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Impact of continuous-cover forestry on soil carbon dynamics in boreal forests through soil organic matter quality, roots and fungi

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Academic dissertation

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ABSTRACT

The boreal forest is the largest forest biome and an important terrestrial storage for carbon, which is mainly stored as soil organic carbon (SOC). Although boreal forests are largely managed, the management effects on SOC storage and quality are not yet completely understood. The dominant management regime is rotation forest management (RFM), which includes clear-cut harvesting. Continuous-cover forestry (CCF) operates without clear-cutting and currently draws attention as an alternative. However, empirical studies in Finland are still sparse as CCF was politically discouraged until 2014.

In this dissertation, I aimed to shed light on the effects of CCF on SOC stabilization compared to RFM. We sampled Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst) forests in central and eastern Finland. The study included RFM treatments (pre- and post-harvest), an uncut control, and various CCF harvesting treatments, adapted to the light demand of the dominating tree species.

In the first sub-study I assessed SOC storage and above- and below-ground litter inputs in pine forests as affected by clear-cuts, retention-cuts, gap-cuts, and uncut forests. SOC quality was assessed by analysing fractions with different chemical stability and short-term incubation in the laboratory. I found the SOC stocks to be similar for all treatments, despite warmer microclimate and decreased litter inputs in clear-cuts. However, clear-cut sites featured lower amounts of labile SOC compounds and higher in-situ decomposition rates.

In the second sub-study I assessed the forest management effects on root density and SOC pools with different stability in spruce forests. Root density was marginally higher in uncut plots than both stages of RFM. Stability indicators reacted ambiguously to the forest management treatment. Like in the first sub-study, the labile SOC pool was reduced after clear-cutting. Uneven-aged CCF plots showed an enrichment in ^{15}N which may indicate an increased role of ectomycorrhizal fungi in soil organic matter formation.

In the third sub-study I analysed the effects of the management regimes on the soil fungal community and functional guilds. I found that clear-cutting altered the community composition and the ecological functionality of soil fungi. Specifically, the abundance, diversity, and richness of ectomycorrhizal fungi declined and their ratio to saprotrophic fungi was lower. Mature stands—uneven-aged and even-aged—also featured different community structures, but their functionality was similar to uncut forests, which highlights the functional redundancy in the fungal community.

This dissertation provides new information on the effects of CCF on the potential long-term storage and stabilization of SOC compared to RFM. Although the short-term effects of clear-cutting on SOC stocks are mitigated over time as SOC accumulates again when the next stands regrow, clear-cutting affects root litter inputs, the quality of SOC, and the fungal community, and RFM may thus cause a risk to decrease the SOC storage in the long term.

Keywords: soil organic matter fractions, natural abundance of stable isotopes, soil fungal community, microbial biomass, amino sugars, condensed tannins

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I still vividly remember the moment when I took the first sample for my doctoral project. It was on a sunny day on *Pehkosensuonsaari*, a peninsula enclosed by a vast bog. I extracted my soil sample—surrounded by the scent of wild rosemary and the buzzing of a thousand mosquitoes—and I thought what a fine life we have as researchers! But I was also wondering if I would have what it takes to complete this thesis. Completing this work took stamina and dedication, but above all guidance, support, and empathy—all of which I received in abundance. I want to extend my deepest gratitude to my supervisors Prof. Eeva-Stiina Tuittila, Prof. emerita Heljä-Sisko Helmisaari, and Assoc. Prof. Kristiina Karhu. Thank you for believing in me, for giving me the opportunity to engage in this endeavour, and for your guidance throughout the process to its completion! Particularly, I wish to thank Kristiina for being a dedicated group leader and navigating all of us through the troublesome COVID-19 times while having a newborn baby at home.

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LIST OF ORIGINAL PUBLICATIONS

The dissertation consists of an introductory review followed by three research articles. In the review the articles are referred to by the roman numerals.

I Roth E-M, Karhu K, Koivula M, Helmisaari H-S, Tuittila E-S (2023) How do harvesting methods applied in continuous-cover forestry and rotation forest management impact soil carbon storage and degradability in boreal Scots pine forests? Forest Ecology and Management 544: 121144. https://doi.org/10.1016/j.foreco.2023.121144

II Roth E-M, Sietiö O-M, Adamczyk B, Xu P, Valkonen S, Tuittila E-S, Helmisaari H-S, Karhu K (2025) Different effects of continuous-cover and rotation forest management on soil organic carbon stabilization in a boreal Norway spruce forest. [submitted manuscript]

III Roth E-M, Sietiö O-M, Valkonen S, Tuittila E-S, Helmisaari H-S, Karhu K (2025) Uneven-aged and even-aged forest management shape the soil fungal community composition in a boreal Norway spruce (*Picea abies* Karst) forest. Science of The Total Environment 965: 178648. https://doi.org/10.1016/j.scitotenv.2025.178648

AUTHOR'S CONTRIBUTION

Eva-Maria Roth (EMR) was responsible for this thesis summary and the main author of the manuscript drafts for publication **I**, **II**, and **III**. EMR planned this research and acquired funding for it, both with the help of her supervisors. EMR planned and conducted fieldwork with the valuable support of colleagues. EMR conducted the laboratory analyses, except for the analysis of condensed tannins which was conducted by Bartosz Adamczyk. Analysis of amino sugars and the chemical fractionation extraction were led by colleagues, and EMR participated in the work. EMR was responsible for data visualisation and interpretation of the results. In paper **III,** EMR conducted the bioinformatics and data analysis with instructions by Outi-Maaria Sietiö.

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SYMBOLS AND ABBREVIATIONS

ANOSIM	Analysis of similarities
ANOVA	Analysis of variance
BA	Basal area of tree stand estimated at breast height (m^2 ha^{-1})
C	Carbon
CC	Clear-cut
^{13}C	Carbon-13 natural stable isotope, containing an additional neutron
CCF	Continuous-cover forestry
DBH	Diameter at breast height (1.3 m)
DTH	Dominant tree height (m)
ECMf	Ectomycorrhizal fungi
ERMf	Ericoid mycorrhizal fungi
ITS	Internal transcribed spacer
MAT	Mean annual temperature (°C)
MAP	Mean annual precipitation (mm)
N	Nitrogen
^{15}N	Nitrogen-15 natural stable isotope, containing an additional neutron
NMDS	Non-Metric Multidimensional Scaling
OTU	Operational taxonomic unit
PCA	Principal component analysis
PCoA	Principal coordinate analysis
PCR	Polymerase chain reaction
PERMANOVA	Permutational multivariate analysis
POC	Particulate organic carbon
MAOC	Mineral associated organic carbon
RFM	Rotation forest management
SAPf	Saprotrophic fungi
SOC	Soil organic carbon
SOM	Soil organic matter

1 INTRODUCTION

1.1 Forest management effects on soil organic carbon cycling in boreal forests

1.1.1 Background

The boreal forest is the largest terrestrial biome, extending over northern Europe, Asia, and North America (Burton et al. 2003). Boreal forests account for 33% of the Earth's forest cover (Chapin et al. 2011) and for about 30% of the global forest carbon (C) stock (Pan et al. 2024). Trees take up C during photosynthesis, store it in their biomass, and allocate it below ground (Prescott 2024). In boreal forests, about 64% of the stored C is found in the soil as soil organic matter (SOM) (Pan et al. 2024), which can persist from decades to millennia (Köster et al. 2014). Globally, SOM is a larger C pool than the atmosphere and global vegetation combined (Scharlemann et al. 2014, Lehmann and Kleber 2015). Hence, boreal forests play a significant role in climate change mitigation (Lal et al. 2021).

Boreal forests are situated in high latitudes and characterized by cold temperatures (Burton et al. 2003). The resulting slow decomposition processes lead to the accumulation of organic matter on the forest floor (Burton et al. 2003). Consequently, boreal forests, which grow more slowly than temperate and tropical forests, store more C in the soil relative to their biomass (Pan et al. 2011). Climate change affects soil organic carbon (SOC) storage, particularly in high latitude regions. These areas experience a higher warming rate than the rest of the globe (Rantanen et al. 2022) and microbial communities in cold soils respond more strongly to rising temperatures (Davidson and Janssens 2006, Karhu et al. 2014). Hence, rising temperatures might turn boreal forest soils into sources of C (Gauthier et al. 2015, Crowther et al. 2016). Because of this susceptibility and due to increasing forest disturbances that cause high SOC losses (Mayer et al. 2023a), boreal forests are considered a potential tipping point ecosystem. If a certain tipping point is exceeded, it might trigger a sudden release of C into the atmosphere, potentially further accelerating climate change (Lenton et al. 2019).

The C stocks in boreal forests have decreased within the last decades worldwide (Pan et al. 2024). According to a recent greenhouse gas inventory, Finnish forests are no longer a C sink, i.e., forest soils emit more C than the standing stock binds (Natural Resources Institute Finland 2025). Boreal forests are largely managed (Gauthier et al. 2015). Thus, it is important to understand the processes driving SOC cycling in boreal forests, and to adapt forest management strategies to protect soil C storage. While it is relatively easy to quantify and compare the aboveground biomass and productivity of different management options, it is more challenging to assess the management effects on the SOC stocks as the accumulation rate is slow against a large and variable background (Jandl et al. 2007, Schrumpf et al. 2011). Hence, effects of different forest management practices on the quality of SOC and SOC stabilization processes are hitherto poorly understood (Jandl et al. 2007, Mäkipää et al. 2023).

1.1.2 Forest harvesting effects on soil organic C

The forest SOC pool is shaped by the balance between inputs (aboveground and belowground) and losses through decomposition or leaching (James and Harrison 2016). Both—inputs and losses—are impacted by forest management (James and Harrison 2016). Carbon absorbed by trees is transported to the soil either as dominantly recalcitrant plant

litter—in the form of leaves, needles, or dead roots—or as more labile compounds exuded by roots and associated mycorrhizae (Prescott 2024) (Figure 1a). The term *recalcitrant* means, here and henceforth, that the organic material is relatively difficult for microorganisms to metabolize or transform. The rhizodeposits, i.e., living root inputs, feed soil microbiota (Dennis et al. 2010, Hirsch et al. 2013). Microbial biomass contains only about 1–2% of SOC in boreal forests (Bauhus and Khanna 1999), but has a rapid turnover time of less than one year (Brookes 2001). Thus, microbial necromass, i.e., microbial residues, can account for up to 80% of SOC (Liang et al. 2019, Buckeridge et al. 2022). In forest ecosystems, microbial necromass accounts for 30% of SOC in the organic layer and 62% in the lower mineral soil (Ni et al. 2020).

