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Uneven-aged and even-aged forest management shape the soil fungal community composition in a boreal Norway spruce (*Picea abies* Karst) forest

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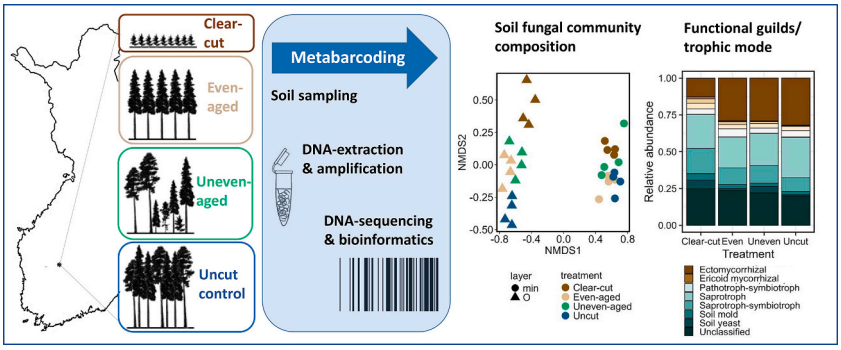
HIGHLIGHTS

- Continuous cover forestry and rotation forestry affect soil fungal community.
- Uneven-aged and even-aged structures alter soil fungal community composition.
- Particularly clear-cutting changes abundance of certain fungal guilds.
- Ectomycorrhizal abundance, diversity and richness decline after clear-cutting.
- Despite changes in potential functionality, results indicate functional redundancy.

GRAPHICAL ABSTRACT



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ABSTRACT

Forest management alters stand density, microclimate, and litter accrual, which all affect soil fungi. Mycorrhizal fungi play a key role in soil organic carbon (C) accumulation in boreal forests. We aimed to compare how uneven-aged continuous cover forestry (CCF) and even-aged rotation forest management (RFM) affect the soil fungal community, to draw conclusions on possible effects for long-term soil C storage. We compared uncut boreal Norway spruce forests to mature uneven-aged (CCF), even-aged and clear-cut forests (the latter two representing late and early stage in RFM). We compared their fungal community composition, species richness and diversity based on metabarcoding of bulk soil samples using sequences of the fungal ITS2 regions, and analysed the response of saprotrophic, ecto- and ericoid mycorrhizal fungal guilds to management practice.

We found that fungal communities differed between all treatments, but species richness and diversity were not impacted. Clear-cuts were most dissimilar to the other treatments and the organic layer was more affected than the mineral soil.

Abundance, diversity and richness of ectomycorrhizal fungi was declined in clear-cuts, leading to dominance of saprotrophic fungi. The abundance of functional guilds in even-aged and uneven-aged stands were similar to

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those in uncut stands. Ericoid mycorrhizae were more abundant in both stages of RFM, but their community composition was not affected by the forest management type.

Despite the altered potential functionality, we found similar C stocks and cellulose decomposition rates in all treatments. This highlights the functional redundancy in the fungal community. Therefore, we conclude that CCF is unlikely to change the long-term soil C storage compared to unmanaged forests. The long-term effects of multiple clear-cutting cycles in RFM on the ecological functionality and possible effects on soil C storage should be further studied for example with sites that have been clear-cut more than once.

1. Introduction

About 32 % of the global carbon (C) stock in forests is stored in boreal forests and the majority of this C is stored in the forest soils as soil organic matter (SOM) (Pan et al., 2011). Boreal forests are largely managed for wood production, hence it is important to understand the effects of different silvicultural regimes on their functions such as C storage (Gauthier et al., 2015). Soil C storage is driven by plant roots and root-associated fungi (Adamczyk, 2021; Averill et al., 2014; Clemmensen et al., 2013; Dijkstra and Cheng, 2007). Mycorrhizal fungi form symbiotic relationships with trees and shrubs, and generate access to nutrients and water in exchange for C compounds that they obtain through the plant hosts (Smith and Read, 2008). In boreal forests, where tree growth is limited by nutrients, especially nitrogen (N), the role of fungi is particularly important (Read et al., 2004). Terrestrial plants allocate about 3.58 Gt C annually underground to the mycelium of mycorrhizal fungi (Hawkins et al., 2023), and the majority—up to 70 %—of the soil C in boreal forests derives from roots and root-associated fungi rather than above-ground litter (Adamczyk et al., 2019; Clemmensen et al., 2013; Kyaschenko et al., 2019). In particular, microbial necromass (including fungal necromass) is proposed to contribute to the stable soil C pool by stabilizing on mineral surfaces and within soil aggregates (Liang et al., 2017). This is called the entombing effect in the microbial carbon pump concept (Liang et al., 2017).

Different mycorrhizal types vary in their abundance and functional role in forest ecosystems. The most common mycorrhizal type in boreal forests are ectomycorrhizae, which are usually associated with trees (Read et al., 2004). Ericaceous understorey plants, such as berry dwarf shrubs, form symbioses with ericoid mycorrhizal fungi (ERMf) (Smith and Read, 2008). Ectomycorrhizal fungi (ECMf) and ERMf occupy complementary niches (Fanin et al., 2022). Saprotrophic fungi (SAPf) are the primary decomposers of soil organic matter (Lindahl and Tunlid, 2015), but ECMf and ERMf also have rudimentary abilities to decompose SOM and scavenge the SOM mainly for N (Heinonsalo et al., 2015; Lindahl and Tunlid, 2015). As ERMf and ECMf compete with free-living saprotrophs for organic N, they may decelerate saprotrophic decomposition according to the “Gadgil hypothesis”, which states that the presence of mycorrhizal fungi suppresses decomposition (Fanin et al., 2022; Gadgil and Gadgil, 1975). In this way, mycorrhizae would enhance the long-term accumulation of SOM (Averill et al., 2014). Recently, Mayer et al. (2023b) found that the effect of ECMf on decomposition depends on soil fertility. ECMf decelerated decomposition under low fertility conditions, which are common in boreal forests. Accordingly, ECMf and ERMf mycorrhizal dominated ecosystems, such as boreal forests, typically show higher soil C stocks than arbuscular-mycorrhizal dominated ecosystems (Averill et al., 2014).

Trees—and forest management that impact tree stands—impact mycorrhizae directly by providing C, and indirectly by altering environmental conditions. Trees sustain and shape the belowground ecosystem by providing root litter, root exudates, and photosynthates to mycorrhizae (Prescott and Grayston, 2023). Trees further regulate soil temperature and moisture and alter the understorey vegetation through shading (Gömöryová et al., 2013). For example, they can suppress ericaceous understorey plants that sustain ERMf (Sietiö et al., 2018) or grasses and herbs that form associations with arbuscular mycorrhiza (Smith and Read, 2008). The quality of the litter supplied by trees and understorey alters soil properties such as soil pH and C/N-ratio (Ostonen et al., 2017). Tree removal in forest management operations alters all of these functions provided by trees, thereby also affecting the soil fungal community.

In forest management, there are two dominating silvicultural systems that we have investigated in this study: rotation forest management (RFM) and continuous-cover forestry (CCF). They likely differ in their impact on soil fungal community. In RFM, basically all trees are harvested by clear-cutting in a mature stand in the end of a rotation period. After clear-cutting, the stand is renewed either by planting, direct seeding, or natural regeneration, and a new young tree stand starts to grow. Rotation forest management works with even-aged stand structures, often consisting of a single tree species (Gustafsson et al., 2020; Pukkala et al., 2012). On the other hand, CCF is characterized by the absence of clear-cutting. Trees are harvested with partial logging methods, usually selection cuttings such as single tree selection or gap cutting (Gustafsson et al., 2020). Logging methods applied in CCF mostly aim at developing and maintaining an uneven-aged structure of the forest stands (Kuuluvainen, 2009) and multi-species stands (Köhl and Baldauf, 2012; Pötzelsberger and Hasenauer, 2015) (Fig. 1). Thus, here we will address CCF and RFM as uneven-aged and even-aged forest management, respectively. Even-aged forest management is currently the predominant management regime in boreal forests (Savilaakso et al., 2021), and the effects of uneven-aged management on soil processes are thus far poorly known compared to the more common even-aged management.

Harvesting is an anthropogenic forest disturbance that affects the soil C storage and decomposition processes (Mayer et al., 2023a). Harvesting via clear-cutting releases a pulse of organic material as harvesting residues and dead roots that tend to benefit saprotrophic fungi. The allocation of C to the soil through living tree roots, which mycorrhizal fungi depend on, ceases completely after the complete tree removal (Prescott and Grayston, 2023). Accordingly, decline in tree fine root biomass (Roth et al., 2023), in soil fungal biomass, and in the abundance of ECMf (Kohout et al., 2018), as well as an increase in saprotrophic fungi has been observed following clear-cutting (Kohout et al., 2018; Kyaschenko et al., 2017). After a disturbance such as a clear-cut, the N availability decreases with time as the SOM becomes more recalcitrant with progressing decomposition. Thus, certain mycorrhizal fungi that can utilize N stored in SOM efficiently become more dominant (Kyaschenko et al., 2017). This is seen in a successional shift in the ECMf species composition following clear-cuts, from dominance of the genera *Piloderma* and *Tylospora* in young post-harvest forest stands to higher abundance of *Cortinarius* and *Russula* in older stands (Kyaschenko et al., 2017; Santalahti, 2018). In a chronosequence study in boreal forests, Clemmensen et al. (2015) found that ECMf dominated earlier in the forest succession, while ERMf became more dominant with advancing succession. While the impact of rotation forest management and associated change in the fungal community composition has been studied thoroughly (Bowd et al., 2022; Hartmann et al., 2012; Kohout et al., 2018; Kyaschenko et al., 2017; Rodriguez-Ramos et al., 2021), the impact of CCF in comparison is difficult to assess since field studies can only consider a moment in time. Forest stand structures in CCF are ideally in a dynamic equilibrium state whereas RFM stands have a certain age (e.g. young/old), a fixed beginning and end. However, a meta-analysis showed a positive relation between stand structural elements (such as canopy

cover or basal area) and the fungal diversity. Particularly ECMf diversity declines with management intensity (Tomao et al., 2020). They suggest selection cuts leading to uneven-aged stands as a measure to preserve fungal diversity. Kim et al. (2021) found the microbial community in CCF similar to that in unmanaged stands, in contrast to clear-cuts that they included as RFM treatment. However, studies assessing later stages in the rotation cycle are still missing (Kim et al., 2021), and a direct comparisons of the fungal community between uneven-aged CCF stands and mature even-aged RFM stands are still lacking (Savilaakso et al., 2021).

