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Forestry history in boreal production and near-natural forests – impacts on biodiversity in wood- inhabiting fungi

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Master of Science in Natural Resource Management

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Abstract

Since the 1940s, stand-based forest management, including clear-cutting, has been the predominant practice in Norway, with approximately 60% of Norwegian forests having undergone at least one cycle of clear-cutting. This forestry practice has led to a significant loss of natural forest structure and coarse dead wood, which are crucial for maintaining natural, ecological processes. Wood-inhabiting fungi (saproxylic fungi) play an important role in forest ecosystems. They decompose dead wood and contribute to nutrient cycling, while their diversity and abundance may give an indication of the forest's biodiversity status.

This thesis aims to investigate the impacts of historical logging activities on the biodiversity of wood-inhabiting fungi in boreal forests, comparing mature forests that previously have been clear-cut with near-natural forests. The field study involved conducting surveys in 12 pairs of forest sites. Each pair consisted of an old, near-natural forest (NN) and a mature production forest established through clear-cutting (CC). All sites were situated in south-eastern Norway and represented bilberry-type spruce-dominated forest. The surveys included registering the number of cut stumps and coring of living trees, supported by pre-existing datasets on dead wood and biodiversity.

Near-natural forests had significantly higher species richness of wood-inhabiting fungi compared to previously clear-cut forests. The study also explored the correlation between volume and diversity of dead wood and biodiversity, confirming that greater volumes and diversity of dead wood were associated with higher species richness. Red-listed species were predominantly found in the near-natural forests. No statistical evidence directly linked management type to species composition, although a pattern suggesting a potential effect of management type was observed. These results offer valuable insights for forest management practices, highlighting the importance of preserving natural forest structures, especially dead wood, to enhance biodiversity.

Sammendrag

Siden 1940-tallet har bestandsskogbruk, inkludert flatehogst, vært den dominerende praksisen i Norge. I dag har omtrent 60% av norske skoger gjennomgått minst én syklus av flatehogst. Denne driftsformen har ført til et betydelig tap av naturlig skogstruktur og død ved, som er viktig for bevaring av naturlige, økologiske prosesser. Vedboende sopp spiller en viktig rolle i skogøkosystemer ved å bryte ned død ved og bidra til næringssyklusen. Soppenes mangfold og overflod kan gi en indikasjon på skogens biologiske mangfold.

Denne masteroppgaven har som mål å undersøke effekten av historiske hogstaktiviteter på biodiversiteten til vedboende sopp i boreale skoger, ved å sammenligne eldre skoger som tidligere har blitt flatehogd med naturskognære skoger. Feltarbeidet inkluderte undersøkelser i 12 skogspår. Hvert par bestod av en eldre naturnær skog (NN) og en eldre produksjonsskog, etablert gjennom flatehogst (CC). Alle områdene var lokalisert i sørøstlige Norge og representerte blåbær-type grandominert skog. Feltundersøkelsene var registrering av antall stubber og boring av levende trær. I tillegg ble eksisterende datasett om død ved og biodiversitet brukt i oppgaven.

De naturnære skogene hadde betydelig høyere artsrikdom av vedboende sopp sammenlignet med tidligere flatehogde skoger. Studien utforsket også sammenhengen mellom volum og diversitet av død ved og biodiversitet, og bekreftet at større volum og diversitet av død ved var assosiert med høyere artsrikdom. Rødlistede arter ble i all hovedsak funnet i de naturnære skogene. Det ble ikke funnet statistisk evidens som knyttet forvaltningstype direkte til artssammensetningen, selv som det ble observert et mønster som antydte en effekt. Disse resultatene gir verdifull innsikt for skogforvaltningen, og understreker hvor viktig det er å bevare naturlige skoger, spesielt død ved, for å ivareta biodiversiteten.

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1 Introduction

About 30% of the Earth's land area is covered by forests, which contain a significant portion of global biodiversity and store most of the terrestrial carbon (FAO & UNEP, 2020). Norway has approximately 121 000 km² of forest which contributes to 37% of the land area, and the Norwegian forests host 48% (1330) of the country's red-listed species (Artsdatabanken, 2021b). Boreal forests are critical for global biodiversity and carbon storage, with Norwegian forests estimated to store 32% of the terrestrial carbon stocks (Bartlett et al., 2020). Intensive forest management practices increase economic value through the extraction of woody biomass, but growing evidence shows that such practices negatively impact biodiversity (Ekman et al., 2024; Mönkkönen et al., 2022; Nordén et al., 2018).

For centuries, Norwegian forests have been managed for timber, fuel, and other by-products. With the onset of the industrial revolution, the demand for wood grew rapidly, leading to the adoption of more intensive forest management practices. By the 1940s, stand-based forest management, which included clear-cutting as a key practice, had become the dominant approach to forestry in Norway (Storaunet & Rolstad, 2020). This shift was driven by a desire to maximise timber production and meet the demands of growing industries. Direct changes in forest structure due to such management practices have been shown to negatively impact forest species and their habitats (Mönkkönen et al., 2022). Research further indicates that the boreal forests are changing in response to natural resource development, including forestry. These changes include habitat loss, transformation of forest types, altered age-class distribution, decreased levels of dead wood and structural diversity, and a shift from interior forest to edge habitats, isolating old-growth forests (Venier et al., 2014).

Today the predominant management practice in Norway, as well as in most of Fennoscandia (Sweden and Finland), is still stand-based forest management. This implies that trees are artificially regenerated by seeding or planting, and close to all trees are harvested by clear-cutting when the forest reaches maturity (Ekman et al., 2024). Norway spruce (*Picea abies*; hereafter spruce) is one of the dominant tree species in Norway and the most important timber species, with nearly 40 million seedlings planted each year. Approximately 7.2 million cubic meters are harvested, with over half being utilised for sawn timber and the remaining for pulpwood production, e.g., paper, cellulose, and wood pulp (NIBIO, 2021). Most productive forests in Norway

are now in a mosaic of even-aged stands at different successional stages, from recently cut and early succession to mature forests (70-120 years). Approximately 60% of the Norwegian forest has experienced one cycle of clear-cutting, while just 1.7% is considered untouched by forestry (Storaunet & Rolstad, 2020).

Managed forests differ from natural forests in terms of disturbance dynamics, turnover time, and structural elements (Paillet et al., 2009). Intensively managed forests typically resemble monocultures characterized by one dominating tree species, even-aged trees, and low deadwood volumes. Monocultures have limited potential to offer the essential habitat structures required for sustaining biodiversity (Ekman et al., 2024). The term “natural forest” has a variety of definitions based on different criteria and uses. In an attempt to establish a general definition for the term in a Norwegian context, the following definition was proposed: “*Natural forests are forests established through natural regeneration of local genetic material where human influence has occurred to such a limited extent, for such a long time ago, or has been conducted in a way that the forest’s natural structure, composition and ecological processes have not been significantly altered*” (Rolstad et al., 2002). A report from 2020 concluded that 30% of the current productive forest area in Norway can be considered natural forests according to this definition (Storaunet & Rolstad, 2020).

In this master’s thesis, the term “near-natural” is used similarly to the “natural forest” definition from Rolstad et al. (2002). In this context, near-natural describes forests that haven’t been clear-cut and have retained key structural characteristics like diverse tree ages, snags, and decaying wood (Rouvinen & Kouki, 2008). Uotila et al. (2002) emphasize that even with mild management activities, such as selective logging, these forests maintain the structural features of natural stands, including an uneven age distribution and a rich understory. Jacobsen et al. (2020) further highlight that near-natural forests support richer saproxylic beetle communities compared to intensively managed stands, primarily due to an abundance of decaying wood and greater habitat diversity.

As cited in Nordén et al. (2018), Siitonen (2001) noted that in Norway, Sweden and Finland forestry practices have resulted in a significant loss of near-natural forest and coarse dead wood, which are crucial for maintaining the natural forest structure. This depletion, estimated at around 90%, has led to severe fragmentation and a reduction in the connectivity of forest habitats. In later decades total forested area and timber volumes have increased in Fennoscandia while the biodiversity decline still

continues (Mönkkönen et al., 2022). The paradox of increasing tree growth, total forest area, and total timber values over the past century, yet decreasing biodiversity, is explored by Mönkkönen et al. (2022). They indicate that the levels of forest structures necessary for sustaining ecologically diverse communities are below what likely existed in Finland under natural reference conditions and in the 1750s. The primary factors contributing to the decline of forest species in Norway are habitat loss and fragmentation resulting from clear-cutting. Specifically, 84% of threatened species in the Norwegian forest are dependent on habitats found in old forests (after NiN 1.0 definition of *gammelskog*) (Artsdatabanken, 2021b). This indicates that intensive forestry has an impact on forest structures, especially dead wood structures, and species diversity.

Conifer trees in boreal forests have the potential to live for centuries, and even after death, the decay process can persist for an additional hundred years. This long decay period creates diverse microhabitats in different parts of the tree, at different stages of decay, offering a dynamic ecological niche over many years (Stokland et al., 2012). Deadwood quality and quantity, including snags and logs at various stages of decay, are crucial for biodiversity. A high abundance of such diverse dead wood may lead to a rich diversity of saproxylic species, including wood-inhabiting fungi (Floren et al., 2015; Parisi et al., 2018). Wood-inhabiting fungi, or saproxylic fungi, play an important role in forest ecosystems. The term “saproxylic” refers to species that, at some stage of their life cycle, are dependent on dead woody material (Stokland et al., 2012). They decompose deadwood and contribute to nutrient cycling, while their diversity and abundance may give an indication of the forest's biodiversity status. Some fungi are generalists capable of colonizing a wide range of wood types, whereas specialists prefer specific wood types, decay stages, or microclimates (Hottola et al., 2009). A forest with less deadwood diversity may have been subject to disturbances such as logging, resulting in lower species diversity. Intensively managed forests, which the current forest landscape in Fennoscandia largely consists of, fail to provide suitable conditions for wood-inhabiting fungi and has led to a decline in the populations of these fungi over recent decades (Hottola et al., 2009).

Cutting intensity, a measure of the extent of logging activities within a given forest site, can be quantified in several ways. For instance, the density of cut stumps provides a direct measure of the intensity of logging activities (Storaunet & Skarpaas, 2022), or the basal area of cut stumps (Penttilä, 2004), the negative of which have

been used as a proxy for naturalness (Nordén et al., 2013). The density and spatial distribution of cut stumps can provide insights into the spatial patterns of logging activities, e.g. a clustering of cut stumps may indicate more intensive logging activities, while dispersed stumps may suggest more selective logging practices. It's also important to note that in addition to human intervention, natural disturbances like pathogens, pests, storms, and fires can cause the death of individual trees or entire stands. These events often enhance light conditions and can be dated by analysing the growth patterns of living trees, including periods of improved growth (growth release). By studying cut stumps, archival data and local knowledge, it is possible to determine if the growth release resulted from natural or anthropogenic causes.

In this master's thesis, I aimed to investigate the intensity and frequency of previous logging activity and forestry in selected forest areas, and the effects that this has on fungal biodiversity. The primary objectives were to (1) explore how forest history affects the biodiversity of wood-inhabiting fungi, and (2) how this relationship is mediated by contemporary forest structure and the diversity and amount of dead wood. I predicted that (1) the biodiversity of wood-inhabiting fungi is greater in near-natural forests compared to clear-cut forests. The difference is expected to be bigger when the intensity of logging in near natural forests is lower. I further predicted that (2) the higher biodiversity observed in near natural forests is due to factors such as the inherent structural complexity of the forests, the diversity and volume of dead wood present, and the level of connectivity between forest patches. My third prediction was that (3) the species composition will change based on the forest history, particularly in relation to logging activities, with an increase in rare species observed in near natural forests.

