha Dawson and Karl Soler Kinnerbäck.

Elin Sjögren Englund and Jesper Rydén has provided much needed and valuable advice on statistics. With the help from the two of you I now have a much better understanding – and appreciation – of statistics.

On a less serious note, I would also like to thank a certain chocolate company whose dark 90% chocolate have aided in the creation of this thesis. Great amounts have been consumed during the process…

Finally, I am thankful for the support from my friends and family. Perhaps most importantly their understanding of my need to prioritize my energy away from them for a (long) while, but still be embraced when I return. Thank you for the space.

Appendix 1

Complementary figures – Materials and Method

R-packages

The following packages were used to perform the analyses in R:

Base (R Core Team 2024), dotwhisker (Solt & Hu 2024), GGally (Schloerke et al. 2024), ggplot2 (Hadley Wickham 2016), MASS (Venables & Ripley 2002) and performance (Lüdecke et al. 2021).

Data distribution

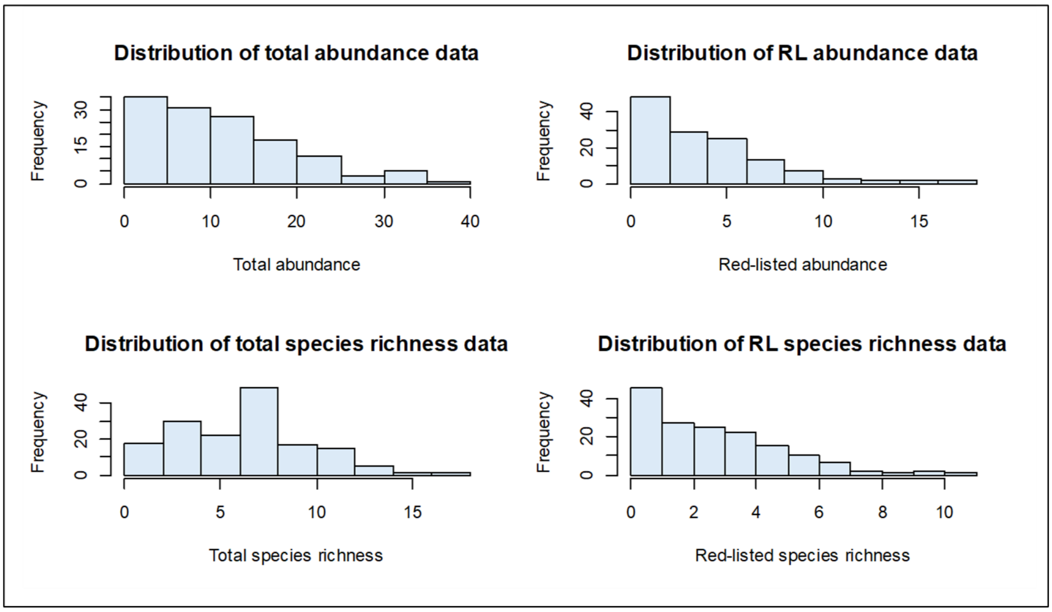


Figure 7 Histograms describing the data distribution of all diversity measures (natural and set-aside patches combined). All three years (2000, 2017 and 2022) pooled for each response variable.

