Diversity of Wood-Inhabiting Fungi Across Managed and Wildfire Boreal Scots Pine Forest Chronosequences

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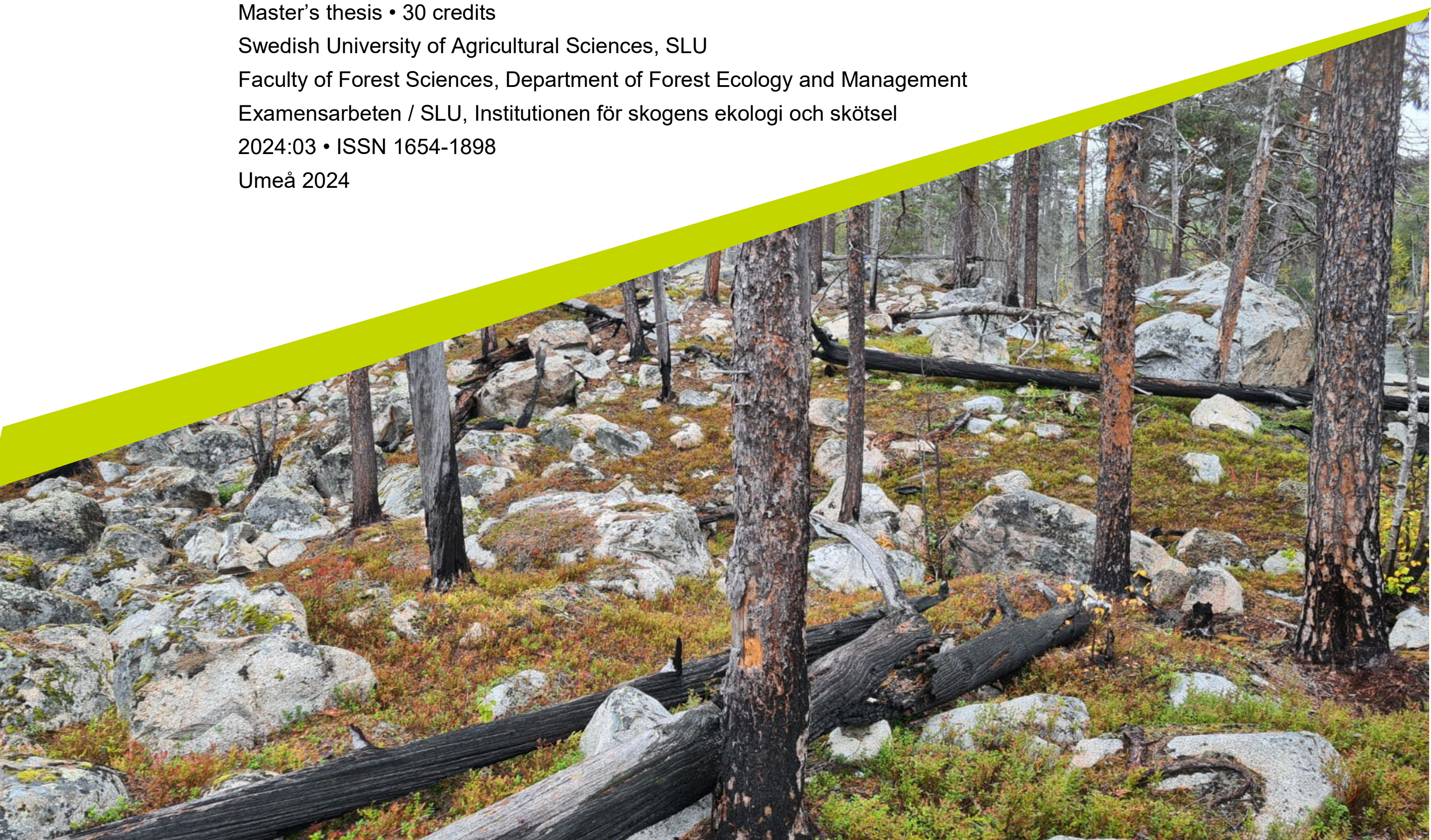

Diversity of wood-inhabiting fungi across managed and wildfire boreal Scots pine forest chronosequences

Mångfald av vedlevande svampar i kronosekvenser av skötta och brända boreala tallskogar

Noel Wieser

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Abstract

I studied how and if clear-cut forestry mimics the disturbance of wildfire by comparing the impacts of these disturbances on coarse woody debris (CWD) volumes, CWD characteristics, as well as species richness of wood inhabiting fungi (WIF) and red-listed species. I compared a wildfire chronosequence with a temporal range of 4-375 years since the last disturbance, and a managed chronosequence ranging between 1-109 years since clearcut. I found that young post-disturbance forests showed the highest CWD volumes. On average, burnt forests showed three times higher CWD volumes, albeit with high variability over time. Characteristics of CWD greatly differed, with fire-disturbed forests showing higher amounts of CWD in larger diameter classes and later decomposition stages. I found that CWD volume predicted species richness of WIF similarly in both chronosequences. Fire-disturbed forests generally reached higher values of WIF species richness; however, when comparing species richness per CWD volume, no significant differences were found between the chronosequences. Species composition differed between the chronosequences, attributed to higher occurrences of red-listed wood fungi in the wildfire chronosequence, particularly those associated with Norway spruce CWD. My study highlights the very different impacts of the fire and clear-cut disturbances on WIF in boreal pine-dominated forests and the need for prescribed burnings to generate charred CWD and thus, maintain natural pine-dominated forests and associated wood fungal species. Furthermore, my results demonstrate the importance of young and old growth post-fire stands as landscape-level habitats and species reservoirs, particularly for red-listed fungal species. Importantly, I found an increase in CWD volumes in the managed forest in the youngest managed stands of the chronosequence, likely due to recent CWD retention efforts over the last few decades due to higher environmental concern in forestry.

Keywords: Biodiversity, fire ecology, species richness, wood-inhabiting fungi, dead wood characteristics, red-listed species

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Abbreviations

CWD	Coarse woody debris
FC	Fire chronosequence
MC	Managed chronosequence
WIF	Wood-inhabiting fungi
NFI	National forest inventory
RF	Retention forestry

1. Introduction

1.1 Background

The emergence of climate change as a significant threat to society and global ecosystems has promoted political commitments in transitioning towards a biobased economy in Sweden. The shift entails the usage of biofuels instead of fossil fuels, substituting plastic with pulp-based products and incorporating more timber into construction practices. The shift towards a bioeconomy has placed greater demands on Sweden´s forest. Concurrently, these forests are also expected to provide other crucial ecosystem services, such as biodiversity, which are leading to trade-offs and conflicts between these expectations (Lindahl et al. 2017). The intensified forestry practices employed to meet societal demands has resulted in a loss of natural forests, which are being replaced with monocultures. Consequently, there is a decline in forest species that depend on old growth forests (Felton et al. 2020; Skogsstyrelsen 2022).

In the forestry field, a common proposition is that clear-cutting mimics the effects of the natural wildfire disturbance, by setting in motion successional processes that resemble those observed in the aftermath of a wildfire (Skogsindustrierna 2023). However, there are significant distinctions in forest structure and development between succession in natural and managed forests. One of the most noteworthy distinctions is the higher presence of coarse woody debris in a natural forest on which many organisms are dependent (Stokland et al. 2012). Fungi are an organism group with several red-listed species that are dependent on natural forest dynamics (Berg et al. 1995). Wood-inhabiting fungi are saproxylic organisms that rely on the availability of coarse woody debris, and are decreasing as a result of intensified forest management practices (Berg et al. 1995; Artdatabanken 2020). Several fungal taxa are used as indicator species for forest continuity and conservation value in the Nordic countries due to their often specialized substrate requirements and sensitivity to environmental changes (Nitare 2020). Natural forest structures have decreased in forest landscapes where clear-cutting has replaced fire as the main disturbance agent.

1.1.1 The evolution of forestry in boreal Sweden

Forest utilization has a long history in Boreal Sweden. Throughout history, people have been utilising the forest for cattle grazing, reindeer herding, firewood, as well as engaging in slash and burn activities (Östlund & Zackrisson 1998). Prior to the 19th century the major influence on the forests of northern Sweden was connected to various agricultural practices which mostly had a marginal effect on the overall structure of the boreal forest (Esseen et al. 1997; Östlund et al. 1997). Sami forestry has also been important in the inland parts of northern Sweden, but has always been of low intensity (Rautio et al. 2016). However, forest utilization has undergone substantial changes during the last 150 years, leading to a successively more intense impact on the forest landscape (Östlund et al. 1997). The industrial revolution in western Europe led to the establishment of "timber frontiers" in regions with remaining forest resources. In northern Sweden exploitation began around 1850 and expanded northwards during the latter part of the 19th century (Östlund & Norstedt 2021). Initial large-scale logging and exploitation during the late 19th century consisted of logging of the largest trees, hereafter referred to as "high grading". High grading, leading to the removal of the largest trees and subsequent loss of ancient trees, had notable impacts on the ecosystem (Josefsson et al. 2010). Nevertheless, high graded stands in the northern parts of Sweden were still relatively intact in terms of structural diversity. From a biodiversity point of view, the maintained heterogeneous structure and continuity of tree cover of high graded stands were still beneficial for many forest dwelling species. However, even limited cuttings carried out a century ago, has the potential to impact contemporary wood inhabiting fungi in boreal forests, due to impact on the available coarse woody debris (CWD) and the distribution of its decay stages (Josefsson et al. 2010).

A more significant transformation of Swedish forests occurred with the introduction of clear-cutting during the first part of the 20th century (Lundmark 2020), which gained momentum on a larger scale during the 1950s (Östlund et al. 1997), and is up until today the prevailing forest management practice. Clear-cut forestry in Sweden is generally carried out by the removal of all or most trees (with the exception of retention areas), followed by soil scarification and planting of a single tree species. The resulting stands are even-aged monocultures with minimal structural complexity, which has resulted in a long-term decline in the mean age of Swedish forests (Ericsson et al. 2000; Axelsson & Östlund 2001). As a part of the "forest restoration program," previously high graded stands, perceived as low producing left-over forests, were revisited, clear-cut and re-planted (Andersson 2023), which had a significant impact on standing stock in the nation-wide growth stock survey (Riksskogstaxeringen 2023b). Fennoscandian forestry is characterized by its high degree of mechanization and efficiency and almost all forested land is used for production of saw timber and wood pulp (Esseen et al. 1997). Forestry has transformed the landscape and key characteristic natural forest structures, such as gap dynamics, fire disturbances, forest continuity and CWD, are now missing in large areas of Sweden, resulting in reduced forest complexity (Esseen et al. 1997).

1.1.2 Fire regime in boreal forests

Fire has historically been the main disturbance agent altering the structure and species composition of natural forests (Zackrisson 1977; Östlund et al. 1997; Linder & Östlund 1998). Fire is a naturally occurring phenomenon but has also been used by people for example to promote grazing, thus altering fire frequencies in the past (Cogos 2020). Forest fires in the boreal region were for the most part of low intensity, however fire frequency varied depending on local conditions (Ryan 2002), which resulted in a multi-dimensional landscape mosaic with high structural forest complexity (Zackrisson 1977). Consequently, many native species in the boreal forest have evolved in the presence of frequent forest fires (Esseen et al. 1997; Östlund et al. 1997). However, since the timber frontier in the beginning of the 1880s, forest fires have actively and efficiently been suppressed, and in the middle of the 20th century the total fire impact on the landscape was very limited (Östlund et al. 1997; Niklasson & Granstrom 2000). Hence, fire has been an essential ecosystem process in the boreal region and its suppression has resulted in far reaching consequences for biodiversity. This includes the decline of fire dependant tree species e.g. *Salix caprea* and *Populus tremula* and associated wood fungi (Östlund et al. 1997). As a result, prescribed burnings have more recently been re-introduced as a tool to benefit fire dependent organisms, increase dead wood volumes and diversity of dead wood characteristics (Hekkala et al. 2016; Ramberg et al. 2018). The ecological importance of fire in the boreal forest is further highlighted by the requirement for large certified forest owners in Sweden to intentionally burn 5% of their land over a consecutive 5-year period as a way of benefitting fire-dependent species (FSC 2020).