2 Materials and methods

2.1 Study area and design.

The field study involved conducting surveys in 12 pairs of sites, as part of the EcoForest project. Each pair consisted of an old, near-natural forest (NN) and a mature production forest established through clear-cutting (CC). All sites were situated in south-eastern Norway (Fig. 1) and represented bilberry-type spruce-dominated forests. Large variations exist in macroscale bioclimatic variables across the study sites, with mean annual temperatures ranging from 0.5 to 5.4 °C (Asplund et al., 2024). Halden and Marker, the southernmost sites, are in the hemiboreal zone, experiencing higher summer temperatures and longer growing seasons. The remaining ten sites are in either the south boreal (Blåfjell and Särkilampi) or middle boreal zones. Blåfjell shares the relatively warm summers with Halden and Marker but has higher summer precipitation and a more oceanic climate. Särkilampi, Braskereidfoss and Hemberget are characterized by continental climates, with broad annual temperature ranges and higher precipitation seasonality. Gullenhaugen, Øytjern, Skotjernfjell, and Langvassbrenna are all located at higher elevations (Table 1), resulting in shorter growing seasons. Storås and Tretjerna represent intermediate bioclimatic conditions (Asplund et al., 2024).

The geographical placement of sites corresponds to differences in historical and contemporary resource utilization, leading to differences in land use and population densities. For example, intensive timber harvesting started earlier in southern coastal regions. Furthermore, higher elevations are typically more remote and have a higher proportion of forests. These distinctions also translate into variations in the connectivity of older spruce forests (Asplund et al., 2024).

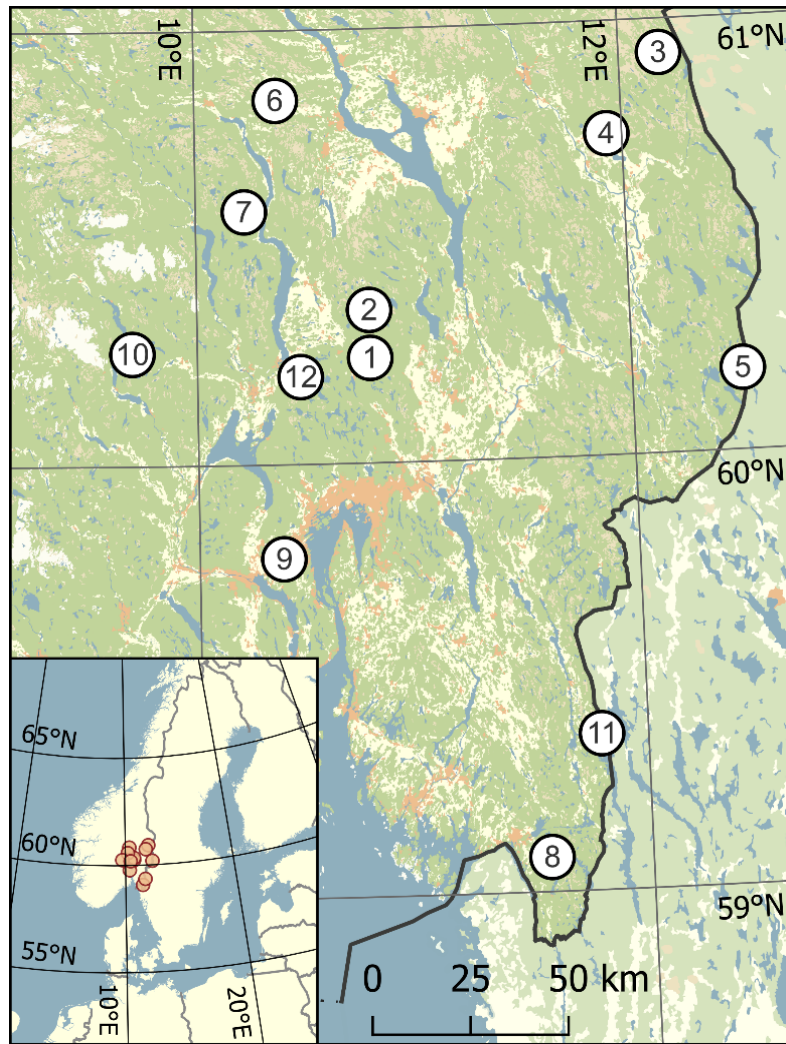


Figure 1. The map illustrates the geographical distribution of the 12 site pairs. The numbers correspond to the overview in Table 1. After Asplund et al. (2024)

The locations of these sites were already determined by the original project’s study design. The previously clear-cut forests have attained maturity class 4 or 5 (Viken, 2021). It is noteworthy that the forests have not been thinned after planting, and none of the stands have been subjected to ditching. They are also on comparable soils and topography. Additional criteria for site selection included approximate uniformity in vegetation type, soil profile, productivity, aspect and canopy gap variation. Furthermore, sites within a pair were constrained to a maximum separation of five kilometres, but the longest distance ended up being 3140 metres. Both near-natural and previously clear-cut forests are assumed to have experienced forestry activities in the past, with varying types, intensity and frequency. These activities are likely to span from cutting of individual trees, to complete clear-cutting.

Table 1. Overview of site pair names, abbreviation, management type, latitude (°N) and longitude (°E), and elevation (m.a.s.l.). After Asplund et al. (2024).

Site nr.	Site name	Abbreviation	Management type	Latitude (°N)	Longitude (°E)	Elevation (m.a.s.l.)
1	Skotjernfjell	SKO	CC	60.2413	10.8084	571
			NN	60.2422	10.7960	610
2	Gullenhaugen	GUL	CC	60.3700	10.7872	591
			NN	60.3526	10.7966	668
3	Hemberget	HEM	CC	60.9211	12.1889	584
			NN	60.9151	12.2065	581
4	Braskereidfoss	BRA	CC	60.7476	11.9264	332
			NN	60.7398	11.9285	427
5	Särkilampi	SAR	CC	60.2005	12.5281	388
			NN	60.1877	12.5080	368
6	Øytjern	OYT	CC	60.8432	10.4090	663
			NN	60.8389	10.3812	640
7	Tretjerna	TRE	CC	60.5773	10.2285	520
			NN	60.5836	10.2265	472
8	Halden	HAL	CC	59.0798	11.5595	197
			NN	59.0798	11.5465	211
9	Blåfjell	BLA	CC	59.7880	10.3865	322
			NN	59.7831	10.3813	264
10	Storås	STR	CC	60.2615	9.7091	432
			NN	60.2591	9.7007	483
11	Marker	MRK	CC	59.3835	11.7590	178
			NN	59.3601	11.9700	187
12	Langvassbrenna	LAN	CC	60.2010	10.4980	548
			NN	60.2018	10.4738	607

2.2 Survey of cut stumps.

To quantify the volumes and densities of different types of cut stumps, a systematic survey was conducted on all cut stumps with a minimum diameter of 5 cm at the top height. The survey plots included transects of 15×133.33 m (0.2 ha). These transects had been established in advance and included a macroplot measuring 15×15 m in the centre. The transect then extended 59.17 m outward from both the northern (or eastern) and southern (or western) side of the macroplot, resulting in an overall extension of 133.33 m in the north-south (or east-west) direction. In cases where the transect could not be fit with either north-south or east-west direction due to the shape of the forest stand, a 90-degree turn was made at the macroplot. To make it easier to ensure that every part of the transect was surveyed, the northern-southern (or eastern-western) part of the transect was subdivided into two 29.58 m cells. The transect comprised in total four cells measuring 29.58×15 m each, in addition to the central 15×15 m macroplot (Fig. 2).

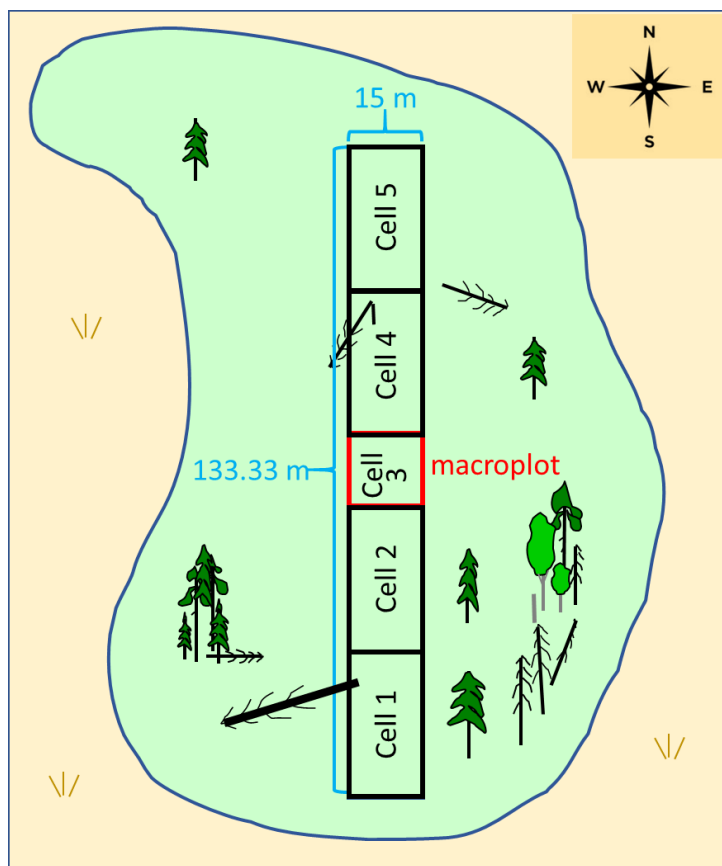


Figure 2. Illustration of the transect. A survey of cut stumps, dead wood, biodiversity and coring of living trees was done within the 133.33×15 m transect. After Nordén et al. (2020).

For each cut stump the following variables were measured: *tree species* (mainly spruce and pine), *diameter* (measured at the top of the stump), *height* (measured from the mean ground level to the top of the stump) and *decay stage class*. The decay stage class was identified by inserting a knife at various points on the stump (Josefsson, 2010) and then given a classification value ranging from 1-5. The five classification categories align with National Forest Inventory, NFI, (Viken, 2021) standards from 2018 and are as follows: **(1)** Recently dead (0-3 years). The bark is still firmly attached or recently loosened due to intensive bark beetle infestation. **(2)** Loose bark, incipient decay. Onset of well-developed fungal mycelium between the bark and the wood. The outer layers of the wood are starting to soften due to the decay, up to 3 cm into the wood. **(3)** Extensively decayed in the outer layers. The wood is completely decayed in its outer layers and can be easily separated with a knife. The core remains solid. **(4)** The wood is loose throughout and sometimes oozes to the ground. There is no inner hard core, and it may be somewhat overgrown. **(5)** Completely disintegrated. Fragments and outlines beneath a layer of vegetation, signifying the complete decomposition of the log.

2.3 Dead wood survey

I utilised a pre-existing dataset on dead wood. All standing and downed dead wood with DBH (diameter in breast height) or basal diameter ≥ 5 cm with the point of birth inside the transect was measured. Variables measured were diameter and length/height, tree species, type of dead wood (e.g. uprooted or broken downed dead wood, snag, fallen tree-top), decay stage (Viken, 2021) and other ecological variables. See Asplund et al. (2024) for more details and volume calculations.

2.4 Coring of living trees

To reveal and date historical logging activities and other disturbances that have caused canopy openings and changes in light conditions within the forest, resulting in growth responses in living trees, we employed two approaches for extracting increment core samples. All core samples were consistently collected at breast height (1.3 m). The increment core samples were also used to calculate stand age and to determine the age of the oldest tree in each site. The DBH weighted mean age is calculated by

summing the products of each tree's age and its basal area, and then dividing by the total basal area of all sampled trees.

In the first approach, a stand-level sample was necessary to be able to identify the historical logging activities and other disturbances. In this approach we aimed to core 20 trees along the transect. The coring was done on spruce and pine trees that were estimated to be at least 40 years older than the cut stumps. For instance, if the cut stumps date back to the 1950s, the cored trees should be at least 110 years old, and preferably even older. As a rule, the coring was limited to trees that were at least 100 years old or had a diameter of at least 25 cm. We selected the two largest or oldest trees within 3 m from each corner of the cell for coring. In the case of the macroplot, only one tree per cell corner was selected because this cell is noticeably smaller than the others.