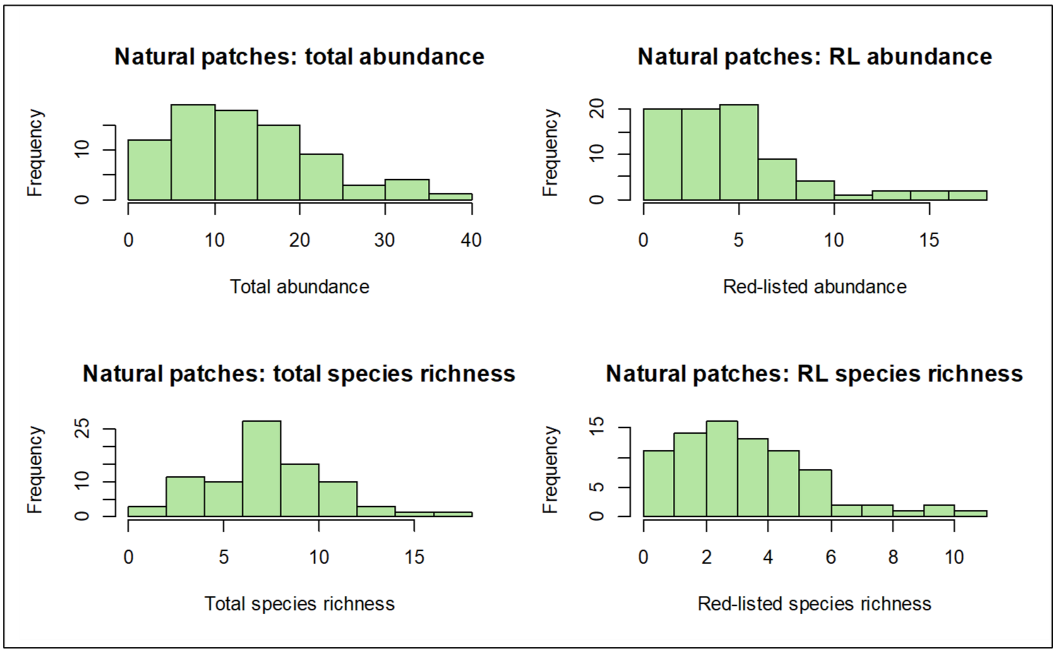


Figure 8 Histograms describing the data distribution of all diversity measures in natural patches. All three years (2000, 2017 and 2022) pooled for each response variable.

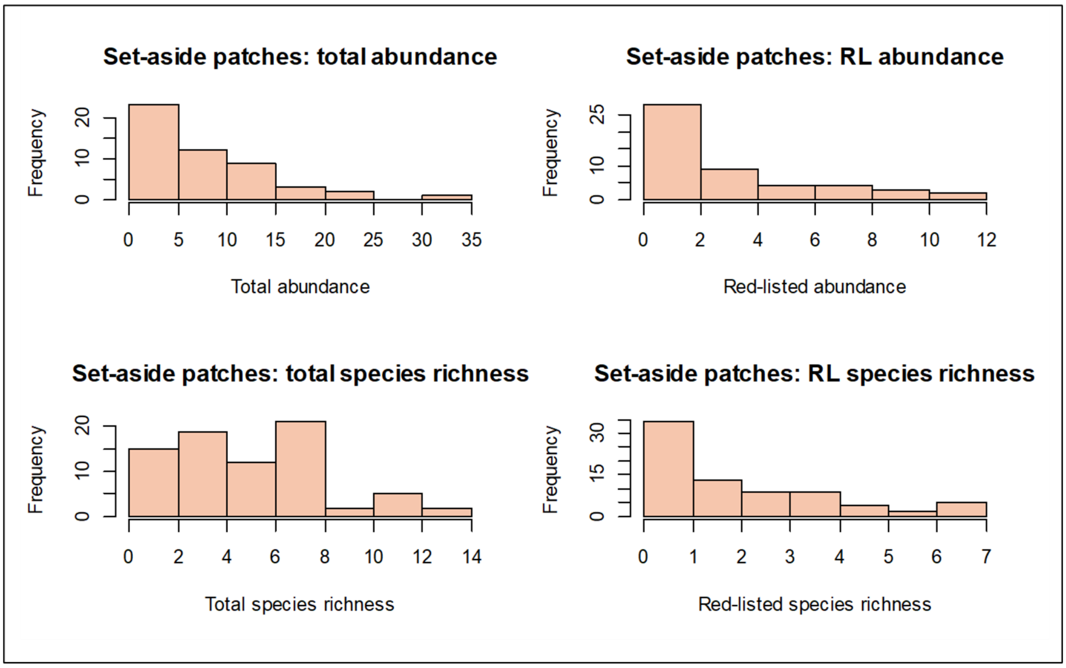


Figure 9 Histograms describing the data distribution of all diversity measures in set-aside patches. All three years (2000, 2017 and 2022) pooled for each response variable, except abundance measures where data was missing for year 2000.