1.1.3 Current state of Sweden’s forests

Throughout the 20th century, Swedish forestry has increased the forest growing stock and simultaneously increased the annual harvest (Riksskogstaxeringen 2023b). This achievement is facilitated by a goal driven, production oriented, and rationalized forestry, where measures such as fertilization, clear-cutting, improved plant material and ditching are standard procedures (Jansson et al. 2011). The intensified forestry practices has consequently resulted in an active loss of biological legacies, as well as a transformation of the forest landscape resulting in habitat loss for many forest dwelling species (Felton et al. 2020).

With the 1993 Forestry Act (*SFS (1993:1096)* 1993), an environmental objective was established parallel with the long-standing goal of maintaining a high wood production. Retention forestry (RF) represents the conventional approach to integrate ecological considerations in contemporary clear-cut forestry practices in Sweden. Retention forestry is legally mandated in Sweden and outlined in the international forest certification standards (FSC, PEFC) (Gustafsson et al. 2010).

The overarching objective of RF is to preserve important biological remnants during the logging period, with the aim to sustain biodiversity, structural coherence, and ecosystem functions over long-term forest cycles. This preservation entails safeguarding important substrates such as lying and standing dead wood which require considerable time to develop, leaving single trees, tree patches, buffer zones bordering lakes, watercourses, and mires (Gustafsson et al. 2010). The organisms that benefit the most from retention forestry are ectomycorrhizal fungi, birds, and lichens (Rosenvald & Lõhmus 2008).

Since the introduction of RF, a clear objective has been to increase dead wood volumes in managed forests. A study by Jonsson et al. (2016), looked at how policy and certification schemes have affected the amount of dead wood using NFI data on dead wood volumes across Sweden. They found that during the studied 15-year period, dead wood in managed Swedish forests have increased with on average $1.5 m^3 ha^{-1}$ which, due to the low initial volumes, corresponds to a 25% increase. The study concludes that despite the increase, amount of dead wood does not align with the desired rate outlined in policy ambitions. Despite two decades of emphasis on the importance of dead wood, there are limited direct effects of these policy ambitions in practice.

Out of 2044 red-listed forests species, fungi together with lichen amount to 900 species (Skogsstyrelsen 2022). Since the introduction of the Swedish red list in its current form, year 2000, fungal species that are dependent on old growth forests has steadily decreased. The Swedish environmental goal “living forests” is not being met and the trajectory towards reaching it appears to be heading in the opposite direction (Artdatabanken 2020; Skogsstyrelsen 2022).

1.1.4 Dead wood and saproxylic fungi

In the Nordic countries, approximately 7500 forest species are saproxylic i.e. dependent on dead trees, either throughout their entire life cycle or during specific stages (Stokland et al. 2012). Therefore, the availability of dead wood is the most important factor influencing biodiversity in boreal forests (Esseen et al. 1997). Wood inhabiting fungi as well as many other organisms are dependent on CWD, (including all dead wood over >10cm in diameter; Dahlberg & Stokland 2004). Furthermore, there are critical thresholds in dead wood quantity and stage of decomposition that affects WIF abundance. There are several studies highlighting the importance of dead wood as a predictor of WIF abundance (Penttilä 2004; Ylisirniö et al. 2012). Increasing CWD volume and the numerous species associated with it, is one of the many functional goals of RF identified by (Gustafsson et al. 2010). Therefore, the dynamics of dead wood volume and decomposition plays a crucial role in maintaining a high species diversity in boreal forests (Bader et al. 1995; Sippola & Renvall 1999).

Accumulation of dead wood within a forest stand depends on three primary factors: site productivity, which governs the rate at which CWD is added to the ecosystem, disturbances, which introduces stochastic elements to an otherwise deterministic equilibrium, and stand succession (Harmon et al. 1986). Fundamentally, the long-term average volume at a site is shaped by the average inputs and decay rates, with disturbances playing a pivotal role in this ecological balance (Siitonen 2001).

There are multiple factors that influence the natural disturbance dynamics in a forest stand. These factors range from stand location, water availability and tree species composition (Ryan 2002). *Pinus sylvestris* has evolved with fire and can consequently survive and benefit from forest fires by developing defence mechanisms such as thick bark and high canopy during its mature life stage (Keeley 2012). In response to damage, pine develops wood rich in resin, commonly known in Swedish as “Kelo” wood. The slow decay rate of pine wood, attributed to its natural richness in tar, creates important substrates for species with different successional niches (Niemelä et al. 2002). In Sweden, a pine can live up to 800 years, and continue standing as dead wood for many decades after it has died. Eventually, as lying dead wood, it slowly decays on the forest floor, utilized by various species throughout these stages (Ehnström 2017). In other words, the substrate delivery time for the most specialized saproxylic fungi and beetles is long. In terms of biodiversity, around 200 beetles are almost fully dependant on pine

CWD. Furthermore, 68 species of butterflies, 500 species of wood inhabiting fungi, and at least 200 mycorrhizal fungal species are pine associated (Ehnström 2017). *Picea abies,* Norway spruce, is more susceptible to rot, and prone to wind damage due to its shallow root system (Ehnström 2017). Therefore, type of disturbance and tree species composition has a big impact on the available dead wood in a forest stand.

Site productivity refers to a biogeographic gradient impacting the deterministic balance of dead wood accumulation. A colder climate and shorter growing seasons result in a lower forest productivity in Fennoscandia's boreal forests, compared to the temperate regions of Europe. Furthermore, productivity varies greatly within Fennoscandia, with the southern parts belonging to the hemi-boreal vegetation zone and northern Sweden belonging to the boreal biome. As a result, productivity potentially reaches around 10 m^3 ha^{-1} in the south declining towards <1m^3 ha^{-1} in the northern scrublands and timberlines (Ahti et al. 1968; Siitonen 2001).

In Sweden's contemporary forest landscape, dead wood volumes greatly differ between primary forests and managed forests. There are estimates of the general CWD volume in old growth forests to range between 60-90 m^3 ha^{-1} in southern Fennoscandia, decreasing towards 20 m^3 ha^{-1} closer to the tree line (Siitonen 2001). The corresponding amount for managed forests, ranges between 2-10 m^3 ha^{-1} depending on the region (Jonsson et al. 2016). In productive forest land in Sweden the national average of dead wood lies around 6 m^3 ha^{-1}, however with significant geographical variation (Fridman & Walheim 1997). In a European context, the current dead wood volumes in managed forests generally amount to 10% of natural forest levels (Stokland et al. 2012). The 7500 saproxylic species in Fennoscandia has seen the amount of deadwood i.e. their habitat, reduced with over 90% in the managed forest landscape of Fennoscandia (Siitonen 2001).

The effect of forest management on CWD and WIF is well documented and the removal of substrate has been shown to reduce species richness and abundance, as well as reducing the amount of red-listed saproxylic fungi (Junninen & Komonen 2011). However, Sippola & Renvall (1999) showed that there is variability among old growth indicator species and their ecological tolerance towards the effects of logging. Wood inhabiting fungi known for preferring old growth forest habitats can survive for extended periods in managed forests, given that they were present before the cutting and their substrate was left intact. However, the species diversity of WIF is heavily reliant on the availability and diversity of decaying dead wood prior to any management practices. Furthermore, a continuous input of CWD is crucial to sustain communities of wood inhabiting fungi in the long-term.

At the stand scale, volume CWD has been shown to be the most important factor in determining species abundance. At the substrate scale, later decomposition stages are acknowledged of having special importance for red-listed species, as supported by studies such as Junninen & Komonen (2011); Ylisirniö et al. (2012). Additionally, size distribution is another important factor explaining what species assemblages occupy dead wood (Juutilainen et al. 2011). The occurrence of red-listed species appears to be closely linked to the presence of large diameter logs in boreal forests (Bader et al. 1995; Sippola et al. 2001; Hottola et al. 2009). According to Juutilainen et al. (2014), earlier research on the effects of forest management on wood inhabiting fungi has concentrated on CWD, even though it has been demonstrated that a substantial part of fungal species also utilize small dead wood pieces.

This thesis is based on data collected from two pine dominated forest chronosequences (age since disturbance gradients) which allows for highly detailed and comprehensive measurements within a carefully defined system. The first chronosequence for this study consists of managed pine forests spanning 110 years since some form of even-aged forest management was initiated, and the second age gradient is a pine dominated natural wildfire chronosequence ranging from 4 to 375 years since a stand replacing wildfire.

Aim and research questions

The purpose of the study is to gain a better understanding of how forestry in Sweden is affecting WIF over time by examining and comparing the abundance of selected fungal taxa in managed and burned forest stands. Many WIF are commonly used as indicator species for identification of primary forests due to their specialized substrate requirements and sensitivity to logging. Consequently, this taxonomic group serves as a compelling subject for long-term investigation into frequency dynamics and alterations in habitat requirements over time following management and natural disturbance. Utilizing two forest chronosequences (representing time since forest fire and time since clearcutting), with data on recorded fungal species, dead wood volume and its characteristics, this study aims to contribute to a better understanding of the temporal dimension and ecological prerequisites after a disturbance, influencing species diversity and red-listed species of WIF, and at what point in time fungal biodiversity is maximized. The questions I will explore are:

- How are the volume and characteristics, i.e., decay stage and diameter class, of CWD developing over time in a managed and wildfire forest chronosequence?

I hypothesize that dead wood volume will vary over time, having higher values initially after the disturbances followed by a decrease, and over time start to increase again. Furthermore, I hypothesize that known important dead wood characteristics such as diameter class and decay stage will greatly differ between the chronosequences and that the wildfire chronosequence will have higher dead wood volumes, greater dead wood tree species diversity and larger dead wood trunks than the managed chronosequence.

- How does stand level species richness and presence of red-listed species differ between a managed and wildfire chronosequence, and how is that related to diversity in dead wood characteristics? Does species richness per dead wood piece (species density) show similar values between the chronosequences over time?

I hypothesize that both species richness and species density will be higher in the wildfire chronosequence, due to higher CWD volumes in larger diameter classes and in later decay stages compared to in the managed chronosequence.

- How does fungal species composition differ between a managed and wildfire chronosequence, and are these differences related to variation in the presence of rare red-listed wood-inhabiting fungi?

I hypothesize that species composition will differ between the chronosequences whereby the presence of rare red-listed species will be higher in the wildfire chronosequence due to higher dead wood volumes and heterogenous CWD characteristics.

2. Method

2.1 Chronosequences

This thesis was based on data collected from two forest chronosequences (age since disturbance gradients). Each chronosequence was comprised of 18 stands located around Arvidsjaur, Norrbotten County (Figure 1). Most of the stands are owned by the state-owned forest company Sveaskog, however some of the fire stands are in nature reserves and managed by the county board. Studying chronosequences, allows for highly detailed and comprehensive measurements within a carefully defined system. The first chronosequence for this study consisted of managed pine forests spanning 110 years since some form of even-aged forest management was initiated. The managed stands have been subject to common silvicultural measures practiced in Sweden, such as pre-commercial thinning and thinning. The second age gradient was a pine dominated natural wildfire chronosequence ranging from 4 to 375 years since a wildfire. The wildfire intensity has varied across the stands and the chronosequence was generally representative of the range of variability in fire severity in boreal-pine forests. Additionally, there were some traces of selective logging in some of the older fire-stands and information on management history was provided by Sveaskog.