In this field study, we aimed to compare the effects of uneven-aged and even-aged forest management practises on the fungal community composition in boreal Norway spruce (*Picea abies* Karst) dominated forests to draw conclusions regarding the future soil organic carbon storage under CCF and RFM. In our sampling, uneven-aged forests represent CCF, whereas clear-cuts and even-aged stands represent the two opposing stages of RFM (post-harvest and pre-harvest). We compared both management practices to an uncut control (Fig. 1).

Our overarching hypothesis was that the uneven age structure, higher stem density, less disturbance to the fungal community and continuous litter inputs through roots and root exudates under CCF would result in different fungal community composition, species richness and functionality compared to RFM. Our focus was on fungi central for SOM decomposition; therefore, we excluded pathogens. More specifically, we hypothesized that:

(1) Uneven-aged CCF forests harbour a more diverse fungal community than even-aged forests as they are structurally more complex in terms of tree species composition and tree age and size and understorey vegetation composition.
(2) Uneven-aged and uncut forests feature a higher abundance of ECMf compared to saprotrophs (higher ECM/SAP-ratio) and harbour a more diverse ECMf community than clear-cut plots. Saprotrophs are more abundant on clear-cuts due to the high amounts of dead plant matter, and because of their competitive advantage according to the Gadgil effect theory.
(3) More open canopy structures in uneven-aged stands enable the growth of ericoid plants in the understorey and lead to a higher abundance of ERMf in uneven-aged forest than in uncut and mature even-aged stands.

2. Materials and methods

2.1. Study area

We collected our data from a long-term silvicultural experiment located in Vessari, Central Finland (62°2′9″N, 24°16′0″E, Fig. 2a, Supporting Information Fig. S2) (Lähde et al., 2001; Pukkala et al., 2016). The experimental site covers about 16 ha at an elevation of about 110 m above sea level (Geological Survey of Finland, 2023). The mean annual temperature at the site ranges between +4 °C and + 5 °C, and the mean annual precipitation between 600 and 650 mm (Finnish Meteorological Institute, 2023). In the Finnish site classification system (Cajander, 1926) the site represents an *Oxalis-Myrtillus* type, i.e., it is mesic and relatively fertile. The soil type is a skeletic albic podzol formed from sandy loam on glacial till, and the humus type is a mor.

The experiment was established in winter 1986/87 to study different forest harvesting strategies and intensities. The forests are Norway spruce dominated and admixed with Rowan (*Sorbus aucuparia* L.), birch (*Betula* spp.) and aspen (*Populus tremula* L.). They originate from natural regeneration after shelterwood cuttings in the 1940s. Uneven-aged and even-aged structures were established with selection cuts and thinning from below, respectively (more detailed description in Pukkala et al., 2016). Since then, selection cutting and thinning from below were repeated three times to retain an average basal area of 17 m^2 ha^{-1} in uneven-aged CCF stands and 19 m^2 ha^{-1} in even-aged RFM stands after each harvesting operation (Supporting Information Table S1, Fig. S1). Clear-cuts included in our study, were created in 2009, partly replanted with Norway spruce and naturally colonized by *Betula* spp. and spruce saplings. Thus, at the time of sampling, clear-cuts where 11 years old, while the three other treatments, the uncut plots, even-aged plots and the old trees in uneven-aged plots where about 85 years old. Uncut controls were not managed since 1986 (Pukkala et al., 2012). Each treatment has four replicates of 50 × 50 m plot size with randomized positions within the experimental site (Fig. 2b).

2.2. Sampling

We sampled four replicate plots of each harvesting treatment ($n = 4$) in September 2020. We took the organic topsoil layer (O-layer) samples with a stainless-steel soil auger with an inner diameter of 6 cm. We sampled the mineral soil layer to a depth of 10 cm using a soil corer with a diameter of 1.9 cm. In total, we took 25 samples from each soil layer on each plot, and pooled these samples to one composite sample per plot for the organic and mineral layer, respectively. The sample layout was a systematic 16 × 16 m grid in the centre of each plot, surrounded by a 17 m buffer zone (Fig. 2c). Subsamples of the pooled samples were manually homogenized and dried with silica gel for DNA extraction (Tedersoo et al., 2014). Within each plot, we installed thermometers and moisture sensors that recorded air and soil temperature as well as soil moisture down to a depth of approximately 14 cm (Wild et al., 2019).

To characterize the different management treatments and their

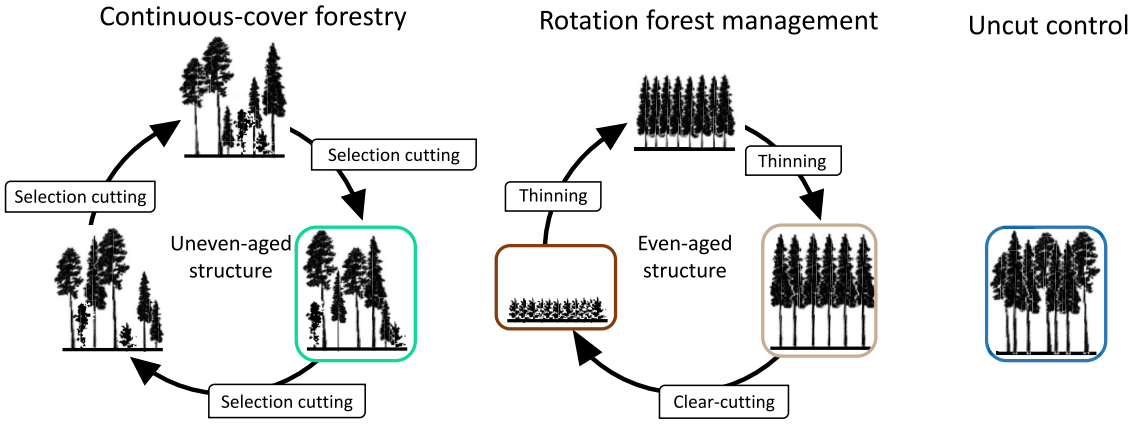

Fig. 1. Comparison of the harvesting cycles depicted for the two silvicultural systems: uneven-aged continuous-cover forestry (left) and even-aged rotation forest management (middle). Framed are the treatments featured in our study: uneven-aged forest (green), even-aged mature forest (beige), young re-growing forest after clear-cutting (brown), and uncut control (blue). Figure has been modified after drawing by T. Aakala in Kuuluvainen et al. (2012).