The decomposition of SOC is influenced by climate and microclimate, soil properties (pH, soil texture, nutrient availability), and the quality of litter (Jandl et al. 2007). From these,

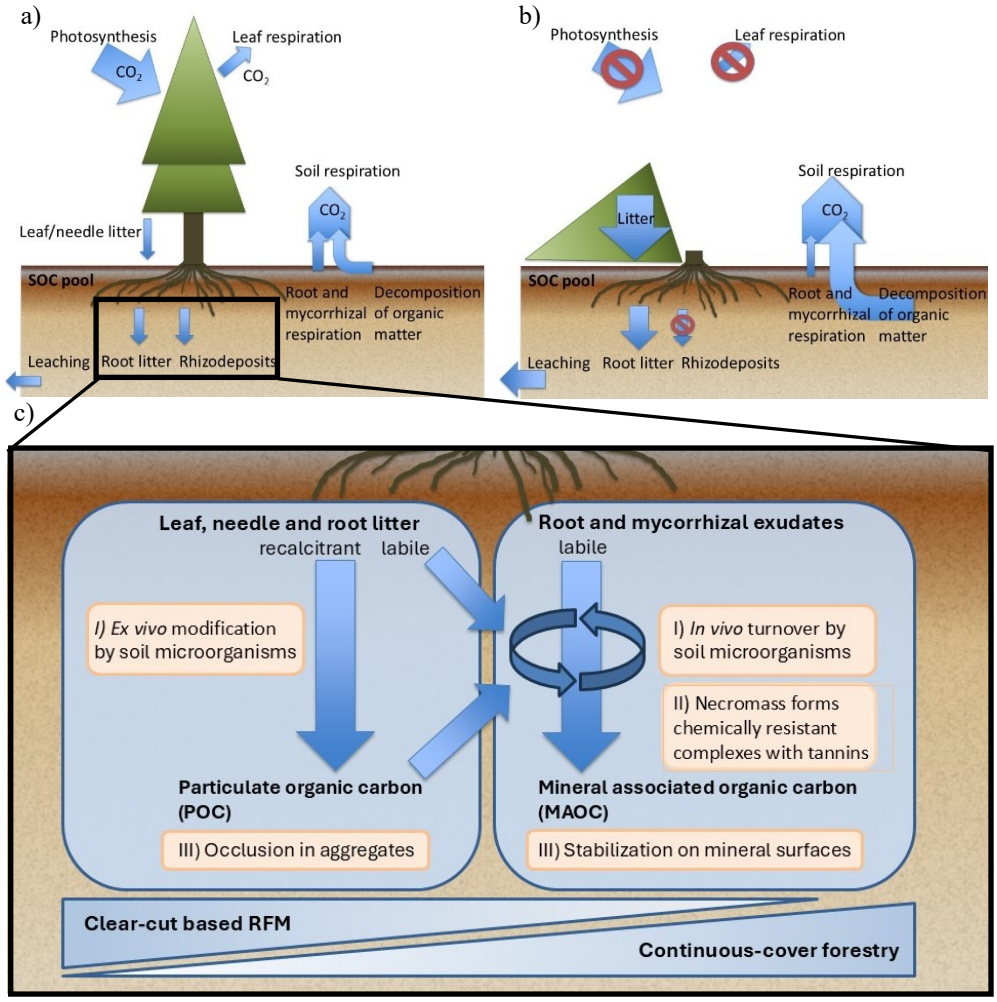

Figure 1. Simplified scheme of the C cycle in the forest (a) and effects of harvesting on C dynamics (b). Zoom-in on the two major pathways of C entering the SOC pool (c), depicting the stabilization mechanisms in the soil and anticipated shifts caused by RFM and CCF.

forest management particularly affects temperature and moisture conditions, as well as litter quality and availability (Mayer et al. 2020).

Forest harvesting is considered an anthropogenic forest disturbance and leads to losses from the SOC stock, particularly from the forest floor (James and Harrison 2016, Mayer et al. 2020, 2023a). The immediate effect of forest harvesting on the soil C pool is an increased input of C as logging residues and dead roots (Strukelj et al. 2015) (Figure 1a and 1b). This might stimulate mineralization processes (Vanguelova et al. 2010) and accelerate decomposition of older SOC in a process called "priming effect" (James and Harrison 2016). In this process, freshly added litter increases microbial activity, and once the substrate is exhausted, microbes resort to the decomposition of older SOC (Broadbent and Bartholomew 1949, Jenkinson et al. 1985). At the same time, rhizosphere priming through root exudates (Karhu et al. 2022) drastically declines with the removal of trees. Following the initial C pulse from logging slash, the litter input is decreased for several years. Hence, the soil C storage declines rapidly after harvesting for several years. These losses are mainly caused by accelerated decomposition processes due to a warmer and wetter stand microclimate, by reduced long-term litter inputs after harvesting, and by increased leaching of dissolved organic C (Mayer et al. 2017, 2020). However, the relationship between harvesting intensity, the magnitude of SOC losses, and the time needed for SOC stock recovery in different boreal forests is still poorly quantified (James and Harrison 2016, Mayer et al. 2020, 2023a).

1.1.3 Rotation forests management and continuous-cover forestry in Finland

The most common harvesting practice worldwide is clear-cutting, and clear-cut-based RFM is currently the most common forest management system in boreal forests worldwide (Burton et al. 2010), and in Fennoscandia in particular (Pukkala et al. 2012, Koivula et al. 2014, Lundmark et al. 2016, Kuuluvainen et al. 2019, Rautio et al. 2025). Rotation forest management is characterized by a repeating cycle: a growing period followed by a final timber harvest as clear-cutting (Table 1). A regeneration phase follows the harvest, often including the introduction of artificial regeneration and/or mechanical site preparation. Before the clear-cut, the stand should be tended with several thinnings, mainly thinning from below (Koivula et al. 2025). RFM leads to even-aged forest stands, predominantly consisting of a single tree species (Pukkala et al. 2012, Gustafsson et al. 2020).

Recently, integrated forest management approaches have emerged to meet changing societal demands, and to widen the focus from solely timber production to other ecosystem services such as C sequestration, soil and water protection, or recreation (Pukkala et al. 2012, Aggestam et al. 2020, Kuuluvainen et al. 2021). Integrated concepts aim to combine wood production and biodiversity conservation instead of spatially segregating them (Aggestam et al. 2020). The emulation of natural disturbance patterns is a common approach in integrated ecological forestry (Seymour and Hunter 1999, Aszalós et al. 2022). Clear-cutting emulates a stand-replacing disturbance; however, only 20–30% of natural disturbances in Fennoscandian forests would be stand-replacing, whereas the majority would be intermediate- to small-scale disturbances (Kuuluvainen and Aakala 2011). Thus, RFM alone does not fully reflect the natural structures and dynamics of boreal forests, and CCF could be one means to diversify forest management practice.

CCF is defined as a group of silvicultural systems that maintain a permanent forest cover (Brunner et al. 2025) (Table 1). Clear-cutting is not applied in CCF, but selective harvesting of single trees or tree groups is used (Gustafsson et al. 2020), hence, respectively called selection system or group system. The term CCF was coined by German forest scientist

Alfred Möller as “Dauerwaldwirtschaft” [continuous forest management] in 1922, based on the idea that the forest is an organism of eternal continuance, and thus its management should be continuous (Möller 1922). One of the aims Möller emphasized was the preservation of the soil environment. In Finland, selective harvesting has been a traditional forest management method, but it was effectively politically banned after the Second World War to increase timber revenues with the Declaration Against Uneven-aged Management (1948-2014) (Pukkala et al. 2012, Cedergren et al. 2025). Selective cuts are a means to harvest timber, enable diameter growth of the remaining trees, and initiate natural regeneration (Lula et al. 2025). Single-tree selection cuts, gap-cuts, or patch-cuts imitate small- and intermediate-scale disturbances, promote uneven-aged stand structures (Kuuluvainen and Aakala 2011), and multiple-species stands (Pukkala et al. 2012). Thus, uneven-aged forest management and CCF are often used as synonyms (Gustafsson et al. 2020).

In another management system—retention forestry—canopy tree cover is continuously maintained in substantial parts of the original stand, with retention trees spread evenly, and/or grouped to maintain structural and functional variation (Gustafsson et al. 2012, 2020). Due to the continuity of the original stand structures, I will hereafter also address retention forestry under the term CCF, but will distinguish clear-cuts with low levels of retention (up to 5%), as these do not suffice to maintain the continuity of structural variation in harvested stands (Kuuluvainen et al. 2019).

Clear-cut harvesting is known to decrease the SOC stocks (Jandl et al. 2007, James and Harrison 2016, Mayer et al. 2020). In boreal forests, these losses amount to about 23% in *Picea* and 14% in *Pinus* forests (Johannesson et al. 2024). After clear-cutting, accelerating tree growth of the new stand, and increasing litter inputs eventually lead to SOC accumulation and recovery of C stocks, when C inputs exceed the C released through decomposition processes (Covington 1981). In podzols—the most common soil type in boreal forests—recovery in the mineral soil can take over 100 years (James and Harrison 2016). Due to a lack of long-term studies, these findings are largely based on chronosequence

Table 1. Overview of the silvicultural systems explored in this dissertation. Roman numerals in parentheses indicate in which sub-study each system is featured. The table is modified after Brunner et al. (2025). The shelterwood system in the original table was replaced by the retention system, a form of the irregular shelterwood system, based on Mitchell and Beese (2002).

Management regime	Silvicultural system	Individual cuttings	Continuous-cover forestry
Selection management	Selection system (**II, III**)	Selection-cutting	Yes
Rotation forest management	Group system (**I**)	Gap-cutting	Yes, when continuous cover is the aim and maintained
	Retention system (**I**)	Variable retention cutting	Yes, when a certain amount of original stand is retained, and continuous cover is the aim and maintained
	Clear-cutting system (**I-III**)	Clear-cutting	No

studies and space-for-time substitution approaches (Covington 1981, James and Harrison 2016, Mayer et al. 2020, Johannesson et al. 2024).

Unintended C losses from the soil during forest operations can be avoided by minimizing disturbances in the soil structure (James and Harrison 2016, Mayer et al. 2020). Thus, partial harvesting methods, such as selection-cutting, gap-cutting, and variable retention, have been suggested to reduce SOC losses (Mayer et al. 2020). CCF might increase carbon sequestration in the soil as the harvesting effects of selective cuts concerning microclimate, litter input, and soil disturbance are moderated compared to clear-cutting (Jandl et al. 2007, Lindroth et al. 2018, Mayer et al. 2020). In peatland forests, partial cutting instead of clear-cutting was found to reduce CO2 emissions from the soil (Korkiakoski et al. 2023), whereas there is still an ongoing debate whether CCF might increase C sequestration in upland forest soils (Högbom et al. 2025). Modelling studies of soil carbon storage under uneven-aged forests have produced conflicting results, some of them leading to a higher C storage (Kellomäki et al. 2019), others to a similar (Peura et al. 2018, Triviño et al. 2023), or a potentially lower C storage (Shanin et al. 2016) compared to RFM. Post-harvest tree density and length of harvesting intervals have been found to be positively correlated with soil carbon stocks (Shanin et al. 2016). Some studies assume CCF to have similar effects on C dynamics as thinnings (Jandl et al. 2007, Lindroth et al. 2018). However, CCF leads to different stand composition and structures, which also affect litter availability, decomposability, and SOC stabilization. A major knowledge gap regarding the effects of CCF on soil C storage is the shortage of empirical studies. The few that exist come to different conclusions. Nilsen and Strand (2013) did not find differences between the SOC stocks in CCF and RFM. Similarly, Strukelj et al. (2015) did not find significant differences between partial cuts and clear-cuts 9 years after the harvesting. Pötzelsberger and Hasenauer (2015) found higher SOC stocks in uneven-aged forests compared to even-aged RFM forests in the upper mineral soil (0–20 cm).

It is challenging to compare the effects of CCF and RFM, as RFM is defined by the rotation cycle with a clear beginning and end, whereas forests under CCF constitute a continuum, so the results are largely determined by the stages compared and by the chosen timeframe. Therefore, in this study I focused on comparing the effects of the different harvesting methods (**I**) and the effects of uneven-aged and even-aged structures (in mature stands) that are typical in CCF and RFM, respectively (**II** and **III**).