The stands selected for the chronosequences were filtered in a geographical information system (GIS) framework based on fulfilling the criteria of mesic soil moisture and pine dominance. They were characterized by a consistent ground vegetation profile, consisting of different ericaceous dwarf shrubs (*V. myrtillus*, *V. vitius ideaea*, and *E. hermaphroditum*) as well as feather mosses. Furthermore, the selection process aimed for the stands to be grouped in clusters, situated in close proximity to each other. As a result, each chronosequence was equally dispersed on the landscape (Figure 1). Studying chronosequences allows for powerful comparisons in how ecosystem services develop over time since a major disturbance, and how forestry versus wildfire disturbances affect those services (Gudrunsson 2013; Clemmensen et al. 2015; Stokland 2021). The project primarily focused on biodiversity change by examining wood-inhabiting fungi diversity from these two chronosequences, with the aim to contribute towards a better understanding of the temporal scales in the recovery, survivability, and dynamics of different fungal taxa after disturbance, and how their abundance varies in a managed versus a wildfire chronosequences.

2.2 Study area

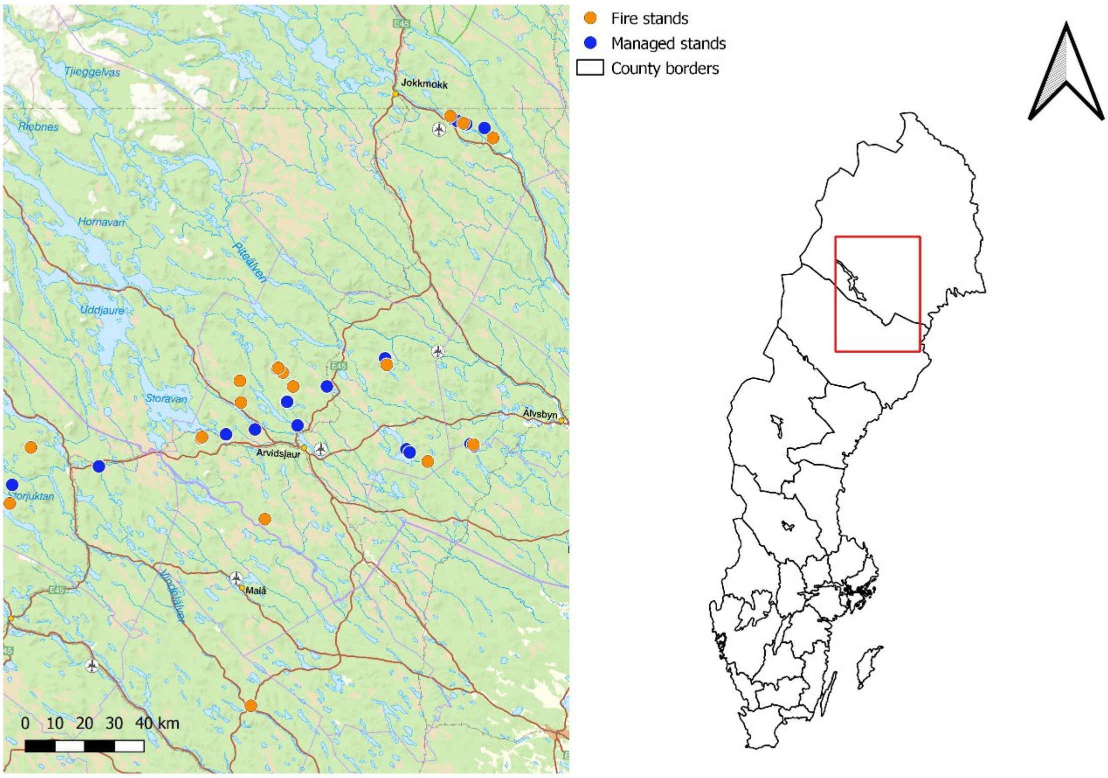

Figure 1. Location of forest stands that make up the two chronosequences. Fire stands are marked as orange and managed stands as blue. The right side of the figure depicts Sweden's county borders, and the square emphasizes the specific area of interest. Copyright for the overview map belongs to Lantmäteriet and the county borders to SCB.

2.3 Inventory method

This study was conducted based on data from a single fruiting body survey carried out for two weeks over 10-15th and 24-29th of September 2023. The inventory was carried out in 36 stands of 1 ha across northern Sweden (Figure 1). The stands each had 5 permanent subplots with a radius of 10 m located in the center and intercardinal corners of the stand. In each subplot, measurements of CWD and inventory of WIF growing on CWD were carried out. The data collection was facilitated by using ESRI field map and then exported to excel.

For the CWD measurement, all lying dead wood above >10 cm in diameter on the largest end, as well as >1 meter long was recorded with three measurements: bottom diameter, top diameter, and length. This was used to calculate the volume of each log in m^3, representing a conical frustum. For each measured log, the species was recorded and a decomposition grade (decay class) was estimated based on a graded scale of 0-4 according to Riksskogstaxeringen (2023a), where 0 = Fresh wood, 1= Hard wood, 2 = Partly decomposed. 3 = decomposed, 4 = Highly decomposed. On each measured log, presence (True/False) of each observed WIF was recorded, treating each species found on a CWD unit as a single record, regardless of the number of fruiting bodies. Observed WIF were identified in the field whenever possible. If identification was not possible in the field, a specimen was collected and later identified in lab with the aid of literature and microscope. A total of 48 specimen of WIF required further identification in the laboratory, which had not been identified at the time of my thesis and were subsequently excluded from the presented analysis. Twenty-eight of these specimens belonged to the wildfire chronosequence and were scattered evenly throughout the stands. The remaining 20 specimens belonged to the managed forests, with 10 recorded in M13 and 5 in M1a, with the remaining 5 evenly recorded across the managed chronosequence.

2.4 Data and statistical analyses

Latin name and conservation status for the recorded WIF was collected from artdatabanken (Artdatabanken 2023). Red-listed species included both threatened (VU, EN) and near threatened (NT) species. The data originated from 36 stands with 5 plots each. I added the data from each plot together resulting in stand level summaries for the dependent variables: species richness, red-listed species and volume dead wood.

The explanatory variable “time since disturbance” was derived from the different sites that were named either F(Fire) or M(Managed) followed by a number indicating elapsed time since the occurrence of the mentioned disturbances. Dead wood volume was summarized per site and upscaled into volume per hectare using the following equation:

$$Volume\ (m^3) \div sample\ plot\ area\ (m^2) * 5 * 10000\ (m^2).$$

Species richness was standardized per volume of CWD by dividing Species richness with dead wood volume, which resulted in the response variable species density, used in one of the models.

To test how CWD volume development over time was different between the chronosequences, I applied a quadratic polynomial linear model using the R statistical software (lm package with a second-degree polynomial; R Core Team 2023). When exploring the data, it became evident that the variables showed a nonlinear relationship that could not be fully captured by a simple linear regression. Thus, I decided to use polynomial linear models instead of simple linear regression models because the inclusion of a quadratic term achieved higher adjusted R-squared values, indicating a better fit to the data. The following polynomial model was applied:

$$Y=\beta_0+\beta_1X+\beta_2X^2+\beta_3Z+\beta_4X\cdot Z+\ \beta_5X^2\cdot Z + \epsilon.$$

In which the dependant variable Y was represented by either: Volume (m^3), volume per ha (m^3 ha^{-1}), species richness, species density and red-listed species. β_0=Intercept, β_1X= linear (time since disturbance or volume per ha (m^3 ha^{-1})), β_2 X^2=Quadratic (time since disturbance or volume per ha (m^3 ha^{-1})), β_3Z= A binary dummy variable that takes the value of either 0 or 1, representing “wildfire” or “managed”, $\beta_4X\cdot Z$= Interaction term, $\beta_5X^2\cdot Z$= Quadratic interaction term, ϵ=Error term that is assumed to be normally distributed. All polynomial models were tested for interaction effects, however if there were no statistically significant interactions, the simplest model with the best R-squared was chosen. We report in the text the R2 for the full model as well as R2 for the individual fits for either the wildfire or managed regressions.

I examined differences in dead wood characteristics by comparing descriptive statics of dead wood by tree species, diameter class and decay stages between the chronosequences. I summarized the stands F4a, F4b, F56a, F56b, M1a and M1b, to improve the visualization on CWD characteristics. Furthermore, to test for relationships between dead wood characteristics and species richness, I applied simple linear regressions (lm package), testing the relationships between species richness (response variable) and dead wood volume in various decay and diameter classes (considered as explanatory variables) using R statistical software (R Core Team 2023).

To test how volume dead wood predicted species richness I applied the same quadratic polynomial model as previously mentioned. The stand M13 was deemed an outlier due to significantly high dead wood volume and low species richness and therefore excluded from the model. Red-listed species and species density was also examined using the polynomial quadratic model.

To test whether species composition differed between the two chronosequences, I applied a non-metric multidimensional scaling (NMDS) ordination via the vegan package (Oksanen et al. 2022). NMDS is a means of visualising the similarity of individual sites. The analysis was based on bray-curtis dissimilarities conducted on presence/absence data of WIF from the 36 sites. Stress-values were assessed to determine the number of dimensions for the NMDS. A stress value of 0.129 was reached with a three-dimensional NMDS using 42 tries. Differences in species composition between managed and primary forest were tested with a pairwise comparison test (PERMANOVA), adjusted using Bonferroni corrected values, via the vegan package (Oksanen et al. 2022). Species were abbreviated using the first three letters of genus and species name, including conservation category, and the "plot" function in R was used to generate a visual representation of the species with a significance $p < 0.05$, derived from using the function "envfit" (Oksanen et al. 2022). The presence of red-listed WIF between the chronosequences was further assessed by examining a table generated from the dataset. The table, summarizing the occurrences of red-listed WIF across the studied stands, is provided in Appendix 1.

The raw excel data was imported into R studio (version 4.3.1, R Core Team 2023), where most of the summary statistics (dplr package, Wickham et al. 2023), and all statistical analyses were conducted. All figures were made using the ggplot package (Wickham 2016) and base R (R Core Team 2023).

3. Results

3.1 Dead wood

3.1.1 Dead wood volume over time

The values of dead wood volume were highest in the fire chronosequence (FC) (Figure 2). These values reached a mean of 57 (± 37 SD) m^3 ha^{-1} (max 127 m^3 ha^{-1}, min 5 m^3 ha^{-1}). Corresponding figures for the managed chronosequence (MC) were mean 20 (± 16 SD) m3 ha^{-1} (max 71 m^3 ha^{-1}, min 0.5 m^3 ha^{-1}). Both time after disturbance ($p=0.04$) and type of chronosequence ($p<0.01$) were significant predictors of dead wood volume, however, the model's explanation power was rather low ($R_{adj}^2=0.3488$), (MC, $R^2=-0.17$, FC, $R^2=0.19$). Initial dead wood volumes were high for both MC and FC immediately after disturbance. Over time, dead wood volume decreased in the MC however exhibiting variability (Figure 2). In the FC, dead wood volume, also declined until ~200 years, after which it started increasing, gradually reaching the initial post disturbance values, and thereby following a U-shape.