The second approach was aimed at dating a logging event identified by the presence of cut stumps. In this approach, we aimed to select 1-3 mature spruce or pine trees within a radius of less than 3 m from the cut stump for coring. The choice of focal cut stumps was based on the presence of neighbouring trees that were at least 40 years older than the estimated age of the cut stumps. This selection criterion is essential because young trees, especially spruce, can exhibit irregular growth patterns. We aimed to date at least three cut stumps along the transect. If fewer than three suitable stumps were initially found, the search for such stumps was expanded to other sections of the stand. The search for suitable stumps was conducted across the entire stand area and limited to a maximum of 2 hours. (Josefsson et al., 2005; Josefsson, 2010; Lundmark et al., 2021; Nordén et al., 2018)

2.5 Biodiversity survey

The fruit bodies of polypore and corticioid wood-inhabiting fungi were surveyed on all standing and downed dead wood (excluding cut stumps) in the transect by co-supervisor Jenni Nordén and species experts Siri Khalsa and Tom Hellik Hofton from Biofokus. One or more fruit bodies on a dead wood unit were counted as occurrence, as common in fruit-body-based surveys of fungi (Nordén et al., 2013).

2.6 Laboratory processing

Both the field work and laboratory work were conducted together with fellow student Ulrik Botten. We mounted approximately 350 core samples onto specially made wooden boards with glue, before we sanded them down with an electric hand planer. The mounting boards were scanned with EPSON Perfection V550 (1200 dpi). The scanned images were then analysed by using the R-package *MtreeRing* (García-Hidalgo et al., 2021). This package made it possible to detect the ring borders and ring width for each core sample.

2.7 Statistical analysis

The statistical analysis of this study was carried out using R version 4.3.2 and RStudio 2023.12.1 Build 402 (R Core Team., 2023). Key packages employed included *tidyverse* (Wickham et al., 2019) and *ggplot2* (Wickham, 2016), for data manipulation and visualization. The primary analytical approach involved the use of Generalized Linear Models (GLM) to analyse the relationship between species richness and various explanatory variables, as well as the effect of forest type. To mitigate potential issues with variable magnitude affecting model outcomes, all variables were scaled to ensure comparability. Further testing of the effect of management type was conducted by performing an ANOVA (analysis of variance) analysis. The *indicspecies* package (v1.7.9, (De Caceres & Legendre, 2009) facilitated the analysis of indicator species through the function *multipatt*. Model selection was performed using the *MuMin* package (Bartoń, 2023). The *dredge*-function within this package was utilized to generate a model selection table, which was ranked based on Akaike Information Criterion (AIC) scores. This criterion balances model fit (e.g. how well the model explains the data) with model complexity (e.g. the number of parameters in the model). Models with lower AIC scores are considered better fitting. The *vegan* package (Oksanen et al., 2022) supported the creation of ordination plots using NMDS (non-metric multidimensional scaling) via the function *monoMDS*. The environmental variables were fitted to the ordination plot using the function *envfit* from the same package.

The management type index categorizes forest areas into two main types: CC or NN, representing previously clear-cut (CC) and near-natural (NN) forests. Species richness denotes the number of different species present within each forest type,

serving as a measure of biodiversity. Stand age is an estimate based on the living cored trees, while the oldest tree is identified based on annual tree ring counts. The total volume of coarse woody debris (CWD) encompasses the volume of all dead wood within the forest area, with detailed calculations outlined in Asplund et al. (2024). Cut stumps were quantified by measuring every stump with a diameter > 5 cm within the transect area, as explained in Chapter 2.2. The W index, as described by Hottola et al. (2009), combines volume and diversity of dead wood. Fdis and Feve indices assess diversity in dead wood, focusing on distance and evenness metrics, respectively. The all.80.a2 index is a measure of connectivity of spruce forests measured as distance-weighted volumes (in $\text{m}^3 \text{ha}^{-1}$) of living spruce in ≥ 80 years old forests, assuming a mean dispersal distance of 0.5 km (i.e. $\alpha = 2$). Downed volume small and downed volume large represent volumes of downed dead wood smaller than 20 cm in diameter ($\text{m}^3 \text{ha}^{-1}$) and 20 cm or more in diameter ($\text{m}^3 \text{ha}^{-1}$), respectively, while total downed volume combines both ($\text{m}^3 \text{ha}^{-1}$). Bioclim 10 signifies the mean temperature of the warmest quarter, crucial for understanding the growing season and biological processes. Bioclim 7 indicates the temperature annual range, serving as a proxy for the climatic oceanity-continentiality gradient. The unique species in site index quantifies species exclusively found in one site pair, providing insights into site-specific biodiversity.

3 Results

3.1 Which variables explain the species richness?

The correlation matrix (Fig. 3) revealed intricate relationships among the variables. A strong positive correlation was observed between stand age and the age of oldest tree, reflecting the even-aged nature of the previously clear-cut forests. The cut stumps index was negatively correlated with species richness, all variables related to dead wood and age of oldest tree. The annual temperature range and the mean temperature of warmest quarter (Bioclim 7 and Bioclim 10) were weakly and negatively correlated with species richness. Moreover, the temperature of warmest quarter showed a negative correlation with connectivity (all.80.a2). Species richness exhibited strong positive correlations with all variables related to dead wood, especially the total volume of coarse woody debris (CWD), the index W (representing volume and diversity of deadwood), the volume of large deadwood and total volume of deadwood. Additionally, a substantial positive correlation was observed with the index of unique species.

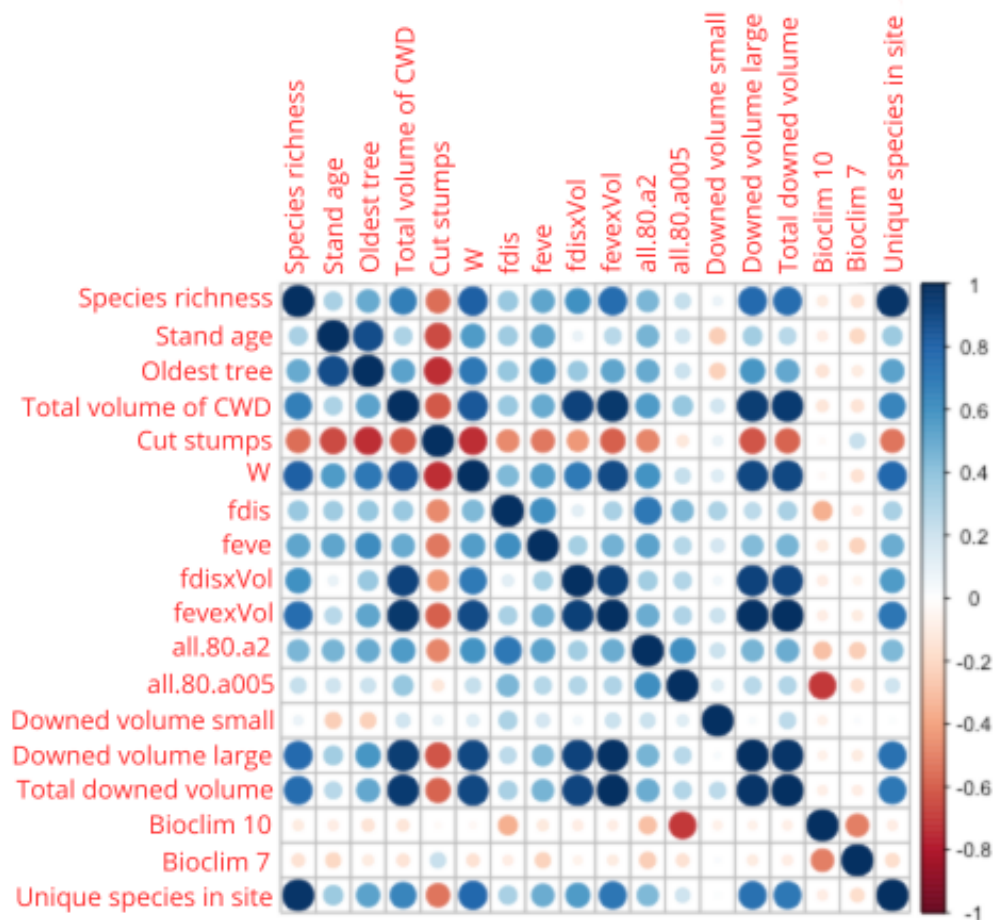


Figure 3. Correlation matrix of measured variables. The response variable in focus was species richness, and the correlation matrix showed strong positive correlations with the dead wood variables. A deeper shade of blue and a larger circle indicated stronger positive correlation, while a deeper shade of red and larger circle indicated stronger negative correlation. Conversely, a lighter colour and smaller circle indicated a weaker correlation.

It is important to acknowledge that several variables related to dead wood are intercorrelated. For instance, the total volume of coarse woody debris and the total volume of downed dead wood are not mutually exclusive, leading to a consistent correlation between them. Likewise, the variable W, which accounts for both the volume and diversity of dead wood, also exhibits a strong correlation with other dead wood variables.

Table 2. Summary table of all models and results from GLM analyses. Models 1-3 test the explanation of species richness, model 4 tests the effect of forest type (previously clear-cut [CC] vs. near-natural [NN] forest), and model 6 tests the explanation of unique species. Bioclim 10 = Mean temperature of the warmest quarter; Bioclim 7 = Temperature annual range; W = Volume and diversity of dead wood. Bold p-values denote significant effects.

Model	Estimate	Std. Error	z	P
Model 1 (species richness)				
(Intercept)	3.481	0.036	95.863	< 0.001
W	0.254	0.323	7.848	< 0.001
Model 2 (species richness in NN)				
(Intercept)	3.656	0.047	77.723	< 0.001
W	0.250	0.047	7.848	< 0.001
Model 3 (species richness in CC)				
(Intercept)	3.306	0.055	59.738	< 0.001
W	0.070	0.056	1.245	0.213
Model 4 (species richness and management type)				
(Intercept)	3.392	0.068	49.594	< 0.001
Management type (NN)	0.420	0.093	4.501	< 0.001
Bioclim 10	0.160	0.098	1.620	0.105
Bioclim 7	0.007	0.067	0.101	0.919
Management type (NN): Bioclim 10	-0.081	0.133	-0.614	0.540
Management type (NN): Bioclim 7	-0.070	0.092	-0.759	0.448
Bioclim 10: Bioclim 7	0.193	0.098	1.970	0.049
Management type (NN): Bioclim 10: Bioclim 7	0.118	0.144	0.820	0.412

Model 6 (unique species in site)				
(Intercept)	2.427	0.062	38.827	< 0.001
W	0.309	0.051	7.631	< 0.001

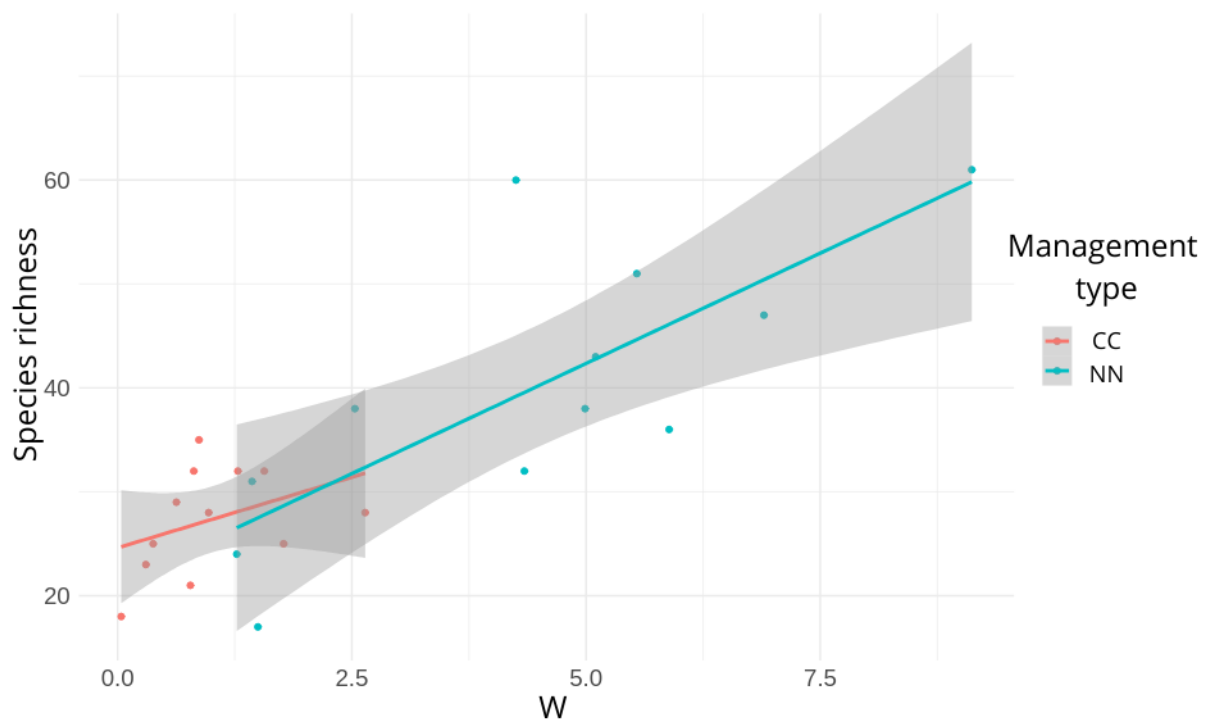


Figure 4. Relationship between species richness and *W* (volume and diversity of dead wood) in 12 site pairs with different forest management history (previously clear-cut forests [CC] and near-natural forests [NN]).