1.2 Stabilization mechanisms of C in the soil

Carbon persists in the soil at different time scales, and until now, the processes behind the accumulation and stabilization of SOC are not yet completely understood (Adamczyk 2021). After C enters the soil through either plant litter or rhizodeposits (Figure 1a), there are several mechanisms that stabilize C in the soil (Figure 1c):

I) Plant residues or rhizodeposits are taken up by soil microbiota, modified *in vivo,* and added to the SOC pool as microbial necromass. Furthermore, microbiota transform plant residues *ex vivo* with extracellular enzymes. Both processes leave behind microbial-derived C which is more resistant to further degradation and adds to the stable SOC pool, and constitute the so-called the entombing effect of the microbial carbon pump (Liang et al. 2017). The *in vivo* process is however, more important for microbial residue C formation (Liang et al. 2017).

II) Secondary metabolites derived from roots, such as condensed tannins, inhibit the decomposition of fungal necromass through the formation of complexes with proteins and chitin (Adamczyk et al. 2019a, 2019b).

III) Soil minerals protect SOC from decomposition, either through occlusion of particulate organic carbon (POC) within soil aggregates or through stabilization as mineral associated organic carbon (MAOC) on mineral surfaces in organo-mineral interactions (Lehmann and Kleber 2015).

The three mechanisms are interconnected. Through these mechanisms, chemically recalcitrant as well as labile SOC may stabilize in the soil (Lehmann and Kleber 2015). The recalcitrant fraction of the aboveground litter contributes to the POC pool, whereas the labile C compounds, for example, from rhizodeposits mainly supply the MAOC pool (Cotrufo et al. 2015). However, MAOC tends to persist longer in the soil, whereas POC cycles faster and is more vulnerable to disturbances (Lehmann and Kleber 2015, Poeplau et al. 2018), as it is not stabilized with mineral interactions. Thus, we would expect POC to show stronger responses to harvesting disturbance, which is strongest in clear-cut harvesting.

Several studies reported that living root inputs are the major contributor to MAOC formation (Sokol et al. 2019, Rossi et al. 2020, Teixeira et al. 2024) while POC is mainly formed from fragmented litter (Lavallee et al. 2020). The two pathways are depicted in Figure 1c. We would expect the pathway rhizodeposits –> MAOC to benefit from CCF as inputs through rhizodeposits are more continuous through time in CCF than in clear-cut-based RFM.

1.3 The functional role of soil fungi in C-cycling in boreal forests

Fungal mycelium is not only an origin of C in the soil, but also plays an important role in the stabilization of SOC (Clemmensen et al. 2015, Adamczyk 2021). Up to 70% of SOC in boreal forests is derived from roots and root-associated fungi rather than aboveground litter (Clemmensen et al. 2013, Adamczyk et al. 2019b, Kyaschenko et al. 2019), and the understanding has emerged that SOC storage is driven by roots and root-associated fungi (Dijkstra and Cheng 2007, Clemmensen et al. 2013, Averill et al. 2014, Adamczyk 2021). Compared to leaf and needle C inputs, which partly dissipate while moving from the litter layer to mineral soil, C inputs entering through roots or mycorrhizal pathway have a higher likelihood of interacting with the soil matrix and being retained (Rasse et al. 2005, Sokol et al. 2019).

There are three ecophysiological guilds of fungi in the soil, that have different lifestyles and functions: symbiotrophs, saprotrophs, and pathotrophs. Symbiotrophs, such as mycorrhizal fungi, form symbiotic relationships with trees and understorey plants. Mycorrhizal fungi generate access to water and nutrients in exchange for C compounds supplied by the plant hosts (Smith and Read 2008). Particularly in boral forests, mycorrhizal fungi are important because of nutrient limitations, especially N (Read et al. 2004). Mycorrhizal fungi have been found to increase the plants ability to use N bound in SOM (Heinonsalo et al. 2015), and their abundance increases when conditions become more N limited (Högberg et al. 2003, 2006). An enrichment in ^{15}N usually indicates an important role of mycorrhizae in N cycling (Lindahl et al. 2007, Clemmensen et al. 2013), because mycorrhizal fungi mainly transfer N depleted in ^{15}N to their plant hosts, thus accumulating ^{15}N in their own biomass (Högberg et al. 1996, 1999). Ectomycorrhizal fungi (ECMf), which usually form associations with trees, are the dominating fungal type in boreal forests (Read

et al. 2004). Ericoid mycorrhizal fungi (ERMf) are associated with ericaceous dwarf shrubs, which are abundant in the ground vegetation of boreal forests (Smith and Read 2008). Saprotrophic fungi (SAPf) primarily decompose soil organic matter (Lindahl and Tunlid 2015); however, ECMf and ERMf also have rudimentary abilities to decompose SOM and mainly scavenge the SOM for N (Heinonsalo et al. 2015, Lindahl and Tunlid 2015). Due to this competition with saprotrophs for organic N, mycorrhizal fungi may suppress decomposition, which is called the "Gadgil effect" (Gadgil and Gadgil 1971, Fanin et al. 2022). ECMf were found to decelerate decomposition in low fertility conditions common for boreal forests (Mayer et al. 2023b). Forest ecosystems dominated by ECMf and ERMf typically show higher soil C stocks than arbuscular-mycorrhizal dominated ecosystems (Averill et al. 2014).

The ratios of SAPf, ECMf, and ERMf determine the balance between accumulation and loss of soil organic matter (Clemmensen et al. 2024). Clemmensen et al. (2024) found in their study that a higher ratio of ECMf to SAPf led to mass loss of humus, whereas a higher ratio of ERMf to SAPf lead to mass gain.

Effects of forest management on soil fungi

After clear-cut harvesting, the allocation of C to the soil via living roots, which sustains mycorrhizae and shapes the fungal community, declines drastically (Yarwood et al. 2009, Prescott and Grayston 2023). Hence, clear-cut harvesting has been found to disturb the belowground fungal and microbial communities (Kohout et al. 2018, Tomao et al. 2020, Kim et al. 2021, Prescott and Grayston 2023), resulting in a decline of soil fungal biomass (Holden and Treseder 2013), and decreased abundance of ECMf (Kohout et al. 2018), and an increased abundance of SAPf (Kyaschenko et al. 2019). Selection cuts have been suggested as a measure to preserve fungal diversity as particularly ECMf diversity declines with management intensity (Tomao et al. 2020). Forests managed with CCF were found to have a similar fungal community to unmanaged stands, in contrast to recently clear-cut forest sites (Kim et al. 2021). However, studies comparing the later stages of the rotation cycle to CCF (Kim et al. 2021) are still missing, and so is the comparison between even-aged and uneven-aged forest structures (Savilaakso et al. 2021).

2. OBJECTIVES

The overall aim of this dissertation was to empirically assess the impact of CCF on SOC storage in boreal forests in comparison to conventional RFM. I expected RFM and CCF to differ in their impact on SOC cycling due to different stand properties, such as stand density and structure, microclimate, and species composition (Jandl et al. 2007), which affect SOC storage through altered litter inputs and altered SOC stabilization processes. It is difficult to find trends in SOC storage because of the high variability (Schrumpf et al. 2011), and management effects on SOC stocks may be below detection limits (Mattila et al. 2022). Therefore, I aimed to draw conclusions regarding the long-term SOC storage capacity, based on changes in SOC quality and degradability, and changes in the soil fungal community, because they affect SOC stabilization mechanisms and can influence the build-up of SOC in the long term.

The specific objectives in the three sub-studies were to:
1) quantify the impact of the forest management system on soil C storage and C inputs into the soil (article **I**).
2) assess the impact of the forest management system on the stability of SOC (articles **I** & **II**).
3) assess the impact of the forest management system on soil fungi involved in C cycling (article **III**).

In brief, we hypothesized that

1) CCF, with a more constant production of aboveground and belowground litter and a colder microclimate under the canopy, would lead to higher SOC stocks than RFM (**I**, **II**).
2) Structural complexity in uneven-aged stands and higher stand density in uncut plots, lead to higher amounts of living tree roots (**II**), which in turn influence SOC stabilization mechanisms.
    - Condensed tannins released by roots retain more fungal necromass in the soil of uneven-aged plots and uncut stands (**II**).
    - Higher root litter inputs lead to higher shares of POC in uncut plots and uneven-aged stands (**II**).
3) Uneven-aged CCF forests harbour a more diverse fungal community than even-aged forests due to their structural complexity and feature a higher abundance of ECMf compared to saprotrophs in contrast to recently clear-cut sites **(III)**.

3. MATERIALS AND METHODS

3.1 Experimental sites

The study was carried out on long-term silvicultural experimental plots of the Natural Resources Institute Finland (Luke). Sub-study **I** featured Scots pine (*Pinus sylvestris* L.) dominated stands in Ruunaa (Lieksa), North Karelia (63°23′25″N, 30°32′18″E) and sub-studies **II** and **III** were conducted on Norway spruce (*Picea abies* (L.) H. Karst.)-dominated forest plots located in Vessari, Central Finland (62°2′9″N, 24°16′0″E, Figure 2). The harvesting treatments considered as CCF complied with the light demand of the dominating tree species. Light-demanding pine stands in Ruunaa were harvested with gap-cuts and retention-cuts in the CCF treatment. Shade tolerant spruce stands were managed with single-tree selection cutting to establish CCF-plots. On both sites, we sampled two opposing stages of RFM. The plots representing the post-harvest stage, were relatively recently clear-cut (10–11 years before our study), naturally regenerated by young trees, or partly replanted. For simplicity, they will be henceforth addressed as clear-cuts. The plots representing the pre-harvest stage of RFM were mature stands ready for harvesting.

The pine-dominated plots in Ruunaa featured in article **I** were established in 2010/11 to study the effects of different forest harvesting practices on forest structures and biota on a landscape level (Koivula et al. 2014). Prior to their establishment, the plots were conventionally managed, mature Scots pine -dominated forests, sporadically admixed with

Figure 2. Location of experimental sites Ruunaa and Vessari in Eastern and Central Finland.

birch (*Betula* L. spp.) and Norway spruce trees. The plots I studied, are located within a four km radius and are 2–7 ha in size. They are positioned at the southern edge of the middle boreal Zone (Ahti et al. 1968) at an elevation of 140–150 m above sea level. They experience a mean annual temperature of about 2.5°C and mean annual precipitation of 650–700 mm (Finnish Meteorological Institute 2023). The medium-low fertility plots are situated on dry, sandy soils, and represent the *Vaccinium* and *Calluna* site type according to the Finnish site-type classification

(Cajander 1926). I identified the soil on these sites as albic podzol (IUSS Working Group 2022) on glacial till, and the humus form as a mor (Zanella et al. 2018) (site parameters shown in Table 2). RFM was represented by the two opposing stages clear-cut (post-harvest) and uncut (pre-harvest). CCF was represented by gap-cuts and retention-cuts. Gap-cuts were established by harvesting groups of trees, leaving gaps with radii of 15–20 m and a surrounding closed stand that was thinned from below. About 20–30% of the initial stand volume were harvested per stand in multiple gaps. In retention-cuts, about 20% of the tree volume was retained, in tree groups, but also dispersed trees. On clear-cut plots, a small amount of trees were retained after harvesting (≤5%), as it is common in Finnish forestry practice (Kuuluvainen et al. 2019) (stand parameters listed in Table 3).

