

The impact of forest management methods on the ectomycorrhizal community and implications for forest productivity in needleleaf forests

OSKAR GÖRANSSON 2023
MVEK12 EXAMENSARBETE FÖR KANDIDATEXAMEN 15 HP
MILJÖVETENSKAP | LUNDS UNIVERSITET
HANDLEDARE: HÅKAN WALLANDER





LUNDS
UNIVERSITET

WWW.CEC.LU.SE
WWW.LU.SE

Lunds universitet

Miljövetenskaplig utbildning
Centrum för miljö- och
klimatforskning
Ekologihuset
223 62 Lund

Abstract

Ectomycorrhizal fungi (ECM) form symbiotic relationships with trees by connecting to the roots, procuring soil nutrients in exchange for carbohydrates, and are an important contributor to plant growth. The forestry practice of clearcutting can be detrimental to the ECM community by removing its source of energy and creating unfavorable soil conditions, acutely reducing ECM diversity. This paper aims to examine existing literature for the effects of clearcutting on the ECM community as well as the potential impact of ECM diversity on plant growth, and attempt to determine if the use of alternate harvesting methods could promote plant growth through preservation of the ECM community.

The following research questions will be answered:

1. What are the impacts of clearcutting on the ECM community compared to alternate harvesting methods?
2. How well do ECM correlate with tree growth?
3. Can the conservation of the ECM community through alternate harvesting methods have a positive impact on forest productivity?

The results indicate that both clearcutting and dispersed tree retention cause a significant loss of ECM diversity. Retention forest patches can lifeboat the ECM community, however it does not speed up the recolonization of seedlings. Conflicting results indicate both a positive and negative correlation between ECM diversity and plant growth, likely depending on specific circumstances. ECM community composition is more closely linked to plant growth, with species adapted to nutrient turnover being the most important, however whether this extends to clearcut sites is uncertain. The reviewed literature was insufficient to draw a conclusion regarding the benefits of a retained ECM community in terms of forest productivity, however if there is no other mature forest in the vicinity, tree retention patches may be necessary for future recolonization of seedlings.

Content

| | |
|---|-----------|
| Abstract | 1 |
| Content | 2 |
| <i>Word list</i> | 3 |
| Introduction | 4 |
| <i>Aim and research questions</i> | 6 |
| Method | 7 |
| <i>Ethical reflection</i> | 7 |
| Results | 9 |
| <i>Changes in ectomycorrhizal composition following different harvesting treatments</i> | 9 |
| <i>The effect of ectomycorrhizal species composition on forest growth</i> | 11 |
| <i>Common ectomycorrhizal indicator species</i> | 12 |
| Discussion | 14 |
| <i>Effects of harvesting on the ECM community</i> | 14 |
| <i>Correlation between ECM community and tree growth</i> | 15 |
| <i>The benefits of ectomycorrhizal preservation in timber production</i> | 16 |
| Conclusions | 18 |
| Acknowledgement | 19 |
| References | 20 |

Word list

ECM - Ectomycorrhizal fungi

Species richness - Amount of different species

Species diversity - Species richness and distribution of species

Relative abundance – Amount of a species in relation to other species, regardless of a change in the total amount of occurring ECM

Community structure – Overall organization, richness, diversity and relative abundance of ECM species in a given ecosystem

Community composition – Makeup of specific identities of ECM species in a given ecosystem

Morphotype - Physical characteristics shared by different species, often but not necessarily related to ecological function

