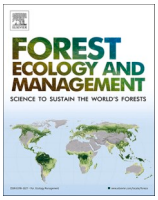
Forest Ecology and Management 598 (2025) 123186

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Tree retention levels and prescribed burning effects on ectomycorrhizal fungal communities in a boreal Scots pine forest

Delphine Lariviere [a,b,*], Line Djupström [a,c], Björn D. Lindahl [d], Anders Dahlberg [e]

[a] The Forestry Research Institute of Sweden (Skogforsk), Uppsala, Sweden
[b] Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Sundsvägen 3, Alnarp SE-230 53, Sweden
[c] Swedish University of Agricultural Sciences (SLU), Department of Wildlife, Fish and Environmental Studies, Umeå SE-901 83, Sweden
[d] Swedish University of Agricultural Sciences, Department of Soil and Environment, Box 7014, Uppsala SE-750 07, Sweden
[e] Swedish University of Agricultural Sciences, Department of Forest Mycology and Plant Pathology, Box 7026, Uppsala SE-750 07, Sweden

ARTICLE INFO

Keywords:
Clearcutting
Ectomycorrhizae
Forest management
Land-use
Pinus sylvestris

ABSTRACT

Ectomycorrhizal fungi (EMF) form essential symbiotic relationships with trees, supporting nutrient cycling and forest health. However, forestry practices such as clear-cutting disrupt this association, threatening EMF survival. This study investigated the effects of tree retention levels and prescribed burning on EMF abundance, species richness, and community composition in old Scots pine forests 4.5 years after logging. Soil samples were analyzed using DNA sequencing, with stand-level replication. Higher retention levels were associated with increased EMF abundance and diversity, while proximity and size of retention trees significantly influenced outcomes. Species richness declined sharply beyond 5–10 m from retained trees. The greatest declines occurred under minimal retention (3 %) and when prescribed burning was combined with a 50 % harvest. Prescribed burning with 50 % tree removal exacerbated EMF losses in the short-term, likely due to the combined effects of harvesting and fire severity, highlighting the need for careful integration of fire management into forestry practices. Community composition shifted noticeably, with disturbance-tolerant taxa replacing dominant species from older forests. Rare species were disproportionately affected by substantial tree removal, while common species persisted. These findings highlight the importance of retaining higher tree densities and strategically placing retention trees. Sustainable management of old boreal Scots pine forests requires tailored retention strategies and cautious planning of harvesting and prescribed burning to balance biodiversity conservation with forestry objectives.

1. Introduction

Forests are complex ecosystems that harbor a rich diversity of life and provide multiple critical ecosystem services, such as carbon sequestration, water regulation, and soil stabilization, which are indispensable for both environmental health and human well-being (Brockerhoff et al., 2017). Globally, forests face challenges due to modern forestry practices that often simplify these ecosystems. This is particularly evident in Fennoscandia, especially in Sweden, where clear-cutting has been the dominant method of forest management since 1950's (Lindbladh et al., 2014, Felton et al., 2020).

Clear-cutting, which involves the removal of most or all trees in an area, leads to habitat loss and a decline in biodiversity, particularly affecting species that rely on forest continuity (Siry et al., 2005). Mycorrhizal fungi rely on the presence of trees to exist. Ectomycorrhiza predominates in boreal forest ecosystems, where only a few host species are present, but belowground fungal diversity is comparably high (Tedersoo et al., 2014). The Pinaceae family is obligatorily associated with ectomycorrhizal fungi (EMF) (Smith and Read, 2010). The trees provide them with carbon in the form of sugars, while the EMF provide the trees with water and nutrients (Futai et al., 2008). EMF are particularly important in Sweden, where 80 % of the forest biomass consists of Scots pine and Norway spruce, and in total 99.5 % of tree species forming ectomycorrhiza (Swedish University Of Agricultural Sciences, 2024). The number of known EMF species in Sweden, largely based on sporocarp observations, is about 1700 of which about at least 500 are known to be associated Scots pine (SLU Artdatabanken, 2025). EMF are vulnerable to clear-cutting as disturbances (Kranabetter et al., 2013,

* Corresponding author at: The Forestry Research Institute of Sweden (Skogforsk), Uppsala, Sweden.
E-mail address: delphine.lariviere@skogforsk.se (D. Lariviere).

https://doi.org/10.1016/j.foreco.2025.123186
Received 4 June 2025; Received in revised form 22 August 2025; Accepted 15 September 2025
Available online 2 October 2025

Sterkenburg et al., 2019, Cline et al., 2005, Jones et al., 2003, Liu et al., 2020), and the severing of symbiotic connections between EMF and their host trees leads to declines in fungal biomass and species richness. (Jones et al., 2003, Nguyen et al., 2012) Sterkenburg et al., 2019).

To mitigate negative impacts of clear-cutting, retention forestry has been widely adopted, particularly in Sweden (Gustafsson et al., 2019). This practice involves leaving specific trees or groups of trees standing during harvesting to preserve structural and biological diversity (Gustafsson et al., 2012). In Sweden, typically 3–10 % of the standing trees per hectare are retained during harvesting (Gustafsson et al., 2020). Retention forestry is globally recognized for its potential to support a range of species, including EMF (Varenius et al., 2017, Cline et al., 2005, Cline et al., 2007). The number, type and spatial arrangement of retained trees vary based on management goals and certification standards, influencing the biodiversity outcomes. While some EMF may persist near forest edges or around retained trees, their survival depends on factors such as retention proximity and type (Varenius et al., 2017, Cline et al., 2005) as well as environmental conditions such as soil acidity, water and nutrients availability, and the dominant tree species (lindahl, Clemmensen, 2017, Prescott and Grayston, 2013, Čugunovs et al., 2020).

In addition to retention forestry, prescribed burning is sometimes used in boreal forest management to mimic natural disturbances, to create structure and enhance species composition in Pine forests (Ramberg et al., 2018). In Scots pine forests, many pines form associations with EMF (SLU Artdatabanken, 2025) whose persistence depends on suitable habitat and hosts, highlighting the importance of management practices that maintain fungal diversity and forest function.

Long-term experiments have advanced understanding of how these practices (individually and in combination) affect EMF and broader forest biodiversity. Studies across boreal forests shows that higher levels of tree retention, alone or in combination with prescribed burning, generally support greater biodiversity, including fungi (Kouki and Salo, 2020, Suominen et al., 2015, Nirhamo et al., 2023, Simard et al., 2021), lichens (Hämäläinen et al., 2016), saproxylic species, and other forest organisms (Tinya et al., 2023); while low retention or/and high-intensity burning can reduce community stability and species richness. The current literature provides a strong foundation for understanding how tree retention affects EMF biomass and diversity over time. Studies have highlighted the importance of living host trees for fungal persistence and shown that maintaining structural elements (Kouki and Salo, 2020, Koivula and Vanha-Majamaa, 2020, Hyvärinen et al., 2006), as well as retention level (Sterkenburg et al., 2019, Kouki and Salo, 2020) and tree arrangement (Cline et al., 2005, Varenius et al., 2017, Luoma et al., 2004), influences fungal community composition.

Our study builds on this foundation, while contributing novel insights by focusing on fine-scale spatial structure of EMF communities relative to individual tree locations, across a large operational-scale experiment, and by using novel techniques, including eDNA metabarcoding, to assess EMF communities. We examine EMF relative abundance and diversity as a function of distance and size of surrounding retained trees. Thus, while not entirely unique in concept, our study complements existing research by providing a detailed spatial lens into EMF responses specifically within a landscape-level experiment. This approach offers operational relevance and direct applicability to forestry planning, especially in regions where retention forestry and fire are increasingly integrated into management regimes.

The objectives of this study were to quantify how different levels of tree retention (from 3 % of tree retained, up to 100 % of tree retained), conservation management (deadwood creation), and prescribe burning may affect EMF communities.

We hypothesized that:

(1) The relative abundance of EMF in the total fungal community would correlate with the number of trees present, i.e., the level of tree retention.
(2) The species richness of EMF would decline proportionally with the proportion of trees logged (tree crown size).
(3) EMF abundance and species richness would decrease with increasing distance from the nearest living retained tree.
(4) The EMF community composition would be minimally impacted by different levels of tree retention, except for the disappearance of low-frequency taxa, particularly when combined with prescribed burning.

These hypotheses address critical knowledge gaps in understanding how operational forestry practices influence EMF communities, with implications for biodiversity conservation and sustainable forest management. By examining these relationships at operational relevant scales, this study provides evidence-based guidance to support both ecological sustainability with practical forestry goals.

2. Material and methods

2.1. Study site and design

The study was conducted at the long-term field experiment Effaråsen, located close to Mora in the province of Dalarna in the southern boreal vegetation zone of Sweden (14°1′1"E 60°58'21"N, Fig. 1). Prior to the long-term-experiment, Effaråsen was an area dominated by Scots pine forests (*Pinus sylvestris L.*) (i.e. >95 %) with tree ages ranging from 100 to 137 years (Fig. 2). The experimental area includes 24 individual stands representing a total of 140 ha of forest. The stand sizes range from 2.3 ha to 14.2 ha with a mean size of 5 ha. The last large scale natural fire happened in 1888, and fire scars are found on both live and dead trees (Fig. 2). The forest stands have relatively low productivity, with a mean annual increment of about 2.5 m^3 per ha. All except one stand had been fertilized 1–2 times 20–40 years ago (Table 1).

In 2012, 24 forest stands were assigned to harvest treatments involving varying levels of tree retention (3, 10, 30, 50, 100 %), deadwood enrichment (NS), and prescribed burning (burn 50 %, burn 100 %) (Table 1). In total 7 treatments, one control, and 3 stands per treatment. Treatments were spatially balanced using restricted randomization and met safety requirements for burning (see map in Fig. 1). To avoid spatial clustering effects, repeated treatments were not located adjacent to each other. The lowest level of retention (3 %) represents the common practice in Swedish forestry, while the higher levels are not commonly applied. These retention levels align with the requirements for certification, such as those set by the Forest Stewardship Council (FSC).

For the treatments where forest harvest was conducted (3, 10,30, 50 %); prior to harvest, single trees and the outer boundaries of retention tree groups (typically including 15–20 trees) were marked to prevent cutting. The location and spacing of these groups varied between stands in accordance with the allotted cutting regimes. Selection prioritized high conservation value Scots pines (*Pinus sylvestris*), old, large-diameter (>25 cm DBH), fire-scarred, or associated with large logs/snags. Four habitat features were created in equal proportions: solitary/groups trees, high stumps (~3 m), felled trees, and girdled/bark-peeled trees. Felled stems were often moved into retention patches. All retained trees (whether live or dead) were included in the calculation of the percentage retained. For further details, see Santaniello et al. (2016). In the same way, the three stands where deadwood enrichment was conducted (NS), no harvest was done but 25 % of trees were left alive, 25 % girdled, 25 % cut as high stumps, and 25 % fell. Finally, six of the 24 stands were burnt in May 2013. The prescribed burnings were carried out during May–June (southern part) and August (northern part) 2013. Of these six stands, three were harvested (50 % of standing volume) before burning, and three stands where no burning nor cutting were carried out served as controls (Table 1).