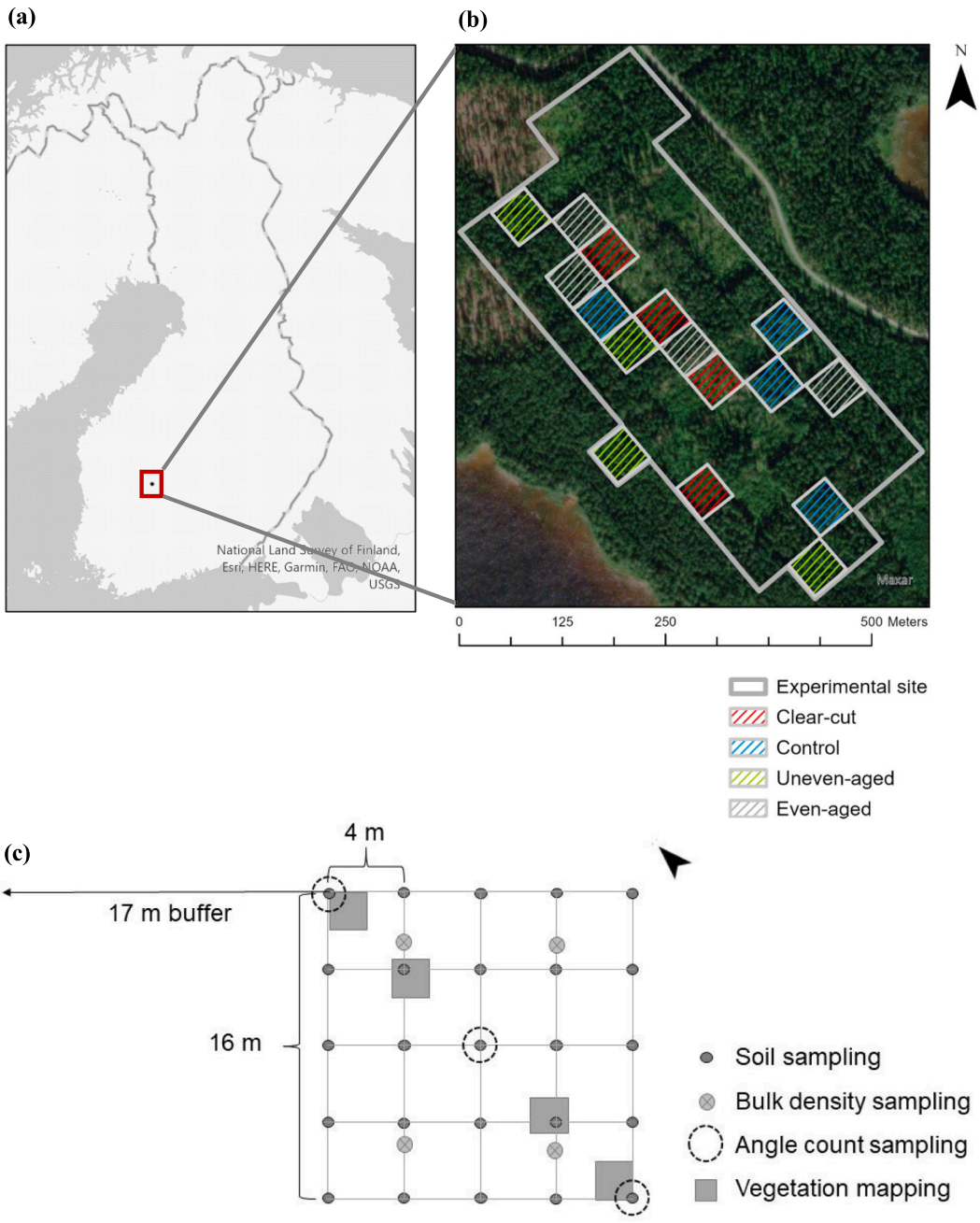

Fig. 2. (a) location of the Vessari study site in Central Finland (b) arrangement of treatments within the experimental site (c) sampling layout.

structural differences we recorded stand parameters. Within the 16 × 16 m soil sampling grid, we measured diameter at breast height (DBH) for all the trees with a DBH > 6 cm, determined dominant tree height (DTH), and measured mean basal area (BA) with three angle-count samples per plot. We recorded the abundance of the various tree species in each plot and calculated their Shannon indices; this was done separately for the upper canopy layer and the saplings in the understorey (Supporting Information Table S2, Methods S1). To quantify the effects of the forest management on the ericoid shrubs in the ground vegetation, we visually estimated the coverage of ericoid shrubs (*Vaccinium myrtillus* L., *Vaccinium vitis-idaea* L. and *Calluna vulgaris* (L.) Hull.) in four 2 m^2 squares each along a diagonal N-S oriented transect in each plot (Reinikainen and Nousiainen, 1995) (Fig. 2c).

2.3. Soil analyses

Samples were air-dried and sieved before further analyses. We analysed C and N concentration of the fine earth fraction of the soil with a LECO CN828 analyser (LECO Corporation, St. Joseph, MI, USA). To draw conclusions on the effects of soil fungi on carbon dynamics, we calculated soil C stocks and conducted in situ decomposition experiments. Soil C stocks were calculated in kg C m^{-2} based on C content and bulk density. Decomposition rate of cellulose was assessed by means of cellulose bags ($n = 14$), which were buried in the soil in two lines along the transect and incubated in situ for 12 weeks throughout the growing season. The mass loss of the bags during this period was used an estimate of the cellulose decomposition rate. We determined particle size distribution by laser diffraction, and measured the pH value in a soil-water suspension. The soil analyses followed the methods as described in Roth et al. (2023).

2.4. Analysis of fungal community

We extracted the total DNA from 500 mg of mineral and 50 mg of organic soil sample (with two lab replicates per sample; their elutes were pooled, $n = 32$ samples) using the NucleoSpin Soil DNA extraction kit (Macherey-Nagel GmbH & Co., Düren, Germany) following the manufacturer's instructions. Samples were homogenized and mechanically disrupted with ceramic beads, and suspended in SL2 Lysis Buffer and 100 μl of Enhancer by shaking horizontally for 5 min with a vortexer. After cell lysis, DNA was precipitated, washed, and eluted following the manufacturer's instructions. We tested for purity and quantity of DNA via ultraviolet-visible spectroscopy with a NanoDrop 2000c (Thermo Scientific) and Qubit fluorometer (Thermo Fisher). The extracted samples were diluted 1:10 before PCR and sequencing.

The fungal ITS2 regions of the extracted dsDNA were sequenced with Illumina® MiSeq at the Institute of Genomics Core Facility, University of Tartu, using the MiSeq v3 600 cycles sequencing kit. Prior to sequencing, the fungal ITS2 regions of the DNA samples were amplified by PCR at the Institute of Genomics Core Facility, using the fungus-specific primers gITS7 (forward: 5′- GTGARTCATCGARTCTTTG) and ITS4 (reverse: 5′-TCCTCCGCTTATTGATATGC) (Ihrmark et al., 2012) and attached to adapter sequences.

The adapter sequences were removed from the raw ITS2 reads at the Institute of Genomics Core Facility, University of Tartu. The general read quality was inspected using the MultiQC bioinformatics tool (Ewels et al., 2016). The sequences were filtered, trimmed and clustered to operational taxonomic units (OTUs) with Mothur (Schloss et al., 2009) following the pipeline described in Sietiö et al. (2018). Briefly, reverse and forward reads were combined and the primers were removed. We removed sequences longer than 350 base pairs (bp), sequences containing ambiguous bases, and homopolymers longer than eight nucleotides. We also removed chimeric sequences and singletons. The sequences were truncated to 230 bp, pairwise aligned and clustered to OTUs and aligned against UNITE database (Version 8.3, Abarenkov et al., 2021) for taxonomic identification. All non-fungal species were excluded from our dataset. The taxonomic information of the obtained OTUs was used to assign them to functional groups using the FUNGuild database (Nguyen et al., 2016). Soil moulds, yeasts and ericoid mycorrhizae were manually assigned to functional groups based on literature.

2.5. Data analysis

All statistical analyses were executed using R Statistical Software version 4.2.0 (R Core Team, 2022). We explored the data by means of the phyloseq package (McMurdie and Holmes, 2013) and the vegan package (Oksanen et al., 2022).

To assess whether the fungal community structure was affected by the management treatment, we visualized it in two-dimensional space using non-metric multi-dimensional scaling (NMDS). The fit of the NMDS ordination was evaluated with Shepards plots and by considering the stress values. We accepted stress values <0.15. We selected the most abundant and best fitting OTUs using the goeveg package (Lampe and Schellenberg, 2023) and plotted them with our community data. To explore covariation between fungal communities and variables altered both directly and indirectly by the management treatment, we overlay the NMDS plot with the following environmental factors: DTH, DBH, BA, stem density and species diversity of mature trees and saplings, soil pH, soil moisture, soil temperature, soil C content, and C/N-ratio. We added soil texture as a site-specific variable that is not affected by forest management.

To analyse the relative importance of the management treatment on fungal community composition we conducted permutational multivariate analysis of variance (perMANOVA) based on Bray-Curtis dissimilarity using the Adonis2 function of the vegan package (Oksanen et al., 2022). To test for statistical differences between the microbial communities of the various treatments we conducted pairwise Analysis of Similarities Test (ANOSIM).

To assess whether the management treatments affect fungal diversity, we calculated the observed species richness and Shannon index (Shannon, 1948) for the whole dataset and for ECMf. The number of species identified as ericoid mycorrhizae was too small to calculate their diversity indices. To estimate the abundance of ECMf, ERMf and SAPf, we calculated relative abundance of observed OTUs for these functional groups and inferred the ECM/SAP-ratio. To calculate statistical differences between treatments we performed parametric one-way Analysis of Variance (ANOVA) with Fisher's F-test after testing for normal distribution with the Shapiro-Wilk test, and for homogeneity of variances with Levene's test. We used unpaired *t*-test with Bonferroni correction as a post-hoc test for parametric ANOVA. If the data were not normally distributed or did not show equal variances, we used Kruskal-Wallis ANOVA followed by Mann-Whitney U post-hoc test with Bonferroni correction. Statistical significance is reported when *p*-values were < 0.05.

3. Results

Soil organic carbon stocks were highest in even-aged plots, and lowest in uncut plots (Fig. 3a). However, these differences were not statistically significant. Also, decomposition rates were similar in the different forest management treatments (Fig. 3b).

3.1. MiSeq sequencing results

We obtained a total of 5,384,638 raw ITS2 sequences from the 32 samples. After quality control, 3,365,960 high-quality and non-chimeric sequences without global singletons remained, which were assigned to 13,152 OTUs with 97 % similarity. After excluding singletons, 9414 OTUs remained. After removing non-fungal species, 0.03 % of the sequences remained unclassified, i.e., 0.56 % of the OTUs. Of the total OTUs, 99.4 % could be assigned to 15 phyla (Table 1), 58.8 % were identified to the genus level, and 29.1 % to the species level.

3.2. Fungal community composition and diversity

Of the 9414 OTUs, the four different treatments shared 1853 OTUs (19.7 %, Fig. 4). Unique OTUs that only occur in one treatment accounted for 15.9 % of the total OTUs. Clear-cuts showed the highest number of unique OTUs ($n = 537$), while even-aged plots had the lowest ($n = 250$) (Fig. 4). Regarding the shared OTUs between two treatments, uncut control plots and clear-cuts shared the lowest number of OTUs, with 504 in common, whereas uneven-aged plots and clear-cuts shared the most: 814 (Fig. 4).