Correlations between environmental variables

Environmental factors were tested for covariation with ggpairs (from package GGally, version 2.2.1 (Schloerke et al. 2024), code in Appendix 2) in R. Figure 11 and 12 shows scatterplot matrices describing correlations between environmental variables for natural patches and set-aside patches respectively. Correlation is low if Pearsons correlation coefficient <0.7.

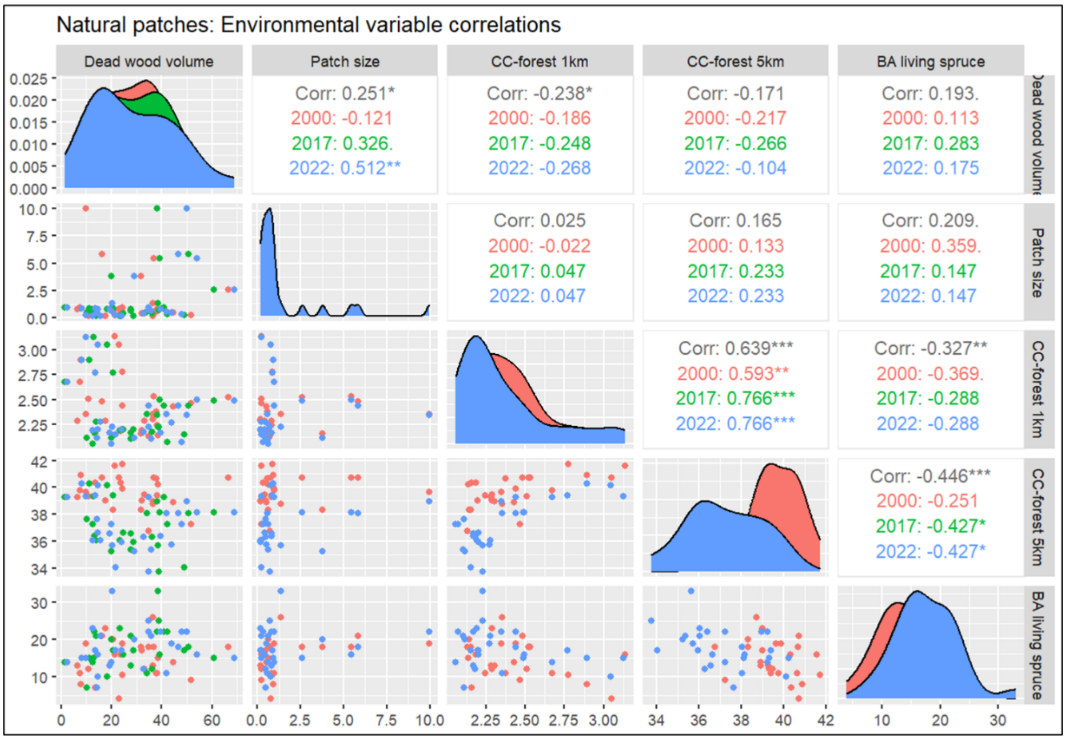


*Figure 10 Scatterplot matrix describing correlations between environmental variables in natural patches. Dot plots represent data points, data distribution is shown diagonally and Pearsons correlation coefficients are shown on the top right side. The correlation coefficients are subdivided into years, with the top value representing the average (grey). For factors with missing values from year 2022, a duplicate of year 2017 is shown. Significant values (p<0.05) are marked by an asterisk. Significance codes: 0.001 '***', 0.01 '**', 0.05 '*', 0.1 '.'*