The model selection procedure indicated that models including variable *W*, which encapsulates both quantitative and qualitative aspects of dead wood, resulted in better model fit compared to those models that included other measures of dead wood when applied to the entire dataset (Table 2) (See appendix Tables 9-12 for AIC scores). Consequently, a positive relationship was observed between species richness and *W* (Fig. 4). The species richness in near-natural forests was explained by the same variable as the whole dataset, variable *W* (Table 2, Model 2). For previously clear-cut forests, the model selection suggested variable *W* again as the key variable responsible for explaining the species richness. However, the regression analysis did not show a statistically significant relationship with *W* (Table 2, Model 3).

3.2 The effect of management type on species richness

Species richness in each forest site is visualized in Figure 5. The mean in the near-natural forests significantly differed from that in the previously clear-cut forests, as detailed in Appendix, Table 5. Moreover, near-natural forests exhibited an overall species richness almost 1.5 times higher than the previously clear-cut forests (see Appendix for calculations).

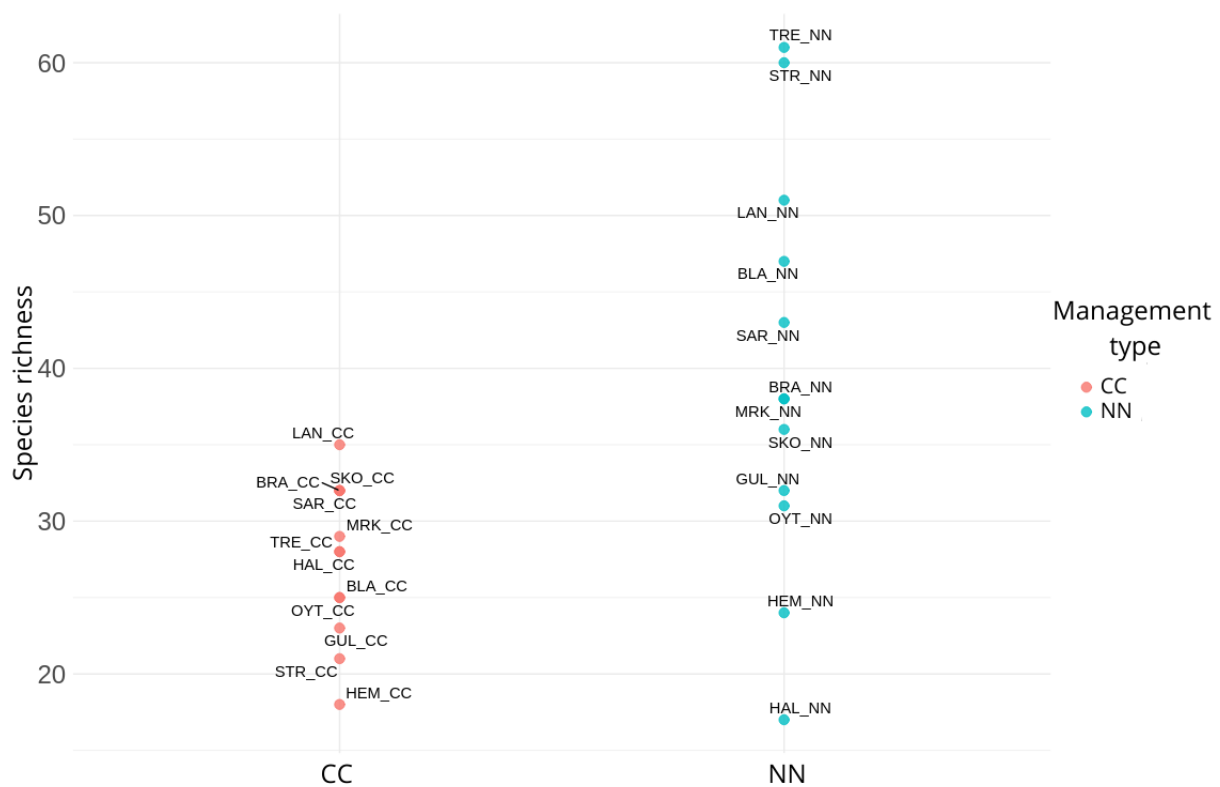


Figure 5. Comparison of species richness in 12 site pairs with different forest management history (previously clear-cut forests [CC] and near-natural forests [NN]). Full names of sites are given in Table 1.

The GLM analysis indicated a significant influence of the near-natural management type on species richness (Table 2, Model 4). The interaction between Bioclim 7 and Bioclim 10 also showed significance. The ANOVA results further confirmed these findings (Table 3). It showed that management type had a substantial impact on species richness, as evidenced by a significant reduction in deviance when this variable was included. The climatic variables, Bioclim 7 and Bioclim 10, contributed to a lesser extent individually. However, the interaction between Bioclim 7 and Bioclim 10, contributed significantly to the model by reducing deviance. The three-way interaction between management type and the two climatic variables did not significantly enhance the model's explanatory power.

Table 3. Results from analysis of variance (ANOVA) testing the effect of forest type (previously clear-cut [CC] vs. near-natural [NN] forest). Bioclim 10 = Mean temperature of the warmest quarter; Bioclim 7 = Temperature annual range.

Model 5 (ANOVA: species richness and management type)	Df	Deviance	Resid_Df	Resid_Dev
NULL			23	90.021
Management type	1	28.079	22	61.942
Bioclim 10	1	0.731	21	61.211
Bioclim 7	1	5.562	20	55.649
Management type: Bioclim 10	1	1.471	19	54.179
Management type: Bioclim 7	1	1.898	18	52.280
Bioclim 10: Bioclim 7	1	12.223	17	40.058
Management type: Bioclim 10: Bioclim 7		0.267	16	39.386

3.3 Red-listed species

Out of the 162 identified species in this study, 15 are listed on the Norwegian Red List 2021 as endangered (EN) (1), vulnerable (VU) (6) or near threatened (NT) (8) (Artsdatabanken, 2021a) (Fig. 6). Most of these red-listed species were primarily found in near-natural forest sites. The only exception was *Chaetoporellus curvisporus* (36), which was identified at the previously clear-cut site in Särkilampi (Appendix, Table 7).

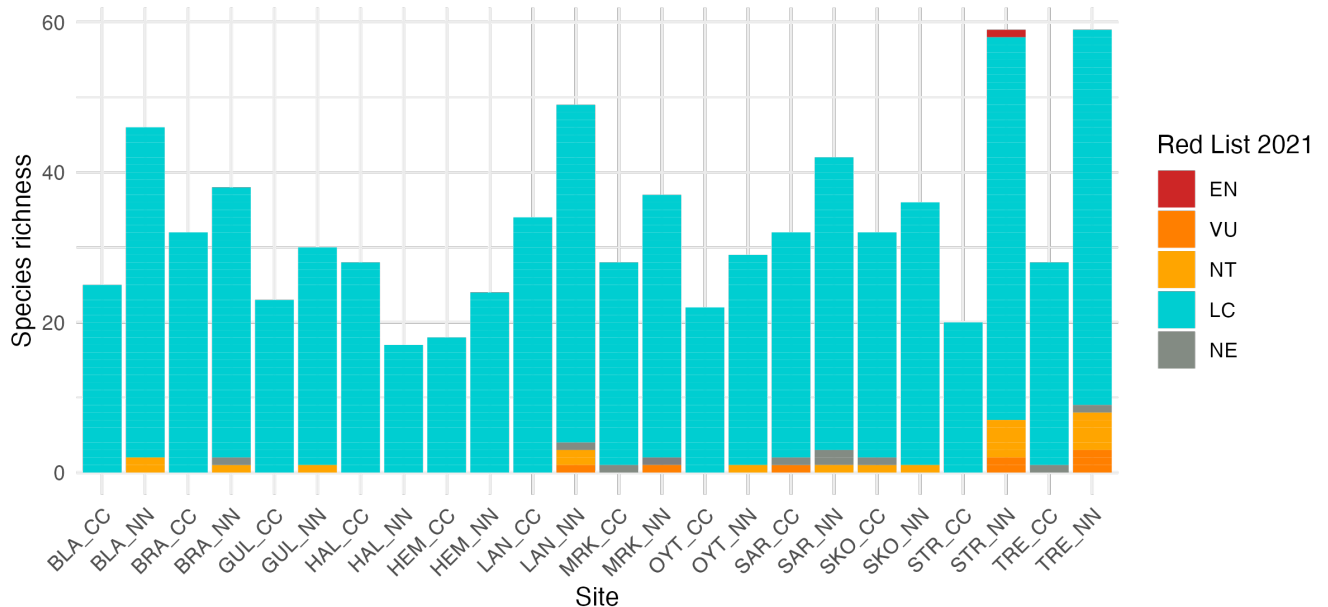


Figure 6: Overview of species richness and red-listed species in each forest site. The colors on the bars correspond to the species red-list status. Full list of species is given in Table

7 (appendix), and full names of sites are given in Table 1. EN = endangered; VU = vulnerable; NT = near threatened; LC = least concern; NE = not evaluated. CC = previously clear-cut forests; NN = near-natural forests.

3.4 Unique species in site

Model 6 (Table 2) tested which variables explained the unique species in each site. It showed that *W* had positive significant effect on the number of unique species. The number of unique species was always higher in near-natural forests compared to previously clear-cut forests, except in Halden where the number of unique species in the previously clear-cut forest was 10, while in the near-natural forest, it was only 4. The biggest difference in unique species between management types was found in Storås and Tretjerna, respectively 8 (CC) and 29 (NN), and 6 (CC) and 28 (NN) (Appendix, Table 6).

3.5 Indicator species analysis

The indicator species analysis revealed a total of four species indicative of near-natural forests, while none were identified for previously clear-cut forests (Table 4). Among these indicator species, three of them are categorized as least concern (LC) and the fourth as near threatened (NT). The presence and frequency of indicator species are displayed in Figure 7 and Table 4. *Athelia decipiens* had the lowest total abundance, while *Globulicium hiemale* showed to be the most frequent occurring species, being present across all near-natural sites, as well as some of the previously clear-cut sites. *Phellinus ferrugineofuscus* had the highest total abundance, primarily due to the presence in Storås and Tretjerna. *Phellinus nigrolimitatus* had the highest abundance in Skotjernfjell.

Table 4. Names of indicator species indicative of near-natural forests. Results from indicator species analysis with Red List status and the species frequency in previously clear cut (CC) and near-natural (NN) forests. LC = Least concern; NT = Near threatened.