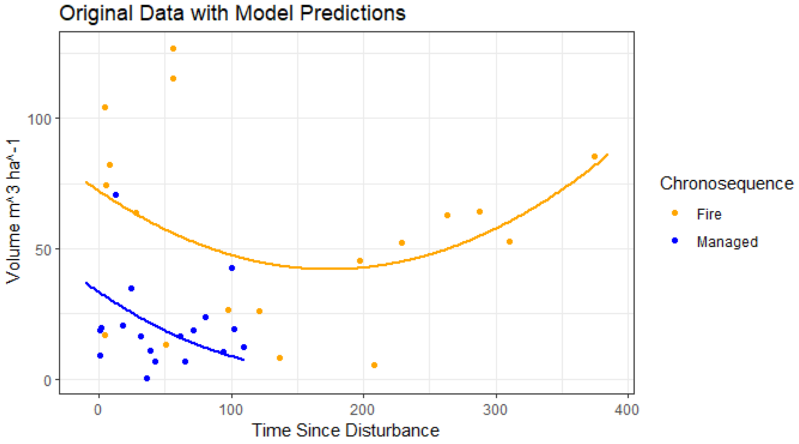

Figure 2: Dead wood volume over time from two chronosequences, each comprised of 18 forest stands located in the Arvidsjaur region. Predicted values are represented by lines and original data plotted for reference, whereby the fire stands are indicated with orange and managed blue.

3.1.2 Dead wood characteristics

Dead wood by tree species

The managed chronosequence (MC) had greater CWD tree species diversity compared to the fire chronosequence (FC). In terms of CWD volume, pine was the dominating tree species in the MC (Figure 3). Generally, there were higher amounts of broadleaved species in the following 24 years after disturbance compared to the later temporal stages of the MC. Spruce CWD appeared after ~ 100 years and gradually became a greater proportion of total CWD. Overall, pine CWD still dominated throughout the chronosequence.

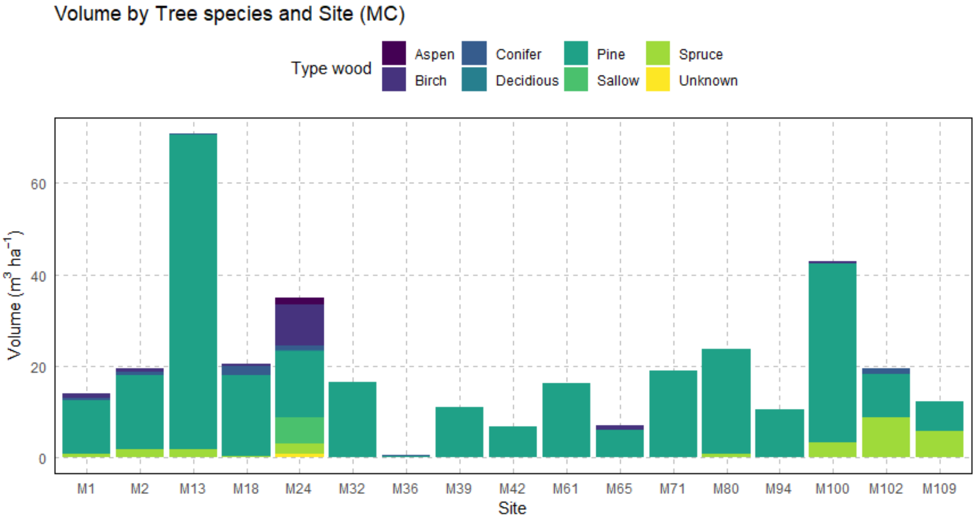

Figure 3. Dead wood volume by tree species for each forest stand in the managed chronosequence. Each site is represented by the letter M as in "managed", followed by a number representing time passed since disturbance (clear-cut).

The fire chronosequence (FC), had a higher proportion of CWD in different tree species compared to MC (Figure 4). Most notable was spruce CWD which occurred throughout the chronosequence; initial spruce volumes were high, however decreased gradually and reached the lowest volumes around 100 years after disturbance, following the same trend as the general CWD volume for all tree species. Spruce CWD reappeared again after around 121 years and then gradually increased up until the end of the chronosequence.

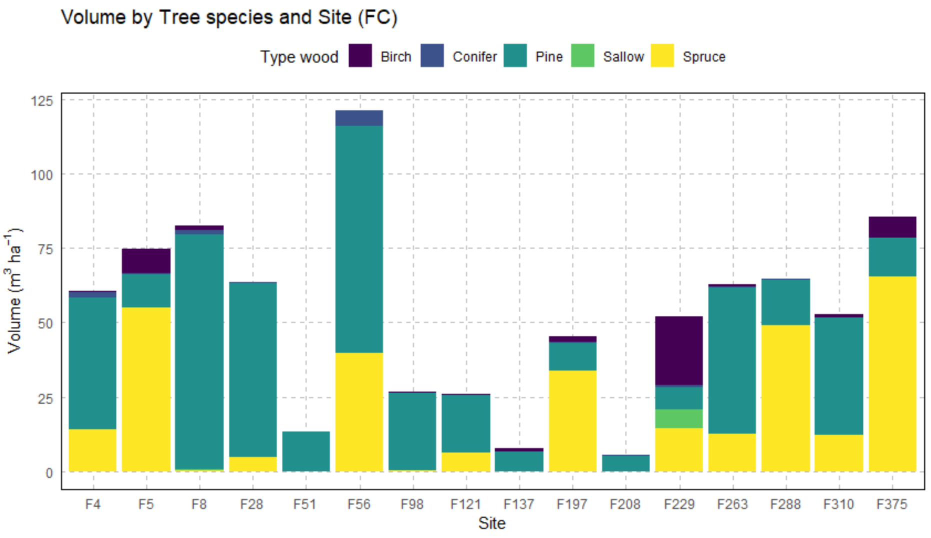

Figure 4. Dead wood volume by tree species for each site in the fire chronosequence. Each site is represented by the letter F as in Fire, followed by a number representing time since disturbance (fire).

Dead wood by decay stages

Generally, in the MC, the two dominating decomposition stages of CWD were hard and partly decomposed. Immediately after disturbance, there were higher volumes of hard CWD compared to the other decay classes, transitioning into partly decomposed and decomposed after 13 years (Figure 5). Higher volumes of very decomposed CWD as a proportion of other decay classes were found between 30 and 60 years after disturbance. Following 65 years after disturbance, hard CWD increased until the oldest stands in the chronosequence. In general, the volume of fresh CWD was low.

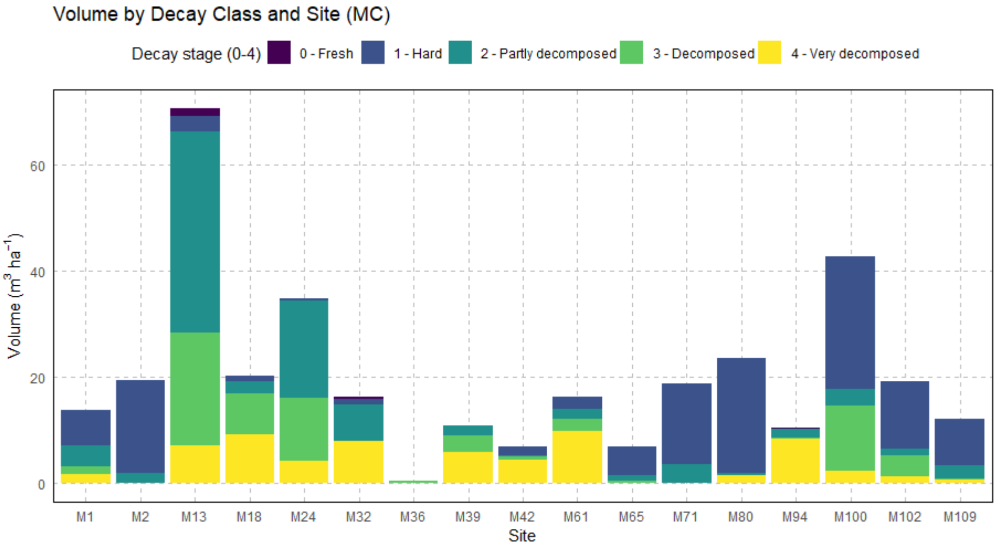

Figure 5. Dead wood volume in decay stages for each site in the managed chronosequence. Each site is represented by the letter M as in managed, followed by a number representing time passed since disturbance (clear-cut).

In the FC, after disturbance, initial decay stages of CWD primarily consisted of the stages hard, partly decomposed and very decomposed (Figure 6). This was the case up until 50 years, after which decomposed wood made up a big proportion until 100 years. Generally, the FC had higher volumes of CWD in decay stage 4 compared to the MC. Very decomposed dead wood was dominant up until 56 years after disturbance, after which it started declining. After ~ 100 years, decay stages hard and partly decomposed increased in their relative proportions and continued to do so until the end of the chronosequence. In general, fresh dead wood was low throughout the chronosequence, with the most noteworthy presence occurring in the oldest stand.

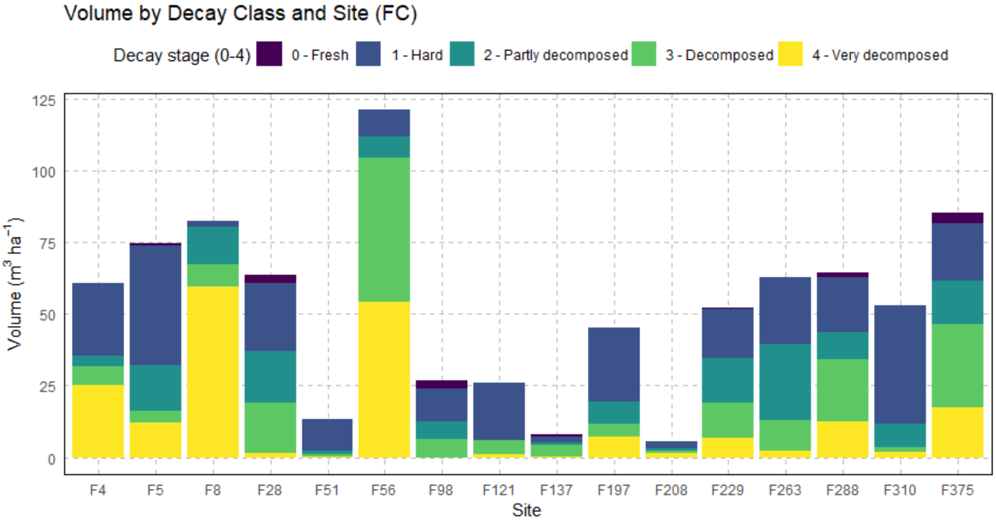

Figure 6. Dead wood volume in decay stages for each site in the fire chronosequence. Each site is represented by the letter F as in Fire, followed by a number representing time since disturbance (fire).

Dead wood by diameter classes

In the MC, the relative proportions of medium and small diameter classes were similar throughout the chronosequence (Figure 7). The largest diameter class occurred in lesser proportions, although it was represented in most of the stands. There was a gradual increase of CWD input in the diameter classes medium and large in the later temporal stages of the MC.

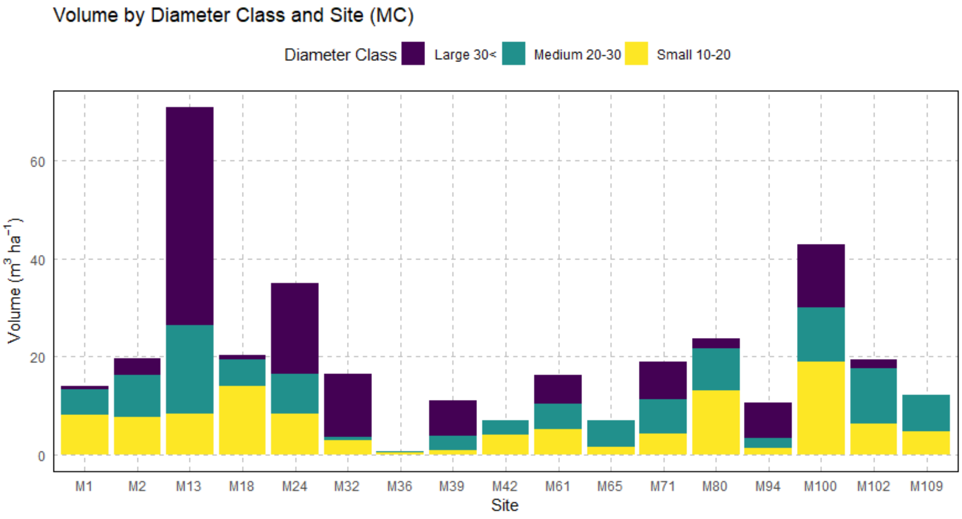

Figure 7. Dead wood volume from each site in the managed chronosequence categorized in diameter classes. Each site is represented by the letter M as in managed, followed by a number representing time passed since disturbance (clear-cut).