Introduction

Mycorrhizal fungi networks permeate the soil in all forest types and play an important role in the function of healthy forest ecosystems (Van der heijden et al., 2014). Ectomycorrhizal fungi (ECM) is the dominant type found in boreal forests, connecting to tree roots through an intercellular net of hyphae as seen in figure 1 (Smith, Read, 2008). It works in symbiosis with trees primarily by collecting nutrients through its extensive mycelium network in exchange for carbohydrates provided by the tree. Apart from their main function some species of the ECM community also play a role in breaking down organic matter and releasing nutrients, converting organic nitrogen to plant-available inorganic nitrogen, as well as protecting the plant root from pathogens. Despite their wide enzyme profile as a whole, many ECM species have a hard time making use of the tougher carbon sources of forest litter and thus prefer carbohydrates in the form of simple sugars from the nutrient exchange with plants (Smith, Read, 2008). As the mycorrhiza coats the finer roots of trees it is also responsible for transporting water to the plant (Garbaye, 2000). Different types of mycorrhiza have unique adaptations that optimize water utilization. For example, in times of drought the considerably thinner mycelium can reach soil micropores containing water that the plant roots can't access, where mycelium with exclusively hydrophilic tips can efficiently scavenge for water. In moist soil, mycelium hydrophilic along its entire length can transport large amounts of water in an enclosing film, simultaneously improving soil conductivity around the root (Garbaye, 2000). Mycorrhiza also plays a role in strengthening plant resistance to pathogens and other stressors (Dreischoff et al., 2020).

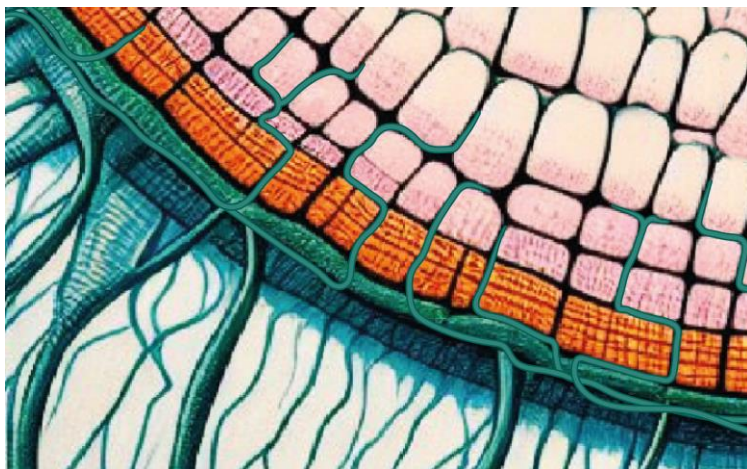


Figure 1. Cross-section of a root. Ectomycorrhizal hyphae (green) connects to the root by growing between the plant cells.

The forest management practice of clearcutting removes their source of energy, making it harder for fungal networks to survive. Some species can recolonize new seedlings through inoculum remaining in the soil (Brundrett et al., 1995), or through surviving on root tips still active after harvest, although this ability is diminished by the soil compaction from machines during harvest (Lazaruk et al., 2005). Newly planted trees may therefore have lesser access to developed ectomycorrhizal networks, potentially limiting growth rate and increasing the need for soil preparation practices such as tillage, where soil is turned over to expose deeper mineral rich soil to new seedlings. Tillage can in turn lead to increased soil erosion and nutrient runoff, degrading the soil quality over time (Klik, Rosner, 2020). The practice of clearcutting is done for economic reasons, as it is simpler and more efficient to harvest an entire field than evaluating which trees to leave behind and working around those. It also provides more lumber per instance of harvesting and

eliminates any canopy coverage that may hinder or cause uneven growth of newly planted trees. Continuous cover forestry, or green tree retention, are alternate management methods that aim to always retain some tree coverage in managed areas, leading to a lower biodiversity loss as a consequence of lumber production as the remaining trees function as microhabitats supporting other forest species (Gauthier et al., 2015). Dispersed tree retention and aggregated tree retention, which can be seen compared to clearcuts in figure 2, are two typical forms of continuous cover forestry.



Figure 2.

Examples of different harvesting treatments. (A) Clearcuts generally leave no trees left standing. (B) Dispersed tree retention retain a variable amount of trees spread out over an area. (C) Aggregated tree retention, or forest patches, leave several clusters of trees with clearcut areas in between.