Species	stat	P	Red List category	CC frequency	NN frequency
<i>Athelia decipiens</i>	0.736	0.025	LC	1	13
<i>Globulicium hiemale</i>	0.848	0.010	LC	9	23
<i>Phellinus ferrugineofuscus</i>	0.688	0.040	LC	2	35
<i>Phellinus nigrolimitatus</i>	0.782	0.005	NT	2	22

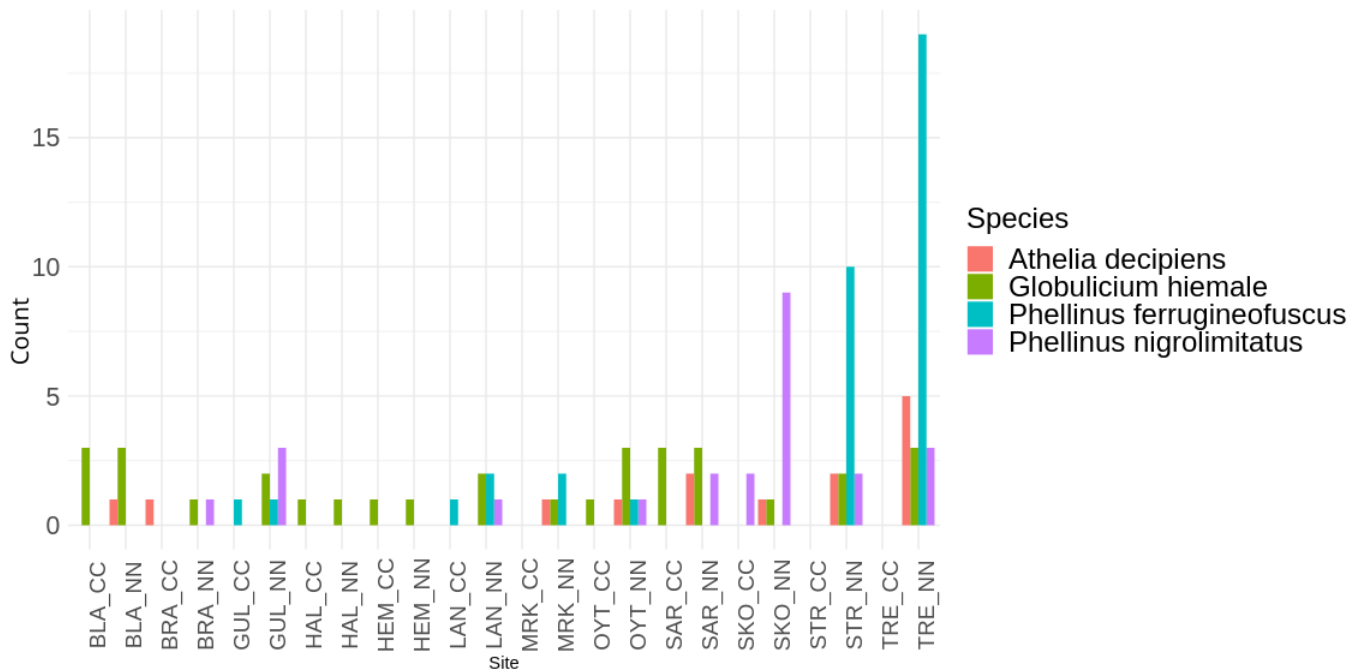


Figure 7. Indicator species and their presence and abundance in the forest sites. *Globulicium hiemale* is present in all near-natural sites, while *Phellinus ferrugineofuscus* has the highest abundance (especially high in near-natural sites in Storås and Tretjerna). Full names of site names are given in Table 1.

3.6 NMDS ordination analysis

Previously clear-cut and near-natural forest sites were widely scattered across most of the ordination space (Fig. 8), and statistical analysis (envfit) showed no significance for management type on species composition. However, there seemed to be a pattern where near-natural sites were more often located to the upper left side of the centre, and previously clear-cut sites were more often located to the bottom/bottom right of the centre. Cut stumps seemed to follow the first axis, which explained most of the variation in the data. Most near-natural forest sites were in the opposite direction of the cut stumps arrow, except from Hemberget, Halden and Øytjern. The previously clear-cut site in Blåfjell deviated from the anticipated pattern, positioned opposite to the cut stumps arrow. It is also interesting that Tretjerna and Storås were quite high up on the second axis regardless of management type, but still separated along the first axis.

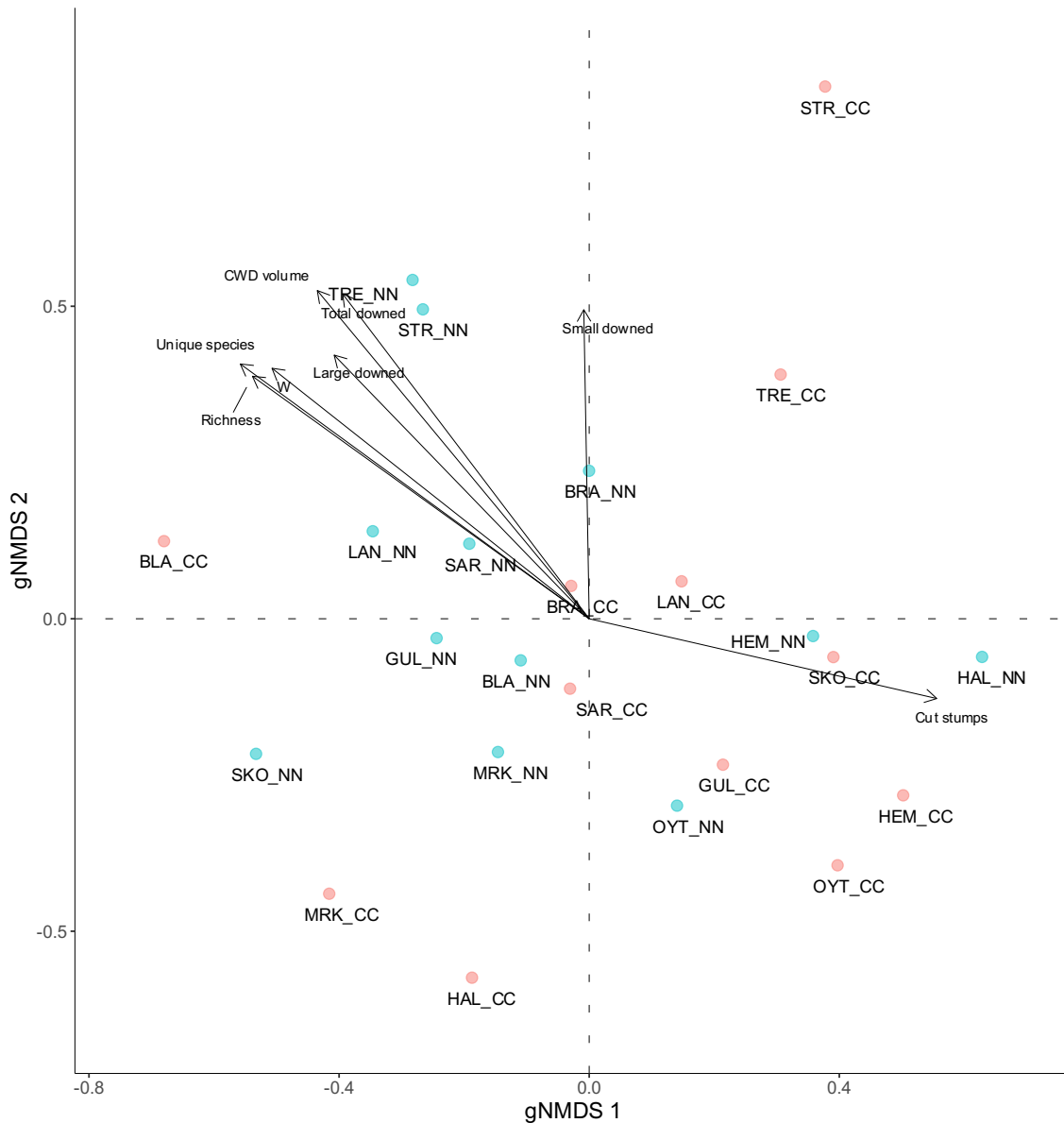


Figure 8. Non-metric multidimensional scaling (NMDS) ordination plot of all 24 sites. The arrows are vectors for the significantly correlated ($p < 0.05$) environmental variables. The direction of the arrow indicates the maximum dissimilarity in the groups, and the length is proportional to the squared correlation coefficient (r^2). CC forests (previously clear-cut) are shown as pink circles, and NN forests (near-natural) as blue circles. Richness = Species richness; Unique species = Number of unique species in site; W = Volume and diversity of deadwood; Large downed = Volume of large, downed deadwood (≥ 20 cm in diameter [$m^3 ha^{-1}$]); CWD volume = Total volume (standing + downed) of coarse woody debris; Total downed = Total volume of downed dead wood; Small downed = Volume of small-diameter, downed dead wood (< 20 cm in diameter [$m^3 ha^{-1}$]). Full names of site names are given in Table 1.

Figure 9 visualise the distribution of species, and the pattern reflects the distribution of forest sites in Figure 8. Red-listed species (red points) were positioned to the left of the second axis (red points). The left side of the ordination space also had a considerably higher density of species, including both every red-listed species and

three out of four indicator species (*A. decipiens* [13], *G. hiemale* [56] and *P. nigrolimitatus* [92]) (Fig. 9). On the upper left side, a cluster of species associated with the near-natural sites in Tretjerna and Storås was formed. In the same area, many of the red-listed species were also located. One extreme outlier on the left side is the species *Chondrostereum purpureum* (37), exclusively located in the previously clear-cut site in Blåfjell. Additionally, a smaller cluster formed on the left side with species *Asterostroma laxum* (11), *Botryobasidium aureum* (22), *Hyphodontia abieticola* (69), *Oligoporus rennyi* (84) and *Trechispora stellulata* (143), all exclusively found in the near-natural site in Skotjernfjell. Similarly, species *Hyphoderma obtusiforme* (66) and *Hyphodontia floccosa* (72) were found solely in the near-natural site in Marker, and *Hyphodontia alutaria* (70) and *Vararia investiens* (156) were found solely in the previously clear-cut site in Halden.

The right side of the second axis displayed fewer species, with only two notable outliers from the previously clear-cut site in Storås (Fig. 9). Despite its relatively low species richness, this site was distinguished from the rest (Fig. 8) due to the presence of two unique species, associated with birch (*Betula*): *Antrodiella pallescens* (9) and *Tyromyces chioneus* (155).