The FC had greater proportions of CWD in larger diameter classes compared to the MC (Figure 8). Most of the volume large CWD was found in the first few decades after a disturbance. Large CWD was notably low during the following 150 years, where after it gradually started increasing 260 years after disturbance and until the end of the chronosequence.

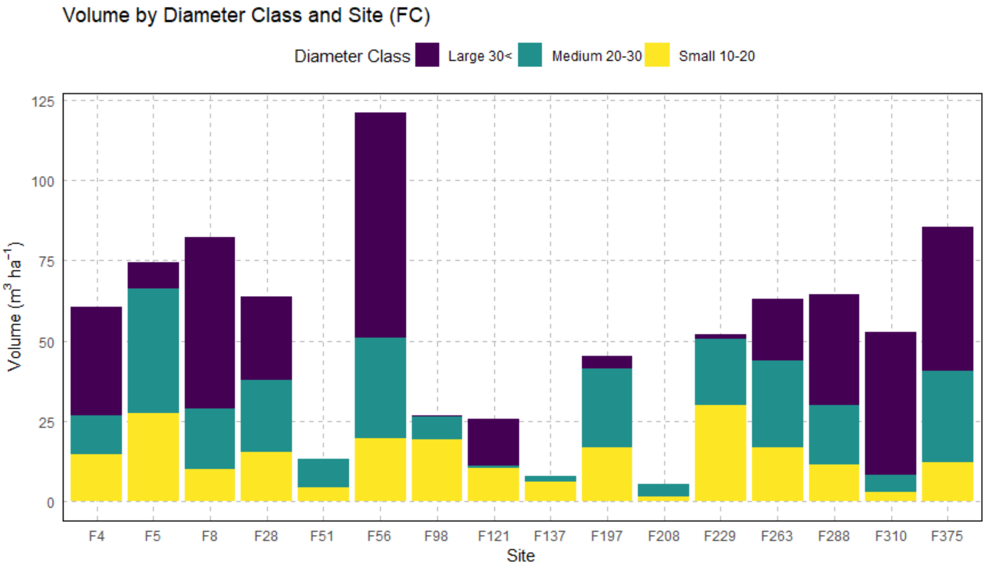

Figure 8. Dead wood volume from each site in the fire chronosequence categorized in diameter classes. Each site is represented by the letter F as in Fire, followed by a number representing time since disturbance (fire).

3.2 Dead wood and species richness

Dead wood volume was found to be a significant factor in explaining species richness ($R_{adj}^2=0.76$, $p<0.001$, $n=36$), and the model showed a good fit for both chronosequences (MC $R^2=0.54$, FC $R^2=0.78$). The chronosequences showed very similar trends, with dead wood positively predicting species richness. Species richness increased with dead wood volume up to ~ 50 m^3 ha^{-1} in the managed chronosequence (MC) (Figure 9). In the FC chronosequence, species richness increased up to ~ 90 m^3 ha^{-1}, after which it reached a breaking point, and eventually started declining (Figure 9). In general, the FC reached both higher values of species richness and dead wood volumes when comparing the chronosequences.

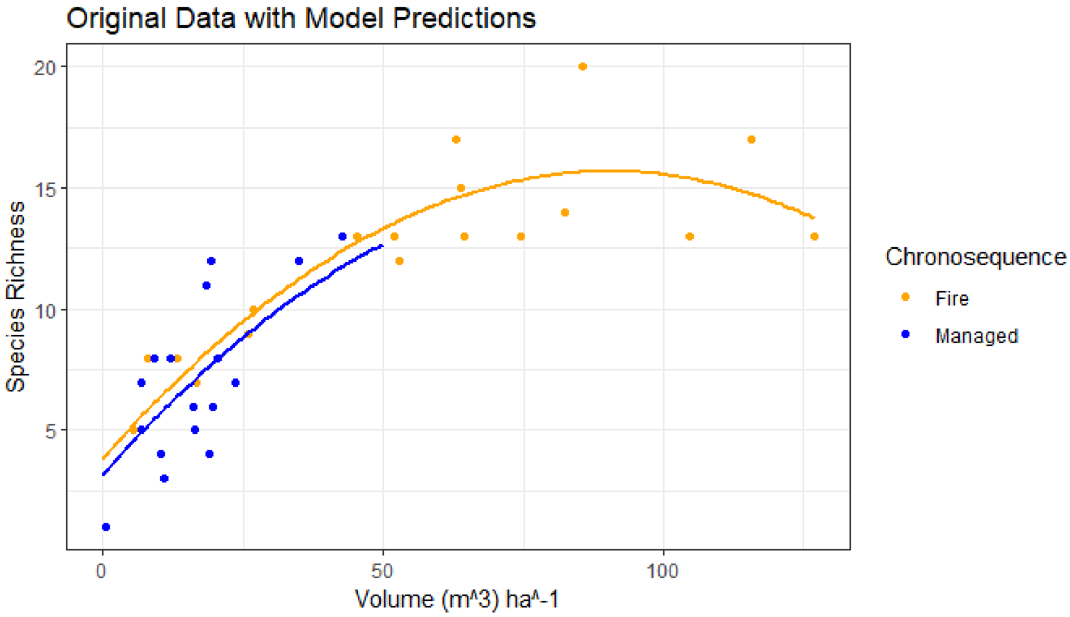

Figure 9. Dead wood volume as a predictor of species richness. Dead wood volume and species richness values originated from two chronosequences, each comprised of 18 forest stands located in the Arvidsjaur region. The figure displays predicted values represented by lines and original data plotted for reference, whereby the fire stands are indicated with orange and managed blue.

3.2.1 Dead wood characteristics and species richness

Decay stage

The linear regressions carried out on dead wood volume in specific decay stages, as a predictor of species richness, showed variability in explanation power and fit (Table 1). In the MC, dead wood volume in decay stages 1 and 4 provided the most robust prediction for species richness. In FC, all dead wood decay stages were significantly related to species richness (Table 1).

*Table 1. Results from linear regressions examining the relationship between species richness and dead wood volume in the different decay stages. Most relationships were positive except for decay stage "fresh" in the managed column which could not be conducted due to limited observations (Not applicable = NA). Significance levels are denoted as follows: *** <0.001** <0.01 * <0.05, non-significance expressed as NS.*

Decay stage	Managed	n	p	Fire	n	p
0-Fresh	NA	0	NA	$R^2 = 0.57$	7	*
1-Hard	$R^2 = 0.59$	15	***	$R^2 = 0.39$	17	**
2-Partly decomposed	$R^2 = 0.16$	17	NS	$R^2 = 0.54$	18	***
3-Decomposed	$R^2 = 0.17$	14	NS	$R^2 = 0.56$	18	***
4-Very decomposed	$R^2 = 0.32$	16	*	$R^2 = 0.35$	16	**

Diameter class

In the fire chronosequence, the volume of CWD within the diameter classes small (10-20 cm), medium (20-30 cm), and large (>30 cm) were significant predictors of species richness (Table 2). Conversely, in the managed chronosequence, volume of CWD within the small and medium diameter classes were identified as significant predictors.

*Table 2. Results from linear regressions examining the relationship between species richness and dead wood volume in specific diameter classes. All relations were positive. Significance levels are denoted as follows: *** <0.001** <0.01 * <0.05, non-significance expressed as NS.*

Diameter (cm)	Managed	n	p	Fire	n	p
10-20	$R^2 = 0.61$	18	***	$R^2 = 0.32$	18	**
20-30	$R^2 = 0.63$	18	***	$R^2 = 0.25$	18	*
>30	$R^2 = 0.025$	13	NS	$R^2 = 0.36$	15	*

3.3 Species richness over time

Values of species richness in the fire chronosequence (FC) were on average 12 (± 3.8 SD), (max 20). In the managed chronosequence corresponding values were mean 7 (± 3.3 SD) (max 13). Species richness was significantly related to time since disturbance ($R_{adj}^2 = 0.49$, $p = 0.019$, $n = 36$), (MC, R^2=0.31, FC, R^2=0.32). Immediately after disturbance, initial values of species richness did not significantly differ between the two chronosequences (p=0.1). After disturbance there was an initial decrease, followed by an increase of species richness in both chronosequences. However, the increasing trend occurred at different temporal stages in the two chronosequences; around 50 years after clear cut and 150 years after fire, respectively (Figure 10). After 50 years in the MC, species richness started to increase back towards the same levels as immediately after clear-cut, at around 109 years, resulting in a U-shaped curve. Further, there was an interactive effect of time since disturbance and chronosequence type (p=0.02), whereby the species richness decreased less rapidly in the initial stages after fire, reached its minimum values at around 100-200 years following fire, after which it increased towards greater species richness values than in the MC.

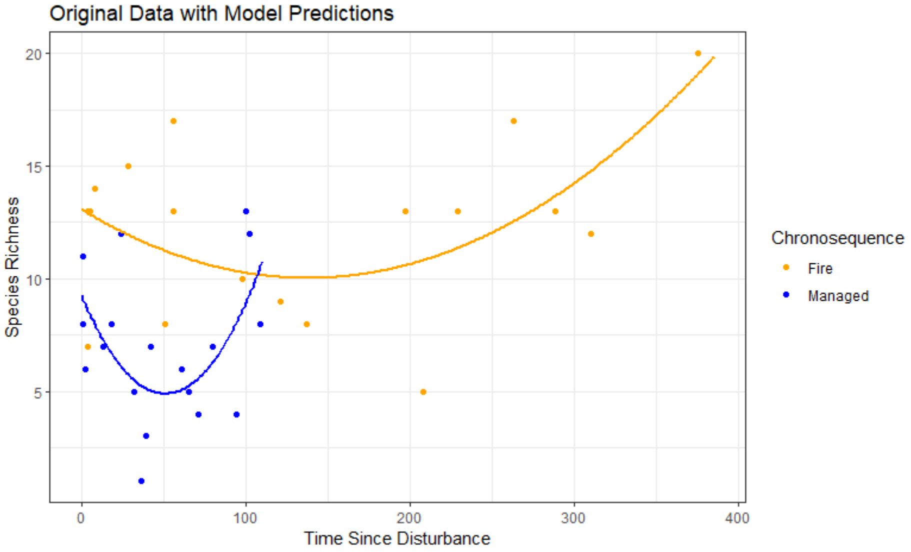

Figure 10. Relationship between species richness and time. Species richness values originate from two chronosequences, each comprised of 18 forest stands located in the Arvidsjaur region. The independent variable time since disturbance, ranged between 4 and 375 years in the FC, and 1 and 109 years in the MC. The figure displays predicted values represented by lines and original data plotted for reference. Fire stands are highlighted in orange, and managed stands in blue.