Although rarely used in modern forestry, continuous cover forestry is of high interest for its efficacy in biodiversity conservation when compared to clearcutting (Kim et al., 2020). This biodiversity conservation extends to the mycorrhizal networks that can survive in the remaining trees and therefore potentially speed up the recolonization of the newly planted forest. Combining this with prescribed burning can further increase biodiversity conservation by creating substrates similar to early-successional natural forests, as the forest ecosystem is adapted to experiencing occasional outbreaks of fire (Suominen et al., 2015). Beyond a shared human responsibility to stop the anthropogenically driven extinction of other species, biodiversity conservation practices are incredibly important for humans to keep benefiting from the many ecosystem services provided by forests. Among these, many benefits of biodiversity can have an impact on the productivity of the forest, further incentivizing alternate harvesting treatments. One of these benefits is pest regulation, as a more biodiverse forest includes more natural enemies of forest pests, which can protect trees and reduce the need for other pest management methods (Brockerhoff et al., 2017). A higher biodiversity in the forest soil can also improve nutrient cycling, soil structure and the previously discussed benefits of ECM, further promoting tree growth.

One important ecological function of the forest ecosystem is its ability to sequester carbon. Forests harbor a wide array of species with different ecological roles that collectively produce its many ecological functions when in balance with each other. However, anthropogenic activity can create unintended effects that disturb this balance of species and alters the expression of certain ecological functions. One important example is the way timber harvest can impact carbon sequestration and in turn the ecosystem service of climate regulation through balancing of atmospheric carbon. A common effect of timber harvest is for the forest to shift from being a carbon sink to a carbon source for some time after harvest (Paul-Limoges et al., 2015). This is in part facilitated by a post-clearcut increase in the relative abundance of saprotrophic fungi, which are adapted to decomposing organic matter that have accumulated during the growth of the forest (Churchland et al., 2013). In a standing forest there is conversely generally a net sequestration of carbon through the continued input of plant litter, some of which is less prone to be broken down by microorganisms, such as lignin. The dominant type of fungi in standing forests usually get their carbon through symbiosis with trees, as is the case with ECM, which facilitates the net sequestration of carbon. Utilizing alternate harvesting methods that maintain an ECM dominated microbiome might therefore reduce the carbon release associated with timber production by maintaining the soil carbon stocks.

Aim and research questions

While many studies have examined the negative effects of clearcutting on ECM, it is not clearly understood how this could impact future timber production. Since ECM plays an important role in tree growth it is possible that harvesting methods that preserve the ECM community could increase forest productivity, providing an economic argument for more environmentally friendly forestry. To come to such a conclusion it is first necessary to understand the impacts of clearcutting, in comparison to alternate harvesting methods, on the ECM community. This part should also provide knowledge of how the ECM community is affected over time, to understand if any initial effects on ECM last long enough to potentially have a meaningful impact on the overall productivity during the entire forest growth cycle. Secondly, the actual correlation between the ECM community and tree growth has to be established. While it is clear that ECM play an important role in a healthy forest ecosystem, this part aims to understand how the contribution of ECM to tree growth is related to factors such as ECM diversity or community composition. This is to finally be able to analyze how specific changes in the ECM community following different harvesting treatments will affect the productivity of each method. The results of this review will as such not provide a conclusive answer to the long term productivity of any management practice, as it will only attempt to relate productivity to changes in the ECM community. Included studies will be limited to ECM communities in managed needleleaf forests, and will not take into account specific soil types or seedling species. This paper will not consider any social or economic value resulting from preservation of ecosystem services or forest biodiversity through continuous cover forestry.

1. What are the impacts of clearcutting on the ECM community compared to alternate harvesting methods?
2. How well do ECM correlate with tree growth?
3. Can the conservation of the ECM community through alternate harvesting methods have a positive impact on forest productivity?