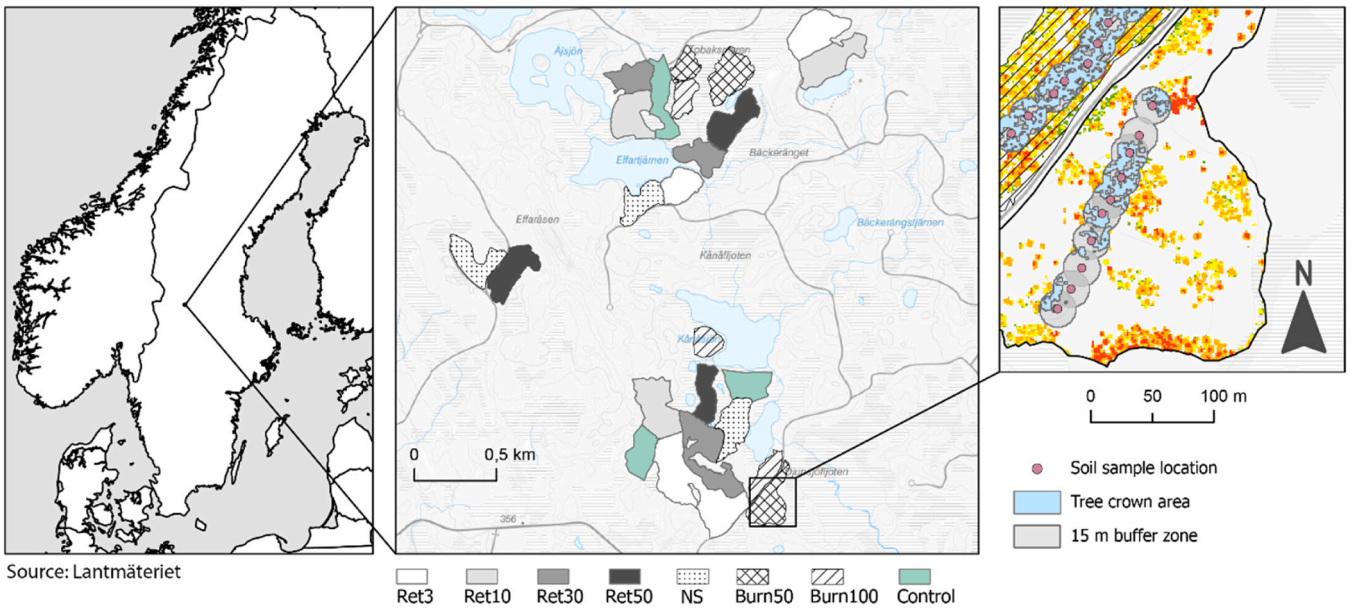


Fig. 1. Map showing the location of the study area, experimental design, soil core sampling layout, and laser-derived data used to assess retention characteristics. The study included 24 forest stands subjected to eight different treatments: four retention treatments (ret3 = 3 %, ret10 = 10 %, ret30 = 30 %, and ret50 = 50 %), a nature conservation management treatment (NS), two prescribed burning levels (Burn100 and Burn50), and a control treatment. Soil samples were collected in 2017. Pink circles indicate the ten sampling points within each stand, while grey areas represent 15-meter buffer zones used to estimate potential tree crown area. The background map on the right displays a height raster layer derived from the Swedish national laser scanning (Skogstyrelssen, 2025), showing canopy height (yellow to red) and interpreted as potential crown height. This layer provides a detailed view of forest structure and spatial variation in canopy conditions.

Fig. 2. Photographs from the Effaråsen site: (left) an overview of the Scots pine forest harvested with a retention group of trees; (center) three soil cores collected per sample, illustrating the sampling methodology; and (right) a fire scar on a high stump of an old Scots pine, highlighting evidence of past prescribed burning.

2.2. Soil sampling & retention data

In September 2017, 4.5 years after logging, ten soil samples (3 cm in diameter) were systematically collected from each stand along 90-meter transects positioned centrally within the stands (Fig. 1). To reduce potential edge effects and immediate spatial dependency, sampling points were positioned toward the center of each stand, separated by at least 10-meter intervals, and GPS coordinates were recorded for each sampling location. This design helps minimize the influence of adjacent stands on the local fungal communities. In certain instances, the sample size was reduced to nine as one sample was lost during processing or handling. Living mosses and mineral soil were removed, so that the samples consisted only of the organic mor layer (Lindahl et al., 2007) (Fig. 2).

At each sampling point, the distance (in meters) to the nearest living tree (regardless of species) was assessed using measuring tape. Additionally, the potential tree crown area (in square meters) above 2 m in height within a 15-meter buffer around each sampling point was estimated using the 2022 height raster from the Swedish laser scanning data (Skogsstyrelsen Swedish Forest Agency, 2025). The “Extract by mask”

Table 1
Overview of the 24 stands included in the experiment. The name of the treatment represents the percentage of retention (Ret3–50 percent) left at clear cut. "C" represents the three untreated control stands with no felling nor regeneration were carried out, "NS" means Conservation management (Naturvårdande skötsel) and include three stands used to represent a management alternative to prescribed burning through the artificial creation of both lying and standing dead wood and girdle trees. "Burn100" includes three stands with only prescribed burning, and "Burn50" three stands where trees were harvested (50 % of standing volume) before burning (Prescribed burning was carried out May/June (south) and August 2012 (north)). Local is representative of the stand location in the landscape: DS- refers to Djupsjön, Eff- for Effaråsen, ETO- for Effartjärnen ost, ETV- for Effartjärnen väst, KS- Kånåsjön, TM- for Tobacksmyren. "Stem/ha" represents the number of trees per hectare before harvest, the age is retrieved from the stand register of the landowner and represents the average age of the stand. And "#" represent the number of soil sample collected for each stand in 2017. ** DS-3, due to its size was divided into two stands and the amount of soil sample doubled.

Name	Treatment	Local	Stem/ha	Size (ha)	Altitude (msl)	Fertilization (year)	Age	#
C	Untreated control	KS	664	4.2	368	1992, 2000	128	10
		DS	636	4.1	377	1992, 2000	117	10
		ETV	264	5.6	391	1992	137	9
Burn100	Prescribed burning with no wood extraction	KS	259	2.3	366	None	156	10
		DS	446	3.2	368	1992, 2000	100	10
		ETV	511	2.8	390	1992	137	10
NS	Conservation management	ETO	395	4.0	380	1992	108	10
		DS	475	5.0	374	1992, 2000	117	10
		Eff	312	4.9	385	1992	111	9
Ret3	Final felling with 3 percent retention	DS	488	14.2	378	1992, 2000	117	19*
		ETO	212	4.1	382	1992	108	10
		TM	539	7.2	405	1982, 1992	134	10
Ret10	Final felling with 10 percent retention	ETV	283	5.9	378	1992	137	9
		KS	488	7.4	391	1992, 2000	117	10
		TM	422	7.7	402	1982, 1992	134	10
Ret30	Final felling with 30 percent retention	DS	490	8.9	376	1992, 2000	117	10
		ETO	414	4.0	385	1992	121	10
		ETV	316	3.9	388	1992	137	9
Ret50	Final felling with 50 percent retention	EFF	411	5.7	391	1992	111	10
		ETO	375	5.5	389	1992	121	10
		KS	449	3.9	370	1992, 2000	117	10
Burn50	Prescribed burning with 50 percent wood extraction	DS	401	5.6	374	1992, 2000	134	10
		ETO	470	5.5	389	1992	121	10
		ETV	297	3.0	393	1992	137	10

Msl= meters above sea level.

tool in ArcGIS Pro was used to extract pixels within a 15-meter radius of each sampling point. Pixels representing heights greater than 2 m (interpreted as potential tree crown) were filtered using the "greater than" tool and converted into polygons using the "Raster to Polygon" tool. The "Summarize Within" tool was then applied to calculate the total area of these polygons representing the estimated crown area around the sampling point (Fig. 1). Distances to the nearest living tree and tree areas were averaged for each sampling point. It is important to note that these crown areas are approximations based on remote sensing data and do not represent direct measurements of individual tree crowns.

2.3. Sequencing of fungal communities

The DNA extraction and sequencing protocols were performed as described by Lindahl et al. (2021). The samples collected in plastic tubes were frozen within 10 h, freezing dried and finely ground in a ball mill. DNA was extracted for fungal community sequencing from 50 mg of organic soil using the NucleoSpin Soil Genomic DNA extraction kit (Macherey-Nagel, Düren, Germany). The ITS2 region of the ribosome-coding operon was PCR-amplified with gITS7 and ITS4 primers, both fitted with unique sample tags, following a standard protocol (Clemmensen et al., 2016) and sequenced on the Sequel I platform (Pacific Biosciences, Menlo Park, CA, USA) at SciLifeLab NGI (Uppsala, Sweden). The methodology was optimized to provide the most accurate reflection of the fungal community composition as possible (Castaño et al., 2020). Sequence data was filtered and clustered using the SCATA bioinformatic pipeline (Swedish University of Agricultural Sciences, 2025). In total, 245 soil samples were analyzed. Sequences were quality checked to remove sequences shorter than 100 bp, with mean quality scores lower than 20, with individual bases with a quality score lower than 3. Sequences were screened for primer sequences, requiring a minimum match of 90 %, and reversed complemented if necessary. Sequences with missing or mismatching 3' or 5' tags were deleted. Globally unique genotypes were removed to reduce the incidence of sequencing errors. Quality filtering removed 35 % of the total sequences, and another 17 % were removed as unique genotypes. The remaining sequences were clustered into species hypotheses (hereafter named species; Kõljalg et al. 2013) through pairwise comparisons with USEARCH (Edgar, 2010) followed by single linkage clustering, with the minimum similarity to the closest neighbor required to enter a cluster set at 99 %. The most abundant sequence from each species was selected as a representative and was identified by BLAST comparisons with the UNITE (Kõljalg et al., 2013) and NCBI databases. After removal of non-fungal sequences, all species that accounted for more than 1 % of the sequences in any sample were evaluated manually for taxonomic identity and ectomycorrhizal status.

3. Data analysis/statistics

3.1. Species richness and relative abundance

The proportion of ITS2 sequences assigned to ectomycorrhizal fungi (EMF) within the total fungal community was analyzed across the samples using a linear mixed-effects model (lmer from the lmerTest R package). The response variable was the log-transformed EMF proportion, retention levels categories were included as a fixed effect and stand included as a random effect to account for the hierarchical sampling design. The control treatment (C) was used as the reference level for the retention level variable. Differences between retention levels were evaluated using a Type III ANOVA with Satterthwaite's method. Post hoc pairwise comparisons were conducted using the emmeans function from the emmeans package (Lenth et al., 2022).