Basidiomycota was the most abundant phylum with a relative abundance of 39.3 % of the total sequences per sample, and containing 35.7 % out of the total OTUs. The second and third most abundant phyla were Ascomycota (34.7 % of sequences and 45.8 % of OTUs) and Mucoromycota (16.48 % of sequences and 8.1 % of OTUs, Table 1, Fig. S4d), respectively. The ten most abundant genera accounted for an average of 46.3 % of the total sequences per sample. *Umbelopsis* (14.1 %) was the most abundant genus, followed by *Mortierella* (8.7 %), *Tylospora* (4.6 %), *Russula* (4.3 %), *Piloderma* (3.6 %), *Cortinarius* (2.8 %) *Penicilium* (2.7 %), *Solicoccozyma* (2.3 %), *Lactarius* (2.2 %) and *Oidiodendron* (2.1 %) (Table 1, Fig. S4b). Due to the similar library sizes of the samples (Fig. S3a), we consider the relative abundance similar to the absolute abundance, and hence do not discuss them separately. For a list of the most abundant species, genera and orders found in our dataset, see Supplementary Fig. S4.

Tylospora, *Russula*, *Piloderma*, *Cortinarius* and *Lactarius* are ectomycorrhizae (Smith and Read, 2008). Their abundance differs between treatments and soil layers. In the mineral soil, *Tylospora*, *Piloderma* and *Cortinarius* were the most abundant in uncut plots and the least abundant in clear-cut plots. Even-aged and uneven-aged plots were

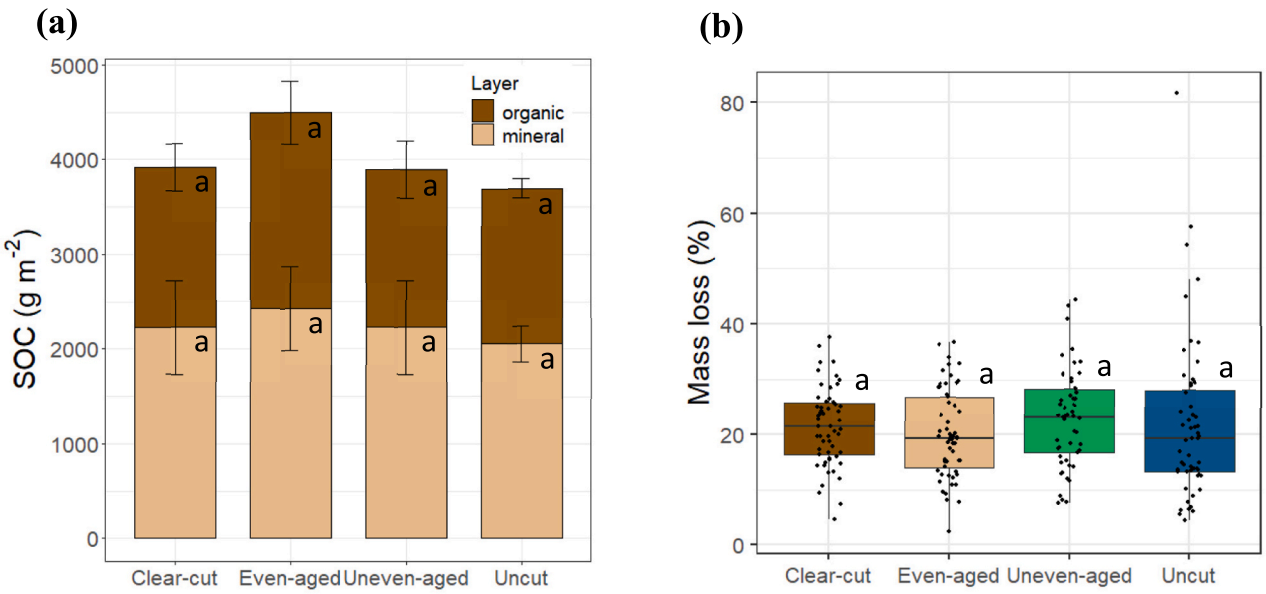

Fig. 3. (a) Soil organic carbon stocks in g m^{-2} in the organic and mineral soil layer. The error bars indicate standard errors of the mean values, (b) Decomposition rates, determined as mass loss of cellulose litterbags during field incubation, depicted for the different treatments. The central line shows the median of the data, and the box depicts the values within the 25 % and 75 % quantiles. Whiskers show the 1.5 interquartile (1.5 IQR) value. Lowercase letters indicate statistical differences ($p < 0.05$).

intermediate. In the organic soil, the pattern was the same for *Piloderma*, and a similar (although nonsignificant) trend was found for *Cortinarius*. *Tylospora* showed the highest abundance in uneven-aged plots and the lowest in uncut plots in the organic layer. Clear-cuts and even-aged plots were intermediate. The genus *Oidiodendron* forms ericoid mycorrhizal associations. There were no significant differences between the treatments, although even-aged and uncut control treatments showed slightly higher values than clear-cuts and uneven-aged plots. The genera *Umbelopsis*, *Penicillium* and *Mortierella* contain fungi with saprotrophic capabilities (Baldrian et al., 2011; Cannon and Kirk, 2007). *Umbelopsis* was more abundant in the uncut plots than the other treatments in the organic soil; in the mineral soil samples, the pattern was not statistically significant. *Mortierella* showed a contrasting pattern. It was least abundant in uncut plots and most abundant in clear-cuts in mineral soils, with a similar non-significant pattern in the organic soil. Glomeromycotae, a phylum of arbuscular mycorrhizal fungi (Smith and Read, 2008), was most abundant in clear-cuts plots and least abundant in uncut plots in both soil layers. In mineral soil samples, it was significantly less abundant in even-aged and uneven-aged stands compared to clear-cut sites (Table 1).

The different treatments shared the same 20 most abundant species (Fig. S4a), except for the ectomycorrhizal fungi *Russula adusta* and *Inocybe boreocarelica* which did not occur in clear-cuts. Some ectomycorrhizal fungi are clearly less abundant on clear-cuts compared to the other treatment with more closed canopy, such as *Tylospora asterophora*, *Piloderma byssinum, Russula adusta* and *Piloderma bicolor*. Other species show higher abundance on clear-cut plots, such as the yeasts *Solicoccozyma terricola* or *Saitozyma podzolica*. Both similarly also show a higher abundance in uneven-aged plots. Ectomycorrhizal *Piloderma bicolor* and saprotrophic *Umbelopsis vinacea* are more abundant in uncut plots than other treatments, whereas *Inocybe boreocarelica* has a high abundance in uneven-aged plots and very low abundance in other treatments.

Observed species richness and Shannon index differed between organic and mineral layer samples, but not between the different management treatments (Table 2). The effect of the treatment was not significant on observed species richness (tested with ANOVA, $p > 0.05$) or on species diversity, i.e., Shannon index (p-value in both cases >0.05). There was an effect of the soil layer on observed species richness ($p >$ 0.001) and the diversity index (p-value in both cases <0.001), which were lower in mineral layer samples compared to the organic layer. Shannon index ranged between 4.3 and 4.6 in the mineral soil samples, and between 5.1 and 5.3 in the organic layer samples, indicating a very high α-diversity in our samples.

The clear separation of mineral soil and organic layer samples along the first NMDS ordination axis demonstrated the dissimilarity between their fungal communities (Fig. 5). As indicated by the environmental vectors, organic layer communities were associated with a higher C/N-ratio, and mineral layer communities were associated with higher pH values (Supporting Information Table S3). The perMANOVA confirms this, as the layer explains 34 % of the variability within the fungal community data (p = 0.001, Table 3). The second ordination axis that ordered the samples from the different treatments from uncut control to clear-cuts was associated with decreasing DBH, DTH, BA, tree density (treedens) and tree diversity (treediv), and with increasing density and diversity of saplings (sapldens and sapldiv, respectively) and coverage of ericoid shrubs (shrubs) (Fig. 5). Accordingly, perMANOVA showed that treatment explains 16 % of the variability overall in the fungal composition data of organic and mineral soil layers combined ($p = 0.001$, Table 3). As the layer explained 34 % of the variability in the combined data, this overshadowed the treatment effects in the combined data. Treatment effects became clearer when looking at both layers separately. According to perMANOVA, treatment explained a higher percentage of the variability in the organic layer than in the mineral soil (38 vs 33 %, p = 0.001 in both cases, Table 3). The fungal communities in uncut, uneven- and even-aged treatments were associated with higher BDH, DTH and BA. Soil moisture (soilmoist), soil temperature (soiltemp) and soil texture (sand) were not significant factors in explaining the fungal community structure ($p > 0.05$). The pairwise ANOSIM test showed that in the organic layer, the fungal communities of all the treatments were significantly different from each other (Supporting Information Table S4). In the mineral soil, the communities in the even-aged plots fell in between uneven-aged and uncut plots, but did not statistically differ from them. All the other treatments (uncut, uneven-aged and clear-cuts) were significantly different from each other (Supporting Information Table S4). In both soil layers, the biggest differences between treatments can be found between clear-cuts and uncut plots, followed by clear-cuts and even-aged plots. Fungal communities in

Table 1
Number of OTUs and percentage of sequences per sample they account for (± standard deviation), recorded for the different phyla and the ten most abundant genera. 'Others' contains the phyla Neocallimastigomycota, Olpidiomycota, Entorrhizomycota, Zoopagomycota, Basidiobolomycota, Entomophthoromycota, Kickxellomycota and Monoblepharomycota. Numbers are listed for the whole dataset and for the four different treatments individually, separated for organic layer and mineral soil. Significant differences between treatments are marked with lowercase letters, and they indicate the differences within the same soil layer (O-layer or mineral soil analysed separately).