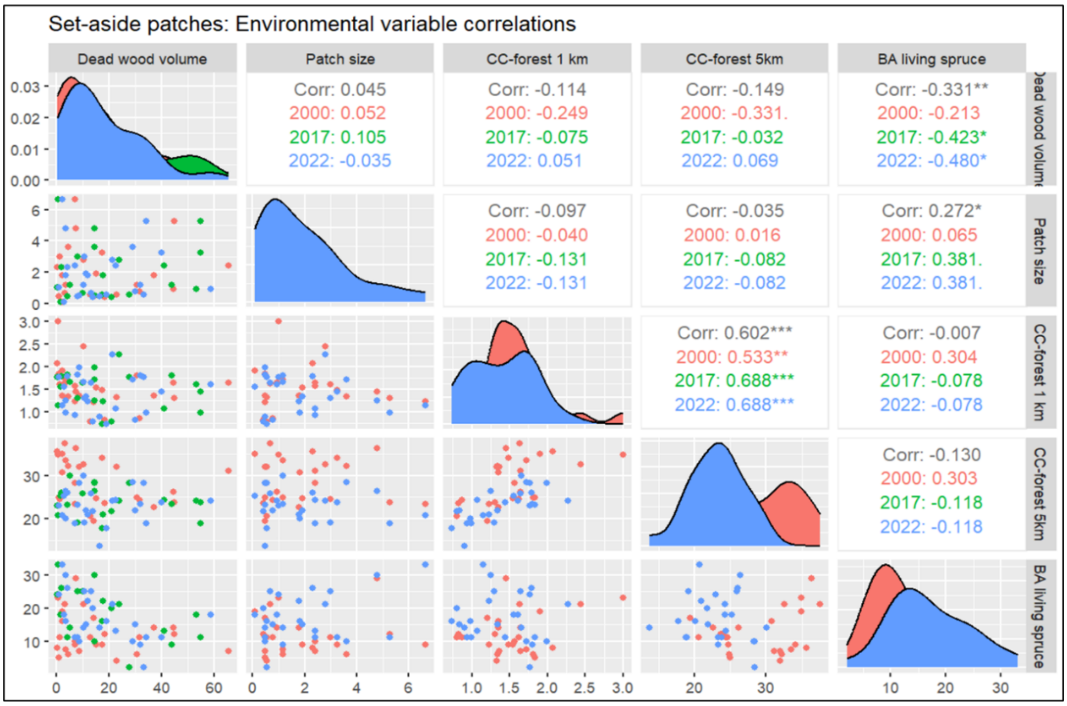


Figure 11 Scatterplot matrix describing correlation between environmental variables in set-aside patches. Dot plots represent data points, data distribution is shown diagonally and Pearsons

*correlation coefficients are shown on the top right side. The correlation coefficients are subdivided into years, with the top value representing the average (grey). For factors with missing values from year 2022, a duplicate of year 2017 is shown. Significant values (p<0.05) are marked by an asterisk. Significance codes: 0.001 '***', 0.01 '**', 0.05 '*', 0.1 '.'*

Species list

Table 6 List of all species detected during inventories of both natural and set-aside patches, across all three years (2000, 2017, 2022). Red-list status according to the Swedish Red List 2020 (SLU Artdatabanken 2020).

Scientific name	**Abbreviation**	**Swedish name**	**Red-listed**
Amylocystis lapponica	Amylap	Lappticka	VU
Amyloporia sinuosa	Amysin	Timmerticka	LC
Amyloporia xantha	Amyxan	Citronticka	LC
Anomoporia bombycina	Anobom	Isabellporing	EN
Antrodia heteromorpha	Anthet	Tickmussling	LC
Antrodiella pallasii	Antpal	Nordlig parasitporing	VU
Antrodiella parasitica	Antpar	Parasitporing	VU
Butyrea luteoalba	Butlut	Gulporing	LC
Cinereomyces lindbladii	Cinlin	Gråporing	LC
Climacocystis borealis	Clibor	Trådticka	LC
Diplomitoporus crustulinus	Dipcru	Sprickporing	VU
Fibroporia norrlandica	Fibnor		DD
Fibroporia unknown	Fibunk		
Fomitopsis pinicola	Fompin	Klibbticka	LC
Fuscoporia viticola	Fusvit	Vedticka	LC
Gloeophyllum sepiarum	Glosep	Vedmussling	LC
Heterobasidium annosum	Hetann	Rotticka	LC
Ischnoderma benzoinum	Iscben	Sotticka	LC
Leptoporus mollis	Lepmol	Kötticka kollektiv	NT
Meruliopsis taxicola	Mertax	Blodticka	LC
Neoantrodia serialis	Neoser	Knölticka	LC
Pelloporus leporinus	Pellep	Harticka	NT
Phellinus chrysoloma	Phechr	Granticka	NT
Phellinidium ferrogineofuscum	Phefer	Ullticka	NT
Phellopilus nigrolimitatus	Phenig	Gränsticka	NT
Postia balsamina	Posbal		DD
Postia caesia complex	Poscae	Blåticke komplex	LC
Postia cyanescens	Poscya		NE
Postia fragilis	Posfra	Blödticka	LC
Postia hibernica	Poshib	Sprödporing	NE
Postia rennyi	Posren	Skörporing	LC
Postia romellii	Posrom		LC
Postia rufescens	Posruf		NE
Postia sericeomollis	Posser	Silkesporing	LC
Postia simulans	Possim		NE
Postia tephroleuca	Postep	Mjölkticka	LC