Species richness was aggregated at the stand level and analyzed across retention levels using a generalized linear mixed-effects model (GLMM) with a Poisson distribution. The data were aggregated to the

stand level and transformed into a binary species matrix, where each species was either present (1) or absent (0). Species richness per stand was calculated by summing the number of species present (i.e., the sum of 1 s). The dispersion of the residuals was checked using the Pearson chi-square statistics, confirming no over or under dispersion. A Type III ANOVA was conducted to analyze the effects of retention treatment. Post-hoc pairwise comparisons were conducted using the emmeans package (Lenth et al., 2022) to evaluate differences in species richness between retention treatment.

The total EMF species richness per retention treatment was estimated by summing unique species occurrences across all stands within each category. Species accumulation curves were generated using the iNEXT package (Hsieh et al., 2022) to visualize differences in species richness among levels, with confidence intervals used to compare sampling completeness and richness patterns.

3.2. Multivariate analyses of community composition

Ectomycorrhizal fungi (EMF) communities were compared at the stand level based on frequencies of occurrence among the 10 soil cores in each stand. We assessed the differences in species composition based on Bray-Curtis dissimilarity using a permutational multivariate analysis of variance (perMANOVA) with the adonis2 function in the vegan R package (Oksanen et al., 2020) and illustrated results by non-metric multidimensional scaling (NMDS), using the metaNMDS function. As many trees died from the fire, the effects of different retention levels are examined with and without the burn treatment. This approach aims to identify the threshold of retention necessary for effective EMF, without considering the influence of additional treatments such as prescribed fire. The stress level was interpreted according to Dexter et al. (2018) where a value of < 0.3 is considered a good fit and allows for reasonable interpretation.

To explore relationships between species composition and environmental variables (Distance to the nearest living tree and tree crown area), an envfit analysis was conducted using the envfit function in the vegan package (Oksanen et al., 2020). Species data were fitted to the NMDS ordination to identify associations between species and the ordination axes. Additionally, the stand averaged crown size within a 15 m radius and distance to the nearest living retention trees per stand, were fitted to the ordination, using the envfit function.

To assess the relationship between the crown area size or the distance to the nearest living tree and the presence of ectomycorrhizal (EMF) fungal individual species, we calculated Pearson correlation coefficients between the canopy size or the distance to the nearest living tree and the incidence frequency of each species. Species incidence was defined as the number of soil cores (out of 10) in which each species was detected per stand. The species were aggregated to taxonomic level. For each species, a two-tailed Pearson correlation test was performed using the cor.test() function in R. To account for multiple comparisons across all species, we applied the Benjamini-Hochberg procedure to control the false discovery rate (FDR). Adjusted p-values were computed using the p.adjust() function with the "BH" method. The ten species with the lowest FDR-adjusted p-values were selected for further interpretation. Then a plot was made showing only the strongly correlated species (with correlation coefficients ≥ 0.7 or ≤ -0.7), separated by positive and negative correlation types.

To evaluate treatment effects on species persistence, soil samples were pooled into three tree-retention categories: (i) no or minimal tree removal (Control, NS, Burn100; $n = 88$), (ii) moderate removal (Ret10, Ret30, Ret50; $n = 88$), and (iii) high removal or mortality (Ret3, Burn50; $n = 69$). For each taxonomic unit, frequency was quantified as the number of samples within a treatment group in which the species was detected. Species not recorded in a given group (frequency $= 0$) were considered locally absent under that retention level. This approach enabled a comparative assessment of species loss across gradients of tree removal intensity.

3.3. Retention tree distance & size

The proportion of EMF, as well as the species richness at the stand level were compared in the different retention level but also correlated to a) the distance to the nearest living tree and b) the size of the retention area using linear correlation models. Since the distance to the nearest living tree is negatively correlated to the size of the retention (stands with larger distances between trees are less associated with larger crown areas, and vice versa.); both variables were investigated in individual models.

4. Results

A total of 18351 sequences attributed to ectomycorrhizal fungi (EMF) were clustered into 123 Species Hypothesis (SH), hereafter called species. Of these, 112 were identified at the species level, whereas the remaining nine percent were identified at the genus level.

4.1. Species richness and relative abundance

The relative proportion of EMF 4.5 years after harvest differed significantly between the various levels of tree retention ($p < 0.01$, $F=3.9$; Table 2). The control treatment had the highest mean proportion of EMF (8.4 % ± 2.01 SE), while burned stands with 50 % retained trees (Burn50) had the lowest proportion of EMF per sample (1.42 % ± 0.53 SE, Table 2). When comparing RT3 to the control, there is a decrease of about 72 % of the EMF proportion, whereas 10, 30 and 50 % retention had a decrease of respectively 54 %, 47 % and 59 % (Table 2).

Species richness also differed significantly between the various levels of tree retention ($p < 0.005$; $Chisq= 37.4$; Table 2). The control (C) had the highest species richness together with the conservation management NS and the 50 % retention treatment (Burn50), whereas the B50 treatment has the lowest, followed by RT3. The confidence intervals vary widely, with Burn50 and the control having wide ranges, indicating more uncertainty and variability in the number of species.

The same pattern is evident in the species accumulation curves (Fig. 2). The assemblage data (collection of species presence or frequency data within a given area or treatment) reveal that infrequent species (e.g., Q3–Q10) are less represented in treatments with higher levels of disturbance (e.g., Burn50 and Ret3). For instance, Burn50

Table 2
Estimated marginal means for species richness per stand (n = 25) and the estimated relative abundance per soil sample (n = 245) of ectomycorrhizal fungi (% EMF) with their standard error of the mean (SE). The table shows the results from the post-hoc test and their comparison (Group), group sharing a letter are not statistically different. The column (% decrease) represents the decrease in % EMF or species richness relative to the control. Additional details and statistical outputs are provided in the Supplementary Material.

Treatment	% EMF (±SE)	% Decrease	Group	Species richness (±SE)	% Decrease	Group
Control	8.4 ± 2.10	0	a	41.0 ± 3.70	0	a
Burn100	6.1 ± 1.56	28	ab	30.3 ± 3.18	26	bcd
NS	5.5 ± 1.45	35	ab	36.0 ± 3.46	12	ab
Ret3	2.4 ± 0.65	72	cd	23.5 ± 2.42	43	de
Ret10	3.8 ± 1.08	54	bc	25.3 ± 2.91	38	cde
Ret30	4.5 ± 1.22	47	abc	26.3 ± 2.96	36	cd
Ret50	3.4 ± 0.98	59	bcd	31.3 ± 3.23	24	bc
Burn50	1.4 ± 0.53	83	d	18.7 ± 2.49	54	e

supports fewer infrequent species (Q3–Q10) compared to the control treatment (Table 3).

4.2. Retention tree distance & size

Proportion of Ectomycorrhizal Fungi: The proportion of ectomycorrhizal fungi (EMF) was higher at shorter distances to the nearest living tree, decreasing as the distance increased. Specifically, the proportion dropped from approximately 35 %–45 % at three meters to around 20 %–25 % when the distance exceeded 15 meters. This relationship was confirmed by a linear model, which showed a significant effect ($F = 10.986$, $p = 0.003$) of the distance to the nearest living tree on the proportion of EMF. Additionally, the proportion of EMF increased by roughly 10 %–15 % as the average tree crown area within a 15-meter radius expanded from 200 to 500 square meters. The linear model also revealed a significant effect of the crown area on EMF proportions ($F = 12.471$, $p = 0.002$, Fig. 4).

Species Richness: Species richness decreased as the distance to the nearest living tree increased, dropping from approximately 35–45 species at three meters to around 20–25 species at distances exceeding 15 m. This trend was confirmed by an analysis of variance, which showed a highly significant effect ($F = 19.745$, $p < 0.001$) of the distance to the nearest living tree on species richness. Additionally, species richness increased by approximately 10–15 species as the average tree crown area within a 15-meter radius expanded from 200 to 500 square meters. This relationship was also highly significant ($F = 31.705$, $p < 0.001$, Fig. 4).

4.3. Community composition

The most frequent species was *Piloderma sphaerosporum* which was found in 56 % of the samples, followed by *Cortinarius semisanguineus* (coll.) (53.16 %) and Cenococcum *geophilum* (coll.) (44 %). These four species were also found in every stand while 14 species were only recorded in single soil core each, and 16 species only in a single stand. The most frequent genera were *Cortinarius,* found in 88 % of the samples, *Piloderma* in 58 %, *Cenococcum* in 44 % and *Russula* and *Suillus* in 43 % of the samples. The most species rich genus was *Cortinarius* with 53 species, followed by the groups tooth fungi (*Phellodon*, *Pseudotomentella*, *Thelephora*, *Tomentella*, and *Pseudotomentella*) with 17 species, crust fungi (*Amphinema*, *Piloderma, Tylospora*) with 14 species, and brittlegills and milkcaps (*Russula* and *Lactarius*) with 10 species.

There was no significant difference in community composition between the retention levels. At the stand level, without any of the prescribed burning stands, the permutational multivariate analysis of variance (PERMANOVA) revealed that retention level classes explained 32 % of the variation in species composition ($R^2 = 0.32$). However, this effect was only marginally significant ($p = 0.06$). The NMDS ordination illustrates differentiation between the various retention levels, with stands with 50 % or more retained trees (NS, C and Ret50) clustering to the lower right and plots with 30 % or less retained trees (ret3, ret10, ret30) located in the upper part (Fig. 5). The NMDS analysis produced a final stress value of 0.2175, indicating an acceptable fit (stress values of 0.1–0.3 are adequate for ecological data). Retention level's relationship with fungal community composition was visualized in the ordination graph (Fig. 5). Multiple regression model by "envfit" function was used to test the effect of environmental variables on the species distribution. The "envfit" function fits vectors of continuous variables to the ordination, with the length of the arrow proportional to the correlation with the ordination. Biplots of species and envfit vectors were generated to visualize the results.

The NMDS plots provide insights into stand groupings by retention treatment and the influence of significant species and environmental variables. In the left plot, the vectors represent significant species identified through the envfit analysis. These arrows indicate the gradient and strength of association between species presence/abundance and the NMDS axes. Sites near the arrowheads are strongly associated with specific species, while the arrow lengths reflect the significance and strength of those associations. The vectors in the right plot highlight the influence of two key variables: "Distance to the nearest tree" and "Crown area." These variables show a trade-off, where sites with larger distances between trees are less associated with larger crown areas, and vice versa. This relationship reflects structural differences in the forest stand based on retention levels. Sparse sites (e.g., low retention treatment like Ret3 or Ret10) tend to have larger tree spacing, while denser sites (e.g., higher retention treatment like Ret50 or Control) are associated with larger crown areas and closer tree spacing.