The spruce-dominated plots in Vessari, featured in articles **II** and **III,** were established in 1985/86 to research different harvesting strategies and intensities (Pukkala et al. 2016). The site originated in the 1940s from natural regeneration after shelterwood cuttings. Uneven-aged structures were established with single-tree-selection cuts in 1985/86, which have been repeated three times since then, whereas even-aged RFM sites were thinned from below. Clear-cuts were created in 2009. Harvesting slash was not removed after the different cuttings. Each treatment plot had a size of 50 × 50 m, and they were randomly arranged within a 16 ha experimental forest. The site is located in the middle boreal zone (Ahti et al. 1968) at an elevation of 110 m above sea level (Geological Survey of Finland 2023), experiencing a mean annual temperature of about +4.5°C and mean annual precipitation of 600–650 mm. The mesic and relatively fertile site represents an *Oxalis-Myrtillus* type according to the Finnish site type classification (Cajander 1926). I classified the soil as a skeletic albic podzol (IUSS Working Group 2022), formed from sandy loam on glacial till, and the humus type as a mor (Zanella et al. 2018) (Table 2). Even-aged mature plots represent the pre-harvest stage of RFM, whereas clear-cuts represent the post-harvest stage. The uncut plots were left unmanaged since 1985 (Table 3).

Table 2. Location and site parameters of the two study sites. Abbreviations used: MAT – mean annual temperature, and MAP – mean annual precipitation. Stoniness is calculated in volume% to a depth of 15 cm in the mineral soil.

Site	**Ruunaa article I**	**Vessari articles II and III**
Location	63°23'25"N, 30°32'18"E	62°2'9"N, 24°16'0"E
Elevation (m)	140-150	110
MAT (°C)	2–3	4–5
MAP (mm)	650–700	600–650
Forest site type	Vaccinium and Calluna type	Oxalis-Myrtillus-type
Soil type	Albic podzol	Skeletic albic podzol
Soil moisture	xeric – sub-xeric	mesic
Organic layer		
Thickness (cm)	5.7	4.4
pH	3.8	4.3
N (%)	0.9	1.3
C/N ratio	47	30
Mineral soil		
Sampling depth (cm)	10	10
pH	4.7	4.5
N (%)	0.04	0.10
C/N ratio	39	28
Stoniness (%)	6.7	34.5
Soil texture	Loamy sand	Sandy loam
Sand (%)	82.0	66.2
Silt (%)	16.8	30.3
Clay (%)	1.2	3.5

Table 3. Basal area (BA), diameter at breast height (DBH), dominant tree height (DTH), and number of saplings per ha are given for the different treatments on each study site. The treatments in Ruunaa are clear-cut (CC), gap-cut, retention-cut, and uncut forest. Treatments featured in Vessari are clear-cut (CC), even-aged (Even), uneven-aged (Uneven), and uncut forest.

Site	**Ruunaa article I**				**Vessari article II and III**			
	CC	Gap	Retention	Uncut	CC	Even	Uneven	Uncut
BA (m^2 ha^{-1})	0.3	8.0	13.7	27.6	0.0	33.7	25.8	52.8
DBH (cm)	0.0	26.7	22.7	22.0	0.0	27.9	16.0	15.5
DTH (m)	0.0	21.6	19.3	21.5	0.0	24.2	23.2	24.6
Saplings (n ha^{-1})	3967	3900	1067	2233	31445	4180	11172	78

3.2. Field sampling and study layout

With the valuable help of colleagues, I took soil samples and conducted the stand inventory in August and September 2020 in Ruunaa and Vessari, respectively. In Ruunaa, the samples (n = 20) were taken every 2.5 m in two rows along pre-existing N-S oriented vegetation transects. The sampling area covered about 225 m^2 in each replicate plot (see sampling layout in Figure 1d, article **I**). We sampled the treatments 1) retention-cuts with 20% retention, 2) gap-cuts, 3) clear-cuts and 4) uncut mature forest.

In Vessari, we established a systematic sampling grid of 16 × 16 m in each plot covering 256 m^2, where samples were taken every 4 m (n = 25). This sampling area was surrounded by a 17 m buffer zone to avoid edge effects (see sampling layout in article **II**: Figure 1a and **III**: Figure 2c). Treatments considered in sub-studies **II** and **III** were: 1) uneven-aged CCF, 2) mature, even-aged RFM, 3) clear-cut, and 4) uncut control.

The organic layer was sampled with a stainless-steel soil corer (inner diameter 6 cm). A thinner auger (inner diameter 1.9 cm) was chosen for the sampling of the upper mineral soil (0–10 cm) due to high stoniness. We pooled the samples to one composite sample per layer and replicate plot before laboratory analyses. Each treatment was replicated 4 times in both sites. All tools were sterilized with ethanol between different plots to avoid cross-contamination.

We took four volumetric soil samples of organic and mineral soil layer in each plot to determine the bulk density (< 2 mm for mineral soil and < 4 mm for organic soil) with the 6 cm diameter soil auger. We estimated stoniness with Viros rod-testing method (Viro 1952). A rod with a diameter of approximately 1 cm was driven into the soil with a small sledgehammer at 12 points in each replicate plot until it hit a stone or boulder.

We measured the stand basal area (BA) with three angle-count samples per plot, using a dendrometer with the BA factor of 1 (Bitterlich 1984, Kramer and Akça 2008). On the sampling areas, we recorded diameter at breast height (DBH), species, and species identity (coniferous or broadleaf) of each tree with a DBH ≥ 6 cm and calculated stem density per plot. Dominant tree height (DTH) was determined as the mean of the 9 trees with the biggest diameter per plot. We also counted the number of saplings and seedlings smaller than 3 m in each plot within a subplot of 6 × 12.5 m and 8 × 8 m in Ruunaa and Vessari, respectively. We visually assessed the ground coverage of functional vegetation groups (dwarf shrubs, herbs, grasses, bryophytes, and lichen) in four 2 m^2 squares on a N-S oriented transect in each replicate plot (**I**: Figure 1d, **II:** Figure 1a). We calculated the coefficient of variation of DBH and the Shannon diversity index of the upper tree layer as indicators for stand structural complexity.

During summer 2021, we incubated cellulose bags (n = 14 per replicate plot) on both sites for 3 months (June, July, August). Additionally, we took soil core samples from the Vessari site to determine total root biomass. In Ruunaa we only collected living roots >2 mm from the 4 volumetric samples per replicate plot. Tree fine root biomass and understorey root biomass were modelled.

Soil moisture and temperature in the plots were recorded with one permanently installed probe (Wild et al. 2019) per plot to assess the forest management effects on the C dynamics caused by different microclimatic conditions in the different treatments.

3.3 Laboratory analyses

3.3.1 General soil characteristics

I analysed several general soil characteristics (data featured in articles **I-III**), that affect soil C storage. The analysis methods are in-depth described in the method description and the supplementary materials of article **I** and the characteristics are briefly explained below.

Soil pH measures acidity and is an important soil parameter that influences the biological activity and the availability of nutrients (Binkley and Fisher 2013). A low pH slows down microbial growth rates, and in this way, limits decomposition of organic matter (Malik et al. 2018). Fungi have a higher tolerance for low pH-values than bacteria and thus tend to dominate in acidic soils (Blagodatskaya and Anderson 1998).

Bulk density describes how tightly the soil is packed in a given volume. An increase in bulk density can limit pore space and thus the activities of roots and aerobic microbes (Binkley and Fisher 2013). Stoniness denominates the relative volume occupied by stones and boulders in a soil (Eriksson and Holmgren 1996), thus reducing the actual volume occupied by soil.

Soil texture denotes the size of the mineral particles in the soil and also affects the accumulation of organic matter (Binkley and Fisher 2013). Specifically, it affects the stabilisation mechanisms of SOC. MAOC, the carbon fraction that is considered to have a long turnover time, is particularly determined by the amount of the fine fractions (silt and clay) in the soil. The amount of available mineral surfaces for sorption or association increases with increasing proportion of silt and clay (Begill et al. 2023).

3.3.2 C stocks and litter inputs

I calculated SOC stocks based on the measured C content, bulk density, stoniness, and volume of each soil layer, as described in article **I**. SOC stocks are frequently overestimated due to incorrect assessment of bulk density and stoniness (Poeplau et al. 2017). However, stoniness was neglected when comparing the effect of the various treatments on the stocks, as, particularly in Vessari, the stoniness would have added a lot of variability.

Root biomass was determined because roots are the major contributor to SOC storage through root litter and root exudates (Balesdent and Balabane 1996, Högberg et al. 2008, Clemmensen et al. 2013). In article **I** coarse tree roots >2 mm were picked from the soil samples, whereas tree fine root biomass was modelled based on stand parameters (Lehtonen et al. 2016a) and understorey root biomass calculated based on ground coverage of functional groups (Lehtonen et al. 2016b). Annual root litter inputs were then calculated based on different turnover rates for the specific root types (Lehtonen et al. 2016a, Ding et al. 2021) (method description in article **I**). For article **II** all the roots were hand-picked from soil cores (n = 3 per plot) dedicated for root picking, and a subsample was separated into coarse roots (>2 mm), fine tree roots (< 2 mm), understorey roots, and dead roots.

I calculated annual total aboveground litterfall (article **I**) using a multiple linear regression model from Starr et al. (2005) based on stand basal area and latitude.

3.3.3 Indicators for SOC stability

The stability of SOC was assessed through physical and chemical fractionations, and with a laboratory incubation. I applied a commonly used physical fractionation method (Christensen

2001) to separate the SOC into fractions with distinct biogeochemical stability and turnover time (Poeplau et al. 2018). “Mineral associated organic carbon” (MAOC), and “particulate organic carbon” (POC), in the mineral soil were determined following suggestions by Lavallee et al. (2020), and as specified in manuscript **II**. For this purpose, I wet-sieved the soil through a 63 µm sieve after shaking with glass beads to break up the aggregates. Addition of hexametaphosphate is recommended to break up aggregates in clay-rich soils; however, our forest soils had relatively little clay, and we were planning to conduct isotope measurements on the samples, and thus wanted to avoid adding salts to the sample. The C stored in the fine fraction (<63 µm) is considered MAOC, as MAOC is associated with silt- and clay-sized minerals. The C stored in the coarse fraction (>63 µm) is considered POC. I chose this simple fractionation method based on particle size, because it has been suggested as an effective tool to assess SOC dynamics, and could be a useful standard method to evaluate a large number of samples (Lavallee et al. 2020).

I further proceeded with a density fractionation of the remaining coarse fraction, separating the purely organic POC from the mineral particles, with the goal to subsequently assess the chemical recalcitrance of the purely organic POC fraction. The coarse fraction was mixed with sodium polytungstate solution, with a density of 1.85 g cm^{-3}, and the "light POC" was collected when floating on top of the liquid, whereas mineral particles and “heavy POC” sunk to the bottom (Figure 3) (Plante et al. 2006, Lavallee et al. 2020).

Subsequently, biochemical recalcitrance of the organic layer (<4 mm) samples and the light POC was analysed with chemical fractionation into non-polar extractives (E-fraction, extracted in dichloromethane), polar extractives (W-fraction, extracted in water), an acid-hydrolysable fraction (A-fraction), and a non-soluble fraction (N-fraction) following a protocol modified after Ryan et al. (1990) and Hilasvuori et al. (2013) (articles **I** & **II**). These fractions have distinct decomposition rates, based on how easily they can be utilized by microbes. Simpler molecules, like glucose, are easily utilized and persist for a shorter time in the soil than complex molecules, such as lignin (Von Lützow et al. 2007). The biochemical recalcitrance increases in the following order: W-fraction < A-fraction < E-fraction < N-fraction (Viskari et al. 2022).