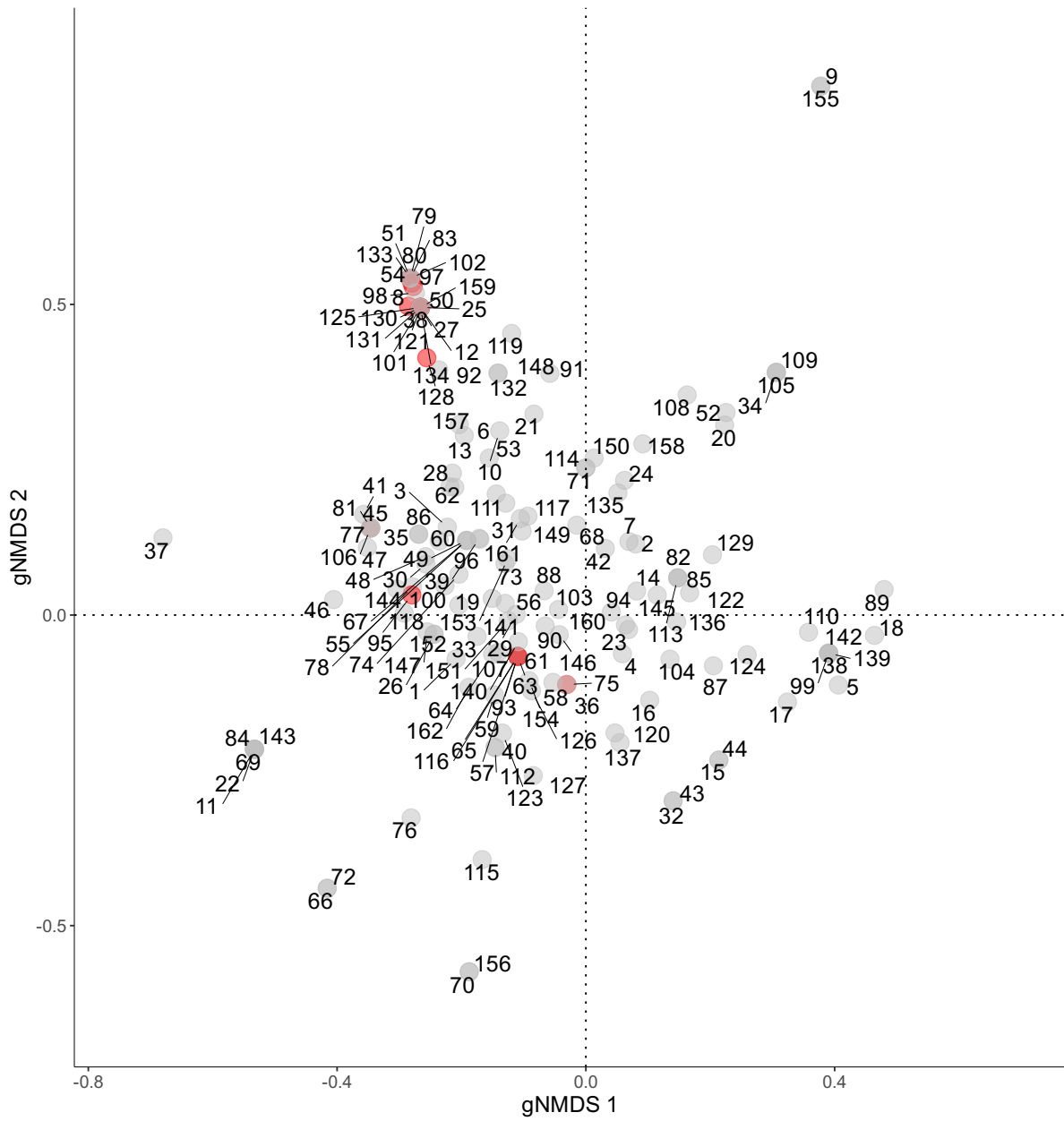


Figure 9. Non-metric multidimensional scaling (NMDS) ordination plot of all 162 species. Red-listed species are shown as red circles, and other species as grey circles. Where species are overlapping, a darker shade of red or grey is present. Full names of species are given in appendix, Table 7.

4 Discussion

My thesis aimed to investigate the intensity and frequency of previous logging activity and the effects this has on fungal biodiversity, including a comparative analysis of biodiversity in wood-inhabiting fungi between mature forests previously subjected to clear-cutting and near-natural forests. An understanding of the long-term effects of clear-cutting on biodiversity is crucial for understanding how human activities influence ecosystems. Biodiversity, particularly in dead wood, is under threat due to deforestation and fragmentation (Stokland et al., 2012). Therefore, understanding the role of dead wood is important for the protection of red-listed species and for encouraging sustainable forestry. My research contributes to filling the knowledge gap by focusing on fungal species and analysing how clear-cutting has impacted their biodiversity. The following discussion will delve deeper into my findings, interpreting them in the context of existing scientific literature.

4.1 Exploring species richness.

The findings in my study supported my first hypothesis that near-natural forests exhibit higher biodiversity of wood-inhabiting fungi compared to previously clear-cut forests. Specifically, near-natural forests had almost 1.5 times higher species richness. In addition to having higher species richness, the results also showed that red-listed species were predominantly found in near-natural forests. According to the study by Ylläsjarvi et al. (2011), species richness, including red-listed fungi, increased with the presence of dead wood. Both model 4 (Table 2) and Model 5 (Table 3) demonstrated that the near-natural management type significantly influenced species richness. This emphasises that near-natural forests are important habitats, offering resources and ecological conditions that previously clear-cut forests can't. The interaction between Bioclim 7 and Bioclim 10 suggests that the effect of one climatic variable on species richness may depend on the level of the other, underscoring the complex interplay between these environmental factors in shaping species richness. However, the three-way interaction between management type and the two climatic variables did not significantly enhance the model's explanatory power, implying that the combined effect of management type and these climatic variables on species richness does not vary significantly across the different levels of these factors.

The correlation matrix (Fig. 3) showed that the cut stumps index was strongly negatively correlated to species richness. In the case of threatened species, Penttilä (2004) found that the number of cut stumps was the best explanatory variable for the number of polypore species. This negative effect of previous logging activities has also been presented by Bader et al. (1995) and Sippola (2001). However, in contrast to these findings, the cut stumps variable did not appear as a significant explanatory variable for species richness in the GLM analyses. Instead, results from the GLM analyses confirmed that the diversity and volume of dead wood (*W*) was a crucial factor influencing biodiversity, supporting the second hypothesis. Previous studies (Hottola et al., 2009; Penttilä et al., 2004) also identified the diversity of dead wood as the best predictor of overall species richness, here in polypore fungi. In my study, *W* significantly influenced species richness in near-natural forests but was not significant in previously clear-cut sites. This could imply that the volume and diversity of dead wood is never large enough in previously clear-cut sites. As shown in Figure 4, the gradient in *W* was too narrow to detect substantial effects. This finding aligns with other studies demonstrating reduced dead wood volume and species richness in clear-cut forests (Asplund et al., 2024; Küffer & Senn-Irlet, 2005; Sippola et al., 2001).

4.2 Perspectives on unique species and indicator species

4.2.1 *Unique species*

There was a consistently higher number of unique species in near-natural sites compared to their previously clear-cut site pair, except for the near-natural site in Halden. This also supports my first hypothesis that near-natural forests generally provide a wider range of habitats and resources, supporting a greater diversity of species. The near-natural site in Halden also had the lowest species richness of all sites. The exception observed in Halden can be explained by its lack of natural forest characteristics (Asplund et al., 2024). It had lower volumes of dead wood and less structural heterogeneity compared to the other near-natural forests. The high number of unique species in the near-natural site in Tretjerna can be observed in conjunction with their forest characteristics. Asplund et al. (2024) reported that the volume of downed dead wood in Tretjerna was 124 m³ ha⁻¹. This was twice as much as the site with the second highest volume (near-natural site in Braskereidfoss; 51.2 m³ ha⁻¹). They also found that Tretjerna had the highest variation in tree heights. The near-

natural site in Storås also had a high number of unique species. However, the explanation for this is not as straightforward as in Tretjerna. Storås held an intermediate position in terms of dead wood volume and the density of cut stumps, suggesting that geographic factors could potentially play a role. In addition, Storås and Tretjerna share intermediate bioclimatic conditions, which, along with geographical factors, could influence the species richness and diversity observed in these areas.

4.2.2 Indicator species

The indicator species found in this study partially align with the indicator species system used in Nordic countries (Jensen et al., 2022). *Phellinus ferrugineofuscus* and *Phellinus nigrolimitatus* are listed as indicator species for old-growth spruce forests. *P. nigrolimitatus* is also red categorized as near threatened (NT) on the Norwegian Red List. A thorough analysis from Stokland and Kauserud (2004) on *P. nigrolimitatus* showed strong evidence of the species association with intermediate to well-decayed (decay stage class 3-5) spruce logs of large dimensions (> 20 cm in DBH). The study also documented clear negative effects of substrate reduction caused by forest management. It's common for previously clear-cut forests to lack dead wood in later stages of decay and with larger dimensions (Asplund et al., 2024; Juutilainen et al., 2014; Stokland et al., 2012). This pattern is typically attributed to the removal of mature trees during logging activities, which disrupts the natural progression of decay and limits the availability of large-dimension logs. This characteristic absence was also observed in this study system, further underscoring the impact of clear-cutting practices on forest structure and, potentially, on biodiversity. In this study, *P. nigrolimitatus* was predominantly found in near-natural sites, except for two occurrences in the previously clear-cut site in Skotjernfjell, further demonstrating the influence of forest management on species distribution.

Despite not being listed as official indicator species, *Athelia decipiens* and *Globulicium hiemale* were presented as indicators for near-natural forests in my study. Stokland and Larsson (2011) categorized them as common species on intermediately decayed conifer trees. However, it was noted that *A. decipiens* was more confined to large-dimension logs, which are less common in previously clear-cut sites, whereas *G. hiemale* was identified as a generalist species, i.e. had no specific preference for log dimension. This could explain why *G. hiemale* was found in 17 out of 24 sites in this study, with at least one occurrence in each of these sites.

Fomitopsis rosea is categorized as a near-threatened species on the Norwegian Red List. The species was exclusively identified within the near-natural sites in Storås and Tretjerna, with 6 and 15 occurrences respectively. Because it only occurred at two sites it was not identified as an indicator species in this study. It is, however, on the list of indicator species in Nordic countries (Jensen et al., 2022). In addition, research by Sippola et al. (2001) identified it as a good indicator of primeval spruce forests in Fennoscandia. The study found that the species was entirely absent from selectively logged sites, mirroring its absence in previously clear-cut sites in my study. Bader et al. (1995) and Bredesen et al. (1997) reported similar findings. This pattern could potentially explain its rarity in most near-natural sites as well. The prevalence of cut stumps in most sites, regardless of management type, may create an environment less conducive for this species, contributing to its limited distribution. This underscores the intricate relationship between forest management practices and the presence and distribution of certain species.

4.3 Effect of management type on species composition

Previous studies have shown that species richness of wood-inhabiting fungi increases with log size (Stokland et al., 2012) and the authors proposed two primary explanations for the relationship: Firstly, larger logs provide more microhabitats with different diameters and decay stages, along with varied moisture levels throughout the wood. Secondly, larger volumes offer more space and resources for species to coexist. Additionally, a third factor is the extended persistence time of large logs which may contribute to longer colonization periods. (Stokland et al., 2012). This contributes to explaining why the dead wood variables (CWD volume, total downed, large downed and W) held significance in the NMDS ordination plot (Fig. 8). The NMDS ordinations revealed a pattern between species composition and our documented, historical logging activities, even though the management type (i.e. CC or NN) did not show statistical significance.

The cut stumps index almost aligned with the first axis (Fig. 8) and near-natural forest sites were predominantly found on the left side of the first axis, while previously clear-cut forest sites were found on the right side. This could suggest that logging activities likely have had an impact on species composition, even if the overall management type distinction did not explain the species composition in my study. The

near-natural sites in Hemberget, Halden and Øytjern deviated from the anticipated pattern, meaning that the species composition found in these sites was more similar to other previously clear-cut sites that were positioned along the cut stumps arrow. Similarly, the previously clear-cut site in Blåfjell was positioned opposite of the cut stumps arrow, implying that the species composition was more like the near-natural sites. Blåfjell also only had 27 cut stumps, which was surprisingly low for a previously clear-cut site. The near-natural sites of Storås and Tretjerna were distinguished by their considerable species richness. These sites both harboured 7 out of the 15 species that are classified as red-listed, underscoring their ecological significance in the context of this study.

Although the management type was not statistically significant in explaining species composition within each forest site, the observed pattern aligns somewhat with my third hypothesis, which suggested that the forest's historical logging activities would influence the species composition. A possible explanation for this could be that many previously clear-cut and near-natural sites exhibited similar species richness levels and indications of past logging activities (density of cut stumps). This observation indicates that factors beyond management type, such as natural variation between forests and the influence of unexplored variables, play a significant role in shaping species composition.

4.4 Methodological uncertainties

The field study methodology had some uncertainties that should be acknowledged. With only 12 pairs of sites, the limited sampling size may have constrained the generalizability of the findings due to environmental differences across regions. The 0.2 ha survey plots for cut stumps might not have fully captured the history of past logging activities, as stumps located outside the transect would have been missed. Additionally, the decay stage classification relied on subjective visual assessment and knife insertion, which could have led to inconsistent results across different surveyors. Finally, the exclusion of cut stumps from the fungi survey might have underrepresented fungal diversity by omitting species specifically associated with cut stumps. Acknowledging these uncertainties is important for accurate interpretation of the results and for guiding future research.

5 Conclusions

The results of this thesis revealed that near-natural sites had significantly higher species richness than the previously clear-cut sites. The volume and diversity of dead wood best explained species richness, while connectivity was not significant. Red-listed species were predominantly found in the near-natural sites. No statistical evidence directly linked management type to species composition, although a pattern suggesting a potential effect of management type was observed.