The relationship between tree crown mean area and distance to the nearest living trees and species frequency was examined for the top three positive and negatively correlated species. The scatter plot with linear regression lines revealed distinct trends among species. Several species exhibited strong positive correlations, indicating that their frequency increased with greater mean area (*Cortinarius aff. Acutus, Cortinarius camphoratus, Leccinium varicolor*). Conversely, other species showed negative correlations, suggesting a decline in frequency as the mean area increased. The same positive (*Suillus bovinus*, *Laccaria laccata (Coll.), Leccinum varlicolor*) and negative (*Suillus variagatus*, *Cortiarius aff. Acutus*, *Lactarius rufus*) pattern are observed with the nearest living tree distance (Fig. 6).

The analysis of species frequencies across the three tree removal groups highlights increasing species loss as tree retention decreases. The first group, with no or minimal tree removal (Control, NS, Burn100; 88 soil samples), shows the lowest impact, with 9 species (6.9 %) no longer recorded. The second group, involving moderate tree removal (Ret10, Ret30, Ret50; 88 soil samples), shows 23 species (17.7 %) absent. The final group, with high tree removal or mortality (Ret3, Burn50; 69 soil samples), exhibits the greatest loss, with 98 species (75.4 %) missing. This trend emphasizes the significant ecological impact of reduced tree

Table 3
Diversity metrics from the iNEXT analysis for the different treatments including the total number of species observed (S.obs), sample coverage (SC), and the frequency of species across ten soil samples (Q1-Q10). The treatments are labeled as C (Control), NS (Conservation management), Burn100 (Prescribed burning), Ret50 (50 % retention), Ret30 (30 % retention), Ret10 (10 % retention), Ret3 (3 % retention), and Burn50 (50 % retention and prescribed burning). T represents the number of soil samples per treatment and U and the number of unique species occurrence, i.e., species that appeared in only one soil sample within a treatment. Because the same SH can occur uniquely in more than one soil sample, U may exceed the total number of SHs detected in the study (123). High values of U highlight the importance of rare fungi and reflect the patchiness of fungal communities across soil samples.

Treatment	T	U	S.obs	SC	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8	Q9	Q10
Control	29	258	76	0.8609	37	16	7	1	2	2	2	2	0	1
Burn100	30	178	63	0.8075	35	11	6	2	1	2	0	0	0	3
NS	29	213	65	0.8724	28	12	13	3	2	0	1	0	0	0
Ret3	39	184	45	0.8876	21	6	1	5	3	1	0	2	0	1
Ret10	29	161	49	0.8619	23	11	3	3	0	1	2	0	1	2
Ret30	29	155	52	0.8110	30	10	3	1	0	0	0	2	2	0
Ret50	30	187	54	0.8863	22	11	7	3	1	2	2	1	0	0
Burn50	30	94	41	0.7398	25	8	0	2	3	0	1	0	1	0

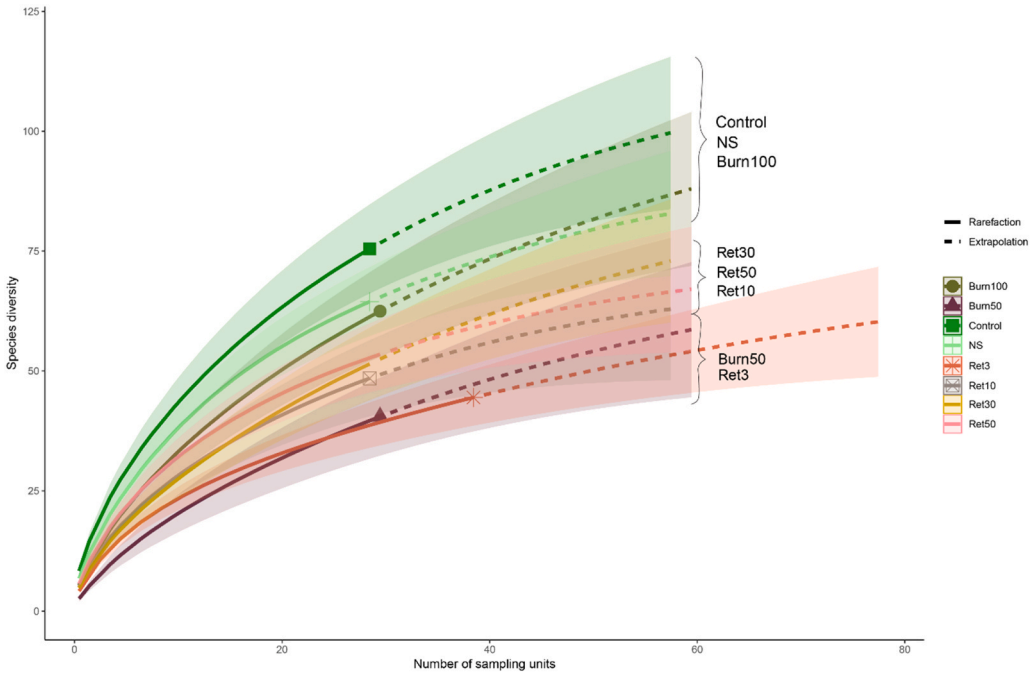


Fig. 3. Rarefaction and extrapolation curves of ectomycorrhizal fungal species richness for different retention levels generated using the iNEXT package in R. Solid lines represent rarefaction curves, while dashed lines indicate extrapolation beyond the observed sample size. The x-axis represents the number of soil samples, and the y-axis represent the accumulated species richness. Shaded regions around the curves show 95 % confidence intervals. Symbols (e.g., circles, squares, triangles) mark observed diversity for each group, with curves projecting expected diversity as sampling effort increases.

retention (Fig. 7).

5. Discussion

This study underscores the significant role of retention trees in supporting ectomycorrhizal fungi (EMF) communities in Scots pine forests 4.5 years after logging. The proximity and local canopy area (potential tree crown size) of retention trees were strongly correlated with EMF abundance and species richness, with closer and larger retention promoting higher EMF diversity and relative abundance. Consequently, higher retention levels were linked to greater EMF abundance and species richness, with the most marked declines observed in low-retention scenarios (Ret3). Interestingly, even with 50 % tree retention, Burn50 emerged as the worst-case scenario, reflecting the short-term potential negative impact of fire. This highlights the needs for careful integration of fire management into forestry practices.

5.1. Proximity and size of retention trees

The abundance and species richness of EMF were significantly influenced by the local canopy area (potential tree crown size) and proximity of living retention trees. Species richness increased from 20 to 25 species at distances over 15 m to 35–45 species within three meters of retention trees. Relative EMF abundance rose by approximately 10 %–15 % as average tree crown area within a 15-meter radius expanded from 200 to 500 square meters. These findings align with previous research that demonstrates declines in mycorrhizal abundance and diversity with increasing distance from forest edges or retention trees (Harvey et al., 1980, Luoma et al., 2004, Parsons et al., 1994). As a consensus, studies across various forest ecosystems show that mycorrhizal abundance tends to decline significantly beyond 1.5–5 m from retention trees or forest edges, disappearing entirely by 7–16 m into clear-cut areas. Similarly, mycorrhizal diversity decreases markedly beyond 5–6 m, with species richness halved at distances of 8–25 m (Cline et al., 2007, Kolaczkowski, 2005, Varenius et al., 2017). These findings underscore the essential role of retention trees in supporting EMF communities, revealing that their influence is primarily confined to a 5–10-meter radius. The highest concentration of fine roots, and therefore the best conditions for mycorrhizal fungi, is typically found 3–6 m from a tree. The distribution of mycorrhizal fungi depends on the extent of roots and the amount of assimilates transported to different distances from trees. Beyond a certain distance from a retention tree, root density decreases, reducing the conditions needed for mycorrhizal fungi to thrive. While some roots can extend farther, approximately 90 % of a Scots pine tree's mycorrhizal root tips are found within six meters of the trunk, mainly under the tree's canopy (Saari et al., 2005). On sandy soils, roots from larger pines may extend 15–20 m whereas on rocky soils or in dense stands, roots are shorter due to competition (Saari et al., 2005). Root availability and distance to retained trees can also influence the species composition of mycorrhizal fungi (Luoma et al., 2006). For example, Varenius et al., 2017 found that the mycorrhizal community within one meter of retained Scots pine trees resembled nearby older forests but differed significantly from areas of young pine stands without retention trees.

5.2. Retention levels

Retention levels had a significant impact on EMF abundance and species richness, as these categories are inherently tied to the number and spatial arrangement of the trees. The average distance from a soil sample to the nearest living tree increased from approximately three meters in control forests and NS treatments to over 15 m at the 3 % retention level. Our results show that while lower retention treatments have greater average distances, the influence of individual nearby trees on EMF abundance operates similarly across all treatments. The 3 % retention treatment showed the steepest decline, with an 80 % reduction in EMF abundance in soil samples compared to control treatments. Total species richness was highest in control (76 species) and conservation management (65 species) treatments but lowest in prescribed burning + 50 % retention (41 species) and 3 % retention (45 species) treatments. A similar study in older pine forests at Ätnarova near Gällivare in