3.3.1 Species density

Time had no significant effect on the variable species density (p=0.35). Additionally, the model showed no significant difference between the chronosequences when comparing the species density, however, with low explanation power ($R_{adj}^2 = 0.02$, p = 0.14, n = 36), (MC R^2=-0.02, FC R^2=0.17). Suggesting that species richness per unit dead wood was similar between the chronosequences (Figure 11). There was a tendency for the ratio to be higher in the managed stands. After ~ 200 years in the FC, the ratio started decreasing.

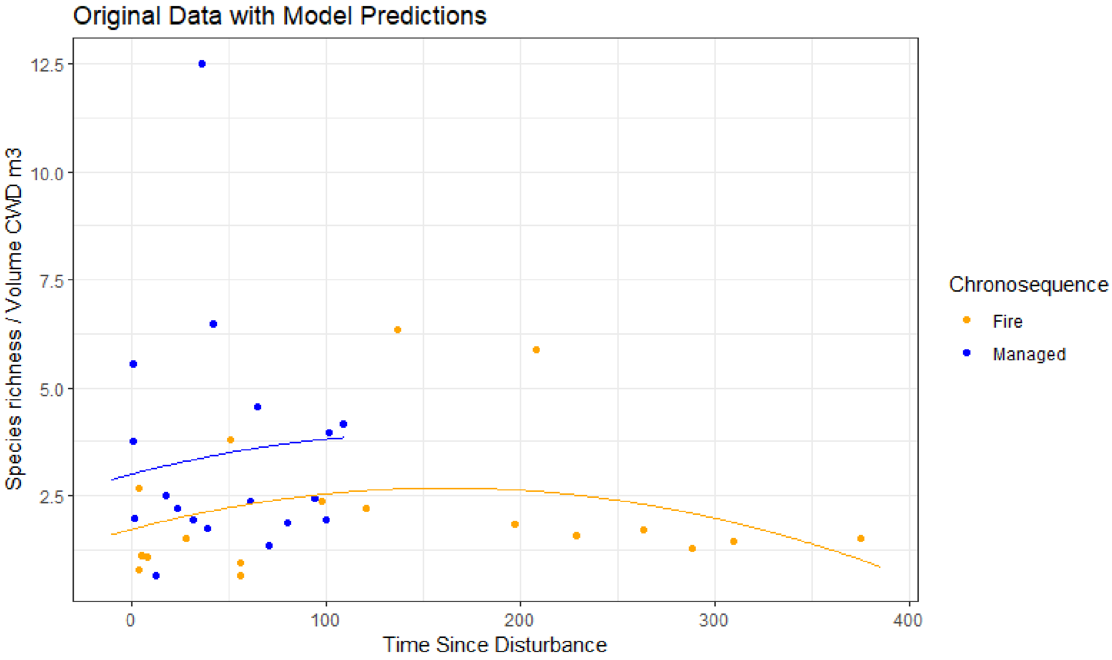

Figure 11. Relationship between species density and time since disturbance from the two chronosequences comprised of 18 stands each, disturbed by either fire or management. The figure displays predicted values represented by lines and original data plotted for reference. Stands disturbed by fire are highlighted in orange and stands disturbed my management in blue.

3.3.2 Species composition

The non-metric multidimensional scaling (NMDS) analysis of species composition revealed distinct fungal community differences between the managed and fire chronosequences (Figure 12). Additionally, the permutational multivariate analysis of variance (PERMANOVA) confirmed that the two groups were significantly different (F=2.78 p<0.02). The species that were most strongly associated with the fire chronosequence (FC) were *Fuscoporia viticola* and *Rhodofomes roseus,* with the latter exclusively occurring in the FC. *Trichaptum abietinum*, *Postia sericeomollis* and *Anomoporia kamtschatica* occurred in both chronosequences.

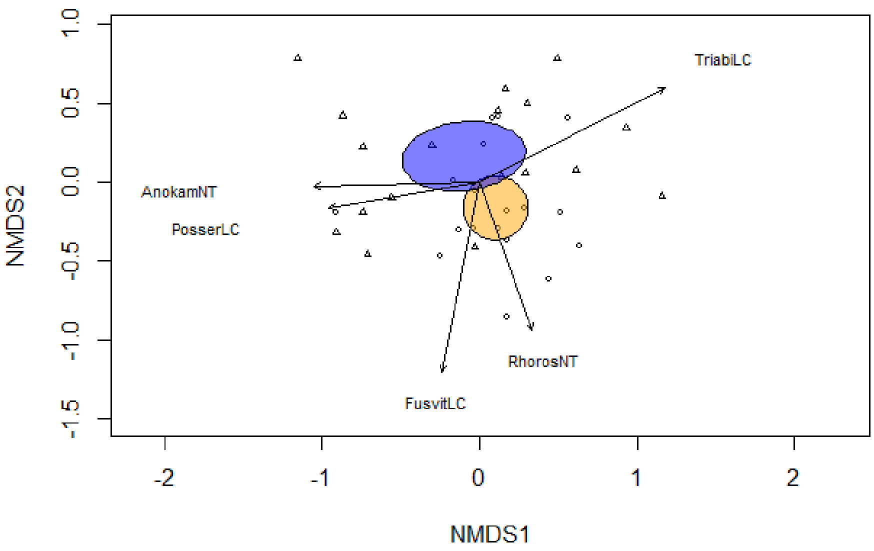

Figure 12. Non-metric multidimensional scaling ordination for presence/absence data (NMDS: stress value= 0.129) of fungal species composition. Circles represent fire sites and triangles represent managed sites. Colored polygons represent the standard error for the grouping based on managed or fire, blue represents managed stands and orange represents fire stands. Abbreviations derived from first three letters of genus and species name, including conservation category.

3.4 Presence of red-listed wood-inhabiting fungi

Mean red-listed species per stand in the fire chronosequence (FC) were 2.8 (± 2.2 SD), (max 9, min 0 and median 2.5). In the managed chronosequence, MC, the corresponding figures were mean 0.89 (± 0.96 SD), (max 2, min 0, and median 0.5). The model´s prediction underscored a significant temporal influence on red-listed species (Figure 13; $R_{adj}^2=0.4735$, p=0.002). Similar to the species richness pattern (Figure 10), red-listed species exhibited an initial decrease, followed by an increase, notably after around 180 years in FC, and reached the max value of red-listed species at the latest temporal stage after disturbance.

Furthermore, a significant difference (p=0.031) was observed between the two chronosequences concerning the presence of red-listed species, (MC $R^2=-0.24$, FC $R^2=0.47$). In the FC, red-listed species ranged between 0 and 9 species and in the MC, between 0 and 2 species. The red-listed species that were present in the MC, were *Anomoporia kamtschatica* NT, *Anthoporia albobrunnea* VU, *Siderna lenis* VU, *Postia lateritia* VU, *phellinidium ferrugineofuscum* NT. With *Anomoporia kamtschatica* being the most frequent.

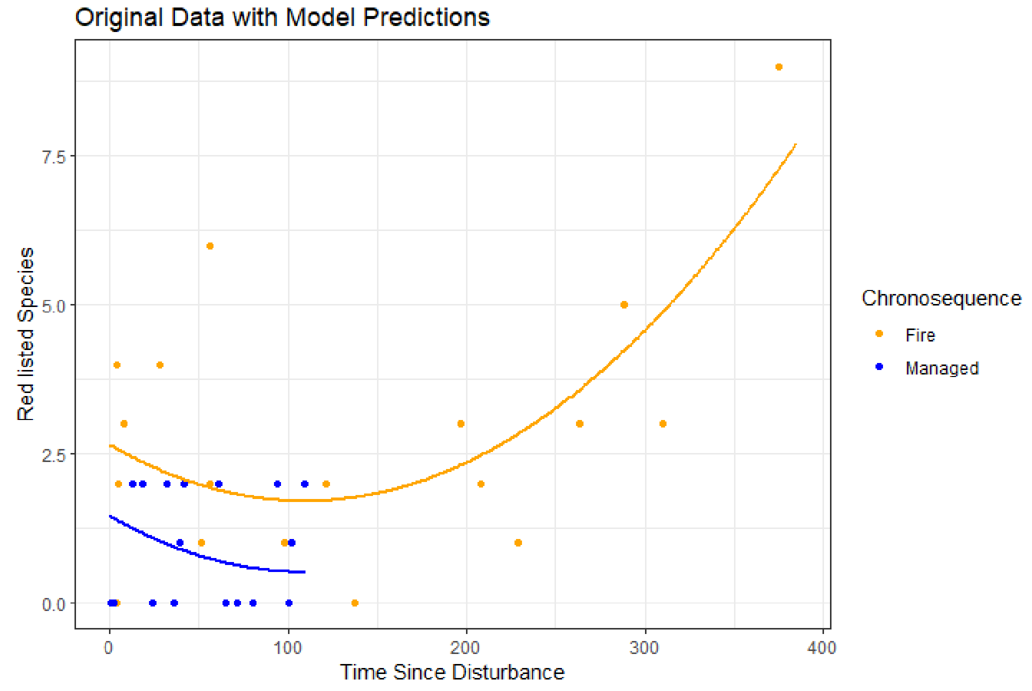

Figure 13. Relationship between red-listed species and time since disturbance for the two different chronosequences. Presence of red-listed species originate from two chronosequences, each comprised of 18 forest stands located in the Arvidsjaur region. Predicted values are represented by lines and original data are plotted for reference. Fire stands are highlighted in orange, and managed stands in blue.

4. Discussion

The purpose of this study was to examine how the disturbances of forest management and fire affects WIF over time, considering that the two disturbances are often proposed as having similar impact on boreal forest ecosystems. This was achieved through a comparative analysis of a managed and a wildfire forest chronosequence, examining how species richness and red-listed species of fungal taxa differed. Managed forests generally had lower species richness and lower presence of red-listed species compared to forests disturbed by fire. When comparing the ratio of species richness to dead wood volume, no significant differences were found. However, the species composition did differ between the chronosequences. The differences in species richness and composition could be explained by ecological predictors such as dead wood volume and diversity in dead wood characteristics. The fire chronosequence showed higher dead wood volumes compared to the managed chronosequence, however, with high variability over time in both chronosequences. Furthermore, dead wood characteristics greatly differed in terms of diameter distribution, tree species type and decay stage, potentially explaining the observed dissimilarity in fungal diversity and composition.

4.1 Dead wood

4.1.1 Dead wood volume

In line with my hypothesis, dead wood volume was on average three times higher in the fire chronosequence (FC) compared to the managed chronosequence (MC). However, as expected, dead wood volumes showed high variability over time (Figure 2). As I hypothesized, dead wood volume was initially high immediately after a fire, ranging between values from ~ 6 m^3 ha^{-1} to ~100 m^3 ha^{-1}, resulting in a mean volume of ~ 60 m^3 ha^{-1} during the first 50 years. These volumes are slightly higher compared to what has been reported previously (e.g. Ylisirniö et al. 2012), who found dead wood volume on young post fire sites to be 38.5 ± 21.7 m^3 ha^{-1}. It has previously been shown that dead wood volumes in boreal forests usually peak in the early successional stages, however, fire intensity and pre fire forest structure highly impacts the outcome (Uotila et al. 2001; Ylisirniö et al. 2012). In the middle temporal stages of the FC, dead wood volume decreased, reaching its minimum values, resulting in a U-shaped line (Figure 2). Similar trends has been observed in previous studies on dead wood dynamics in boreal forests (Clark et al. 1998; Siitonen 2001). The observed decrease in dead wood over time is commonly linked to the decomposition of existing dead wood. Dead wood volume typically starts to increase again after larger trees from the original pioneer cohort begin to die (Luyssaert et al. 2008; Aakala 2010). The dead wood volumes of the old growth stands in FC ranged between 60 and 80 m^3 ha^{-1}, which is in line with estimates from other studies from the boreal biome (Siitonen 2001; Hekkala et al. 2016).