My thesis provides important insights into the relationship between historical logging activities and biodiversity in wood-inhabiting fungi. It contributes to reinforcing the importance of preserving and increasing the volume and diversity of dead wood and limiting logging activities to support rich fungal biodiversity. For further research, it would be interesting to study if the findings from this study are consistent across other taxonomical groups.

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Appendix

Table 5. Results of a Welch Two Sample t-test comparing the mean species richness in previously clear-cut and near-natural forests. The mean species richness was found to be significantly lower in CC as compared to NN forests. The p-value of this test is 0.009, indicating a statistically significant difference between the two management types. CC = previously clear-cut; NN = near natural.

Metric	Value
Mean in CC	27.33
Mean in NN	39.83
Difference	12.50
p-value	0.009

Calculation of ratio and percentage difference in species richness in previously clear-cut and near-natural forests:

$$\text{Percentage difference: } \left(\frac{12.5}{27.33} \right) \times 100\% = 45.73729\% \approx 45.7\%$$

$$\text{Ratio} = \frac{39.83}{27.33} = 1.457373 \approx 1.46$$

Table 6. List of number of unique species in site. Full names of sites are given in Table 1. CC = previously clear-cut; NN = near-natural.

Site ID	Management type	Unique species in site
BLA_CC	CC	6
BLA_NN	NN	17
BRA_CC	CC	12
BRA_NN	NN	14
GUL_CC	CC	6
GUL_NN	NN	13
HAL_CC	CC	10
HAL_NN	NN	4
HEM_CC	CC	3
HEM_NN	NN	4
LAN_CC	CC	12
LAN_NN	NN	25
MRK_CC	CC	10
MRK_NN	NN	15
OYT_CC	CC	6
OYT_NN	NN	10
SAR_CC	CC	11
SAR_NN	NN	20
SKO_CC	CC	11

SKO_NN	NN	15
STR_CC	CC	8
STR_NN	NN	29
TRE_CC	CC	6
TRE_NN	NN	28

Table 7. Full list of wood-inhabiting fungi. Species marked with * are indicator species (chapter 3.4). LC = Least concern; NT = Near threatened; VU = Vulnerable; EN = Endangered; NE = Not evaluated.

Number	Species	Red List category	CC frequency	NN frequency
1	<i>Alutaceodontia alutacea</i>	LC	3	7
2	<i>Amphinema byssoides</i>	LC	23	27
3	<i>Amylocorticium cebennense</i>	LC	1	5
4	<i>Amylostereum chailletii</i>	LC	2	3
5	<i>Antrodia heteromorpha</i>	LC	1	2
6	<i>Antrodia serialis</i>	LC	10	65
7	<i>Antrodia sinuosa</i>	LC	2	3
8	<i>Antrodiella citrinella</i>	NT	0	11
9	<i>Antrodiella pallescens</i>	LC	1	0
10	<i>Asterodon ferruginosus</i>	LC	9	18
11	<i>Asterostroma laxum</i>	LC	0	1
12	<i>Athelia bombacina</i>	LC	0	2
13	<i>Athelia decipiens</i> *	LC	1	13
14	<i>Athelia epiphylla</i>	LC	17	21
15	<i>Athelia fibulata</i>	LC	1	0
16	<i>Athelia neuhoffii</i>	LC	2	2
17	<i>Athelidium stridii</i>	LC	4	1
18	<i>Athelopsis glaucina</i>	LC	1	3
19	<i>Athelopsis subinconspicua</i>	LC	0	5
20	<i>Basidioradulum radula</i>	LC	3	1
21	<i>Boidinia furfuracea</i>	LC	1	4
22	<i>Botryobasidium aureum</i>	LC	0	1
23	<i>Botryobasidium botryosum</i>	LC	45	65
24	<i>Botryobasidium candicans</i>	LC	1	1
25	<i>Botryobasidium ellipsosporum</i>	LC	0	1
26	<i>Botryobasidium intertextum</i>	LC	0	1
27	<i>Botryobasidium laeve</i>	LC	0	3
28	<i>Botryobasidium obtusisporum</i>	LC	19	25
29	<i>Botryobasidium subcoronatum</i>	LC	7	10
30	<i>Botryohypochnus isabellinus</i>	LC	2	4

31	<i>Butyrea luteoalba</i>	LC	2	2
32	<i>Byssoctricium pulchrum</i>	LC	0	1
33	<i>Ceraceomyces eludens</i>	LC	15	18
34	<i>Ceraceomyces serpens</i>	LC	1	0
35	<i>Cerinomyces crustulinus</i>	NE	0	2
36	<i>Chaetoporellus curvisporus</i>	VU	1	0
37	<i>Chondrostereum purpureum</i>	LC	1	0
38	<i>Cinereomyces lindbladii</i>	LC	0	2
39	<i>Conferticum ochraceum</i>	LC	1	4
40	<i>Coniophora arida</i>	LC	0	2
41	<i>Coniophora olivacea</i>	LC	0	9
42	<i>Coniophora puteana</i>	LC	2	1
43	<i>Corticium boreoroseum</i>	LC	0	1
44	<i>Cristinia helvetica</i>	LC	1	0
45	<i>Crustoderma corneum</i>	VU	0	1
46	<i>Cylindrobasidium evolvens</i>	LC	6	3
47	<i>Cystostereum murrayi</i>	LC	0	4
48	<i>Dacryobolus sudans</i>	LC	2	4
49	<i>Eonema pyriforme</i>	NE	0	1
50	<i>Exidiopsis calcea</i>	LC	0	1
51	<i>Fibricium lapponicum</i>	VU	0	3
52	<i>Fomes fomentarius</i>	LC	27	11
53	<i>Fomitopsis pinicola</i>	LC	21	78
54	<i>Fomitopsis rosea</i>	NT	0	21
55	<i>Ganoderma applanatum</i>	LC	0	1
56	<i>Globulicium hiemale*</i>	LC	9	23
57	<i>Gloeophyllum odoratum</i>	LC	0	1
58	<i>Gloeophyllum sepiarium</i>	LC	1	6
59	<i>Hastodontia hastata</i>	LC	12	17
60	<i>Heterobasidium parviorum</i>	LC	3	6
61	<i>Hymenochaete fuliginosa</i>	LC	0	1
62	<i>Hyphoderma argillaceum</i>	LC	4	9
63	<i>Hyphoderma capitatum</i>	NT	0	1
64	<i>Hyphoderma cremeoalbum</i>	LC	0	3
65	<i>Hyphoderma definitum</i>	LC	0	1
66	<i>Hyphoderma obtusifforme</i>	LC	1	0
67	<i>Hyphoderma occidentale</i>	LC	0	1
68	<i>Hyphoderma sibiricum</i>	LC	1	1
69	<i>Hyphodontia abieticola</i>	LC	0	1
70	<i>Hyphodontia alutaria</i>	LC	1	0
71	<i>Hyphodontia cineracea</i>	LC	0	1
72	<i>Hyphodontia floccosa</i>	NE	3	0
73	<i>Hyphodontia pallidula</i>	LC	5	10

74	<i>Hyphodontia subalutacea</i>	LC	5	4
75	<i>Hypochnicium eichleri</i>	NE	1	0
76	<i>Hypochnicium lundellii</i>	LC	1	1
77	<i>Hypochnicium punctulatum</i>	LC	0	2
78	<i>Jaapia ochroleuca</i>	LC	1	4
79	<i>Junghuhnia collabens</i>	VU	0	1
80	<i>Leptoporus mollis</i>	NT	0	1
81	<i>Leucogyrophana sororia</i>	LC	0	1
82	<i>Membranomyces delectabilis</i>	LC	1	0
83	<i>Mucronella calva</i>	LC	0	1
84	<i>Oligoporus rennyi</i>	LC	0	1
85	<i>Oligoporus romellii</i>	LC	1	0
86	<i>Oligoporus sericeomollis</i>	LC	0	2
87	<i>Peniophora pithya</i>	LC	8	5
88	<i>Peniophorella praetermissa</i>	LC	10	20
89	<i>Phanerochaete gigantea</i>	LC	3	4
90	<i>Phanerochaete sanguinea</i>	LC	6	4
91	<i>Phanerochaete sordida</i>	LC	3	2
92	<i>Phellinus ferrugineofuscus*</i>	LC	2	35
93	<i>Phellinus laevigatus</i>	LC	0	1
94	<i>Phellinus lundellii</i>	LC	2	6
95	<i>Phellinus nigrolimitatus*</i>	NT	2	22
96	<i>Phellinus viticola</i>	LC	17	54
97	<i>Phlebia centrifuga</i>	NT	0	12
98	<i>Phlebia livida</i>	LC	0	2
99	<i>Phlebia radiata</i>	LC	1	0
100	<i>Phlebia segregata</i>	LC	0	6
101	<i>Phlebia subulata</i>	VU	0	1
102	<i>Physisporinus vitreus</i>	LC	0	1
103	<i>Piloderma byssinum</i>	LC	30	51
104	<i>Piloderma fallax</i>	LC	8	7
105	<i>Piloderma lanatum</i>	NE	1	0
106	<i>Piloderma olivaceum</i>	LC	0	1
107	<i>Piloderma sphaerosporum</i>	LC	2	2
108	<i>Piptoporus betulinus</i>	LC	5	2
109	<i>Porpomyces mucidus</i>	LC	2	0
110	<i>Postia alni</i>	LC	0	1
111	<i>Postia caesia</i>	LC	24	49
112	<i>Postia calvenda</i>	NA	0	1
113	<i>Postia fragilis</i>	LC	1	0
114	<i>Postia tephroleuca</i>	LC	0	1
115	<i>Pseudoxenasma verrucisporum</i>	LC	1	1
116	<i>Pycnoporellus fulgens</i>	NT	0	1

117	<i>Resinicium bicolor</i>	LC	7	5
118	<i>Resinicium furfuraceum</i>	LC	1	8
119	<i>Serpula himantioides</i>	LC	2	4
120	<i>Sidera lunata</i>	LC	1	1
121	<i>Sistotrema autumnale</i>	LC	0	1
122	<i>Sistotrema brinkmannii</i>	LC	9	9
123	<i>Sistotrema muscicola</i>	LC	2	0
124	<i>Sistotrema octosporum</i>	LC	0	2
125	<i>Sistotremastrum suecicum</i>	LC	0	1
126	<i>Skeletocutis amorpha</i>	LC	0	2
127	<i>Skeletocutis biguttulata</i>	LC	8	2
128	<i>Skeletocutis brevispora</i>	VU	0	7
129	<i>Skeletocutis carneogrisea</i>	LC	9	14
130	<i>Skeletocutis exilis</i>	NT	0	2
131	<i>Skeletocutis jelicii</i>	EN	0	1
132	<i>Skeletocutis kuehneri</i>	LC	0	2
133	<i>Skeletocutis papyracea</i>	LC	0	1
134	<i>Spongiporus undosus</i>	LC	0	1
135	<i>Stereum rugosum</i>	LC	20	10
136	<i>Stereum sanguinolentum</i>	LC	31	25
137	<i>Tomentellopsis echinospora</i>	LC	8	6
138	<i>Tomentellopsis zygoesmoides</i>	NE	1	0
139	<i>Trametes betulina</i>	LC	1	0
140	<i>Trechispora farinacea</i>	LC	9	11
141	<i>Trechispora hymenocystis</i>	LC	0	2
142	<i>Trechispora mollusca</i>	LC	1	0
143	<i>Trechispora stellulata</i>	LC	0	1
144	<i>Trechispora subsphaerospora</i>	LC	2	5
145	<i>Trichaptum abietinum</i>	LC	72	77
146	<i>Tubulicrinis accedens</i>	LC	1	5
147	<i>Tubulicrinis calothrix</i>	LC	5	11
148	<i>Tubulicrinis confusus</i>	NE	0	2
149	<i>Tubulicrinis glebulosus</i>	LC	2	5
150	<i>Tubulicrinis sororius</i>	LC	1	2
151	<i>Tubulicrinis subulatus</i>	LC	5	6
152	<i>Tulasnella violea</i>	LC	0	1
153	<i>Tylospora asterophora</i>	LC	4	2
154	<i>Tylospora fibrillosa</i>	LC	26	29
155	<i>Tyromyces chioneus</i>	LC	1	0
156	<i>Vararia investiens</i>	LC	5	0
157	<i>Veluticeps abietina</i>	LC	1	12
158	<i>Vesiculomyces citrinus</i>	LC	31	12
159	<i>Xenasmatella christiansenii</i>	LC	0	1

160	<i>Xenasmatella vaga</i>	LC	34	40
161	<i>Xylodon asperus</i>	LC	22	27
162	<i>Xylodon brevisetus</i>	LC	15	17

Table 8. Selection table from dredge-function for Model 1. All.80.a2 = connectivity; Bioclim 10 = Mean temperature of the warmest quarter; Bioclim 7 = Temperature annual range; Cut stumps = Number of cut stumps >5 cm in diameter; Total downed = Total volume of downed deadwood; Oldest tree = Oldest tree in the stand; Stand age; Average age of trees within the stand; W = Volume and diversity of dead wood.