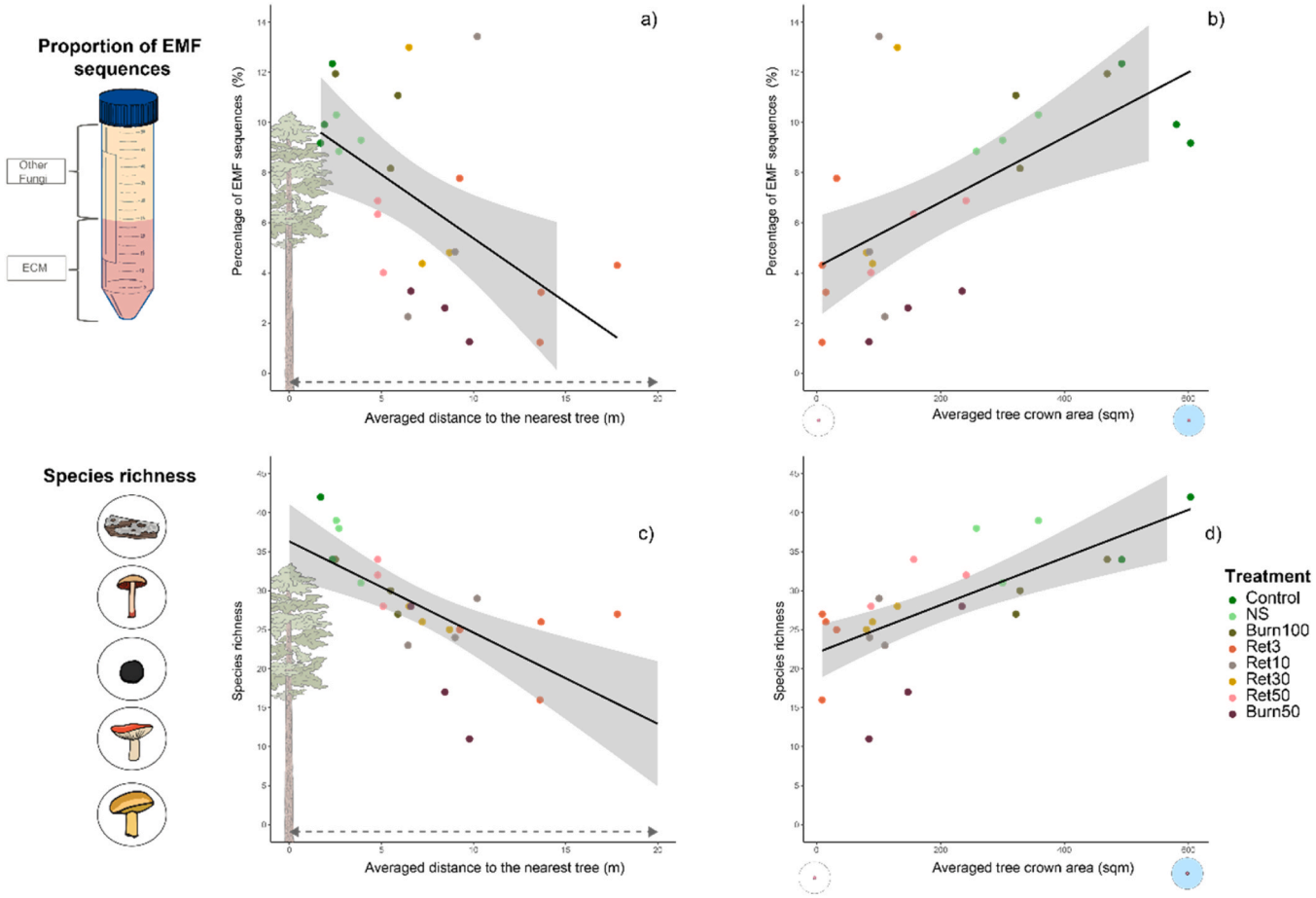


Fig. 4. Relationships between forest structural variables and fungal metrics (% ectomycorrhizal fungi and species richness). (a) relationship between the averaged distance to the nearest living tree (m) and % ectomycorrhizal fungi sequences. (b) relationship between the average tree crown area (sqm) and % ectomycorrhizal fungi sequences. (c) relationship between the average distance to the nearest living tree (m) and species richness. (d) relationship between the average tree crown area (sqm) and species richness. Points are colored by retention (Control, NS, Burn100, Ret3, Ret10, Ret30, Ret50, and Burn50), and shaded areas represent 95 % confidence intervals around the regression lines.

northern Sweden (Sterkenburg et al., 2019) found a sharper decline in the relative abundance of EMF DNA markers and species richness at low conservation levels, with almost no fungal DNA in clear-cuts without retained trees. Even moderate harvesting (40 % tree removal) led to noticeable declines. This stronger effect compared to our study may be due to the longer post-harvest period at Effaråsen (4.5 vs. 3 years). Mycorrhizal recovery is also faster in southern climates; for example, at Tönnersjöheden in Halland, mycelial growth peaked already 10–20 years after harvesting, though species richness remained low (Wallander et al., 2010).

Long-term experiments in Finland have demonstrated that retention of living trees helps buffer forest communities against the negative effects of disturbance. Retained trees support the maintenance of fungal and saproxylic diversity, even in areas subjected to intensive management (Hyvärinen et al., 2006). These findings highlight that retention forestry not only preserves mycorrhizal inoculum potential but also secures habitat continuity for wood-decaying fungi and other forest biota.

However, it is important to note that not all retention is equally effective. The term “ecologically meaningful retention” refers to retention practices that are sufficient in quantity, quality, and spatial arrangement to support biodiversity and ecosystem functions (Gustafsson et al., 2019). This typically involves retaining at least 10–30 % of the original stand, including a mix of tree species and sizes, and arranging retained trees in groups or patches rather than as isolated individuals. Such configurations help maintain microclimatic conditions, soil stability, and mycorrhizal networks. In contrast, minimal retention (such as the 3 % level tested in our study) is unlikely to provide these ecological benefits.

Taken together, these findings highlight that retention forestry, when implemented at ecologically meaningful levels (Gustafsson et al., 2019), can play a crucial role in preserving fungal communities in managed boreal landscapes. Yet, current operational practices often fall short of these thresholds, underscoring the need for improved guidelines and policy support to ensure that retention strategies effectively contribute to biodiversity conservation.

5.3. *Community composition*

In general, EMF communities are characterized by a relatively small number of frequent and dominant species, while most species are rare. The overall community composition, as depicted in the ordinations, reflects the common and dominant species. The changes are primarily due to an increase in the occurrence of some frequent species, where almost half of them belong to the *Cortinarius* (webcap) genus and are associated with higher retention levels. Meanwhile, the crust fungus (*Piloderma sp.*), though also negatively affected by harvesting, was not as impacted as other species, and its occurrence was less dependent on the number of retention trees compared to other mycorrhizal fungi. This shift, where *Cortinarius* species that dominate mycorrhizal communities in older forests are replaced by various crust fungi species after harvesting and over several decades, has been observed in multiple studies (Wallander et al., 2010, Kyaschenko et al., 2017, Lindahl et al., 2021). A

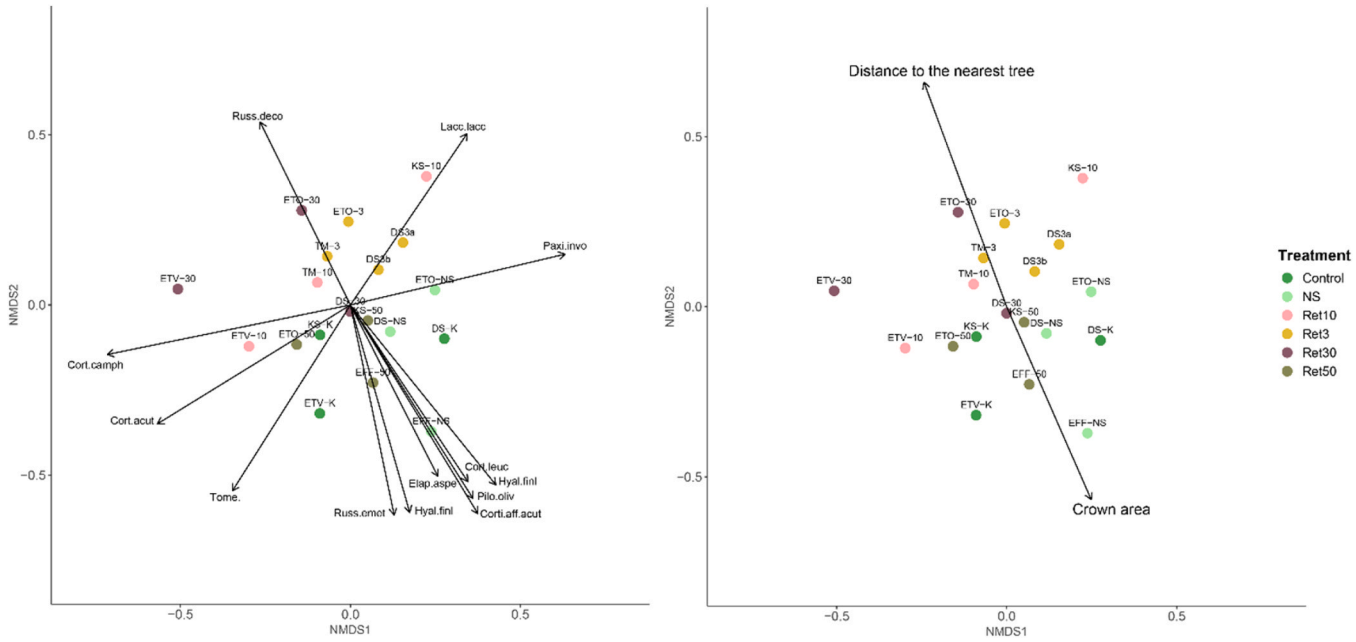


Fig. 5. Non-metric multidimensional scaling (NMDS) ordination plots showing community composition across retention treatment (Control, NS, Ret10, Ret3, Ret30, Ret50). In the left plot, points represent stands colored by retention level, with arrows indicating key species driving variation, only species with p-values < 0.005 are represented; their length and direction reflect the strength and influence of each species (e.g., Russ. dec. and Lacc. lacc. influence NMDS1, while Cort. camph. and Cort. acut. influence NMDS2). The right plot highlights two significant environmental factors, distance to the nearest tree and crown area, with arrows showing their strength and direction. The proximity of points reflects the similarity of community composition, where closer points represent more similar communities. The plot helps visualize the relationships between retention treatment, community composition, and environmental factors.

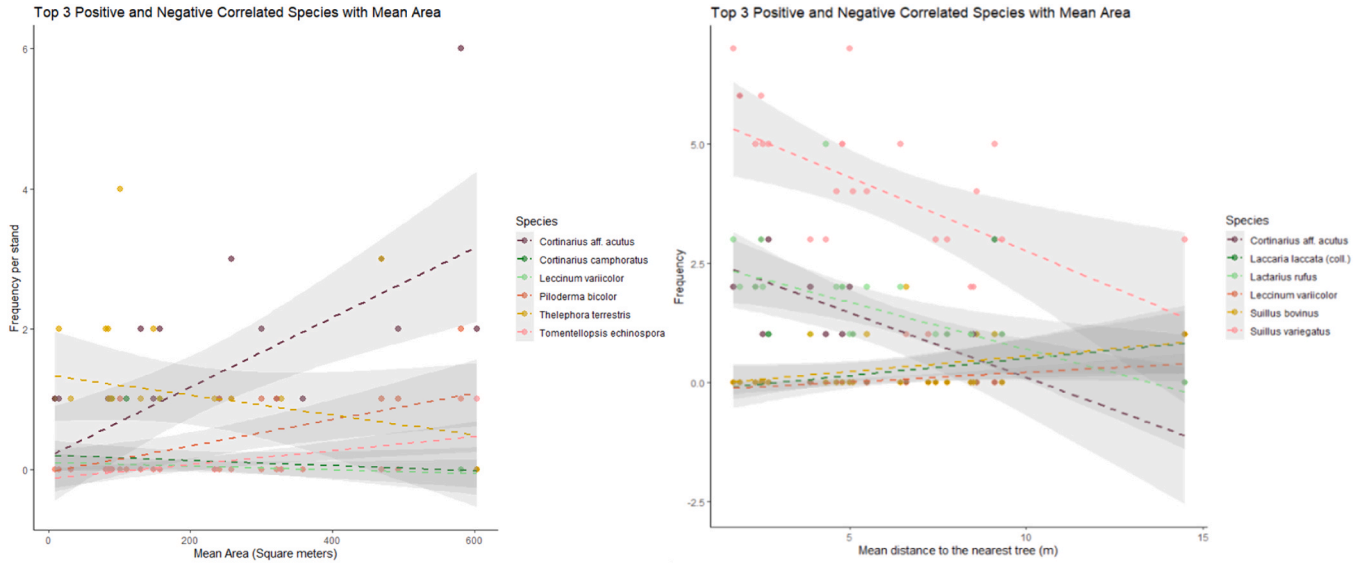


Fig. 6. Relationships between species frequency and tree metrics: (Left) Top three positive and negative correlations between species frequency (across 10 soil samples per stand) and mean tree area within a 15 m radius. (Right) Species frequency plotted against distance to the nearest living tree (in meters). The fitted linear models, along with confidence intervals, highlighted the variability in these relationships across species.

probable explanation is that many crust fungi have lower sugar demands from trees and thrive in the slightly more nutrient-rich conditions that often occur after harvesting disturbances (Jörgensen et al., 2025). Such shifts in species composition may have long-term consequences for the functional properties of mycorrhizal communities, as *Cortinarius* species have a greater capacity to mobilize organically bound nutrients compared to crust fungi.