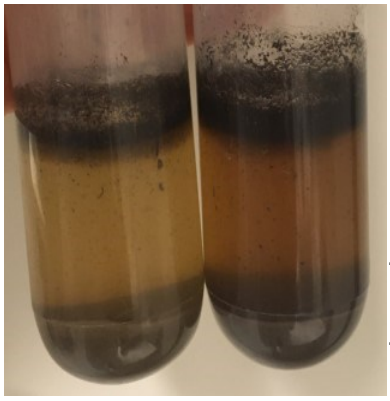

Figure 3. Separating the coarse fraction of the soil (>63 µm) into light POC (floating on top) and heavy POC mixed with mineral particles (sinking to the bottom), using a sodium polytungstate solution with a density of 1.85 g cm^{-3}.

Table 4. Overview of the chemical fractions: used solvents, extracted substances (Ryan et al. 1990, Wieder and Starr 1998, Von Lützow et al. 2007), and the annual decomposition rate, indicating their stability as used in the Yasso model (Tuomi et al. 2011).

Fraction	Extraction solvent	Compounds in fraction	Decomposition rate (a^{-1})
W Polar	Hot water	Simple sugars, polyphenols	5.90 ± 0.08
A Acid-soluble	Sulfuric acid	Cellulose and hemicellulose	0.72 ± 0.09
E Non-polar	Dichloromethane	Fats, oils, waxes,	0.28 + 0.07/-0.04
N Non-extractable		Non-extractable compounds including Klason lignin	0.01 + 0.01/-0.00

These fractions were chosen because they correspond to the decomposition compartments used in the carbon and decomposition model Yasso (Liski et al. 2005). The model is widely used in Finland, for example, to report SOC changes to the United Nation Framework Convention on Climate Change (UNFCCC) (Ťupek et al. 2019), and our data can be used for model development and testing.

I conducted a 28-day laboratory incubation of the forest soil samples and measured the CO_2 evolution during this period (article **I** and **II**, detailed method description in article **I,** including the supplementary material). During a laboratory incubation, the decomposition rate of the SOC can be assessed under standardized moisture and temperature conditions (Berg and Laskowski 2005). A short-term laboratory incubation can be considered a means to biologically determine the size of the labile SOC pool, as the labile pool decomposes quickly (Alvarez and Alvarez 2000).

3.3.4 Decomposition rate in the field

To evaluate the decomposition rate of organic material in situ I used litter-bag incubation as a common standard method (Berg and Laskowski 2005). The litter bags were exposed to field conditions for 12 weeks, and the decomposition rate was then determined in the laboratory as the mass loss during this time (method description in article **I** & **III**). We used cellulose as a standardized litter inside mesh bags with a mesh size of 1 mm, allowing mycelial and fine root ingrowth. This way, we could assess the effects of forest microclimate, and fine roots and hyphae on the decomposition rate. We positioned the litterbags on the interface between organic and mineral soil layers.

3.3.5 Indicators of SOC quality

Microbial biomass C, fungal necromass and abundance of natural isotopes were assessed as indicators for SOC quality. Microbial biomass is considered the main component of the active/labile SOC pool, regulates SOM transformations, and has a short turnover time (Von

Lützow et al. 2007). Hence, it has been suggested as an indicator for long-term SOC trends (Sparling et al. 1998, Von Lützow et al. 2007) that cannot yet be observed in a shorter timescale. I analysed microbial biomass C with chloroform fumigation extraction, following the method of Vance et al. (1987) (article **I** and **II**). The flush of microbial biomass C was measured without using a correction factor, similarly to Leckie et al. (2004).

Amino sugars (glucosamine, galactosamine, mannosamine) and muramic acid have been used as indicators for dead microbial residues, because they stabilize in the soil after the death of the microbial biomass (Glaser et al. 2004, Engelking et al. 2007, Liang and Balser 2008, Joergensen 2018, Liang et al. 2019, Buckeridge et al. 2022). They are components of the cell walls of bacteria, fungi, and actinomycetes, but not of higher plants (Glaser et al. 2004, Liang et al. 2019). It has been found that living microbial biomass contributes negligible amounts to the total soil amino sugar content (Glaser et al. 2004), and hence, amino sugars can serve as biomarkers for the contribution of microbial necromass to the soil C storage. Glucosamine, which stems from the chitin in fungal cell walls, is considered a biomarker for fungal necromass. Muramic acid occurs almost exclusively in bacterial cell walls and is used as an indicator for bacterial necromass (Engelking et al. 2007). We analysed the content of amino sugars according to Zhang and Amelung (1996). The samples were first hydrolysed with HCl, followed by a derivatization procedure, during which amino sugars were converted to aldononitrile derivatives. We calculated fungal necromass C by subtracting bacterial glucosamine from total glucosamine to equal fungal glucosamine, and using a conversion factor of 9 (Appuhn and Joergensen 2006, Joergensen 2018, detailed method description in manuscript **II**).

Studies have shown that microbial necromass often preferentially forms associations with minerals (Kopittke et al. 2018) and that it forms complexes with root-derived condensed tannins, and in this way stabilizes in the soil (Adamczyk et al. 2019a). We analysed condensed tannins with an acid-butanol assay, modified after Smolander et al. (2005), to examine the potential for these stabilization processes in the different management treatments.

The abundances of stable isotopes ^{13}C and ^{15}N are commonly used as indicators in studying SOC dynamics, due to their fractionation during decomposition (Fry 2006b). In the process of microbial C cycling, natural isotopes ^{13}C and ^{15}N usually enrich in the SOC (Clemmensen et al. 2013, Kyaschenko et al. 2019), because isotopes are discriminated in chemical reactions due to their higher molecular weight (Fry 2006a). Isotopic fractionation during SOM recycling and necromass accumulation leads to an enrichment of ^{13}C and ^{15}N in the soil with soil depth (Dijkstra et al. 2006, Krüger et al. 2024). Mycorrhizal fungi contribute to the enrichment of ^{13}C and ^{15}N with decomposition, as their necromass is enriched in these isotopes (Etcheverría et al. 2009).

3.3.6 Analysis of soil fungal community

To study the microbial communities, I applied metabarcoding, which is considered a powerful tool and has gained popularity in ecological studies due to the development of high-throughput methods (Ihrmark et al. 2012). Metabarcoding refers to the analysis of amplicon sequence data from environmental DNA: a primer marks a certain region of DNA that is characteristic for the taxonomic group of interest and is used as a genetic marker. This region is amplified via polymerase chain reaction (PCR) and then sequenced. Hence, the primer determines which taxa will be amplified and detected. The result is a potpourri of data from various taxa, which can be used as a proxy for the actual community of interest after some

processing (Shelton et al. 2023). We conducted metabarcoding to examine the fungal community in the soil for possible effects of the management regime (uneven-aged CCF vs even-aged RFM). We extracted DNA from organic and mineral soil samples, as described in article **III**. The internal transcribed spacer 2 region of the ribosome was amplified, which is the genetic marker for fungi (Ihrmark et al. 2012). It was targeted using the fungus-specific primers gITS7 (forward: 5′-GTGARTCATCGARTCTTTG) and ITS4 (reverse: 5′-TCCTCCGCTTATTGATATGC) (Ihrmark et al. 2012). The fungal ITS2 region was PCR-amplified and sequenced with the Illumina® MiSeq system at the Institute of Genomics Core Facility, University of Tartu. Before the data analysis, the sequences were filtered, trimmed, and clustered into operational taxonomic units (OTUs) with MOTHUR, according to the workflow described by Sietiö et al. (2018). The OTUs were aligned to the UNITE database to identify the taxa (Abarenkov et al. 2021). The obtained taxonomic information was then used to assign the OTUs to functional groups, i.e., fungal guilds using the FUNGuild database (Nguyen et al. 2016; detailed method description in article **III**).

3.4 Data analysis

Statistical analyses were conducted using the software R version 4.2.0 (R Core Team 2022). The data were first examined for normal distribution with Shapiro-Wilk test and for homogeneity of variances with Levene's test. If either one or both criteria were fulfilled, I compared treatments with parametric one-way analysis of variance (ANOVA) followed by a post-hoc test. If criteria were not fulfilled, I used non-parametric Kruskal-Wallis ANOVA followed by Mann-Whitney U test (with Bonferroni correction) to compare the treatments for differences (**I-III**).

To reduce the number of dimensions of the dataset, I conducted principal component analysis (PCA) after scaling the dataset and visualized the relationships between environmental variables and variables describing SOC quality with a biplot showing the first two dimensions (**I**). With PCA, the multiple variables are combined into principal components based on assumed linear relationships between variables and objects are given a new set of coordinates in the principal component space based on the similarity of the variables' scores for the object (Paliy and Shankar 2016).

I compared POC and organic layer chemical fractions using paired samples t-test (in case of normal distribution), or Wilcoxon signed-rank test on paired samples (if not normally distributed), because the observations were not independent (**II**). I visualized the relationships between the environmental variables with a correlation matrix based on Pearson's correlation coefficient (**II**). Selected correlations were further explored with simple linear regression analysis.

Soil temperature and moisture under the different managements were assessed with linear mixed-effects models for each month, based on daily means with treatment set as fixed effect and plot and date as random effect (**II**). Linear mixed effect models were also used to analyse the treatment effect on ground coverage of understorey plants, with treatment set as a fixed effect, and plot as a random effect (**II**). The distribution of model residuals was visually assessed by means of diagnostic plots. Proportional response variables were logit-transformed before the analyses.

The fungal community data were explored using the phyloseq package. The effects of the forest management on the fungal community structure were visualized in two-dimensional space by means of non-metric multi-dimensional scaling (NMDS). In NMDS, the data are

fitted to a pre-chosen number of dimensions (in our case k=2) based on dissimilarity ranks calculated between objects (Paliy and Shankar 2016). NMDS plots were overlain with vectors depicting environmental factors, which are directly or indirectly altered by forest management (**III**).

I conducted permutational multivariate analysis (PERMANOVA) based on Bray-Curtis dissimilarity to analyse the relative importance of the management treatment for the fungal community composition. PERMANOVA is a nonparametric multivariate ANOVA comparing dissimilarities between interclass objects to dissimilarities between intraclass objects (Paliy and Shankar 2016). A pairwise analysis of similarities (ANOSIM) test was used to test for statistical differences between fungal communities of the different management treatments. The ANOSIM test is a multivariate statistical test of significance that is used to compare classes (in our case treatments) based on the ranks of object distances within classes, similar to the NMDS ordination technique (Paliy and Shankar 2016).

I calculated observed species richness and the Shannon index for the fungal communities and ectomycorrhizal communities to examine the effects of the forest management treatment on fungal diversity. To assess the effects of the management treatments on fungal guilds, I calculated the relative abundance of observed OTUs for these functional groups and inspected the ratio between ectomycorrhizal and saprotrophic fungi.

4. RESULTS AND DISCUSSION

4.1 Forest management impacts on microclimate, litter inputs, and SOC stocks

The effects of CCF and RFM on stand microclimate and SOC stocks were assessed in both pine and spruce forests (Ruunaa and Vessari, respectively; articles **I** and **II**). The annual litter inputs to the soil under the different management regimes (aboveground and belowground) were estimated in pine forests (Ruunaa; article **I**).