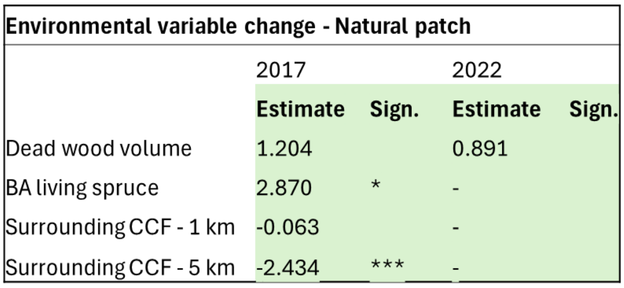
Rhodoformes roseus	Rhoros	Rosenticka	NT
Skeletocutis amorpha	Skeamo	Gullticka	LC
Skeletocutis biguttulata	Skebig	Gärdselticka	LC
Skeletocutis brevispora	Skebre	Ulltickeporing	VU
Skeletocutis chrysella	Skechr	Grantickeporing	VU
Skeletocutis delicata	Skedel		DD
Skeletocutis exilis	Skeexi		LC
Skeletocutis kuehneri	Skekue	Kilporing (s.lat.)	NT
Skeletocutis odora	Skeodo	Ostticka	VU
Skeletocutis papyracea	Skepap	Svällticka	LC
Skeletocutis stellae	Skeste	Kristallticka	VU
Steccherinum collabens	Stecol	Blackticka	VU
Trechispora mollusca	Tremol	Spröd mjölporing	LC
Trichaptum abietinum	Triabi	Violticka	LC
Trichaptum fuscoviolaceum	Trifus	Violtagging	LC
Trichaptum laricinum	Trilar	Violmussling	NT
Corticoid species			
Asterodon ferruginosus	Astfer	Stjärntagging	NT
Cystostereum murrayi	Cysmur	Doftskinn	NT
Laurilia sulcata	Lausul	Taigaskinn	VU
Phlebia centrifuga	Phlcen	Rynkskinn	NT

Complementary figures – Results

Temporal change in environmental variables

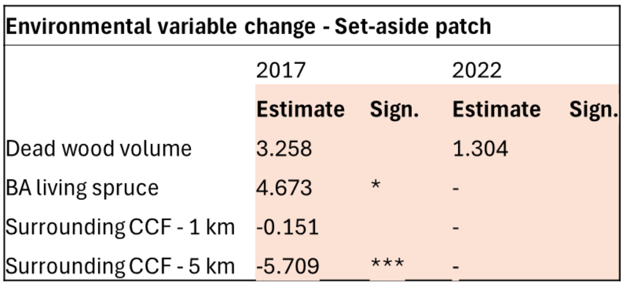
*Table 7 Temporal changes in environmental variables in (A) natural patches and (B) set-aside patches. Tables presents regression results from 8 different linear models, one for each environmental variable (dead wood volume, basal area of living spruce and surrounding continuous cover-forest 1 and 5 km) in each patch type. Year 2000 serves as the reference to year 2017 and 2022. BA living spruce exhibited a significant (p<0.05) increase and surrounding continuous cover-forest (5 km) a significant decrease between year 2000 and 2017. No other changes were significant. Note that data from year 2022 only was available for dead wood volume. Values for the remaining three variables were assumed to have remained stable between 2017 and 2022. Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.'*