It is also possible that certain species were detected only from spores present in the soil samples or that DNA from the pre-harvest period was preserved in the soil (Carini et al., 2020). The assemblage data shows that infrequent species were less represented in treatments with higher disturbance. when 30 % or less of the trees are retained it is not enough to preserve less infrequent species and that rare species may benefit from higher retention level than 3 % (Sterkenburg et al., 2019). It remains unclear to what extent re-establishment of different species occurs in managed forests and whether the species composition approaches that of older forests during a rotation period. The fact that certain groups, *e.g. Piloderma* species, are favored and dominate in secondary forests established after clear-cutting likely hinders and delays the re-establishment of *Cortinarius* species, as more disturbance-tolerant

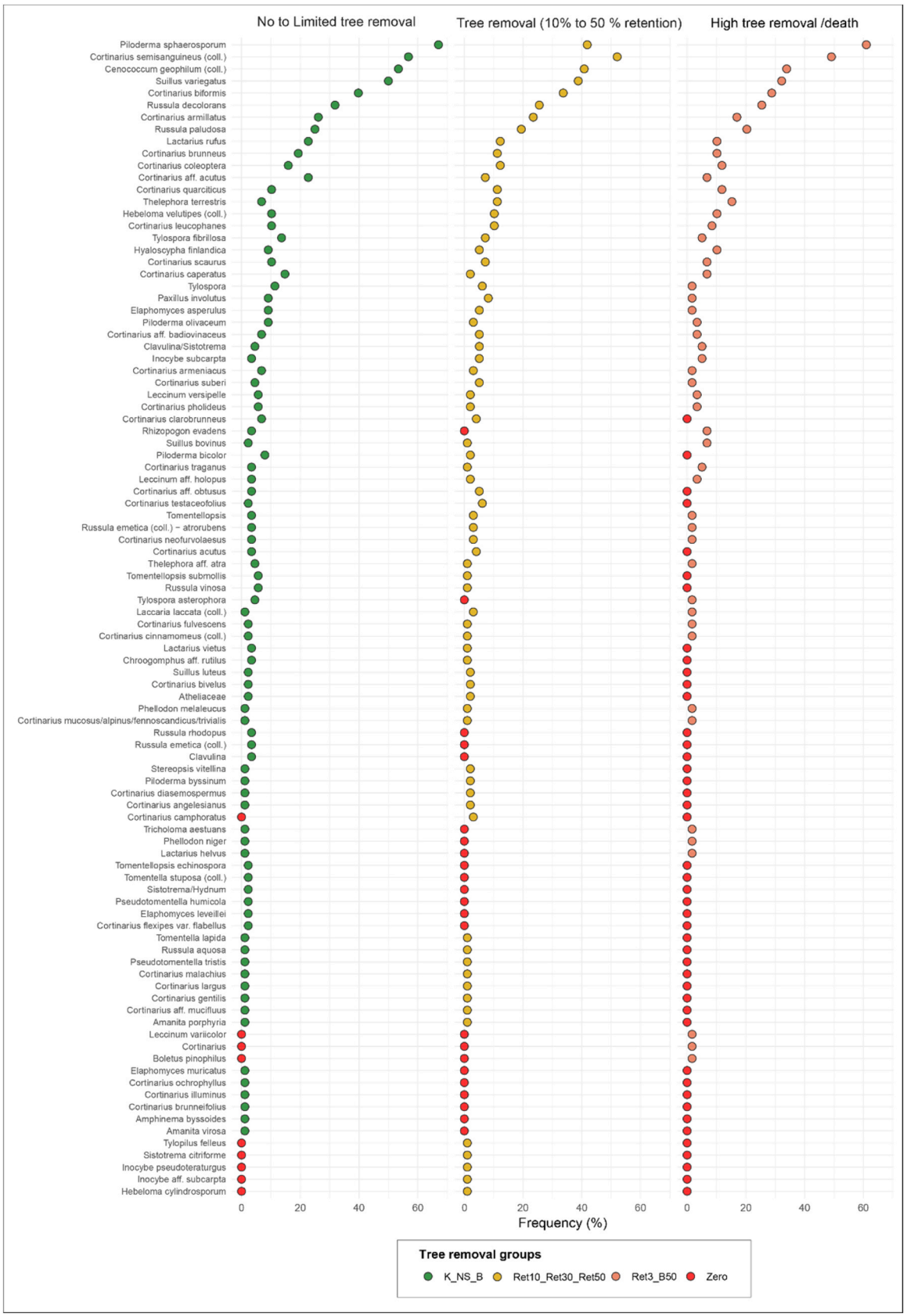


Fig. 7. Frequency of each taxonomic species according to the tree removal group. The first group represents treatments with no or minimal tree removal, including the Control (C), Nature Conservation Management (NS), and the prescribed burn treatment without tree removal (Burn100) with a total of 88 soil samples. The second group includes treatments with moderate tree removal (10–50 % retention), comprising Ret10, Ret30, and Ret50 with a total of 88 soil samples. The final group represents treatments with high tree removal or tree mortality, including Ret3 (3 % retention) and the prescribed burn treatment with 50 % retention (Burn50) with a total of 69 soil samples. The red dots represent the 0 frequency, species that are not/no longer occurring in the inventory for the group.

fungi compete with *Cortinarius* for space and resources in the soil and for access to tree roots (Kyaschenko et al., 2017, Sterkenburg et al., 2019). Previous studies have shown that changes in fungal diversity regarding dominant species remain significant for at least 50 years after pine forest harvesting (Varenius et al., 2016). Higher densities of permanently retained trees is one way to reduce the effects of harvesting and accelerate the return to a richer community with preserved functionality.

5.4. Influence of prescribed burning

Prescribed burning strongly affected EMF community composition, particularly in stands where 50 % harvesting was combined with fire. These areas showed notably low species richness, likely due to tree mortality, altered soil chemistry, and changes in microhabitats (Dahlberg et al., 2001, Čugunovs et al., 2020). Increases in soil pH from alkaline ash, the presence of charred logs, and the loss of living hosts further contributed to the shift in fungal communities (Čugunovs et al., 2020, Junninen et al., 2008, Kouki and Salo, 2020). Previous studies have shown that EMF are highly sensitive to fire severity in the short term (Salo and Kouki, 2018, Dahlberg et al., 2001, Yang et al., 2020); largely because higher severity reduces the number of surviving trees that sustain fungal networks (Jones et al., 2003; Nguyen et al., 2012). We acknowledge that the Burn50 and Burn100 treatments differ not only in retention level but also likely in fire severity, making it difficult to fully separate these effects. Although we did not measure fire severity directly, the stronger effect observed in Burn50 suggests that severity and retention interacted to reduce EMF persistence, with greater host-tree loss likely driving the observed decline.

At the same time, our results indicate that retention buffers negative impacts by maintaining living trees and fungal continuity. This highlights the critical role of timing, fire severity and retention level as interactive drivers of fungal diversity. Implementing prescribed burns prior to harvesting can further preserve surviving hosts, limit additional mortality and their associated fungal networks, thereby reducing additional mortality and promotes long-term biodiversity (Suominen et al., 2018).When carefully timed and combined with retention, prescribed burning may even enhance biodiversity through deadwood creation and increased structural complexity (Suominen et al., 2015, Suominen et al., 2019, Nirhamo et al., 2023).

5.5. Practical implications

Our findings have clear implications for forest management and biodiversity conservation. Most notably, they demonstrate that higher levels of tree retention, along with strategic placement, are essential for mitigating the negative effects of forest harvesting on ectomycorrhizal fungi (EMF). Minimal retention levels, such as 3 %, were shown to be insufficient for maintaining the biodiversity and potential functional capacity of EMF communities. Instead, retention strategies should aim for ecologically meaningful levels (typically >10–30 % of the original stand), with a focus on the strategic placement of trees, considering factors such as distance, species, and size (Gustafsson et al., 2019). This approach can guide the planning of silvicultural practices, including determining optimal retention levels, in alignment with the conservation value of the forest and the presence of key target species essential to preserve. However, the effectiveness of retention forestry depends not only on how much is retained, but also on how well those trees survive. Studies have shown that mortality among retained trees can be high, especially in small or exposed patches, reducing their long-term ecological value (Hallinger et al., 2016).This is particularly problematic for fungi and other organisms that rely on habitat continuity (Nordén and Appelqvist, 2001, Adnan et al., 2022). Therefore, retention planning should also consider site conditions, wind exposure, and patch size to improve the survival of retained trees and ensure that their biodiversity benefits persist over time.

In addition to retention strategies, understanding the role of prescribed burning is crucial for developing management approaches that balance fire management with biodiversity preservation. Fire is an important natural disturbance in Scots pine forests for many species, but it can negatively affect EMF communities in the short term. However, when carefully planned alongside harvesting, prescribed burning can have positive long-term effects, enhancing EMF communities depending on the intensity, frequency, and timing of the burns. In the short term, prescribed burning can reduce EMF diversity and the abundance of certain species due to habitat disruption and altered soil conditions. However, in the long term, it may promote the colonization of fire-adapted EMF species, benefiting certain taxa that thrive in post-fire conditions.Our findings suggest that timing is critical; burning before harvesting (as in the Burn100 treatment) helps preserve living trees and fungal networks, minimizing ecological damage.