Method

Literature reviewed in this paper was found through web of science between 2023-04-01 to 2023-06-01. Papers older than 25 years or with no citations were assumed to be outdated or of low quality/scientific relevance. The following parameters were used in the search:

| Database | Search terms | Boundaries |
|----------|---|---|
| WoS | clear-cut* OR clearcut* OR clearfell* AND ectomycorrhiz* OR ecto-mycorrhiz* AND change* OR composition AND conifer* OR pine* OR spruce* OR fir* | All rows sorted by topic |
| WoS | "tree growth" OR "forest growth rate*" OR "sapling growth" OR "seedling growth" AND ectomycorrhiz* OR ecto-mycorrhiz* | First row required in title, second row topic |

Initial selection of papers was made using title and abstract to determine relevance to the question formulation. For the first research question, the paper was only reviewed if the title and abstract indicated that researchers had measured indicators for the ECM community, such as diversity, species richness or relative abundance, before and after a harvesting treatment. For the second research question, papers were reviewed if title and abstract indicated that the researchers had attempted to draw correlations between sapling or mature forest growth and specific ECM species or general parameters of the ECM community like diversity, species richness or relative abundance. Papers deemed relevant in the first selection were then read, and evaluated primarily based on the methodology to determine if the study design could produce relevant results. Besides adhering to common scientific methods of multiple sampling locations, and using statistical analyses to assess differences between sites, papers used to answer the first research question were required to use some form of molecular analysis of ECM samples to accurately be able to determine changes in the ECM community, as other techniques such as visual analysis of morphotypes only provides indications of the potential presence of certain families or genres. For the second research question, seedling growth had to be monitored for a minimum of 3 years, with molecular analysis of associated ECM carried out once a year to evaluate how ECM communities changed alongside seedling growth. The examined studies in each search block were organized according to common findings, and a comprehensive review was carried out to answer their corresponding research question. Alternate factors that could impact the results were identified and discussed.

Ethical reflection

There is an ethical dilemma in trying to put an economic value on nature preservation focused forestry in comparison to conventional forestry, as in if the results establish that there is no economic value in continuous cover forestry over clearcutting, could this paper be used as an argument to continue and expand the practice of clearcutting? There is much research covering the ongoing biodiversity loss throughout managed forests, and the conservation of species that may go extinct cannot be conclusively defined in economic terms. Despite this, or perhaps because of this, modern forestry is dominated by what

is thought to be the most economically efficient method of clearcutting, which also happens to cause a large biodiversity loss. This paper is not meant to argue for conducting forestry purely based on an economic viewpoint, but rather aims to determine if conventional forestry has been overlooking the economic benefit of continuous cover forestry, as such an argument might be one of the few ways to redirect forestry practices towards biodiversity conservation.

Results

To answer the research questions a total of 15 appropriate studies were found, 10 related to the impacts of harvesting treatments on the ECM community, and 5 related to the correlation between the ECM community and tree growth.

Table 1.
Number of studies found from each search term.

| Database | Search terms | Boundaries | # Results | # Selection 1 | # Selection 2 |
|----------|---|---|-----------|---------------|---------------|
| WoS | clear-cut* OR clearcut* OR clearfell* AND ectomycorrhiz* OR ecto-mycorrhiz* AND change* OR composition AND conifer* OR pine* OR spruce* OR fir* | All rows sorted by topic | 101 | 27 | 10 |
| WoS | "tree growth" OR "forest growth rate*" OR "sapling growth" OR "seedling growth" AND ectomycorrhiz* OR ecto-mycorrhiz* | First row required in title, second row topic | 98 | 19 | 5 |

Changes in ectomycorrhizal composition following different harvesting treatments

Table 2.
Overview and short summary of the results from papers used to answer the first research question.