A



Environmental variable change - Natural patch				
	2017		2022	
	Estimate	**Sign.**	**Estimate**	**Sign.**
Dead wood volume	1.204		0.891	
BA living spruce	2.870	*	-	
Surrounding CCF - 1 km	-0.063		-	
Surrounding CCF - 5 km	-2.434	***	-	

B

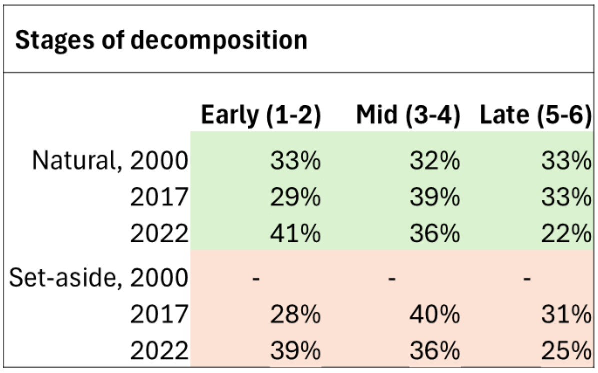


Environmental variable change - Set-aside patch				
	2017		2022	
	Estimate	**Sign.**	**Estimate**	**Sign.**
Dead wood volume	3.258		1.304	
BA living spruce	4.673	*	-	
Surrounding CCF - 1 km	-0.151		-	
Surrounding CCF - 5 km	-5.709	***	-	

Complementary figures – Discussion

Stages of decomposition

Table 8 Stages of decomposition in surveyed logs. The percentage is the number of logs in a certain decomposition stage, out of the total number of logs measured each year, e.g. 33% of all logs measured in natural patches in year 2000 was in early decomposition stage. Decomposition was not measured in set-aside patches in the year 2000. Amounts were overall stable, with a slight increase in early stages of decomposition in 2022 and a subsequent decrease in late stages the same year.



Stages of decomposition			
	Early (1-2)	**Mid (3-4)**	**Late (5-6)**
Natural, 2000	33%	32%	33%
2017	29%	39%	33%
2022	41%	36%	22%
Set-aside, 2000	-	-	-
2017	28%	40%	31%
2022	39%	36%	25%

Appendix 2

R Code for analyses

The following code was used for models and analyses. Code for data tidying and visualization excluded.

Raw data can be sent upon request. Contact Mari Jönsson (mari.jonsson@slu.se) for further information.

Diversity changes over time in natural and set-aside patches

```
# Total abundance, negative binomial
Mod.TotalAbun.nb <- glm.nb(TotAbun ~ PatchType + SurveyYear, data
= data_full)

# Total species richness, negative binomial
Mod.TotalSR.nb <- glm.nb(TotSR ~ PatchType + SurveyYear, data =
data_full)

# Redlisted abundance, negative binomial
Mod.RLAbun.nb <- glm.nb(RLAbun ~ PatchType + SurveyYear, data =
data_full)

# Redlisted species richness, negative binomial
Mod.RLSR.nb <- glm.nb(RLSR ~ PatchType + SurveyYear, data =
data_full)
```

Patch type difference

```
# Total abundance, negative binomial
GL_NB.TotAbun <- glm.nb(TotAbun ~ PatchType, data = data_full)

# Red-listed abundance, negative binomial
GL_NB.RLAbun <- glm.nb(RLAbun ~ PatchType, data = data_full)

# Total species richness, negative binomial
GL_NB.TotSR <- glm.nb(TotSR ~ PatchType, data = data_full)

# Red-listed species richness, negative binomial
GL_NB.RLSR <- glm.nb(RLSR ~ PatchType, data = data_full)
```