The average CWD volume in the MC was substantially higher compared to other studies on the subject (Fridman & Walheim 1997; Uotila et al. 2001; Ylisirniö et al. 2012). I also found that dead wood volumes in the early temporal stages of the MC are much higher compared to the middle temporal stages (Figure 3), which could potentially be attributed to logging residues and retention forestry, which has developed during the last decades in forest management (Gustafsson et al. 2010, 2012). Further, the dead wood volume in the older managed stands are in line with similar studies on the subject (Ylisirniö et al. 2012).

To summarise, the disturbances fire or clear cut had different impacts on the availability of dead wood volume throughout the chronosequences. Forests disturbed by fire had on average three times higher CWD volumes compared to clear cut forests. Young post-fire forests had higher CWD volumes, illustrating the importance of fire as a disturbance to create habitat for saproxylic organisms. The managed chronosequence had surprisingly high dead wood volumes in the first decades after management, a result that could potentially be explained by implemented retention practices stemming from the 1993 forestry act.

4.1.2 Dead wood characteristics

In general, the managed chronosequence (MC) showed homogeneity in terms of wood characteristics compared to the fire chronosequence (FC) (Figure 3-8). Higher volumes of spruce CWD throughout the FC was observed when comparing CWD by tree species. The diversity of CWD tree species in the FC is potentially explained by the pre-disturbance stand structure, potentially influenced by previous low intensity forest fires that led to a pine dominated forest with a relatively high proportion of spruce, which would explain the high volumes of spruce CWD observed in the FC. Spruce CWD in the later successional stages can partly be explained by the successive ingrowth and mortality of spruce (Engelmark 1987). Low CWD tree species diversity in the MC also illustrates the efficiency of clear-cutting in favouring selected tree-species.

There were notable differences between the chronosequences in CWD decay stage distribution (Figure 5-6). The first few decades after a disturbance, the fire chronosequence (FC) generally had higher CWD volumes in the later decay stages compared to the managed chronosequence (MC). While not measured in this study, a potential reason behind the low volumes of CWD in later decay stages in the MC, is that pre-disturbance CWD could have been damaged during harvesting, which could have accelerated the breakdown of wood or altered the decomposition dynamics. In the FC, CWD volume was more evenly distributed among the different decay stages. The heterogeneity of the decomposition stages in the FC, suggests that there is a wider variety of substrates which allows for a greater diversity of WIF occupying different successional niches. My results also point to how different decay stages differ in their predictive capacity in relation to species richness of WIF. In the FC, all decomposition stages were significant predictors of species richness, however the later stages of decomposition showed stronger relationships with species richness compared to the earlier decay stages. These findings align with prior studies, highlighting that at the substrate scale, decay stage is the strongest determinant for species richness. Furthermore, the later decomposition stages are acknowledged of having special importance for red-listed WIF in boreal forests, which were more frequent in the FC, as supported by (Junninen & Komonen 2011; Ylisirniö et al. 2012). These studies contribute to the conclusion that dead wood in advanced decomposition stages significantly influences the presence of red-listed species in boreal forests.

Diameter class has also been acknowledged as an important CWD characteristic explaining species richness, with special importance for red-listed species (Bader et al. 1995; Hottola et al. 2009). My results showed that the diameter classes “small” and “medium” were important predictors of species richness in both chronosequences. Furthermore, CWD >30 cm was an important predictor in explaining species richness in the fire chronosequence (Table 2).

The two disturbances had widely different impacts on dead wood characteristics in the forest stands. In general, forests disturbed by fire displayed higher heterogeneity with greater dead wood volumes in larger diameter classes and later decomposition stages. These are characteristics that have been suggested as prerequisites for red-listed wood fungi in Sweden’s boreal forests (Hottola et al. 2009; Junninen & Komonen 2011; Ylisirniö et al. 2012).

4.1.3 Dead wood and species richness

Dead wood volume was shown to be a strong determinant in species richness of WIF (Figure 7). These results align with prior studies suggesting that diversity of local species richness of WIF is strongly correlated with quantity of CWD (Junninen & Komonen 2011). Furthermore, it has been shown that the correlation between dead wood volume and species richness of saproxylic organisms is stronger in the boreal biome compared to the temperate biome (Lassauce et al. 2011). It is worth mentioning that while increased dead wood volume is beneficial for saproxylic organisms, the stage of decay is likely more influential in determining what species can occupy it (Hekkala et al. 2016).

Ylisirniö et al. (2012), found a non-linear relationship between CWD volume and species richness, with a breaking point in the increase of species richness at around 35 m^3 ha^{-1}. I identified a breaking point of species richness at ~ 90 m^3 ha^{-1} (Figure 9), and the differences in breaking points could potentially be attributed to higher dead wood volumes and different tree species composition in my study system. Although not specifically examined in this study, previous findings have shown a breaking point for the occurrence of red-listed WIF in spruce forests at around 20 m^3 ha^{-1}(Penttilä 2004). Furthermore, in boreal forests, there are estimates of a general threshold value of 20-30 m^3 ha^{-1}, for the maintenance of saproxylic organisms (Müller & Bütler 2010).

Collectively, these findings suggest that on a stand scale, CWD volume is an important determinant in explaining species richness in boreal forests. Furthermore, my results show that species richness can increase with dead wood volume up to much higher values than previously shown.

4.2 Species richness over time

In line with the hypothesis, the fire chronosequence (FC) generally had higher species richness compared to the managed chronosequence (MC). This result can partially be attributed to higher CWD volumes (Figure 10). I previously showed that volume of CWD was a significant predictor of species richness in both chronosequences (Figure 9), and the species richness trends over time mirrors that of the dead wood volume.

Immediately after a fire, depending on intensity and extent, dead wood volume has been shown to increase and create a supply of dead wood for at least 50-70 years, providing new input of habitat and substrate allowing for new species to colonize, and the development of new fungal communities (Dahlberg 2002; Ylisirniö et al.

2012). However, wildfire can also have a destructive short-term effect on fungal communities by destroying fungal mycelia and reducing inoculum potential by consuming CWD (Penttilä 2004). Previous studies have identified changes in fungal communities on dead wood a few years after a fire compared to the pre-fire fungal community (Olsson & Jonsson 2010; Berglund et al. 2011).

Hence, my results point to reduction of dead wood due to decomposition, over time since disturbance, together with a reduction in new input of dead wood, being a likely driver of my findings of a decline in species richness up until ~70 years for the MC and ~190 years for the FC. After these time points, a gradual increase in CWD contributed to an increase in species richness in the FC. Despite a noted decrease in dead wood volume in the MC (Figure 2), there was an observed increase in species richness (Figure 10). This finding is interesting and calls for further investigation into the specific species recorded and their substrate requirements, which could provide insights into the dynamics of WIF in older managed forests.

4.2.1 Species density

I found no support for my hypothesis that species density would be higher in the fire chronosequence, which suggests that species richness per unit dead wood was similar between the chronosequences. Species density decreased with time in the older stands in the FC, a result potentially explained by dead wood volume increasing at a disproportionally higher rate resulting in reduced species density. This also raises the question whether the absence of appropriate CWD characteristics prevented species richness from reaching higher values. Dead wood volume in more advanced decay stages is proportionately smaller compared to the other decay stages (Figure 6). This finding is noteworthy since old growth wood-inhabiting fungal species are known to prefer large trunks in medium or advanced decay stages (Sippola & Renvall 1999; Josefsson et al. 2010). A more heterogeneous distribution of decay stages would have resulted in a greater habitat diversity and potentially more species. In the FC, old stumps gave evidence of past forest management in some of the later successional stands. Limited cuttings carried out a century ago, has continuous impact on WIF in boreal forests, due to impact on the available CWD and the distribution of its decay stages (Josefsson et al. 2010). Hence, it is likely that without any human interference, CWD volumes would be higher in the old growth stands and distributed more evenly in the different decay stages. This could facilitate species that can occupy diverse successional niches.

4.2.2 Species composition

The NMDS analysis highlighted a significant difference in species composition between managed and fire-disturbed forests which was in line with the hypothesis. The fire chronosequence generally displayed higher dead wood volumes, and a greater diversity of dead wood characteristics such as diameter distribution, decay stages and tree species, which are key determinants in influencing species composition. Notably, two species associated with the FC, *Fuscoporia viticola* and *Rhodofomes roseus,* both recognized as spruce associated species, emerged as key drivers of this observed dissimilarity (Figure 12). The presence of spruce CWD, and the species associated with it, is most likely one of the main drivers behind the observed dissimilarity in species composition between the chronosequences. Tree species composition has been shown to be one of many important parameters that impacts the availability of substrate, which in turn affects species assemblages (Ylisirniö et al. 2012).

4.3 Red-listed species

In line with the hypothesis, the fire chronosequence (FC) generally had a higher presence of red-listed species compared to the managed chronosequence. However, at certain points in time following a disturbance, the chronosequences shared similar frequencies. Apart from greater dead wood volumes in the FC, a potential explanation for higher presence of red-listed species, could be the more pronounced diversity of CWD characteristics, such as the presence of unique dead wood substrates created by fire, i.e. charred wood and resin rich pine wood, referred to as "kelo" wood, which provides a niche for a variety of highly specialized WIF (Niemelä et al. 2002).

The temporal dimension in the FC ranged between 4 and 375 years and represents changes in successional dynamics marking a shift from pine dominated forests towards increasing proportion of spruce (Engelmark 1987; Figure 4). Furthermore, time affects dead wood characteristics such as decay stage and diameter distribution, which varied greatly throughout the FC. Addition of spruce CWD in the later temporal stages of the FC, potentially allowed for new successional niches to increase the presence of red-listed species from the initial levels. Time since fire has been shown to influence species composition from being pine associated in natural recent fire stands, shifting towards spruce associated in old fire stands Gudrunsson (2013), which I also found in my study system (Figure 4). During the later temporal stages after fire, CWD started to gradually increase reaching its initial values, which correlates well with the higher presence of red-listed species (Figure 2,13).

As previously mentioned, the NMDS (Figure 12) highlighted two spruce associated species (one red-listed), that were drivers of the dissimilarity in species composition between the chronosequences. While an increase in the abundance of red-listed species might be perceived as positive, there is a long-term concern: the competitive advantage of spruce over pine poses a threat to the already red-listed pine associated WIF. This highlights the need for prescribed burnings to provide new CWD input, reduce tree species competition and maintaining natural pine-dominated forests to safeguard pine associated wood fungi in the long-term. The red-listed species that were found in the managed chronosequence were predominantly pine associated. *Anomoporia kamtschatica, Anthoporia albobrunnea and Siderna lenis* are all utilizing charred and resin rich pine wood, "Kelo" wood (Artdatabanken 2023). The substrate is created over long time spans and is slow in its decomposition rate. It is safe to say that this substrate is barely recreated in the managed stands, which implies that there is an extinction debt for species dependent on this unique substrate in the managed forest. Furthermore, it highlights the need for prescribed burning to create necessary substrates in both protected areas and managed forests, to safeguard viable populations of the species associated with it. Additionally, these results are in line with the findings of Sippola & Renvall (1999), who showed that species diversity of lignolocolous fungi in managed stands are dependent on the availability and diversity of decaying wood created before clear-cut forestry.

In the MC, presence of red-listed species ranged between zero and two occurrences, making it difficult to correlate the occurrences with the examined parameters. Consequently, it is challenging to draw conclusions on methods to increase the occurrence of red-listed species in managed forests. I have shown that over time, volume of CWD and diversity in CWD characteristics influence the presence of red-listed species in the FC. However, there are several other factors that need to be considered such as "naturalness" of the site, wood fungi dispersal and reproduction (Penttilä 2004; Ylisirniö et al. 2012).