Forest canopy provides shade and insulation, and thus, clear-cutting typically leads to an increase in mean temperature and diurnal and seasonal temperature variation (Palviainen et al. 2004, Kulmala et al. 2009, 2014, Kumpu et al. 2018). The soil temperature measurements on both sites showed corresponding effects of clear-cutting. In the pine forests, soil temperatures during the summer months were higher in clear-cuts than the other treatments. In the spruce stands, the soil temperature in clear-cuts was higher during summer compared to the other treatments, whereas during winter, it was mostly lower (**II**: supplementary Figure S1 and Table S2). The treatments with canopy in the spruce forests (uncut, uneven-aged, and even-aged) featured soil temperatures more similar to each other. The removal of a canopy may drastically decrease interception and thus more precipitation reaches the ground, which typically increases soil moisture in boreal forests (Kulmala et al. 2014). Accordingly, soil moisture was higher in clear-cuts and gap-cuts during the vegetation period in the pine stands, where the canopy was removed or partly removed (**I**: supplementary Figure S1). In Vessari spruce forests, soil moisture was mainly not affected by the forest management treatment (**II**: supplementary Figure S3 and Table S3), probably because the site is moister, and the soil has a higher water holding capacity due to the finer soil texture.

Forest management significantly affected the annual aboveground and belowground litter inputs from trees and understorey in the pine forests (**I**: Table 1). As expected, clear-cut plots showed the lowest annual inputs and uncut plots the highest inputs. Gap-cuts and retention-

cuts, as harvesting methods applied in CCF, had intermediate annual litter inputs that were similar to each other.

Despite the altered microclimate and litter inputs, the SOC contents and stocks of the different treatments on both sites in organic layer and mineral soil were not statistically different (Figure 4). Clear-cutting in Ruunaa was conducted in 2010/2011, and in Vessari in 2009; thus, I expected a declined C storage in clear-cut plots on both sites based on results from earlier studies (Covington 1981, James and Harrison 2016, Johannesson et al. 2024). Whereas the clear-cut sites in Vessari already exhibited a dense sapling layer, which might cause a recovery effect, this was not the case in the Ruunaa pine forests (Table 3). Similarly to our results, Madsen et al. (2025b) did not find differences in the SOC stocks of even-aged RFM stands and uncut (near-natural) stands, despite differences in the aboveground litterfall and soil respiration. Johannesson et al. (2024) modelled SOC stock recoveries in Nordic and Canadian forests based on national soil inventory data and found that pine-dominated forests needed 48 years until organic layer SOC stocks recovered to pre-cutting level, whereas organic layer stocks under spruce-dominated forests did not recover within the 53-year modelling period. However—similar to our results—there was also no loss recorded in the 0–10 cm mineral soil layer in their study. Triviño et al. (2023) modelled SOC stock development under different forest management options in Finland for 100 years and found an uncut set-aside treatment to yield the highest SOC stocks. Similarly, Menichetti et al. (2025) found, via modelling, the set-aside scenario to have a higher SOC storage than clear-cut forests with recovery times of 37 years for spruce and 69 years for pine. Our results show that modelling results and results from space-for-time approaches cannot be easily replicated in empirical studies and more field studies are needed to confirm these results.

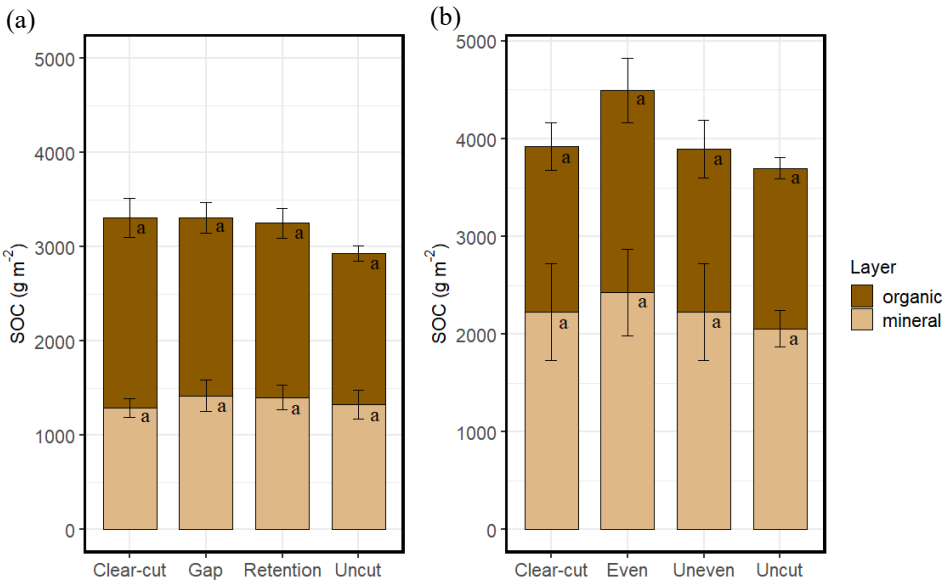

Figure 4. Soil organic carbon (SOC) stocks in g m^{-2} in the organic layer and upper mineral soil layer in (a) pine forests (Ruunaa), and (b) spruce forests (Vessari), displayed for the various management treatments. Error bars indicate the standard error of the mean. Stoniness has not been considered in these plots, as it would have increased variability, particularly in Vessari. Lowercase letters indicate statistical differences between treatments.

In the spruce forests in Vessari, we found higher SOC stocks in the mineral soil compared to the pine forests in Ruunaa (Figure 4). This can be attributed to the higher clay and silt content, and thus, higher potential for C to stabilize on mineral surfaces (Cotrufo et al. 2019, Begill et al. 2023). Furthermore, spruce stands tend to have higher litter inputs than pine stands, and higher nutrient concentrations in the litter (Ukonmaanaho et al. 2008, Hansson et al. 2013b, 2013a, Ransedokken et al. 2024), which may impact the SOC stocks as well (Vesterdal et al. 2013).

4.2 Forest management impacts on SOC quality and stability through roots

4.2.1 Root biomass, root secondary metabolites and SOC quality

Roots impact the SOC quality and stability in various ways, as explained in the introduction, and hence, we quantified root biomass in CCF and RFM in pine (article **I**) and spruce forests (article **II**). These two studies were partly similar, measuring SOC stocks, microbial biomass C, chemical stability fractions, and lab decomposition. Additionally, in the spruce forest (article **II**), the following parameters were also measured: condensed tannins, fungal necromass C, physical fractions (POC and MAOC), and occurrence of natural isotopes.

I expected clear-cutting in RFM to decrease root density, whereas structural complexity in uneven-aged CCF would increase root density compared to even-aged mature RFM stands. Root biomass was impacted by the forest management treatment on both sites (**I**: supplementary Table S2 and **II**: Figure 2). In agreement with the hypothesis, uncut plots showed the highest root biomass, and clear-cut plots the lowest. In Ruunaa pine forests, gap-cuts and retention-cuts featured amounts similar to the uncut plots. In the Vessari spruce forests, even-aged stands showed amounts similar to clear-cut plots. Root biomass in uneven-aged plots was intermediate between clear-cuts and uncut plots. The similarity between these treatments indicates that the saplings on the clear-cut sites in Vessari (Table 3) already have a dense root network. In the pine stands, the forest management particularly affected the fine root biomass, which was modelled based on basal area and other stand variables (**I**: Methods S1). In the spruce forests, the fine root biomass (determined by hand-picking) increased similarly with the stand basal area in the organic layer, and with stem density (**II**: Figure 3). Because of their high turnover, fine roots have a particularly high impact on the SOC cycle (Ding et al. 2021). We could link neither total nor fine root biomass to variation in tree diameter, and only coarse root biomass showed an increase with tree species diversity (both measures of stand structural complexity) (**II**: Figure 3). Hence, structural complexity did not clearly increase living tree root biomass, and our hypothesis was not fully supported. This result resonates with earlier studies, which also could not link fine root biomass to tree species diversity (Domisch et al. 2015, Finér et al. 2017).

In addition to litter inputs through dead roots, fine roots exude labile organic compounds (Heinzle et al. 2023), leading to higher microbial abundance and activity in the rhizosphere (Sokol and Bradford 2019). This may lead to an acceleration of decomposition, as these microbes start to “mine” organic matter to acquire organic N (Heinonsalo et al. 2015, Meier et al. 2017). Nitrogen mining is particularly important in N-poor soils, typical for the Arctic and subarctic (Hicks et al. 2020). In Ruunaa and Vessari, the mineral soil C/N ratios were 39 and 28, respectively (Table 2) indicating limited N availability (Schimel 2003).

Fine roots may, on the other, hand also decelerate decomposition processes and contribute to SOC stabilization through exudation of secondary metabolites, such as condensed tannins

(Adamczyk et al. 2019b). Tannins inhibit enzymes that microbes use to decompose organic material (Benoit and Starkey 1968) and form complexes with chitin, thus retaining fungal necromass in the soil (Adamczyk et al. 2019b). While we found significantly decreased condensed tannins in the organic layer on clear-cut plots (**II**: Figure 4a), we could not find a difference in the concentration of fungal necromass in the soil (**II**: Figure 8 a–d), i.e., we found no evidence for the stabilization of fungal necromass through condensed tannins.

However, the natural abundance of ^{15}N and ^{13}C that we analysed in the organic layer, POC, and MAOC (article **II**), showed contradicting results. The enrichment of ^{15}N and ^{13}C indicates the advancing level of decomposition of organic material and accumulation of microbial necromass (Lindahl et al. 2007, Clemmensen et al. 2013, Krüger et al. 2024). The abundance of both heavy isotopes increased with soil depth, from organic layer to POC, and furthermore from POC to MAOC (Figure 5), which supports the notion that POC acts as a precursor of MAOC (Angst et al. 2021). The enrichment of ^{15}N with soil depth is typical for N-limited conditions (Högberg et al. 1996). Mycorrhizal fungi mine SOM for N and transfer mostly ^{15}N-depleted N to their host plants, while the isotope accumulates in their necromass. Plants redeposit litter depleted in ^{15}N back onto the soil surface (Högberg et al. 1996, 1999).

Organic soil samples from uneven-aged CCF were enriched in ^{15}N compared to the other treatments, and in POC, they were enriched compared to clear-cuts. This may indicate an increased contribution of mycorrhizae to N cycling in uneven-aged plots (Högberg et al. 1996, 1999). This indication was corroborated by the strong correlation of $\delta^{15}N$ in POC with soil fungal necromass, and with the relative abundance of ECMf in the soil (**II**: supplementary Figure S6).

The depletion of ^{13}C in clear-cuts, on the other hand (as observed in POC and MAOC), reflects the high amounts of relatively recently added fresh litter from harvesting residues. The increase of ^{13}C from the organic layer to POC, and then to MAOC, indicates more microbial-derived compounds and fewer plant-derived compounds (Lavallee et al. 2020).