| Research paper | Findings |
|-------------------------------|--|
| Byrd et al. (1999) | Clearcutting changes community composition and decreases species richness |
| Parladé et al. (2019) | Clearcutting & partial clearcutting reduces relative abundance and diversity of ECM |
| Rodriguez-Ramos et al. (2021) | Clearcutting reduces relative abundance and diversity of ECM |
| Kyashenko et al. (2017) | Clearcutting decreases ECM abundance and diversity, gradual recovery as stand age increased |
| Twieg et al. (2007) | Clearcutting decreases ECM diversity, sharp recovery around canopy closure |
| Wallander et al. (2010) | Maximal mycelial production during canopy closure |
| Varenius et al. (2017) | Similar changes to ECM community composition following clearcutting and seed tree retention, decreases in relative abundance and diversity |

| | |
|--------------------------|---|
| Varenius et al. (2016) | 50 years after clearcutting ECM community was relatively similar to natural forests |
| Lazaruk et al. (2005) | Similar decrease in active ECM root tips in areas impacted by harvest machinery regardless of harvesting treatment |
| Churchland et al. (2021) | Decreased ECM relative abundance regardless of harvesting treatment, but maintained soil nutrient concentrations for green tree retention |

One paper by Byrd et al. (1999) studied changes in ECM community composition and abundance by analyzing root tips supplemented with fruiting bodies in naturally regenerated clearcut stands compared to undisturbed areas in and near Yellowstone national park. The researchers found that clearcutting has significant effects on fungal communities. While many dominant ECM species were resilient to the clearcutting event and maintained their relative abundance and overall community structure in both sites, a majority of the ECM species found in undisturbed sites disappeared and were replaced by new ones after a clearcut event, concluding a significant change in community composition and a loss in species richness.

Another study by Parladé et al. (2019) examined changes in soil fungal communities of clearcut and partial clearcut stands through DNA analysis of soil core samples. This study found that both cutting treatments sharply reduced the relative abundance and diversity of ECM, being largely displaced by saprotrophs and arbuscular mycorrhiza. The total clearcut treatment also had a large absolute increase of pathogenic, parasitic, and endophytic fungi. Similarly Rodriguez-Ramos et al. (2021) used DNA analysis of soil cores and found that clearcutting caused a shift away from ECM to saprotrophic fungi, decreasing both ECM relative abundance and species diversity.

Kyashenko et al. (2017) found that ECM abundance and diversity decreased severely and was replaced by saprotrophic fungi after clearcutting by DNA analysis of soil core samples. As stand age of the next generation of trees increased the ECM slowly displaced the saprotrophic fungi, and overall ECM species richness increased significantly with forest age. The late colonization by certain ECM species was theorized by the authors to stem from competition of well-established generalist species hindering recolonization, as the patchy forest landscape should support dispersion from nearby forests. Twieg et al. (2007) also examined ECM succession with forest age by analyzing root tips and found that after clearcutting ECM diversity was significantly lower than control in 5-year old stands. In the 26-year old stands ECM diversity had recovered well, coinciding with canopy closure. ECM diversity had only increased slightly when comparing 26-year old stands to both 65- and 100-year old stands. Similarly a study by Wallander et al. (2010) studying ECM mycelial growth using mesh bags found that maximal ECM mycelial production occurred during canopy closure in 10-20 year old Norway spruce. Fast-growing *T. fibrillosa* was significantly more dominant in 10-30 year old stands accounting for 80% of ECM amplicons, while in 30-90 year old stands *T. fibrillosa* was reduced to 43% of ECM amplicons and ECM species richness increased.

In a study by Varenius et al. (2017) researchers examined what effects the retention and utilization of seed trees after harvest would have on the recolonization of ECM communities in new trees. The researchers used DNA analysis to determine that ECM community composition in the regenerated forests differed significantly from old natural stands but became more similar in older regenerated stands. There was however no significant difference in ECM community composition between the clearcut stands and the seed tree regenerated stands. The local ECM community composition around the retained seed trees was similar to old natural stands, but this composition did not spread to the surrounding regenerated trees. The authors theorize that as ECM communities did not differ between regeneration methods, how they develop is more dependent on environmental filtering following harvest, for example changes in soil chemistry such as elevated pH and increased levels of inorganic nitrogen. More generalist species might as such dominate the ECM composition and hinder the diversification of the ECM communities for several decades. Adding to this, a previous study from Varenius et al. (2016) suggests that 50 years after clearcutting the ECM community is relatively similar to natural forests in species richness as 13 of the 20 most common ECM species were found, also using DNA analysis. The authors argue that the main source for recolonization of ECM is wind carried spores from nearby forests, which generally travel a few hundred meters. Re-established ECM communities are thus limited to the composition of nearby communities.