Together, these findings support a more integrated approach to forest management; one that combines ecologically meaningful retention with carefully timed prescribed burning to support long-term ecosystem resilience and biodiversity.

5.6. Limitations and future directions

This study offers valuable insights into EMF responses to tree retention and prescribed burning, but several limitations should be noted. First, the research was conducted in a Scots pine dominated ecosystem, which may limit generalizability to other forest types or climatic zones. EMF communities can respond differently across forest types, such as spruce or mixed hardwoods. Second, the experimental design was not fully factorial; prescribed burning was applied only to Burn100 and Burn50 treatments, limiting our ability to isolate fire effects across the retention gradient. While our results suggest that burning combined with harvesting negatively impacts EMF richness, we cannot fully separate fire effects from those of tree removal. However, studies with more comprehensive designs (Kouki and Salo, 2020, Suominen et al., 2015) support our interpretation that retention mitigates fire-related impacts on fungal communities. Third, the relatively short timeframe (4.5 years post-logging) may not capture long-term EMF recovery. Although some dispersal between adjacent stands is possible, our design likely minimized this influence. Long-term resilience often unfolds over decades. For example, Rianhard et al. (2025) found that EMF richness remained reduced nearly 30 years after harvesting, especially at forest edge; highlighting persistent fragmentation effects and the need for extended monitoring.

Future research should explore long-term EMF recovery, including their roles in nutrient cycling and ecosystem stability. EMF are just one component of forest fungal communities; saprotrophs, endophytes, and pathogens also respond to disturbance and contribute to ecosystem processes. Including these groups would provide a more complete picture of fungal dynamics. Additionally, future studies should examine interactions among fungal and tree species, and the combined effects of multiple disturbances. Advances in molecular tools now allow exploration of functional traits underlying plant–fungi interactions, which could inform conservation strategies to enhance forest resilience under changing environmental conditions (Stewart et al., 2018).

6. Conclusion

This study provides important insights into how tree retention and prescribed burning influence ectomycorrhizal fungi (EMF) communities in Scots pine forests. Our results underscore the critical role of tree retention in sustaining EMF abundance and diversity, with proximity to living retention trees and local canopy area (crown size) identified as key factors. Notably, minimal retention levels (e.g., 3 %) were insufficient to support EMF communities 4.5 years after logging, especially for rare species. These findings highlight the need for ecologically meaningful retention, which includes adequate quantity, strategic placement, and consideration of tree survival.

While prescribed burning was only applied to a subset of the experimental stands, its effects were still notable. Burning combined with 50 % harvesting, resulted in the most pronounced short-term reductions in EMF richness, likely due to habitat disruption, altered soil chemistry and increased tree mortality. However, when burning was applied without harvesting, its impact was minimal, suggesting that timing is critical. Burning before harvest may help preserve living trees and fungal networks, reducing unintended ecological damage.

In conclusion, sustainable forest management in boreal ecosystems requires an integrated approach that combines ecologically meaningful tree retention with carefully timed and context-aware prescribed burning. By aligning harvesting practices with biodiversity conservation goals, it is possible to enhance fungal biodiversity, maintain functionality, and promote long-term resilience.

CRediT authorship contribution statement

Björn Lindahl: Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization. **Anders Dahlberg:** Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization. **Delphine Lariviere:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation, Conceptualization. **Line Djupström:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This study was funded by FRAS (Future Forest Management in Southern Sweden), a collaborative research program involving three leading forest research institutions in southern Sweden: the Swedish University of Agricultural Sciences (SLU), Linnaeus University (LNU), and Skogforsk (The Forestry Research Institute of Sweden). The original Effaråsen forest experiment was conducted and financed by Skogforsk. We would like to thank the staff at the Department of Forest Mycology and Plant Pathology for their work in conducting the molecular workflow, from sample collection to bioinformatics processing and the generation of the final fungal OTU data.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123186.

Data availability

The data will be openly available on SND. The temporary DOI is shared in the Title page.

References

Adnan, M., Islam, W., Gang, L., Chen, H.Y.H., 2022. Advanced research tools for fungal diversity and its impact on forest ecosystem. Environ. Sci. Pollut. Res. 29, 45044–45062.

Brockerhoff, E.G., Barbaro, L., Castagneyrol, B., Forrester, D.I., Gardiner, B., González-Olabarria, J.R., Lyver, P.O.B., Meurisse, N., Oxbrough, A., Taki, H., 2017. Forest biodiversity, ecosystem functioning and the provision of ecosystem services. Biodivers. Conserv. 26, 3005–3035.

Carini, P., Delgado-Baquerizo, M., Hinckley Eve-Lyn, S., Holland-Moritz, H., Brewer Tess, E., Rue, G., Vanderburgh, C., Mcknight, D., Fierer, N., 2020. Effects of spatial variability and relic DNA removal on the detection of temporal dynamics in soil microbial communities. mBio 11. https://doi.org/10.1128/mbio.02776-19.

Castaño, C., Berlin, A., Brandström Durling, M., Ihrmark, K., Lindahl, B.D., Stenlid, J., Clemmensen, K.E., Olson, Å., 2020. Optimized metabarcoding with pacific biosciences enables semi-quantitative analysis of fungal communities. N. Phytol. 228, 1149–1158.

Clemmensen, K.E., Ihrmark, K., Durling, M.B., Lindahl, B.D., 2016. Sample preparation for fungal community analysis by High-Throughput sequencing of barcode amplicons. In: MARTIN, F., UROZ, S. (Eds.), Microbial Environmental Genomics (MEG). New York, NY: Springer New York.

Cline, E., Vinyard, B., Edmonds, R., 2007. Spatial effects of retention trees on mycorrhizas and biomass of Douglas-fir seedlings. Can. J. For. Res. 37, 430–438.

Cline, E.T., Ammirati, J.F., Edmonds, R.L., 2005. Does proximity to mature trees influence ectomycorrhizal fungus communities of Douglas-fir seedlings? N. Phytol. 166, 993–1009.

Čugunovs, M., Tuittila, E.-S., Kouki, J., 2020. Proximity to charred logs in burned forests likely affects decomposition processes in the soil. Silva Fenn. 54.

Dahlberg, A., Schimmel, J., Taylor, A.F.S., Johannesson, H., 2001. Post-fire legacy of ectomycorrhizal fungal communities in the Swedish boreal forest in relation to fire severity and logging intensity. Biol. Conserv. 100, 151–161.

Dexter, E., Rollwagen-Bollens, G., Bollens, S.M., 2018. The trouble with stress: a flexible method for the evaluation of nonmetric multidimensional scaling. Limnol. Oceanogr. Methods 16, 434–443.

Edgar, R.C., 2010. Search and clustering orders of magnitude faster than BLAST. Bioinformatics 26, 2460–2461.

Felton, A., Löfroth, T., Angelstam, P., Gustafsson, L., Hjältén, J., Felton, A.M., Simonsson, P., Dahlberg, A., Lindbladh, M., Svensson, J., Nilsson, U., Lodin, I., Hedwall, P.O., Sténs, A., Lämås, T., Brunet, J., Kalén, C., Kriström, B., Gemmel, P., Ranius, T., 2020. Keeping pace with forestry: Multi-scale conservation in a changing production forest matrix. Ambio 49, 1050–1064.

Futai, K., Taniguchi, T., Kataoka, R., 2008. Ectomycorrhizae and their importance in forest ecosystems. In: SIDDIQUI, Z.A., AKHTAR, M.S., FUTAI, K. (Eds.), Mycorrhizae: Sustainable Agriculture and Forestry. Dordrecht. Springer Netherlands.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D. B., Lõhmus, A., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W.J.A., Wayne, A., Franklin, J.F., 2012. Retention forestry to maintain multifunctional forests: a world perspective. BioScience 62, 633–645.

Gustafsson, L., Bauhus, J., Asbeck, T., Augustynczik, A.L.D., Basile, M., Frey, J., Gutzat, F., Hanewinkel, M., Helbach, J., Jonker, M., 2019. Retention as an integrated biodiversity conservation approach for continuous-cover forestry in Europe. Ambio 49, 1–13.

Gustafsson, L., Hannerz, M., Koivula, M., Shorohova, E., Vanha-Majamaa, I., Weslien, J., 2020. Research on retention forestry in Northern. Eur. Ecol. Process. 9, 1–13.

Hallinger, M., Johansson, V., Schmalholz, M., Sjöberg, S., Ranius, T., 2016. Factors driving tree mortality in retained forest fragments. For. Ecol. Manag. 368, 163–172.

Hämäläinen, A., Hujo, M., Heikkala, O., Junninen, K., Kouki, J., 2016. Retention tree characteristics have major influence on the post-harvest tree mortality and availability of coarse woody debris in clear-cut areas. For. Ecol. Manag. 369, 66–73.

Harvey, A.E., Jurgensen, M.F., Larsen, M.J., 1980. Clearcut harvesting and ectomycorrhizae: survival of activity on residual roots and influence on a bordering forest stand in Western Montana. Can. J. For. Res. 10, 300–303.

Hsieh, T., Ma, K., Chao, A., Hsieh, M.T., 2022. R package 'iNEXT' 3.0.0 ed. Vienna, Austria: The R Fundation.

Hyvärinen, E., Kouki, J., Martikainen, P., 2006. Fire and Green-tree retention in conservation of red-listed and rare deadwood-dependent beetles in Finnish boreal forests. Conserv Biol. 20, 1711–1719.

Jones, M.D., Durall, D.M., Cairney, J.W.G., 2003. Ectomycorrhizal fungal communities in young forest stands regenerating after clearcut logging. N. Phytol. 157, 399–422.

Jörgensen, K., Clemmensen, K.E., Fransson, P., Manzoni, S., Wallander, H., Lindahl, B.D., 2025. A trait spectrum linking nitrogen acquisition and carbon use of ectomycorrhizal fungi. N. Phytol. N./a.

Junninen, K., Kouki, J., Renvall, P., 2008. Restoration of natural legacies of fire in european boreal forests: an experimental approach to the effects on wood-decaying fungi. Can. J. For. Res. 38, 202–215.

Koivula, M., Vanha-Majamaa, I., 2020. Experimental evidence on biodiversity impacts of variable retention forestry, prescribed burning, and deadwood manipulation in fennoscandia. Ecol. Process. 9, 11.

Kolaczkowski, O. 2005. *Effects of spatially dispersed green-tree retention on ectomycorrhiza diversity.* Master of Science (M.S.), Oregon State University.

Kõljalg, U., Nilsson, R.H., Abarenkov, K., Tedersoo, L., Taylor, A.F., Bahram, M., Bates, S. T., Bruns, T.D., Bengtsson-Palme, J., Callaghan, T.M., 2013. Towards a unified paradigm for sequence-based identification of fungi. Wiley Online Libr.