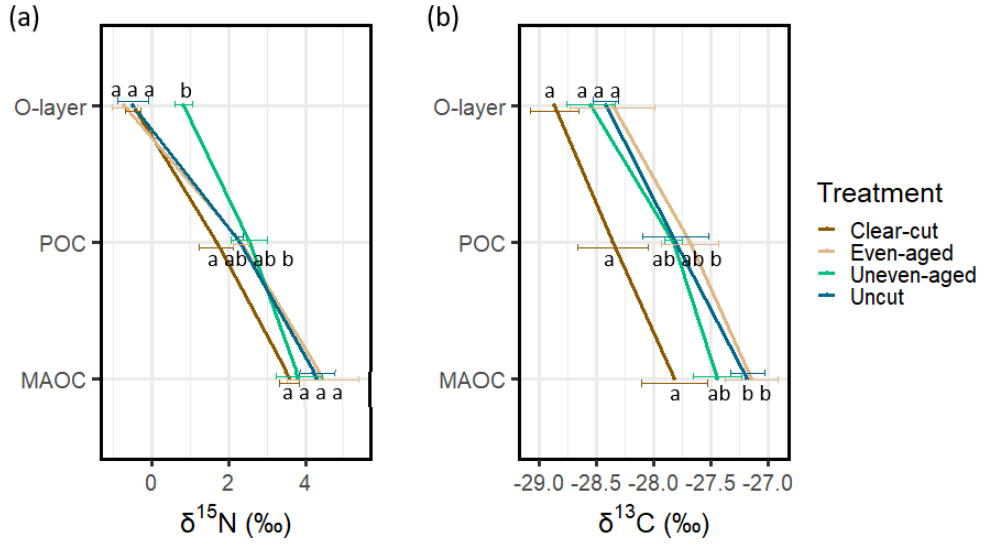

Figure 5. Mean $\delta^{15}N$ and $\delta^{13}C$ values ± standard deviation in the organic layer, POC, and MAOC, analysed in Vessari spruce forests. Different lowercase letters indicate statistical differences between treatments, tested with ANOVA and Tukey's post hoc test.

4.2.2 Forest management impacts on SOC stability

As expected, we could not find changes in the SOC stocks in the different management treatments, but we found changes in the SOC stability and the processes behind the accumulation and decomposition of SOC. During laboratory incubation, the organic layer soil samples from both pine and spruce forests showed a significant effect of the forest management treatment on the cumulative short-term respiration, which represents the labile fraction of the SOC (Figure 6, articles **I** and **II**). In both sites, uncut plots showed a higher fraction of labile SOC, and clear-cut plots showed a lower fraction of labile SOC.

In pine forests, gap-cuts and retention-cuts featured intermediate cumulative respiration values, whereas in spruce forests, managed mature stands (even-aged and uneven-aged) showed lower respiration, similar to clear-cut plots. In the pine stands, the chemical fractionation corroborated these findings, with smaller shares of the labile fractions (polar, non-polar, and acid-extractable) in clear-cut sites than in uncut sites (with gap and retention-cuts being intermediate) (**I**: Figure 7).

However, in the spruce stands, we could not detect an effect of the forest management treatments on the different chemical fractions, neither in organic layer nor in mineral soil POC (**II**: Figure 6). This highlights the impact of site conditions on study results and implies that more studies on different sites under the two tree species are needed to determine the effects of forest management on the chemical stability of SOC.

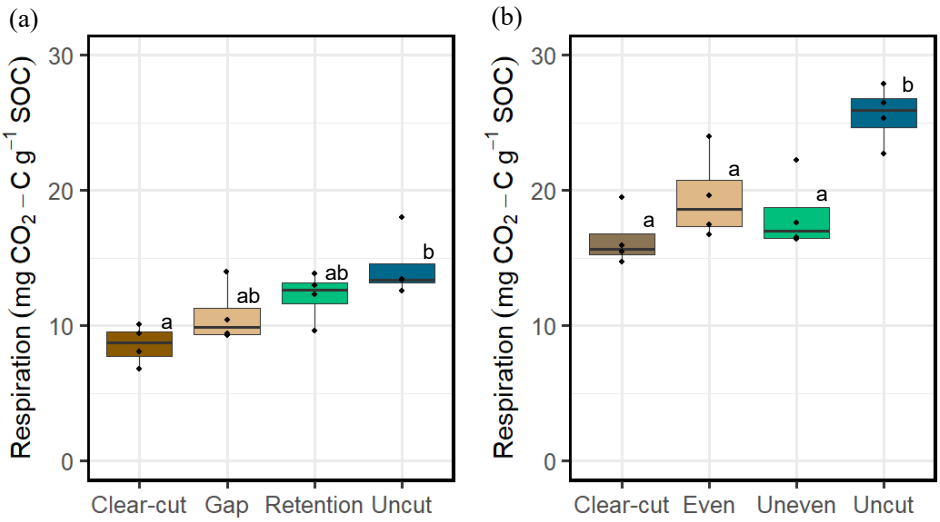

Figure 6. Cumulative carbon dioxide –carbon respired under laboratory conditions, expressed in mg g^{-1} SOC, from organic layer samples taken in (a) pine stands (Ruunaa) and (b) spruce stands (Vessari). In Ruunaa, gap-cuts and retention-cuts were analysed as different cuts applied in CCF. In Vessari, even-aged stands represent RFM, and uneven-aged stands represent CCF. The central line of the box shows the median of the data, and the box represents the data between the 25th and 75th percentile. The whiskers represent 1.5 times the interquartile range (1.5 × IQR). Different lowercase letters indicate significant differences at $p < 0.05$.

In the spruce forests, the cumulative respiration was highly correlated with the amount of POC in the mineral soil (**II**: supplementary Figure S6), similarly to the results found by Alvarez and Alvarez (2000), which indicates the lability of this fraction.

The *in-situ* decomposition rate of cellulose bags that were incubated in the pine forests was higher in clear-cuts and gap-cuts than in retention-cuts and uncut plots (**I**: Figure 5). It was tightly linked to the soil temperature measured in the field, which was also higher in these treatments (**I**: Figure 8). In the spruce stands, the decomposition rate was not affected by the different management treatments (**III**: Figure 3a). Whereas under standardized laboratory conditions, the SOC quality is the limiting factor for decomposition processes (assessed through measuring respiration), in the field, other factors limit the decomposition, such as soil moisture and temperature. The SOC pool is shaped by inputs through litter and outputs through decomposition. The higher decomposition rate in clear-cuts and gap-cuts, combined with the lower litter inputs in clear-cuts, may indicate decreased potential for SOC accumulation in RFM after clear-cutting. This is already reflected in the accumulation of chemically labile fractions in uncut plots and retention-cuts. Management effects can usually first be seen in the labile fractions, and these changes may indicate how management will affect the more stable C compounds in the long term (Awale et al. 2017, Bongiorno et al. 2019).

I expected that the different root densities under RFM and CCF would affect the stabilization of SOC in POC and MAOC, and conducted physical fractionation on mineral soil samples from the Vessari spruce forests (presented in article **II**). The SOC stored in the mineral soils could be separated into about 56% MAOC, about 36% POC, and about 8% heavy POC. The fractions were, contrary to our hypothesis, not significantly affected by the forest management (**II**: Figure 5). This might be due to the great variability introduced during the laboratory separation as material can be lost in the process, or traces of heavy sodium polytungstate might remain in the sample (despite careful washing). In future work, I would recommend separating based on particle size only and not following up with a separation based on density, which we conducted to obtain the purely organic material for chemical fractionation and analysis of natural isotopes.

MAOC correlated with soil moisture and with the silt and clay content in the soil (**II**: supplementary Figure S6), which determines the amount of mineral surfaces available for carbon–mineral associations (Cotrufo et al. 2019, Begill et al. 2023). Interestingly, soil POC content showed a positive linear relationship with fungal necromass in the soil, instead of a

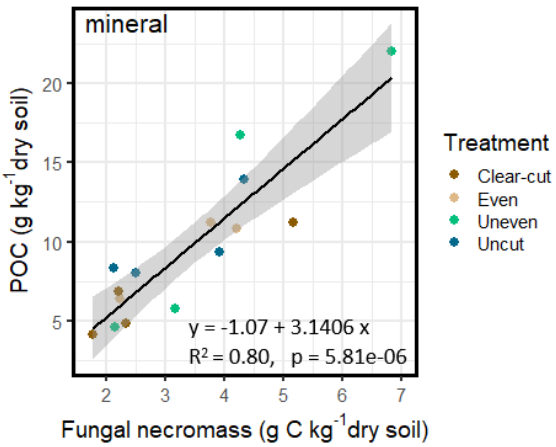

Figure 7. Linear relationship between soil fungal necromass (in g C kg_{-1} dry soil) and POC (g kg^{-1} dry soil) in the mineral soil in Vessari.

relationship with root density, which we had suspected (Figure 7). It has been frequently suggested that microbial residues particularly contribute to the MAOC. However, our result suggest that fungal residues might be an important contributor to the POC fraction, which has also been indicated in some studies (Angst et al. 2021). There are, however, contradicting results about the contribution of microbial necromass to POC and MAOC, and additional studies would benefit the understanding of the formation of stabilized SOM (Angst et al. 2021).

4.3 Forest management impacts on fungal community

As presented and discussed in article **III,** I analysed the effects of the forest management regime on the fungal community and the functional fungal guilds in spruce forests in Vessari. I examined clear-cut plots and even-aged mature plots (as post-harvest and pre-harvest stages of RFM), uneven-aged plots (CCF), and uncut control forests.

The forest management significantly affected the fungal community composition in the organic layer and mineral soil, with a stronger impact on the organic layer (**III**: Table 3). Basal area, dominant tree height, and stem density were the environmental factors with the strongest impact on the fungal communities (**III**: supplementary Table S3). This probably indicates the presence of roots, which also showed relationships with these stand variables. The fungal community differed between all treatments in the organic layer (Figure 8). In the mineral soil, the community in even-aged plots was similar to the ones in uneven-aged and uncut plots. All the other treatments differed from each other. Uncut plots and clear-cut plots featured the most dissimilar communities in the organic layer and mineral soil. Observed species richness and Shannon diversity did, however, not differ between management treatments in either soil layer (**III**: Table 2).

I analysed the effects of CCF and RFM on functional fungal guilds to draw conclusions regarding SOC accumulation. Mycorrhizal fungi have been shown to promote the accumulation of SOM, as they compete with saprotrophic decomposers (Gadgil and Gadgil 1971, Averill et al. 2014, Kyaschenko et al. 2017, Fanin et al. 2022). The abundances of functional guilds in even-aged and uneven-aged stands were similar to those in uncut stands, whereas the clear-cut community was more dissimilar (Figure 9).

Abundance of ECMf declined in clear-cuts compared to the other treatments, leading to a dominance of saprotrophic fungi (Figure 9). Ectomycorrhizal abundance increased with increasing stem density and basal area (**III**: supplementary Figure S5), but not sapling density, which emphasises the importance of older trees in sustaining the ECMf community. Accordingly, there was a marginally lower ECMf/SAPf ratio in clear-cuts than in uneven-aged CCF stands (and even-aged and uncut stands were intermediate). The ectomycorrhizal community composition was affected by the forest management treatment, with clear-cuts being most dissimilar from the other treatments (**III**: Figure 7). Also, diversity and richness of ECMf declined in clear-cuts (**III**: Table 4). Though, it appears that the fungal community changes induced by clear-cutting would not affect soil carbon storage in the later stages of the rotation period, as the functionalities of the soil fungi in the mature stands (even-aged, uneven-aged, and uncut) resembled each other.

A declined ECMf/SAPf-ratio, as observed in clear-cut sites, may lead to a stimulation of SOM decomposition according to the Gadgil theory and has been connected to a mass loss of humus by Clemmensen et al. (2024).