One study by Lazaruk et al. (2005) examined changes in ECM community following different levels of disturbance, including clearcuts and 20%, 50% and 75% green tree retention (GTR) ellipses, by collecting active fine root tips and identifying morphotypes. Researchers found that ECM species richness and diversity were both almost four times greater in residual tree strips compared to clearcuts or machine corridors. In the residual strips, amount of active root tips was similar to control. While a lower amount of active root tips are to be expected in clearcuts, the same was seen in machine corridors of GTR-sites, indicating that the soil compaction from machines kill off roots and accompanying ECM.

Churchland et al. (2021) studied changes in the microbial community following harvest by comparing clearcutting, dispersed tree retention and aggregate tree retention (forest patches) through phospholipid fatty acid (PLFA) analysis. The results indicate that ECM relative abundance declined significantly in clearcut and dispersed tree retention, with a shift to a bacteria-dominated microbial community. In aggregate tree retention the forest patches allowed ECM a better environment to maintain a similar community composition to uncut forests. Soil nutrient concentrations were however maintained for both types of tree retention treatment, suggesting that although ECM abundance decreased in dispersed tree retention, the overall microbial community was still efficient in decomposition and nutrient cycling.

The effect of ectomycorrhizal species composition on forest growth

Table 3.

Overview and short summary of the results from papers used to answer the second research question.

| Research paper | Findings |
|--------------------------|---|
| Kranabetter, J (2004) | Less diverse ECM community adapted to disturbance increased seedling growth in clearcuts |
| Guignabert et al. (2018) | Seedlings in clearcuts had larger increases in biomass than in seed tree retention plots |
| Heinonsalo et al. (2007) | Lower ECM diversity increased seedling growth only in seedlings planted before harvesting |
| Karst et al. (2011) | Increased ECM morphotype richness had a positive correlation with seedling growth |
| Anthony et al. (2022) | Strong correlation between seedling growth and ECM community composition specialized in nutrient turnover |

One study by Kranabetter, J (2004) transplanted hybrid spruce seedlings from both a mature forest (<5 meters from forest edge) and a disturbed site (along road edges with exposed mineral soil) with similar light conditions over to a clearcut site to compare the seedling growth rate. Seedlings from the mature forest harbored higher ECM morphotype richness than seedlings from the disturbed site. After three years the ECM community of mature forest seedlings became more similar to the disturbed site seedlings. Disturbed site seedlings showed a slightly greater height increment of 25%, indicating that the less diverse disturbed site ECM community had an advantage in the clearcut environment.

Guignabert et al. (2018) compared seedling growth and ECM colonization in seed tree regeneration and clear-cut plots also containing naturally regenerated seedlings and found no significant difference between the harvesting treatments. Seedlings in clearcuts had the largest increase in biomass, likely in part due to more light exposure compared to seed tree regeneration. The researchers identified ECM morphotypes and percent colonization by visually examining root tips.

One study by Heinonsalo et al. (2007) studied scots pine seedling performance and ECM community dynamics following clearcutting. Different set of seedlings were planted before (set 1) and after (set 2) clearcutting, as well as in an interface zone 10 meters into the clearcut plot from the nearest standing trees.

Seedlings in set 1 showed seven times greater growth in clearcut plots compared to interface or control after four years of growth, while no difference was seen in set 2 between the different plots. The morphological ECM diversity was greater for seedlings in the interface zone than clearcut plot for both sets, although more pronounced in pre-clearcut transplanted seedlings (set 1). The researchers suggest that seedlings in the interface zone retain an ECM community structure similar to that of the standing forest because of the close proximity to the control zone, while in the clearcut zone the ECM community is allowed to adapt for optimal growth in clearcut conditions, hence the significant improvement in growth rate.