4.4 Implications for forest management

The key findings from this study have indicated a substantial difference in the post-disturbance outcomes for forest stands affected by the disturbances clear-cutting and wildfire, in terms of important ecosystem components such as CWD volume and diversity of WIF. Therefore, drawing similarities between the clear-cutting and fire disturbances can contribute to a misconception (Skogsindustrierna 2023), erroneously implying that both disturbances are natural processes with similar impacts on boreal forests. Furthermore, it is noteworthy that this misconception might contribute to the acceptance of clear-cutting, failing to acknowledge its negative effects on red-listed WIF.

In general, the measured CWD volumes in the managed forest stands were notably high compared to other studies, reaching estimates of threshold values for the maintenance of saproxylic species in boreal forests (Müller & Bütler 2010). However, this is not the case for most of the managed forests in Sweden (Fridman & Walheim 1997; Jonsson et al. 2016). The ecological resilience of Sweden's forests is being negatively affected by intensified forestry, and the last decades transformation of the Swedish forest landscape has resulted in a decreasing trend for many forest dwelling organisms, including WIF (Skogsstyrelsen 2022). My findings support this outcome by highlighting a lower species richness and lower presence of red-listed WIF in the studied managed forests. Furthermore, I have shown that clear-cut forestry has transformed Sweden's old-growth forests into monocultures, resulting in lower volumes of CWD in my study system, which has resulted in changes in species composition and reduced species richness of fungi dependent on CWD.

The Swedish environmental goal "living forest" is not being met and with the current management practices the trend towards reaching it appears to be heading in the wrong direction, with an ongoing upward trend in the red listing of forest species (Skogsstyrelsen 2022). Therefore, continuous conservation practices in forest management are encouraged such as retention of CWD, living conservation trees and tree patch retention providing input of CWD, all of which are standard procedures in the certification norms (FSC 2020). Retention forestry is still in its early stages in terms of conclusive results on biodiversity, however, the practices have increased the dead wood volumes in the managed forest landscape of Sweden (Gustafson et al. 2016; Jonsson et al. 2016). I show that volume CWD and its characteristics are key determinants in the maintenance of WIF in the boreal forest. Since many organisms in the boreal forest have evolved with fire, prescribed burnings could be a potential tool to provide substrate and habitat for these organisms. Additionally, burning has been shown to be the most effective restoration measure in the short and long term to increase deadwood volumes and the distribution of its decay stages (Hekkala et al. 2016).

4.5 Improvements and limitations

Forty-eight specimens were excluded from the analysis due to pending further identification, resulting in uncertainty about their status as unique species. Twenty-eight of these specimens were recorded in the fire-disturbed forests and were scattered relatively evenly across 13 stands in the fire chronosequence. The remaining twenty specimens belonged to the managed forests, with 10 recorded in M13 and 5 in M1a, with the remaining five evenly recorded across the managed chronosequence. Although the absence of these specimens impacts the results of this study, it is noteworthy that most of the specimens originated from the fire chronosequence, and their inclusion would have most likely further increased the robustness of the results.

The inventory of WIF was conducted as a single survey. There are known reliability issues associated with single surveys, e.g., single survey based on fruiting bodies never catches the whole wood-inhabiting fungal community (Halme & Kotiaho 2012) and WIF abundance can vary from year to year. All the surveys were conducted during the same time of the year when most fruiting bodies were visible, as well as within a short timeframe, which minimized the risk of a time-mismatch between probabilities in finding fruiting bodies across the sites.

Dead wood measurements were conducted on logs measuring above 10 cm in the largest end and there is a risk of not fully capturing the fungal community when excluding dead wood pieces below 10 cm (Juutilainen et al. 2014). However, measuring all dead wood debris would be time consuming. The analysis excluded standing dead wood, a variable that could have provided valuable insight into the anticipated future input of CWD in the two chronosequences.

The extent of the disturbances in the fire chronosequence may differ between stands with forest fires of varying intensity, resulting in different post-fire stand structure. This introduces a level of uncertainty and variability when comparing stands within the chronosequences and makes comparisons to other studies on the subject difficult.

Furthermore, some of the “old-growth” stands in the fire chronosequence had apparent traces of previous historical management practices. Historical management, mainly consisting of high grading has to some extent affected the available CWD in these stands today. Trees that would otherwise have died of natural causes and contributed to the CWD of a particular stand are instead lacking, impacting the available substrate for wood-inhabiting fungi and consequently species occurrences (Josefsson et al. 2010); however, this is difficult to quantify given that mortality can be unpredictable.

Forestry practices are continually evolving, therefore, the data from the managed stands is a result of the prevailing management practices and policy conditions from that respective time point in history. In the older stands, manual felling and natural regeneration using seed trees was the common practice. In contrast, forestry today is highly mechanized and rationalised, carried out with forest machines and with additional regard to nature conservation.

Comparing two chronosequences with different time ranges is not optimal when aiming to draw conclusions based on notable differences in the examined parameters. A different approach could have been to compare similar time ranges; however, that would have resulted in a loss of data from the fire chronosequence. Additionally, comparing the whole age range, captures the landscape situation of the two land-use designations. By presenting the two chronosequences as done in this study makes it possible to compare the stands and speculate on how managed stands with a stand age older than >120, would look in comparison to the older burnt stands. In a way, the managed chronosequence is representing reality of a managed forest rotation in northern Sweden, where forest stands are usually harvested after around 100 years. Furthermore, examining a longer time range in the fire chronosequence gives valuable insights in how ecological succession dynamics act over time.

4.6 Conclusion

I studied how dead wood and its characteristics, species richness, red-listed species and composition of wood-inhabiting fungi differed between a managed and a wildfire forest chronosequence. The aim was to assess the immediate and long-term impact of disturbances, namely clear-cutting and wildfire, on CWD and fungal diversity.

I found that forests disturbed by fire had on average three times the amount of CWD compared to managed forests, although showing high variability over time since disturbance. Furthermore, CWD characteristics greatly differed between the chronosequences, with the most noteworthy being higher dead wood volumes in later decomposition stages, higher volumes in larger diameter classes, and more CWD tree species diversity in fire-disturbed forests, all of which have been shown to be important parameters for predicting the occurrence of red-listed wood-inhabiting fungal species, contributing to higher species richness in fire-disturbed forests in my study system.

I found that dead wood volume was a strong predictor of species richness in both chronosequences up to 90 m^3 ha^{-1} in the fire chronosequence and 50 m^3 ha^{-1} in the managed chronosequence. In general, the fire chronosequence reached higher values of species richness both immediately after disturbance and over time. However, when comparing species density there was no difference between the chronosequences.

Further, I showed that species composition significantly differed between the chronosequences and the species of wood fungi driving the dissimilarity were mainly spruce associated. The finding highlights the need for prescribed burnings to maintain natural pine forests from being outcompeted by spruce, and safeguard threatened pine associated wood fungi. Furthermore, I showed that, over time, forests disturbed by fire had a higher presence of red-listed wood fungi and that the red-listed fungal species occurring in the managed forests were mainly associated with charred and resin rich pine wood, a substrate likely retained from the pre-disturbed forest structure.

These results highlight how the two disturbances, clear-cutting and wildfire, have radically different impacts on forest ecosystems and it is apparent that the natural disturbance of wildfire creates higher volumes and diversity of CWD characteristics, which is advantageous for a wider diversity of WIF, including threatened species missing in large parts of Sweden’s managed forest landscape.

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Popular science summary

More than half of Sweden's land is covered by forests, and the forest industry plays an important role in Sweden's economy. Forest management, often involving clear cutting, has been important in raising forest growing stock and wood availability. The efficient and rationalized forestry practices have positioned Sweden as a leading forestry nation. As climate change poses challenges, the role of forests as a partial solution to addressing these issues has been understood. In the contemporary forest debate, much of the discussion is centred on how we can manage forests to mitigate the effects of climate change. The forest industry has drawn similarities between the natural disturbance wildfire and clear-cutting, emphasizing its appropriateness in the northern parts of Sweden where wildfires were historically prevalent. However, the importance of forests goes beyond their role in carbon uptake, they are equally crucial for biodiversity. The current trend is negative for many forest dwelling species in Sweden's forest today, with species successively being added to the red-list. The dilemma of managing forest to mitigate climate change parallel with consideration for biodiversity is leading to trade-offs.

To further understand the effects of the forest management activity of clear-cutting on biodiversity, I examined the differences between managed forests and burnt forests in terms dead wood quantity, dead wood characteristics and their impact on wood-inhabiting fungi.

I found that the two disturbances had distinctly different ecological effects on post-disturbance stand structure. Burned forests had on average three times the amount of dead wood, characterized by later decomposition grades, larger diameter sizes and a wider diversity of dead wood tree species. Higher dead wood volumes correlated with higher species richness of wood inhabiting fungi. Fire-disturbed forests had greater diversity of wood inhabiting fungi and more red-listed species compared to managed forests. This outcome can partially be explained by the greater diversity of dead wood characteristics in fire-disturbed environments. My findings show that managed and burnt forests widely differ in terms of dead wood volume, species diversity and red-listed species. The results further emphasize the trade-offs between clear-cut forestry and the consequential reduction in biodiversity.

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Appendix 1

Site				
F121	Phellinidium ferrugineofuscum NT	Anomoporia kamtschatica NT		
F137				
F197	Porodaedalea chrysoloma NT	Phellinidium ferrugineofuscum NT	Rhodofomes roseus NT	
F208	Sidera lenis VU	Anomoporia kamtschatica NT		
F229	Phellinidium ferrugineofuscum NT			
F263	Phellinidium ferrugineofuscum NT	Rhodofomes roseus NT	Porodaedalea chrysoloma NT	
F28	Anomoporia kamtschatica NT	Anthoporia albobrunnea VU	Phellinidium ferrugineofuscum NT	Skeletocutis brevispora VU
F288	Phellinidium ferrugineofuscum NT	Rhodofomes roseus NT	Amylocystis lapponica VU	Phellopilus nigrolimitatus NT
F310	Rhodofomes roseus NT	Phellinidium ferrugineofuscum NT	Phellopilus nigrolimitatus NT	
F375	Postia lateritia VU	Phellopilus nigrolimitatus NT	Porodaedalea chrysoloma NT	Antrodiella parasitica VU
F4a	Rhodofomes roseus NT	Porodaedalea chrysoloma NT	Perenniporia subacida VU	Diplomitoporus crustulinus VU
F4b				

F5	Rhodofomes roseus NT	Perenniporia subacida VU		
F51	Anomoporia kamtschatica NT			
F56a	Phellopilus nigrolimitatus NT	Anthoporia albobrunnea VU		
F56b	Neoantrodia infirma EN	Rhodofomes roseus NT	Anomoporia kamtschatica NT	Anthoporia albobrunnea VU
F8	Odonticium romellii NT	Sidera lenis VU	Anthoporia albobrunnea VU	
F98	Anomoporia kamtschatica NT			
M100				
M102	Phellinidium ferrugineofuscum NT			
M109	Phellinidium ferrugineofuscum NT	Asterodon ferruginosus NT		
M13	Anomoporia kamtschatica NT	Phellinidium ferrugineofuscum NT		
M18	Anomoporia kamtschatica NT	Phellinidium ferrugineofuscum NT		
M1a				
M1b				
M2				
M24				
M32	Postia lateritia VU	Anomoporia kamtschatica NT		
M36				
M39	Anomoporia kamtschatica NT			
M42	Anomoporia kamtschatica NT	Sidera lenis VU		
M61	Anomoporia kamtschatica NT	Anthoporia albobrunnea VU		
M65				
M71				

M80				
M94	Anthoporia albobrunnea VU	Anomoporia kamtschatica NT		

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