Relationships with environmental variables within patch types

Natural patches (Granlandet):

```
# Total abundance, negative binomial
scale_model_GL_TotAbun.2 <- glm.nb(TotAbun ~ SurveyYear +
PatchArea_ha + LogVolperHa + forest1km_Survey + forest5km_Survey
+ BASpruceLiving, data = scale_GL_relevant)

# Red-listed abundance, negative binomial
scale_model_GL_RLAbun.2 <- glm.nb(RLAbun ~ SurveyYear +
PatchArea_ha + LogVolperHa + forest1km_Survey + forest5km_Survey
+ BASpruceLiving, data = scale_GL_relevant)

# Total species richness, poisson
scale_model_GL_TotSR.2.p <- glm(TotSR ~ SurveyYear + PatchArea_ha
+ LogVolperHa + forest1km_Survey + forest5km_Survey +
BASpruceLiving, family = poisson(link = "log"), data =
scale_GL_relevant)

# Red-listed species richness, poisson
scale_model_GL_RLSR.2.p <- glm(RLSR ~ SurveyYear + PatchArea_ha +
LogVolperHa + forest1km_Survey + forest5km_Survey +
BASpruceLiving, family = poisson(link = "log"), data =
scale_GL_relevant)
```

Effect size plot created with `dwplot()` from dotwhisker package.

Set-aside patches:

```
# Total species richness, poisson
scale_model_NB_TotSR.2.p <- glm(TotSR ~ SurveyYear + PatchArea_ha
+ LogVolperHa + forest1km_Survey + forest5km_Survey +
BASpruceLiving, family = poisson(link = "log"), data =
scale_NB_relevant)

# Red-listed species richness, poisson
scale_model_NB_RLSR.2.p <- glm(RLSR ~ SurveyYear + PatchArea_ha +
LogVolperHa + forest1km_Survey + forest5km_Survey +
BASpruceLiving, family = poisson(link = "log"), data =
scale_NB_relevant)
```

Effect size plot created with `dwplot()` from dotwhisker package.

Changes in environmental variables

Natural patches (Granlandet):

```
# Dead wood volume
År_dödved.GL <- lm(LogVolperHa ~ SurveyYear, data =
subset_Naturalpatch)

# Basal area of living spruce
```

```
År_gran.GL <- lm(BASpruceLiving ~ SurveyYear, data =
subset_Naturalpatch)

# Surrounding continuous cover forest (1 km)
År_forest1km.GL <- lm(forest1km_Survey ~ SurveyYear, data =
subset_Naturalpatch)

# Surrounding continuous cover forest (5 km)
År_forest5km.GL <- lm(forest5km_Survey ~ SurveyYear, data =
subset_Naturalpatch)
```

Set-aside patches:

```
# Dead wood volume
År_dödved.NB <- lm(LogVolperHa ~ SurveyYear, data =
subset_SetasidePatch)

# Basal area of living spruce
År_gran.NB <- lm(BASpruceLiving ~ SurveyYear, data =
subset_SetasidePatch)

# Surrounding continuous cover forest (1 km)
År_forest1km.NB <- lm(forest1km_Survey ~ SurveyYear, data =
subset_SetasidePatch)

# Surrounding continuous cover forest (5 km)
År_forest5km.NB <- lm(forest5km_Survey ~ SurveyYear, data =
subset_SetasidePatch)
```

Correlations between environmental variables

```
# Scatterplot matrix, natural patches

subset_Naturalpatch %>%
  ggpairs(columns = c("LogVolperHa", "PatchArea_ha",
"forest1km_Survey", "forest5km_Survey", "BASpruceLiving"),
          aes(color = SurveyYear),
          title = "GRANLANDET",
          columnLabels = c("Dead wood (m3/ha)","Patch size (ha)",
"Surrounding forest 1km", "Surrounding forest 5km", "BA Living
spruce"))


# Scatterplot matrix, set-aside patches

subset_SetasidePatch %>%
  ggpairs(columns = c("LogVolperHa", "PatchArea_ha",
"forest1km_Survey", "forest5km_Survey", "BASpruceLiving"),
          aes(color = SurveyYear),
          title = "NYCKELBIOTOPER",
          columnLabels = c("Dead wood (m3/ha)","Patch size
(ha)","Surrounding forest 1km", "Surrounding forest 5km", "BA
Living spruce"))
```

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