One study by Karst et al. (2011) examined the contribution of ECM communities to seedling growth rate in relation to some abiotic factors such as watering regime and soil pH by visually determining morphotype and utilizing DNA analysis of each morphotype. The results indicated that morphotype richness and ECM community composition had a positive correlation to sapling growth, although to a much lesser extent than watering regime and pH.

One large scale study by Anthony et al. (2022) collected ECM community samples from 137 ICP Forest level II sites (International co-operative programme on assessment and monitoring of air pollution effects on forests), 87 of which had paired ECM community and forest inventory data. The researchers identified several environmental variables that correlated to tree growth rate without a high correlation to the ECM community, such as temperature, stand density and nitrogen deposition, which enabled an examination of the effect of ECM community variation on growth rates. While fungal richness and diversity was positively but not significantly correlated with growth rates, ECM community composition had a strong correlation, in particular communities specialized in metabolizing nutrients such as inorganic nitrogen.

Common ectomycorrhizal indicator species

Following is an overview of different taxa of ECM that appeared in highest frequencies in each corresponding study. A higher level of taxa might be less indicative of the optimal conditions or performance of the taxa, as it includes fungi with increasingly different adaptations. However the genus level is commonly used to describe fungi of similar adaptations or characteristics.

Among the species with a notably higher relative abundance in the clearcut plot than the undisturbed plot were *Cenococcum geophilum*, *Suillus*, *Thelephoraceae*, *Cortinarius* and *Russulaceae* (Table 1)(Byrd, et al., 1999). *Russula* genera was very low in 5-year old stands, but increased dramatically with age. *Piloderma* and *Cortinarius* also increased with stand age. *Rhizopogon vinicolor* was far more dominant on 5 year old stands than in older stands (Table 1)(Twieg, et al., 2007). *Cortinarius* genus, which is adapted to accessing complex nutrient pools and increasing turnover of organic carbon and nitrogen pools, was much more prevalent in old natural stands than regenerated stands (Table 1)(Varenius, et al., 2017). The only morphotype observed in all clearcut stands was *Tomentella*, indicating that this is an early stage broad generalist (Table 1)(Lazaruk, et al., 2005). The relative abundance of *Amphinema byssoides* was significantly higher for the disturbed site seedlings (Table 1)(Kranabetter, J, 2004). Cutting treatments reduced the abundance of *Boletus* and *Eurotiales* (Table 1)(Parladé, et al., 2019). *Piloderma* and *Tylospora* were dominant in younger stands, while *Cortinarius* and *Russula* became dominant in older stands (Table 1)(Kyashenko, et al., 2017). Significant losses of *Russula*, *Cortinarius* and *Piloderma* were found following clearcutting (Table 1)(Rodriguez-Ramos, et al., 2021).

Table 4.

Fungi highlighted in the studies sorted by taxa and context of most common occurrence. Numbers in parentheses indicate the number of studies with similar results.

| Taxa | Undisturbed/Older stand | Disturbed/Younger stand |
|---------|-------------------------|-----------------------------|
| Species | | <i>Rhizopogon vinicolor</i> |

| | | |
|--------|--|---|
| Genus | <i>Russula</i> (3), <i>Piloderma</i> (2), <i>Cortinarius</i> (4), <i>Boletus</i> | <i>Suillus</i> , <i>Cortinarius</i> , <i>Tomentella</i> , <i>Tylospora</i> , <i>Piloderma</i> |
| Family | | <i>Thelephoraceae</i> , <i>Russulaceae</i> |
| Order | <i>Eurotiales</i> | |

Two dominant *Wilcoxina* morphotypes showed a correlation to growth rate (Table 2)(Karst, et al., 2011). ECM community composition linked to fast growth rates differed for needle vs. broadleaf forests, with *Russula ochroleuca* being the only fast growth indicator species in both types of forest. Common taxa correlated with fast growth in needleleaf forest were *Atheliaceae* and *Cenococcum*, while taxa correlated with slow growth were *Imleria badia*, *Thelephoraceae* and *Russulaceae*. The less common *Piloderma fallax* and *Piloderma byssinum* were fast growth indicator species in needleleaf forests (Table 2)(Anthony, et al., 2022).