Kouki, J., Salo, K., 2020. Forest disturbances affect functional groups of macrofungi in young successional forests – harvests and fire lead to different fungal assemblages. For. Ecol. Manag. 463, 118039.

Kranabetter, J.M., De Montigny, L., Ross, G., 2013. Effectiveness of Green-tree retention in the conservation of ectomycorrhizal fungi. Fungal Ecol. 6, 430–438.

Kyaschenko, J., Clemmensen, K.E., Hagenbo, A., Karltun, E., Lindahl, B.D., 2017. Shift in fungal communities and associated enzyme activities along an age gradient of managed pinus sylvestris stands. ISME J. 11, 863–874.

Lenth, R., Singmann, H., Love, J., Buerkner, P., Herve, M., 2022. R package 'Emmeans' 1.8.3 ed. Vienna, Austria: The R Fundation.

lindahl, B.D. & Clemmensen, K.E.. 2017. Fungal ecology in boreal forest ecosystems. In: (Ed), M. F. (Ed.) *Molecular Mycorrhizal Symbiosis*,. First Edition Ed.: John Wiley & Sons Inc.

Lindahl, B.D., Ihrmark, K., Boberg, J., Trumbore, S.E., Högberg, P., Stenlid, J., Finlay, R. D., 2007. Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest. N. Phytol. 173, 611–620.

Lindahl, B.D., Kyaschenko, J., Varenius, K., Clemmensen, K.E., Dahlberg, A., Karltun, E., Stendahl, J., 2021. A group of ectomycorrhizal fungi restricts organic matter accumulation in boreal forest. Ecol. Lett. 24, 1341–1351.
Lindbladh, M., Axelsson, A.-L., Hultberg, T., Brunet, J., Felton, A., 2014. From broadleaves to spruce–the borealization of Southern Sweden. Scand. J. For. Res. 29, 686–696.
Liu, Y., Li, X., Kou, Y., 2020. Ectomycorrhizal fungi: participation in nutrient turnover and community assembly pattern in forest ecosystems. For. [Online] 11.
Luoma, D.L., Eberhart, J.L., Molina, R., Amaranthus, M.P., 2004. Response of ectomycorrhizal fungus sporocarp production to varying levels and patterns of Green-tree retention. For. Ecol. Manag. 202, 337–354.
Luoma, D.L., Stockdale, C.A., Molina, R., Eberhart, J.L., 2006. The spatial influence of pseudotsuga menziesii retention trees on ectomycorrhiza diversity. Can. J. For. Res. 36, 2561–2573.
Nguyen, N.H., Hynson, N.A., Bruns, T.D., 2012. Stayin' alive: survival of mycorrhizal fungal propagules from 6-yr-old forest soil. Fungal Ecol. 5, 741–746.
Nirhamo, A., Hämäläinen, K., Junninen, K., Kouki, J., 2023. Deadwood on clearcut sites during 20 years after harvests: the effects of tree retention level and prescribed burning. For. Ecol. Manag. 545, 121287.
Nordén, B., Appelqvist, T., 2001. Conceptual problems of ecological continuity and its bioindicators. Biodivers. Conserv. 10, 779–791.
Oksanen, J., Blanchet, F.G.U.I.L.L.A.U.M.E., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., Minchin, P., hara, R.O., Simpson, G., Solymos, P., Stevens, H., Szoecs, E., Wagner, A.N.D.H., 2020. R package 'Vegan' 2.5-7 ed. Vienna, Austria: The R Foundation.
Parsons, W.F.J., Knight, D.H., Miller, S.L., 1994. Root gap dynamics in lodgepole pine forest: nitrogen transformations in gaps of different size. Ecol. Appl. 4, 354–362.
Prescott, C.E., Grayston, S.J., 2013. Tree species influence on microbial communities in litter and soil: current knowledge and research needs. For. Ecol. Manag. 309, 19–27.
Ramberg, E., Strengbom, J., Granath, G., 2018. Coordination through databases can improve prescribed burning as a conservation tool to promote forest biodiversity. Ambio 47, 298–306.
Rianhard, O.M., Kranabetter, J.M., Penkova, L.V., Durall, D.M., Jones, M.D., 2025. Ectomycorrhizal fungal community succession and fragmentation across forest edges nearly three decades postharvest. *plants, people*. PLANET 7, 1510–1523.
Saari, S.K., Campbell, C.D., Russell, J., Alexander, I.J., Anderson, I.C., 2005. Pine microsatellite markers allow roots and ectomycorrhizas to be linked to individual trees. N. Phytol. 165, 295–304.
Salo, K., Kouki, J., 2018. Severity of forest wildfire had a major influence on early successional ectomycorrhizal macrofungi assemblages, including edible mushrooms. For. Ecol. Manag. 415-416, 70–84.
Santaniello, F., Line, D.B., Ranius, T., Rudolphi, J., Widenfalk, O., Weslien, J., 2016. Effects of partial cutting on logging productivity, economic returns and dead wood in boreal pine forest. For. Ecol. Manag. 365, 152–158.
Simard, S.W., Roach, W.J., Beauregard, J., Burkart, J., Cook, D., Law, D., Murphy-Steed, A., Schacter, T., Zickmantel, A., Armstrong, G., Fraser, K.M., Hart, L., Heath, O.R.J., Jones, L., Sachs, N.S., Sachs, H.R., Snyder, E.N., Tien, M., Timmermans, J., 2021. Partial retention of legacy trees protect mycorrhizal inoculum potential, biodiversity, and soil resources while promoting natural regeneration of interior Douglas-Fir. Front. For. Glob. Change 3.
Siry, J.P., Cubbage, F.W., Ahmed, M.R., 2005. Sustainable forest management: global trends and opportunities. For. Policy Econ. 7, 551–561.
Skogsstyrelsen (Swedish Forest Agency). 2025. Skogliga grunddata – Höjdmodell från laserskanning [Online]. Skogsstyrelsen. Available: https://www.skogsstyrelsen.se/e-tjanster-och-kartor/karttjanster/skogliga-grunddata/ [Accessed 2025-05-12].
SLU Artdatabanken. 2025. Artfakta [Online]. Available: https://www.artfakta.se [Accessed 2025-05-07].
Smith, S.E. & Read, D.J. 2010. *Mycorrhizal symbiosis*, Academic press.
Sterkenburg, E., Clemmensen, K.E., Lindahl, B.D., Dahlberg, A., 2019. The significance of retention trees for survival of ectomycorrhizal fungi in clear-cut Scots pine forests. J. Appl. Ecol. 56, 1367–1378.
Stewart, J.E., Kim, M.-S., Klopfenstein, N.B., 2018. Molecular genetic approaches toward understanding Forest-Associated fungi and their interactive roles within forest ecosystems. Curr. For. Rep. 4, 72–84.
Suominen, M., Junninen, K., Heikkala, O., Kouki, J., 2015. Combined effects of retention forestry and prescribed burning on polypore fungi. J. Appl. Ecol. 52, 1001–1008.
Suominen, M., Junninen, K., Heikkala, O., Kouki, J., 2018. Burning harvested sites enhances polypore diversity on stumps and slash. For. Ecol. Manag. 414, 47–53.
Suominen, M., Junninen, K., Kouki, J., 2019. Diversity of fungi in harvested forests 10 years after logging and burning: polypore assemblages on different woody substrates. For. Ecol. Manag. 446, 63–70.
Swedish University Of Agricultural Sciences 2024. Skogsdata 2024: aktuella uppgifter om de svenska skogarna från SLU Riksskogstaxeringen. *Skogsdata.* Umeå.
Swedish University Of Agricultural Sciences. SCATA Bioinformatic Pipeline [Online]. Available: http://SCATA.mykopat.slu.se [Accessed 2025-05-07].
Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N.S., Wijesundera, R., Ruiz, L.V., Vasco-Palacios, A.M., Thu, P.Q., Suija, A., Smith, M.E., Sharp, C., Saluveer, E., Saitta, A., Rosas, M., Riit, T., Ratkowsky, D., Pritsch, K., Põldmaa, K., Piepenbring, M., Phosri, C., Peterson, M., Parts, K., Pärtel, K., Otsing, E., Nouhra, E., Njouonkou, A.L., Nilsson, R.H., Morgado, L.N., Mayor, J., May, T.W., Majuakim, L., Lodge, D.J., Lee, S.S., Larsson, K.-H., Kohout, P., Hosaka, K., Hiiesalu, I., Henkel, T. W., Harend, H., Guo, L.-D., Greslebin, A., Grelet, G., Geml, J., Gates, G., Dunstan, W., Dunk, C., Drenkhan, R., Dearnaley, J., Kesel, D.E., Dang, A., Chen, T., Buegger, X., Brearley, F., Bonito, F.Q., Anslan, G., Abell, S., S, Abarenkov, K., 2014. Global diversity and geography of soil fungi. Science 346, 1256688.
Tinya, F., Doerfler, I., Groot, D.E., Heilman-Clausen, M., Kovács, J., Mårell, B., Nordén, A., Aszalós, B., Bässler, R., Brazaitis, C., Burrascano, G., Camprodon, S., Chudomelová, J., Čížek, M., D'andrea, L., Gossner, E., Halme, M., Hédl, P., Korboulewsky, R., Kouki, N., Kozel, J., Lõhmus, P., López, A., Máliš, R., Martín, F., Matteucci, J.A., Mattioli, G., Mundet, W., Müller, R., Nicolas, J., Oldén, M., Piqué, A., Preikša, M., Rovira Ciuró, Ž., Remm, J., Schall, L., Šebek, P., Seibold, P., Simončič, S., Ujházy, P., Ujházyová, K., Vild, M., Vincenot, O., Weisser, L., W, Ódor, P., 2023. A synthesis of multi-taxa management experiments to guide forest biodiversity conservation in Europe. Glob. Ecol. Conserv. 46, e02553.
Varenius, K., Kårén, O., Lindahl, B., Dahlberg, A., 2016. Long-term effects of tree harvesting on ectomycorrhizal fungal communities in boreal Scots pine forests. For. Ecol. Manag. 380, 41–49.
Varenius, K., Lindahl, B.D., Dahlberg, A., 2017. Retention of seed trees fails to lifeboat ectomycorrhizal fungal diversity in harvested Scots pine forests. FEMS Microbiol. Ecol. 93 fix105.
Wallander, H., Johansson, U., Sterkenburg, E., Brandström Durling, M., Lindahl, B.D., 2010. Production of ectomycorrhizal mycelium peaks during canopy closure in Norway spruce forests. N. Phytol. 187, 1124–1134.
Yang, T., Tedersoo, L., Lin, X., Fitzpatrick, M.C., Jia, Y., Liu, X., Ni, Y., Shi, Y., Lu, P., Zhu, J., Chu, H., 2020. Distinct fungal successional trajectories following wildfire between soil horizons in a cold-temperate forest. N. Phytol. 227, 572–587.