	OTU count	% of samplesequences	Organic Layer						Mineral soil					
			Clear-cut		Even-aged		Uneven-aged		Clear-cut		Even-aged		Uneven-aged		Uncut	
Ascomycota	**4314**	34.7 ± 6.9	41.05 ± 5.45		42.67 ± 7.31		37.75 ± 2.37		33.57 ± 5.07		32.80 ± 2.42		27.89 ± 2.42		26.44 ± 3.26	
Penicilium	184	2.7 ± 2.7	6.93 ± 3.64		4.54 ± 2.70		2.76 ± 2.40		1.16 ± 0.22		0.69 ± 1.03		1.39 ± 1.03		0.79 ± 0.42	
Oidiodendron	226	2.1 ± 1.0	1.35 ± 0.29		2.10 ± 0.94		1.19 ± 0.22		1.92 ± 0.06		3.03 ± 1.02		2.63 ± 1.02		3.43 ± 0.71	
Basidiomycota	**3358**	39.3 ± 6.7 3	35.25 ± 3.17		39.43 ± 3.97		42.97 ± 4.20		38.73 ± 4.74		31.37 ± 6.71		39.16 ± 3.80		42.34 ± 3.80		45.37 ± 7.32	
Tylospora	191	4.6 ± 4.7	0.91 ± 0.53	ab	1.38 ± 0.62	ab	2.64 ± 1.74	b	0.46 ± 0.32	a	1.87 ± 0.96	a	10.09 ± 2.08	b	8.38 ± 2.08	ab	11.19 ± 2.52	b
Russula	243	4.3 ± 3.1	1.66 ± 1.69		4.83 ± 1.70		3.52 ± 2.41		5.76 ± 3.79		2.92 ± 2.30		6.27 ± 3.95		6.10 ± 3.95		3.54 ± 1.20	
Piloderma	202	3.6 ± 3.5	0.86 ± 0.52	a	7.40 ± 2.78	b	6.36 ± 2.72	b	8.47 ± 2.32	b	0.27 ± 0.31	a	1.69 ± 0.44	ab	1.05 ± 0.44	a	2.94 ± 1.52	b
Cortinarius	273	2.8 ± 2.5	0.95 ± 0.37		2.61 ± 2.04		4.38 ± 1.35		4.78 ± 4.21		0.07 ± 0.04	a	2.96 ± 1.06	ab	1.27 ± 1.06	a	5.23 ± 2.42	b
Solicoccozyma	93	2.3 ± 2.7	2.42 ± 0.95	a	0.41 ± 0.14	b	0.93 ± 0.42	b	0.14 ± 0.08	b	5.90 ± 2.21	a	1.62 ± 4.03	bc	5.77 ± 4.03	ab	1.13 ± 0.75	c
Lactarius	109	2.2 ± 2.2	1.81 ± 1.93		1.38 ± 0.47		2.70 ± 1.09		2.09 ± 0.34		1.00 ± 0.66		4.04 ± 1.48		1.73 ± 1.48		2.56 ± 2.08	
Mucoromycota	**764**	16.5 ± 7.6	10.82 ± 6.10		7.71 ± 2.89		8.37 ± 2.65		16.00 ± 4.55		21.58 ± 2.83		20.85 ± 5.31		22.50 ± 5.31		24.06 ± 5.95	
Umbelopsis	581	14.1 ± 8.2	7.00 ± 3.33	a	4.60 ± 2.13	a	4.63 ± 0.55	a	13.42 ± 3.89	b	19.89 ± 2.41		18.85 ± 5.26		21.39 ± 5.26		23.08 ± 5.96	
Mortiellomycota	**629**	8.8 ± 3.5	11.93 ± 2.56		9.69 ± 2.34		10.16 ± 1.06		8.87 ± 1.46		12.68 ± 4.33	a	6.88 ± 2.50	b	6.41 ± 2.50	b	3.78 ± 1.07	b
Mortierella	614	8.7 ± 3.5	11.76 ± 2.50		9.50 ± 2.36		10.01 ± 0.97		8.68 ± 1.36		12.59 ± 4.37	a	6.87 ± 2.50	ab	6.39 ± 2.50	b	3.77 ± 1.07	b
Rozellomycota	**147**	0.2 ± 0.1	0.22 ± 0.14		0.17 ± 0.06		0.20 ± 0.11		0.06 ± 0.01		0.24 ± 0.10		0.22 ± 0.05		0.17 ± 0.08		0.17 ± 0.09	
Chytridiomycota	**72**	0.2 ± 0.2	0.30 ± 0.29		0.06 ± 0.03		0.14 ± 0.05		0.14 ± 0.07		0.06 ± 0.05		0.06 ± 0.06		0.50 ± 0.48		0.03 ± 0.03	
Fungi unclassified	**53**	0.0 ± 0.0	0.08 ± 0.07	a	0.02 ± 0.02	ab	0.04 ± 0.03	ab	0.01 ± 0.01	b	0.04 ± 0.04		0.02 ± 0.02		0.03 ± 0.03		0.01 ± 0.01	
Glomeromycota	**23**	0.0 ± 0.1	0.13 ± 0.12	a	0.01 ± 0.01	ab	0.01 ± 0.02	ab	0.00 ± 0.00	b	0.11 ± 0.08	a	0.01 ± 0.02	b	0.01 ± 0.01	b	0.01 ± 0.01	b
Other	**54**	0.3 ± 0.5	0.22 ± 0.09		0.25 ± 0.32		0.36 ± 0.17		0.77 ± 0.68		0.35 ± 0.20		0.01 ± 0.01		0.16 ± 0.11		0.14 ± 0.21	

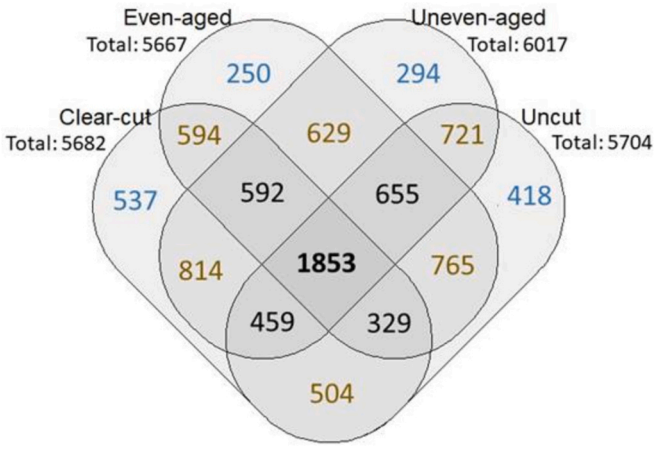

Fig. 4. Venn diagram showing the number of unique operational taxonomic units (OTUs) for each treatment in blue colour, OTUs shared between two treatments in brown, the OTUs shared between three treatments in black and OTUs shared between all treatments in bold font.

uneven-aged plots were more similar to the ones found in clear-cuts, however the differences between them were still statistically significant.

3.3. *Ectomycorrhizae and ericoid mycorrhizae*

Ectomycorrhizal fungi were less abundant on clear-cuts compared to the other treatments (Fig. 6a, Table 4). Abundance of ECMf declined with increasing stem density and basal area (Supporting Information Fig. S5a,b), and was unaffected by the density of saplings (Supporting Information Fig. S5c). There were no significant differences in the abundance of saprotrophs between the treatments. We found a marginally lower ECM/SAP-ratio in clear-cuts than in even-aged and uneven-aged plots. The lower ECM/SAP-ratio compared to uncut plots was not significant (Table 4).

Ericoid mycorrhizae were more abundant in the organic layer of clear-cut plots and even-aged plots than uncut plots. Uneven-aged plots were intermediate, and were not significantly different from the other treatments. Ericoid shrub cover showed a similar pattern. Uncut plots had the lowest cove, while the other three treatments were similar to each other (Fig. 6b). However, the relationship between ericoid shrub cover and ERMf abundance was not significant (Supporting Information Fig. S5f). As true ERMf we identified *Oidiodendron maius* and *Hyaloscypha hepaticicola* (previously *Rhizoscyphus ericae*, syn. *Pezoloma ericae*). The ERMf abundance in the organic layer showed a negative linear relationship to the stem density and basal area of the upper tree layer (Supporting Information Fig. S5d, e), i.e., it decreases with increasing stand density.

The main variation found for ECMf (Fig. 7a) using NMDS resembled that found for the total fungal community (Fig. 5). It showed a clear distinction in the communities between the two soil layers (Fig. 7a). Accordingly, perMANOVA showed that the soil layer explained 23 % of the variation within the ECMf community structure (Table 5). The different treatments that ordered samples along the second NMDS axis (Fig. 7) were found to explain 19 % of the variation in the ectomycorrhizal community (Table 5). The ectomycorrhizal communities in both the mineral and organic soil of clear-cuts were clearly dissimilar from the ones in the other treatments, while the communities in the other treatments appeared to be more similar to each other (Fig. 7a). The ERMf community structure was not significantly affected by the management treatment or the soil layer (Table 5, Fig. 7b).

The observed species richness of ECMf was lower in clear-cuts than in the other treatments in both soil layers. The Shannon index showed a trend towards a higher species diversity in the ectomycorrhizal community in the organic layer of uncut control plots compared to clear-cuts

Table 2
Average number of obtained sequences per sample, mean observed OTU richness (number of OTUs observed in each sample) and Shannon index for each treatment and layer (± standard deviation). We tested for differences between mean values of different treatments with ANOVA followed by post-hoc unpaired t-test with Bonferroni correction. Different lowercase letters indicate significant differences between treatments within each layer.