	Intercept	all.80.a2	Bioclim 10	Bioclim 7	Cut stumps	Total downed	Oldest tree	Stand age	W	df	logLik	AICc	delta	weight
1	3.481								0.254	2	-79.767	164.1	0	0.157
2	3.481							0.040	0.271	3	-79.300	165.8	1.693	0.067
3	3.481						0.037		0.278	3	-79.500	166.2	2.094	0.055
4	3.480		-0.026						0.252	3	-79.526	166.3	2.146	0.054
5	3.481				0.026				0.272	3	-79.662	166.5	2.417	0.047
6	3.481			-0.014					0.251	3	-79.696	166.6	2.486	0.045
7	3.481	-0.006							0.257	3	-79.759	166.7	2.611	0.043
8	3.481					0.0003			0.253	3	-79.767	166.7	2.629	0.042
9	3.480					-0.09		-0.077	0.374	4	-78.874	167.9	3.747	0.024
10	3.480		-0.030					-0.043	0.271	4	-78.991	168.1	3.982	0.021
11	3.480		-0.034				-0.047		0.283	4	-79.123	168.4	4.245	0.019
12	3.481			-0.021				-0.044	0.270	4	-79.151	168.4	4.301	0.018
13	3.480		-0.044	-0.037					0.246	4	-79.177	168.5	4.354	0.018
14	3.481						0.009	-0.046	0.268	4	-79.294	168.7	4.588	0.016
15	3.481	0.005						-0.041	0.269	4	-79.295	168.7	4.589	0.016
16	3.481				0.002			-0.039	0.273	4	-79.299	168.7	4.597	0.016
17	3.480			-0.015			-0.038		0.277	4	-79.419	168.9	4.837	0.014
18	3.480					-0.03	-0.046		0.309	4	-79.441	169.0	4.882	0.014
19	3.480		-0.025		0.022				0.268	4	-79.450	169.0	4.898	0.014
20	3.480	-0.019	-0.031						0.263	4	-79.452	169.0	4.902	0.014

Table 9. Selection table from dredge-function for Model 2. All.80.a2 = connectivity; Bioclim 10 = Mean temperature of the warmest quarter; Bioclim 7 = Temperature annual range; Cut stumps = Number of cut stumps >5 cm in diameter; Total downed = Total volume of downed deadwood; Oldest tree = Oldest tree in the stand; Stand age; Average age of trees within the stand; W = Volume and diversity of dead wood.

	Intercept	all.80.a2	Bioclim 10	Bioclim 7	Cut stumps	Total downed	Oldest tree	Stand age	W	df	logLik	AICc	delta	weight
1	3,656								0.250	2	-44.347	94.0	0	0.189
2	3,654							-0.078	0.238	3	-43.069	95.1	1.111	0.108
3	3,654						-0.062		0.267	3	-43.519	96.0	2.010	0.069
4	3,654		-0.062						0.246	3	-43.643	96.3	2.258	0.061
5	3,646		-0.184	-0.200				-0.186	0.160	5	-38.589	97.2	3.151	0.039
6	3,650		-0.104				-0.098		0.273	4	-41.857	97.4	3.402	0.034
7	3,642		-0.222	-0.183			-0.188		0.251	5	-38.727	97.5	3.427	0.034
8	3,656	-0.024							0.265	3	-44.283	97.6	3.539	0.032
9	3,656			-0.015					0.246	3	-44.309	97.6	3.591	0.031
10	3,656					0.019			0.231	3	-44.326	97.7	3.623	0.031
11	3,656				0.005				0.253	3	-44.345	97.7	3.662	0.030
12	3,652		-0.076					-0.087	0.232	4	-42.048	97.8	3.782	0.028
13	3,653			-0.067				-0.107	0.218	4	-42.419	98.6	4.525	0.020
14	3,652					-0.111		-0.114	0.342	4	-42.609	98.9	4.904	0.016
15	3,663					0.204				2	-46.836	99.0	4.977	0.016
16	3,653				-0.065			-0.101	0.187	4	-42.746	99.2	5.179	0.014
17	3,653	0.068						-0.109	0.189	4	-42.750	99.2	5.188	0.014
18	3,654						-0.024	-0.063	0.247	4	-42.991	99.7	5.669	0.011
19	3,654		-0.255	-0.311				-0.264		4	-43.146	100.0	5.978	0.009
20	3,653	-0.073	-0.087						0.292	4	-43.160	100.0	6.006	0.009

Table 10. Selection table from dredge-function for Model 3. All.80.a2 = connectivity; Bioclim 10 = Mean temperature of the warmest quarter; Bioclim 7 = Temperature annual range; Cut stumps = Number of cut stumps >5 cm in diameter; Total downed = Total volume of downed deadwood; Oldest tree = Oldest tree in the stand; Stand age; Average age of trees within the stand; W = Volume and diversity of dead wood.

	Intercept	all.80.a2	Bioclim 10	Bioclim 7	Cut stumps	Total downed	Oldest tree	Stand age	W	df	logLik	AICc	delta	weight
1	3,308									1	-36,177	74,8	0	0,156
2	3,306								0,070	2	-35,416	76,2	1,411	0,077
3	3,306							0,061		2	-35,631	76,6	1,841	0,062
4	3,307						0,049			2	-35,812	77,0	2,204	0,052
5	3,307					0,044				2	-35,875	77,1	2,329	0,049
6	3,307	0,040								2	-35,933	77,2	2,446	0,046
7	3,302					-0,355			0,418	3	-34,106	77,2	2,459	0,046
8	3,307			-0,037						2	-35,978	77,3	2,536	0,044
9	3,308		0,029							2	-36,048	77,4	2,675	0,041
10	3,308				0,011					2	-36,160	77,7	2,899	0,037
11	3,305							0,052	0,063	3	-35,033	79,1	4,313	0,018
12	3,305						0,041		0,066	3	-35,165	79,3	4,576	0,016
13	3,305				0,031				0,078	3	-35,274	79,5	4,794	0,014
14	3,306		0,020						0,067	3	-35,360	79,7	4,965	0,013
15	3,306					0,042		0,059		3	-35,362	79,7	4,970	0,013
16	3,306			-0,018					0,065	3	-35,375	79,7	4,995	0,013
17	3,306				0,043			0,079		3	-35,404	79,8	5,055	0,012
18	3,306	0,009							0,065626	3	-35,406	79,8	5,059	0,012
19	3,306		0,034					0,064		3	-35,456	79,9	5,159	0,012
20	3,306						-0,126	0,182		3	-35,464	79,9	5,175	0,012

Table 11. Selection table from dredge-function for Model 4. All.80.a2 = connectivity; Bioclim 10 = Mean temperature of the warmest quarter; Bioclim 7 = Temperature annual range; Cut stumps = Number of cut stumps >5 cm in diameter; Total downed = Total volume of downed deadwood; Oldest tree = Oldest tree in the stand; Stand age; Average age of trees within the stand; W = Volume and diversity of dead wood.

	Intercept	Management type	Bioclim 10	Bioclim 7	Management type: Bioclim 10	Management type: Bioclim 7	Bioclim 10: Bioclim 7	Management type: Bioclim 10: Bioclim 7	df	logLik	AICc	delta	weight	
1	3,412	+	0,096	-0,042			0,245		5	-85,499	184,3	0	0,503	
2	3,416	+	0,182	-0,037	+		0,257		6	-84,182	185,3	0,975	0,309	
3	3,412	+	0,094	-0,034		+	0,244		6	-85,479	187,9	3,568	0,084	
4	3,414	+	0,200	0,013	+	+	0,248		7	-83,655	188,3	3,980	0,069	
5	3,392	+	0,160	0,007	+	+	0,193	+	8	-83,319	192,2	7,907	0,010	
6	3,305	+	-0,079	-0,101					4	-91,451	193,0	8,676	0,007	
7	3,308	+							2	-94,597	193,8	9,435	0,004	
8	3,305	+		-0,060					3	-93,287	193,8	9,444	0,004	
9	3,303	+	-0,023	-0,098	+				5	-90,715	194,8	10,434	0,003	
10	3,309	+	-0,031						3	-94,232	195,7	11,333	0,002	
11	3,306	+	-0,079	-0,075		+			5	-91,275	195,9	11,553	0,002	
12	3,307	+		-0,035		+			4	-93,124	196,4	12,022	0,001	
13	3,307	+	0,014	-0,028	+	+			6	-89,766	196,5	12,143	0,001	
14	3,307	+	0,029		+				4	-93,343	196,8	12,461	0,001	
15	3,615		0,083	-0,045			0,235		4	-99,675	209,5	25,124	0,000	
16	3,510		-0,085	-0,100					3	-	105,372	217,9	33,613	0,000
17	3,514								1	-	108,637	219,5	35,124	0,000
18	3,513			-0,056					2	-	107,480	219,5	35,201	0,000
19	3,513		-0,037						2	-	108,121	220,8	36,483	0,000

Table 12. Selection table from dredge-function for Model 6. All.80.a2 = connectivity; Bioclim 10 = Mean temperature of the warmest quarter; Bioclim 7 = Temperature annual range; Cut stumps = Number of cut stumps >5 cm in diameter; Total downed = Total volume of downed deadwood; Oldest tree = Oldest tree in the stand; Stand age; Average age of trees within the stand; W = Volume and diversity of dead wood.

	Intercept	all.80.a2	Bioclim 10	Bioclim 7	Cut stumps	Total downed	Oldest tree	Stand age	W	df	logLik	AICc	delta	weight
1	2,427								0,391	2	-69,926	144,4	0	0,167
2	2,425			-0,047					0,385	3	-69,675	146,5	2,126	0,058
3	2,424					-0,072			0,464	3	-69,687	146,6	2,149	0,057
4	2,426		-0,041						0,389	3	-69,725	146,6	2,226	0,055
5	2,426				0,042				0,421	3	-69,828	146,9	2,431	0,050
6	2,427							-0,004	0,392	3	-69,925	147,0	2,626	0,045
7	2,427	-0,003							0,393	3	-69,926	147,1	2,627	0,045
8	2,427						0,002		0,390	3	-69,926	147,1	2,628	0,045
9	2,423		-0,083	-0,090					0,375	4	-69,033	148,2	3,748	0,026
10	2,423		-0,050			-0,086			0,477	4	-69,391	148,9	4,464	0,018
11	2,424					-0,149		-0,072	0,571	4	-69,396	148,9	4,473	0,018
12	2,423				0,079	-0,104			0,553	4	-69,398	148,9	4,478	0,018
13	2,425			-0,058	0,064				0,429	4	-69,461	149,0	4,604	0,017
14	2,424			-0,041		-0,061			0,448	4	-69,502	149,1	4,685	0,016
15	2,424					-0,086	-0,027		0,496	4	-69,642	149,4	4,966	0,014
16	2,426		-0,038		0,035606				0,414	4	-69,656	149,4	4,992	0,014
17	2,426	-0,016		-0,049					0,393	4	-69,657	149,4	4,995	0,014
18	2,426			-0,049				-0,012	0,389	4	-69,658	149,4	4,998	0,014
19	2,424	-0,016				-0,076			0,477	4	-69,669	149,4	5,018	0,014
20	2,425			-0,047			-0,001		0,385	4	-69,675	149,5	5,031	0,014



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