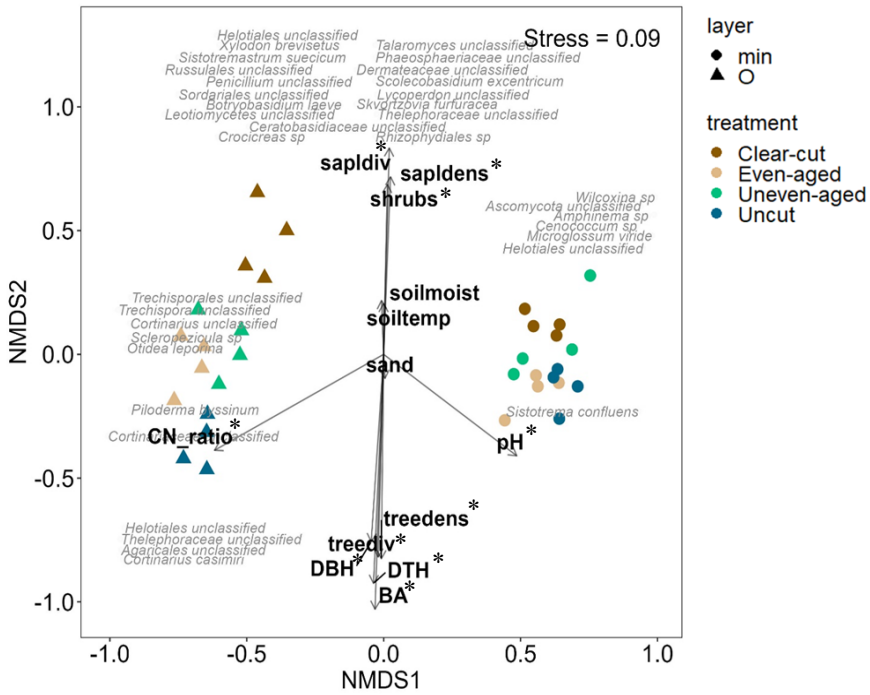

Figure 8. NMDS plot showing the fungal community composition in Vessari in the different management treatments and soil layers. Environmental factors affecting the composition are overlain and marked with an asterisk if they had a significant influence on the fungal community. Factors characterizing the forest stand: dominant tree height (DTH), diameter at breast height (DBH), basal area (BA), upper tree layer diversity and density (treediv, treedens), and sapling diversity and density (sapldiv, sapldens), and cover of ericoid shrubs (shrubs). Factors characterizing the soil: soil pH (pH), soil moisture (soilmoist), soil temperature (soiltemp), soil texture (sand), and C/N ratio.

However, the decomposition rate and SOC storage in our plots were unaffected by the management treatments, similarly to Madsen et al. (2025a, 2025b), even when the ECMf/SAPf ratio was altered. This highlights plasticity and redundancy in the soil fungal community in Vessari, which appears to exhibit a high response diversity (Simard 2008); i.e., even though the fungal community is altered by disturbance (clear-cutting), it remains resilient due to its high species richness: declines in one species' abundance or functionality are offset by other species (Ross et al. 2023).

Yet, it remains unknown whether repeated clear-cutting would eventually alter this response diversity through repeated altering of the fungal community, and lead to changes in the functionality of the soil fungi. Long-term changes in the ectomycorrhizal community after clear-cutting have been found before, and researchers have voiced concerns over the possible effects of repeated clear-cutting on biodiversity and ecological functionality (Lunde et al. 2025). Even though the fungal community in CCF is different from uncut forests, it is unlikely to change the long-term soil C storage compared to unmanaged forest, as the functionality of fungal guilds remains similar.

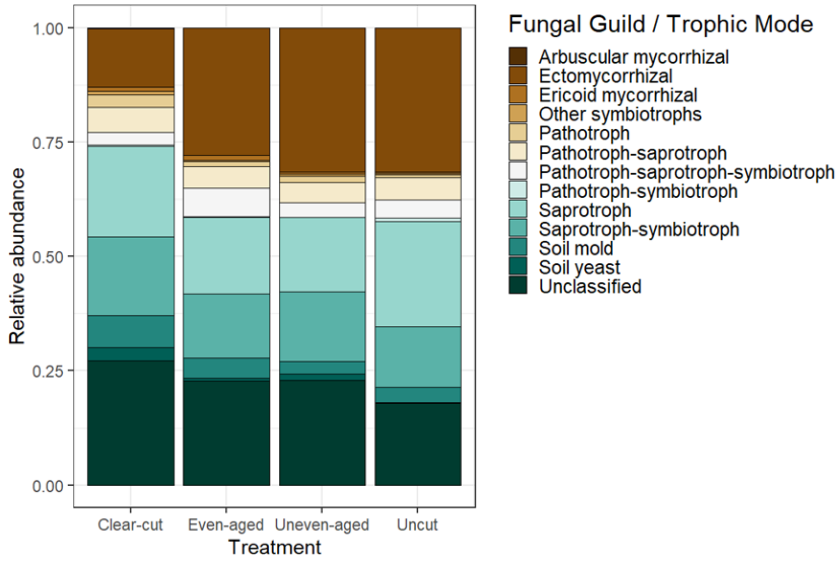

Figure 9. Fungal guilds indicating the potential functionality of the observed fungal taxa in the various treatments, based on normalized OTU counts. "Unclassified" fungi include OTUs that yielded no answer when aligned to the UNITE database and fungi that were assigned with a confidence ranking of "possible".

Changes in fungal species composition, ECMf diversity, and richness may, furthermore, have implications for seedling establishment and competition (Jones et al. 2003) that affect the C pool recovery after harvesting. Seedlings growing in uneven-aged plots may benefit from a richer ECMf community, which could enhance tree growth and increase C inputs to the soil. Yi et al. (2024) found that a higher diversity of fungal associations increases forest resilience, for example, leading to less foliar damage and higher predation on insects. A higher resilience decreases the possibility of soil C losses induced by forest disturbances.

4.4 Limitations of this study

When comparing CCF and RFM in a field study, it is difficult to include the aspect of time. A forest stand managed with CCF is ideally an infinite continuum with a dynamic uneven-aged structure. A stand managed with RFM exists for one rotation period, with a clear beginning and end, and evolves through different age stages. It is thus difficult to choose a point in the stand development to compare between CCF and RFM. We tried to account for this by considering the post- and pre-harvest stage of RFM. However, modelling studies have better tools to consider this aspect of time.

As common in field studies that research soil processes, also my study did not easily find definite results. In field studies, many environmental factors (soil temperature, moisture, C/N ratio, soil texture, etc.) are affecting the results and thus processes that have been observed in laboratory studies might not easily be reproduced in the field. The changes of soil C stocks in the field are difficult to observe as they are relatively small against a large and variable storage forming the background (Schrumpf et al. 2011).

Laboratory analyses are laborious and costly and thus it is a common practice, to pool samples to reduce the workload, as also done here. However, reducing the number of observations comes with the price of increasing the tendency of overfitting when applying statistical modelling (Wenger and Olden 2012). Due to our limited number of observations (16 per soil layer), I resorted to simple statistical analyses when analysing the pooled soil samples: ANOVA (parametric or non-parametric) or simple regression analysis with only one explanatory variable to avoid overfitting. PCA was furthermore used to reduce the number of dimensions (i.e., environmental factors). In future research, it would be useful to corroborate some of my findings with higher sample numbers to gain more insight on the impact of environmental factors and their interactions.

We could not take any samples in deeper mineral soil layers due to the high stoniness on both sites, even though a review study suggests that forest management might affect the deep soil C pool even stronger than in the upper mineral soil (James and Harrison 2016). The deep soil C pool is large, despite low C concentrations because of the big volume of this soil layer, but is scarcely researched. Studies suggest, that deep soil C is to a greater extent formed from microbial necromass (Ni et al. 2020) and may have a higher temperature sensitivity than topsoil C (Hicks Pries et al. 2017). Therefore, it would be very important and interesting to study forest management effects on this important C storage in the future.

5. CONCLUSION

Boreal forests capture and store significant amounts of C, and thus have an important role in climate change mitigation. On the other hand, they are also intensely managed to meet societal demands for timber. In this dissertation, I compared the effects of two management regimes—continuous-cover forestry and rotation forest management—on SOC storage, by taking a closer look at SOC fractions as indicators for quality and stability, and at the soil fungal community involved in C-cycling.

In the first study, conducted in pine forests, I found that there may be a potential for greater SOC accumulation under CCF over time, due to higher and continuous litter inputs in continuously managed forests, paired with a lower decomposition rate caused by lower soil temperatures. An accumulation of chemically labile SOC fractions in retention-cuts and uncut plots may indicate an increase in total SOC eventually, based on the assumption that labile SOC is a precursor for stabilized SOC. The decomposition rate in canopy gaps was similar to clear-cuts. Therefore, retention-cuts could be the better management choice for CCF on less fertile pine sites when the management aim is to increase the SOC storage.

The second study, conducted in spruce forests, showed that SOC stability and quality indicators react with different sensitivity to changes in the management practise. The chemical and physical fractionation did not yield any significant differences for the different treatments. However, cumulative lab respiration indicated more easily decomposable SOC in uncut plots. In the future, it would be important to study to which extent stabilized SOC is formed by microbial residues and to which extent by plant-derived organic matter, and how these components are affected by forest management practice. There was indication that POC is to a greater extent formed from fungal necromass instead of plant tissue than presumed. As anticipated, root density was declined in RFM compared to uncut forests, and condensed tannins in the soil increased with basal area and root density, leading to lower amounts of tannins in clear-cuts. However, I did not find support for the hypothesis that condensed

tannins retain fungal necromass. As these mechanisms have been observed in controlled mesh bag studies, it might also mean that they are difficult to detect at field scale, even if they exist. A higher abundance of ^{15}N in uneven-aged plots indicated, however, that there was a higher contribution of mycorrhizal fungi to SOM formation, and a lower abundance of ^{13}C indicated less decomposed organic material in clear-cut plots. Hence, even though I did not find direct effects of the different management systems on the SOC stocks, they affected the stabilization mechanisms of SOC. Clear-cutting decreased the amount of easily decomposable SOC, while CCF benefited the mycorrhizal involvement in SOM formation.

The result on the higher mycorrhizal involvement under CCF was supported by the findings of the third article, which showed that the ectomycorrhizal abundance, diversity, and richness were reduced by clear-cutting. Also, the ratio of ectomycorrhizae to saprotrophs was marginally smaller in clear-cuts than CCF plots, which may accelerate decomposition processes and lead to losses of SOC. However, we could not find the expected difference in the decomposition rate of cellulose in the field. This highlights the high response diversity of the fungal community in our study. An increasing relationship found between ECMf abundance and basal area suggests that a certain threshold (basal area) of older trees should remain after harvesting CCF plots to sustain the ECMf community, rather than conducting a strict target diameter cut. The fungal community structure was different in all treatments and thus clearly affected by forest management. As uneven-aged CCF, however, showed a similar composition of functional fungal guilds to uncut forests, it is unlikely to affect the SOC storage through the altered fungal community in the long term. Whether RFM has a long-term effect through the altered ecological functionality and fungal community remains still unclear and should be studied, for example, with research plots that have experienced more than one clear-cut.

Carbon sequestration in the forest is only one tool to mitigate climate change, and its effects are limited. It is equally important to focus on a long-term usage of the harvested timber and, of course, to drastically cut carbon emissions. The effect of forest disturbances on SOC storage should also be further studied, as they have recently become more frequent and severe, and this trend is predicted to accelerate. Therefore, we must be careful to protect the carbon storages in the forest with management actions and focus on building forests resilient to climate change. Our forest management decisions today shape the conditions of the forests that we leave to future generations.

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