Treatment	No. of Sequences			Observed OTU richness				Shannon index			
O-layer											
Clear-cut	111,345	±	17,847	2213	±	150	a	5.3	±	0.2	a
Even-aged	100,894	±	11,822	1907	±	271	a	5.1	±	0.4	a
Uneven-aged	127,946	±	10,413	2201	±	115	a	5.2	±	0	a
Uncut	113,539	±	4520	2062	±	142	a	5.1	±	0.1	a
Mineral soil											
Clear-cut	89,490	±	22,002	1475	±	220	a	4.6	±	0.1	a
Even-aged	97,873	±	16,059	1374	±	107	a	4.4	±	0.1	a
Uneven-aged	98,711	±	13,173	1437	±	47	a	4.5	±	0.2	a
Uncut	101,689	±	10,694	1415	±	96	a	4.3	±	0.1	a

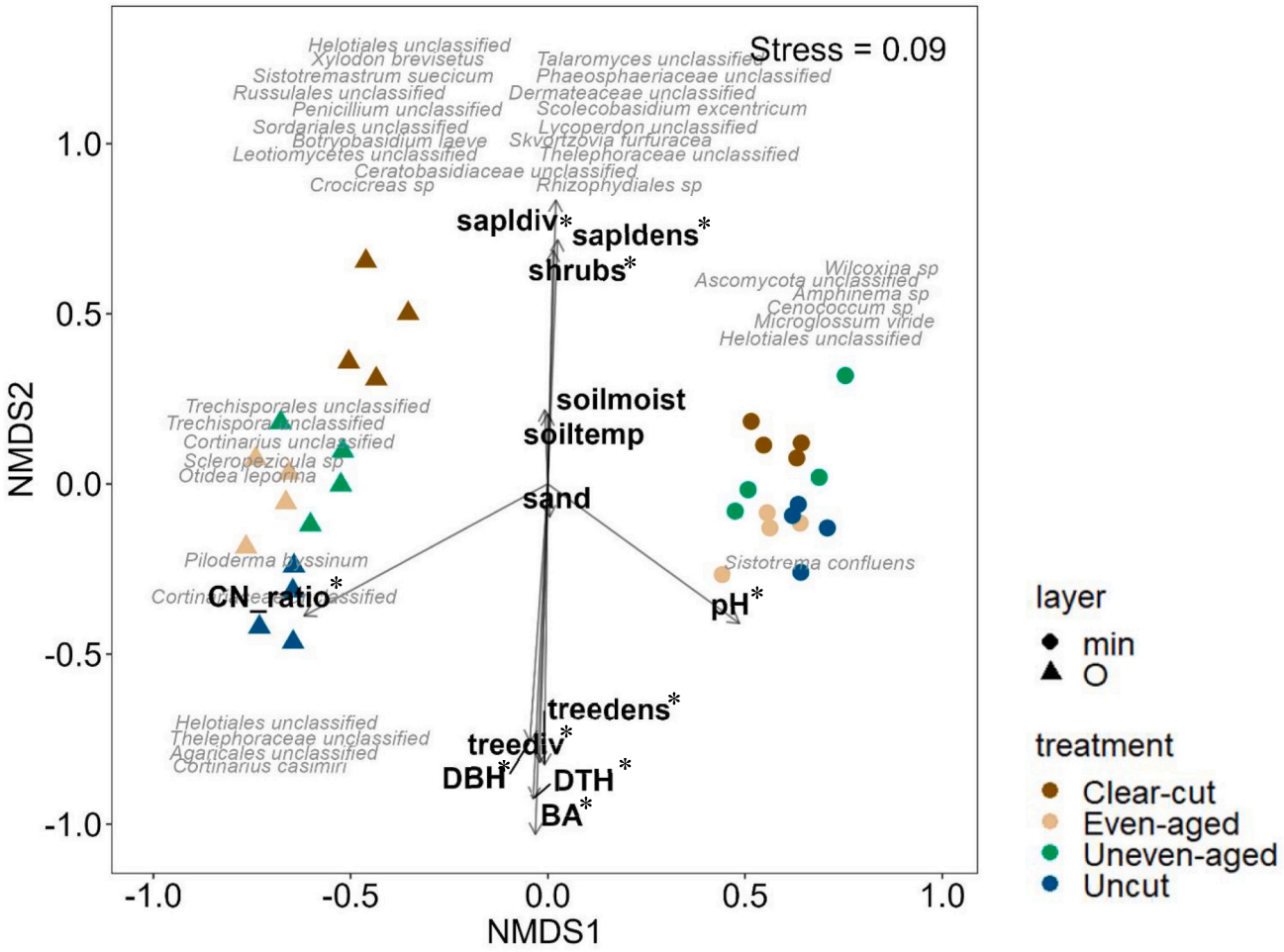

Fig. 5. NMDS with two ordination axes (k = 2) displaying the 10 % most abundant and 5 % best fitting species/OTUs for the organic layer and mineral soil combined. We fitted environmental variables characterizing the forest stand: dominant tree height (DTH), diameter at breast height (DBH), basal area (BA), diversity and density (stem/ha) of upper tree layer (treediv, treedens) and saplings (sapldiv, sapldens), and cover of ericoid shrubs (shrubs). Variables characterizing the soil include: soil pH (pH), soil moisture (soilmoist), soil temperature (soiltemp), soil texture (sand) and C/N-ratio. Significant variables are marked with *.

(Table 6).

4. Discussion

We compared two stages of RFM—mature even-aged forests stands (pre-harvest) and re-growing stands after clear-cutting (post-harvest)—to uneven-aged (CCF) and uncut forests. Our study showed that forest management shapes the fungal community composition, not only through clear-cutting, but also through even- and uneven-aged stand structures. Furthermore, the silvicultural system impacts the potential ecological functionality of soil fungi.

In particular, clear-cutting affected the fungal community structure, which was highly and significantly dissimilar from the community in the uncut and the partially cut (mature even-aged and uneven-aged) plots in both soil layers. The strong effect of clear-cutting on the fungal community found 11 years after the harvesting aligns with the results of

Table 3
Results from perMANOVA for the impact of management treatment and soil layer on fungal community based on the Bray-Curtis distance between OTUs, and the impact of treatment on fungal community for organic and mineral soil layers separately.

	R2	F-value	p-value
perMANOVA all data:			
R-formula: adonis2 (otus.dist ~ treatment + layer)			
Treatment	0.16	2.93	0.001
Layer	0.34	18.09	0.001
Organic layer: adonis2 (otus.dist ~ treatment)			
Treatment	0.38	2.45	0.001
Mineral soil: adonis2 (otus.dist ~ treatment)			
Treatment	0.33	1.97	0.001

other studies (Kim et al., 2021; Kohout et al., 2018; Simard, 2008). The even-aged and uneven-aged structures that were established 33 years before our study through partial harvesting (thinning and single-tree selection, respectively) led to different fungal communities, which also differed from uncut plots. This is in line with the results of Kim et al. (2021), who also found that the fungal community in CCF treatments was different from unmanaged plots. Similarly to Choma et al. (2021), we found that the effect of forest management on fungal community composition was stronger in the organic layer than mineral soil. These results imply that the fungal community in the organic topsoil layer is more sensitive to forest management practices than the deeper soil layers, or there might be a delay in the response of deeper soil layers. Generally, the SOM stocks in organic layers are known to be more strongly affected by forest management practices than in deeper soil layers (James and Harrison, 2016).

The communities of uncut plots and even-aged plots were more dissimilar from the clear-cut plots compared to the uneven-aged community; the uneven-aged communities were more similar to those in clear-cuts. Uneven-aged forests have a sparser canopy and lower basal area than uncut and mature even-aged forests, and their microclimate and light conditions within canopy gaps often resemble those in clear-cuts. Therefore, we could also expect locally similar conditions under canopy gaps as in clear-cut sites, whereas under the partially remaining canopy, the microclimate and shading is similar to a closed mature stand (Kumpu et al., 2018; Roth et al., 2023). Uneven-aged stands might offer good conditions for plant species and their associated fungi, which are usually associated with clear-cuts, as well as species that can be found under closed canopy. This can also be seen in the great variability in ericoid shrub coverage in the uneven-aged stands. Furthermore, the tree species identity might also affect the community (Hofmann et al., 2023). Favourable light conditions may increase growth of broadleaved species on clear-cuts and uneven-aged stands, and deciduous litter inputs possibly also benefit saprotrophs. Soil temperature and moisture did not have direct significant effects on the fungal community. The community was shaped by tree and sapling density, tree stocks (BA, DTH and DBH) and tree and sapling diversity, followed by variables related to soil quality (soil pH and C/N-ratio). Tedersoo et al. (2014) found fungal richness to be decoupled from plant diversity on a global scale. In their study, the best predictors for fungal richness and community composition were climatic factors followed by edaphic and spatial variables. However, on a local scale, this appears to be reversed. Our results align with a study in a temperate mixed forest, where Gömöryová et al. (2013) found that the soil microbial community is more affected by interactions with vegetation than changes in the microclimate.

Our hypothesis 1 on more diverse fungal community in uneven-aged CCF plots than in even-aged plots due to the structural complexity of uneven-aged forests was not supported. In contrast, we recorded the highest Shannon diversity and species richness on clear-cut plots (although not statistically significant). In contrast, Paillet et al. (2010) found a decrease in soil fungal richness associated with forest management, regardless of the management intensity. However, they did not include any studies with clear-cuts in their analysis. Our results also contradict those outlined in a meta-analysis, which showed that uneven-aged stands generally have a higher fungal species richness than young even-aged forests a few years after clear-cutting (Savilaakso et al., 2021). Our results agree with the findings of Kohout et al. (2018), who reported an increase of OTU richness after clear-cutting. The increased richness they found, was caused by an increase of saprotrophic fungi.

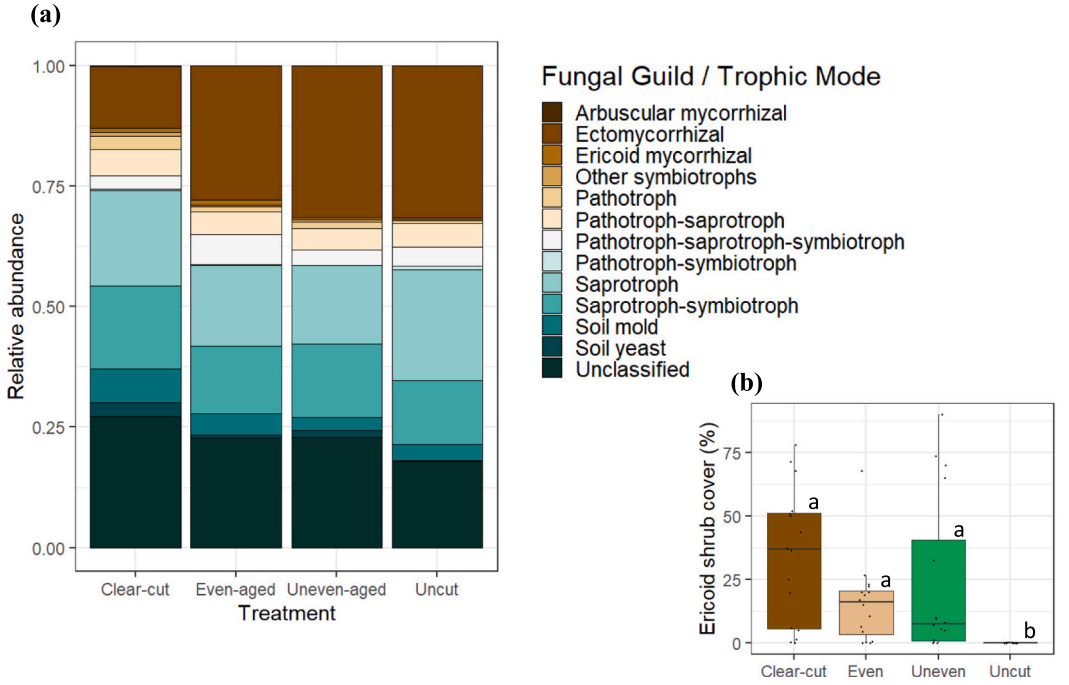

Fig. 6. (a) Potential functionality of the observed fungal taxa assigned through FUNGuild database in the various treatments based on normalized OTU counts. 'Unclassified fungi' include OTUs that yielded no answer when aligned with UNITE database and fungi that were assigned with a confidence ranking of 'possible'. (b) Ericoid shrub ground cover in % in the different treatments.

Table 4
Relative abundance in % for ECMf, SAPf and ERMf, and ECM/SAP-ratio of relative abundance (± standard deviation). We tested for differences between mean values of different treatments with ANOVA followed by post-hoc unpaired *t*-test with Bonferroni correction. Different lowercase letters indicate significant differences with $p < 0.05$. Letters in parentheses show marginally significant differences with $p < 0.1$.

Treatment	Abundance														
	ECMf	±	SD		SAPf	±	SD		ERMf	±	SD		ECM/SAP	±	SD	
All data																
Clear-cut	12.82	±	6.30	a	23.60	±	6.41	a	0.95	±	1.21	a	0.73	±	0.60	a
Even-aged	28.52	±	7.08	b	21.06	±	6.69	a	0.63	±	0.59	a	1.70	±	0.69	(b)
Uneven-aged	28.73	±	5.58	b	22.70	±	7.49	a	0.28	±	0.28	a	1.72	±	0.97	(b)
Uncut	32.23	±	7.56	b	27.29	±	7.95	a	0.15	±	0.17	a	1.43	±	0.76	ab
O-layer																
Clear-cut	13.8	±	8.2	a	19.6	±	6.4	a	0.97	±	0.18	a	0.98	±	0.8	a
Even-aged	28.2	±	4.1	b	16.6	±	2.8	a	0.98	±	0.54	a	2.09	±	0.6	ab
Uneven-aged	31.4	±	2.5	b	16.2	±	1.2	a	0.53	±	0.08	ab	2.47	±	0.8	(b)
Uncut	31.6	±	6.2	b	22.9	±	5.3	a	0.28	±	0.14	b	1.66	±	0.8	ab
Mineral soil																
Clear-cut	11.9	±	4.8	a	27.6	±	3.5	a	0.94	±	1.84	a	0.47	±	0.3	a
Even-aged	28.9	±	10.0	b	25.5	±	6.7	a	0.27	±	0.42	a	1.32	±	0.6	a
Uneven-aged	26.0	±	6.8	ab	29.2	±	4.1	a	0.03	±	0.03	a	0.96	±	0.3	a
Uncut	32.9	±	9.7	b	31.6	±	8.3	a	0.02	±	0.01	a	1.20	±	0.7	a

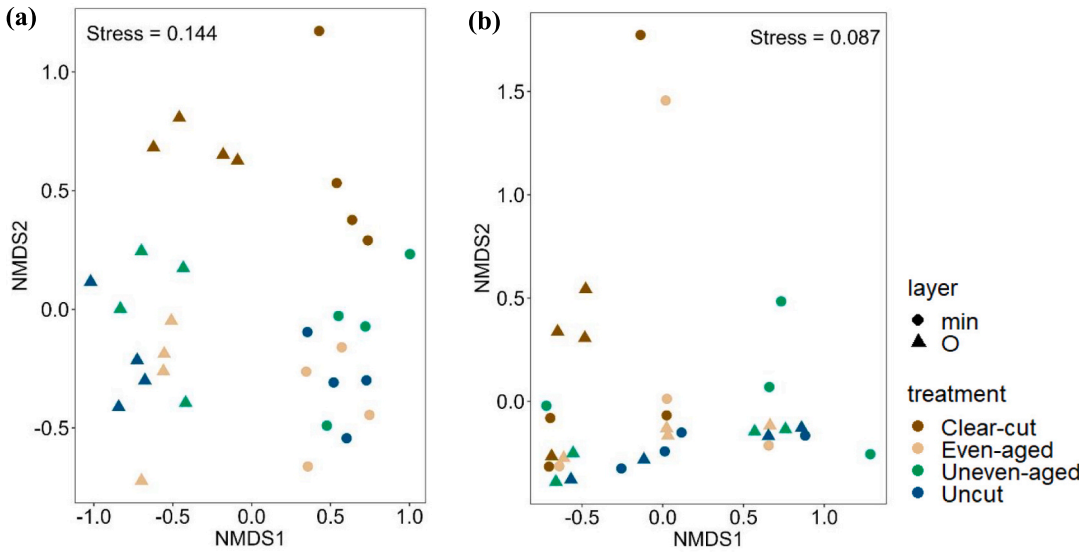

Fig. 7. NMDS with two ordination axes (k = 2) for the ECMf community structure (a) and ERMf community structure (b) for organic and mineral soil combined.

Table 5
Results from perMANOVA for the impact of management treatment and soil layer on ECMf and ERMf community based on the Bray-Curtis distance between OTUs.

	R2	F-value	p-value
perMANOVA ECMf:			
R-formula: adonis2 (otus.dist.ecm ~ treatment + layer)			
Treatment	0.19	2.88	0.001
Layer	0.23	10.50	0.001
perMANOVA ERMf:			
R-formula: adonis2 (otus.dist.erm ~ treatment + layer)			
Treatment	0.17	1.90	0.08
Layer	0.04	1.21	0.31

This indicates that different taxa react differently to the disturbance, depending on their trophic mode and habitat preferences. Forest-dependant species are known to have an advantage in uneven-aged or mature even-aged stands, whereas open-habitat specialists benefit from clear-cutting (Savilaakso et al., 2021). We also found a higher abundance of arbuscular mycorrhizal fungi after clear-cutting, which were contributing to OTU richness and Sannon diversity in clear-cut plots.

Our hypothesis 2, on higher abundance of ECMf and a more diverse ECMf community in uneven-aged and uncut forests compared to clear-cut plots was supported by our results. In clear-cuts, the abundance of ECMf fungi was indeed significantly lower than in the other treatments, which corroborates the first part of our hypothesis and is in line with the results of similar studies (Centenaro et al., 2024; Hasby, 2022; Kohout et al., 2018; Kyaschenko et al., 2017; Parladé et al., 2019; Rodriguez-Ramos et al., 2021; Twieg et al., 2007). However, contrasting results have also been found (Choma et al., 2021; Rähn et al., 2023). The lower abundance of ECMf in clear-cuts is caused by the absence of host trees that mycorrhizal fungi depend on (Prescott and Grayston, 2023; Smith and Read, 2008). We also found that ectomycorrhizal species amongst the most abundant species in our dataset, dropped out completely in clear-cuts, such as *Russula adusta* and *Inocybe boreocarelica,* or were less abundant compared to the other treatment, such as *Tylospora asterophora*, *Piloderma byssinum, Russula adusta* and *Piloderma bicolor*.

Table 6
Observed OTU richness and Shannon index for ectomycorrhizal communities in the different treatments, presented for all data combined, and for the organic layer (O-layer) and mineral soil separately. We tested for differences between mean values of different treatments with ANOVA followed by post-hoc unpaired *t*-test with Bonferroni correction. Different lowercase letters indicate significant differences. Letters in parentheses show marginally significant differences with $p < 0.1$.

	Treatment	Observed OTU richness	±	SD		Shannon index	±	SD	
All data									
	Clear-cut	152.8	±	47.6	a	2.9	±	0.5	a
	Even-aged	266.1	±	50.7	b	3.0	±	0.4	a
	Uneven-aged	288.3	±	59.1	b	3.2	±	0.3	a
	Uncut	293.6	±	45.8	b	3.2	±	0.4	a
O-layer									
	Clear-cut	171.3	±	50.2	a	3.1	±	0.2	a
	Even-aged	282.8	±	40.2	b	3.2	±	0.3	ab
	Uneven-aged	332.3	±	49.4	b	3.4	±	0.1	ab
	Uncut	326.8	±	42.3	b	3.6	±	0.1	(b)
Mineral soil									
	Clear-cut	134.3	±	43.1	a	2.7	±	0.7	a
	Even-aged	249.5	±	60.3	b	2.7	±	0.2	a
	Uneven-aged	244.3	±	23.3	b	3.0	±	0.2	a
	Uncut	260.5	±	13.4	b	2.8	±	0.3	a

Abundance of ECMf increased with increasing basal area and stem density as anticipated, but showed no relationship with sapling density. This highlights the importance of old trees in sustaining the ECMf community.

The second part of hypothesis 2 on a higher abundance of saprotrophs in clear-cut plots was also supported. We found a lower observed species richness of ECMf in clear-cuts than in the other treatments, which is in agreement with the results of several other studies (Tomao et al., 2020; Twieg et al., 2007). Some ECMf may not be able to persist in the absence of mature trees (Kranabetter and Friesen, 2002), which would explain the declined species richness after clear-cutting. The species diversity of ECMf was marginally lower in the organic layer of clear-cuts than in uncut plots, but not different from partially cut even-aged (RFM) or uneven-aged (CCF) plots. This is in line with the results of Jones et al. (2003), who found that the diversity of ECMf fungi reacts inconsistently after clear-cutting even if ECMf abundance is generally declining. Grebenc et al. (2009) also found a decline in ECMf diversity and richness in canopy gaps after partial harvesting.

As expected, the ECM/SAP-ratio was smaller in clear-cuts than in even-aged or uneven-aged stands, but contrary to our hypothesis, the ratio in uncut plots was not significantly higher than in clear-cuts. This might be due to the comparably high abundance of saprotrophs in uncut plots. For example, the genus *Umbelopsis* that was most abundant in uncut plots, even though it has been identified as an indicator of disturbed forests soils (Sukdeo et al., 2018), might be benefiting from the high amounts of dead wood in uncut plots. Competition for light in dense uncut forests leads to high tree mortality (Hülsmann, 2016), which sustains saprotrophic fungi. Despite the higher ECM/SAP-ratio, there were no statistical differences in the abundance of saprotrophs between the treatments. Based on the assumption that ECMf compete with decomposers, and thus slow down soil carbon cycling and promote the accumulation of SOM (Averill et al., 2014; Averill and Hawkes, 2016; Gadgil and Gadgil, 1975; Kyaschenko et al., 2017), the declined ECM/SAP-ratio in clear-cut sites may indicate a stimulation of SOM decomposition.

We also found differences between the treatments on the genus level of ECMf, in agreement with their known ecological niches. *Cortinarius* and *Russula*, which are genera typically associated with older forests (Kyaschenko et al., 2017; Santalahti, 2018), were more abundant in mature stands (even-aged, uneven-aged or uncut) and less abundant in clear-cuts. On the other hand, *Piloderma* and *Tylospora,* usually dominant in young forests (Kyaschenko et al., 2017; Santalahti, 2018), were least abundant on clear-cut plots—even though we found a dense cover of young saplings on clear-cuts—and more abundant in the other treatments that include mature trees. This resonates with the results of Sukdeo et al. (2018), who identified *Cortinarius*, *Russula* and also *Piloderma* as genera that are indicative of undisturbed forest soils. *Cortinarius* was less abundant in the mineral soil of clear-cuts than uncut plots, but also uneven-aged plots. This may be caused by the higher amount of young re-growing trees and canopy gaps, and again illustrates that conditions in uneven-aged plots might locally resemble conditions in clear-cuts (Kumpu et al., 2018).

In hypothesis 3, we expected a higher abundance of ERMf in uneven-aged plots compared to even-aged and uncut forests due to more ericoid host plants in the ground vegetation. However, our hypothesis was not supported. On the contrary, ERMf were least abundant in uncut plots and more abundant in both stages of RFM, i.e., clear-cuts and even-aged plots. The abundance in uneven-aged plots was intermediate. Ericoid mycorrhiza have the ability to efficiently decompose recalcitrant SOM (Perotto et al., 2018; Smith and Read, 2008) and are thus more abundant in late stages of succession where SOM quality is on average lower than in earlier stages of succession (Clemmensen et al., 2015). Especially on clear-cuts their decomposer abilities might benefit ERMf due to the high amount of dead organic material. In our case, the ERMf abundance was regulated through the stand density (stem density ha^{-1} of the upper tree layer) and basal area (m^2 ha^{-1}), which regulate the understorey via availability of light reaching the soil surface. Lower stand density was associated with higher ERMf abundance. High stand density and low ericoid shrub coverage in uncut stands also coincide with low ERMf abundance, however, we could not find a clear significant relationship between ericoid shrub cover and ERMf abundance. In contrast to the abundance, community structure of ERMf was not significantly affected by forest management.

It is difficult to draw conclusions about the future soil C storage under RFM and CCF based on our data. According to the Gadgil hypothesis, mycorrhizal fungi may decrease the decomposition of SOM as they compete with saprotrophic fungi for SOM in nutrient mining (Gadgil and Gadgil, 1975). We found lower ECMf abundance, species richness and Shannon diversity in clear-cuts, and a significantly lower ratio of ECMf to SAPf. However, SOC storage and cellulose decomposition rate did not differ between treatments. This highlights the plasticity and functional redundancy in a diverse fungal community and indicates a high response diversity in our studied forests (Simard, 2008). It furthermore shows that the microbial community composition is highly dynamic, whereas changes in the soil C stocks happen at a slower pace (Baldrian, 2017). There was a tendency of increased ECMf abundance and biodiversity in the uneven-aged forests, approaching that of mature uncut forests. There are three mechanisms by which this could lead to higher or more stable soil C stock over time: 1) A large part of the old, stable SOC in forests has been shown to be ectomycorrhizal litter and roots (Clemmensen et al., 2013), 2) Ectomycorrhizal dominance could slow down decomposition rates due to competition for nitrogen with

decomposers (Averill and Hawkes, 2016), and 3) Ectomycorrhizal symbioses enhance seedling growth and stand productivity (Simard, 2008) and thus the flow of C to the soil. The importance of these mechanisms for the development of C stocks over time in CCF compared to RFM remains to be investigated in more detail. This could be done by comparing pairs of centuries-old uncut forests and forests under RFM that have been managed for an equal period. However, suitable pairs for such comparisons are difficult to find, and comparable forests under long-term CCF management are in practice non-existent.

We do not know if the ECMf community would recover from clear-cutting until the end of the rotation period and if the response diversity would remain high over a longer time span, i.e., several rotations and clear-cuts. Maintaining fungal diversity is important for forest ecosystem functioning and ecological resilience (Simard, 2008). A loss of diversity due to forest management is potentially harmful even if there is functional redundancy (Talbot et al., 2014).

5. Conclusion

Our comparison of uneven-aged and even-aged forests showed that the fungal community was affected by these management practices. Compared to an uncut forest, CCF and RFM changed the community structure of soil fungi in general, and of ECMf in particular. In the clear-cut plots with young re-growing even-aged stands, we found changes not only in fungal community composition, but also in the functionality of soil fungi compared to mature managed and unmanaged stands. After clear-cutting, ECMf were less abundant, their diversity and richness were declined, and the ECM/SAP-ratio was lower. On the other hand, overall species richness and diversity were not affected by clear-cutting. Our results emphasize the importance of large old trees to sustain an abundant ECMf community. We therefore suggest that also in CCF a certain number of large trees should be retained to maintain the ECMf community rather than conducting strict target diameter harvesting. In the mature stands (managed and unmanaged), the fungal communities were different from each other, but the ecological functionality of the soil fungi was similar. As uneven-aged forests did not differ from uncut forests in their potential soil fungal functionality, CCF is unlikely to change the fate of soil carbon storage through alterations of soil fungal community compared to unmanaged forests. Even though even-aged plots also showed a potential functionality similar to uncut forests, clear-cutting shifted the stands from ectomycorrhizal to saprotroph-dominated in RFM. How these differences develop over time and whether they add up over several rotation periods should be further studied to determine the effects of altered fungal composition and potential ecological functionality on soil C storage in RFM.

The higher ECMf-diversity that we found in CCF compared to RFM forests may have benefits to forest resilience. The role of belowground biodiversity in this process should be further studied.

CRediT authorship contribution statement

Eva-Maria Roth: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Outi-Maaria Sietiö:** Writing – review & editing, Validation, Software, Methodology, Formal analysis, Conceptualization. **Sauli Valkonen:** Writing – review & editing, Resources. **Eeva-Stiina Tuittila:** Writing – review & editing, Supervision, Funding acquisition. **Heljä-Sisko Helmisaari:** Writing – review & editing, Supervision, Funding acquisition. **Kristiina Karhu:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

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Declaration of competing interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2025.178648.

Data availability

The data supporting our findings in this study are stored at the National Center for Biotechnology Information (NCBI) and are openly available under http://www.ncbi.nlm.nih.gov/bioproject/1112306.

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