Table 5.

Fungi highlighted in the studies sorted by taxa and implications on growth effect.

| Taxa | Fast growth | Slow growth |
|---------|---|--|
| Species | <i>Russula ochroleuca</i> , <i>P. fallax</i> , <i>P. byssinum</i> | <i>Imleria badia</i> |
| Genus | <i>Wilcoxina</i> , <i>Cenococcum</i> | |
| Family | <i>Atheliaceae</i> , <i>Cortinariaceae</i> | <i>Thelephoraceae</i> , <i>Russulaceae</i> |

Discussion

Effects of harvesting on the ECM community

Maintaining the biodiversity of forest ecosystems is crucial to preserve the many ecosystem functions that all species rely on for survival (Brockerhoff et al., 2017). The ECM community in particular plays an important role in keeping the forest ecosystem healthy and stable by contributing to nutrient cycling, carbon sequestration and plant health. Clearcutting has a significant negative impact on both above and below ground biodiversity, including the ECM community, potentially having a long term negative impact on many ecosystem services (Rosenvald, Lohmus, 2008). It's possible that this loss of biodiversity could negatively affect the productivity of managed forests over the long term, defeating the purpose of clearcutting, which is done for economic reasons, while also ensuring a loss of biodiversity and ecosystem services. One notable way biodiversity loss could affect forest productivity is through a less diverse ECM community, as they contribute to nutrient acquisition and plant resilience (Smith, Read, 2008). Using green tree retention forestry instead, biodiversity loss following harvest can be significantly reduced (Rosenvald, Lohmus, 2008). As such this paper attempts to examine existing literature for correlations between the ECM community and plant growth, to see if alternate harvesting methods that favor biodiversity conservation could carry an economic incentive that might speed up the adoption of such methods.

From the reviewed studies it was hard to conclusively determine whether clearcutting mainly reduces ECM abundance, species richness or community composition, most likely because it depends on several different factors such as nutrient availability, soil type, climate or seedling species. One important factor could be how well other types of microorganisms manage to establish following a disturbance. The studies by Parledé et al. (2019), Rodriguez-Ramos et al. (2021) and Kyashenko et al. (2017) are examples where other types of fungi managed to dominate the relative fungal abundance, in particular saprotrophic fungi, even when green tree retention was applied. This could mean that the conditions following both types of harvesting methods are less favorable for ECM, allowing them to be outcompeted by other types of fungi. Lindahl et al. (2002) discusses the competition for nutrients between saprotrophic fungi and ECM, but they could also compete for space or water when soil nutrients are not limiting. Even as soil conditions return to normal, it's possible that the harsher competition induced by harvest could delay the recolonization of less competitive species, at least until the ECM regains a considerable competitive advantage for example in the form of carbon as seedlings become more developed. Twieg et al. (2007) did find that ECM diversity had recovered well as canopy closure occurred, indicating that the ECM community reacts and expands quickly in response to optimal photosynthetic activity. Varenus et al. (2017) also found no difference in community composition between green tree retention and clearcuts, and Guignabert et al. (2018) found equal amount of ECM colonization between the two methods.

Despite ECM communities remaining on the roots of retained trees, they don't seem to speed up the colonization of new seedlings based on the reviewed studies. Colonization through hyphae contact in the soil is a slow process, starting out just around the retained trees (Cline et al., 2005), and many ECM species can't survive as inoculum for the several decades it takes for proper diversification to appear. Hence the main avenue for recolonization is likely spores from wind dispersion, as pointed out by Varenus et al. (2016), which generally only occurs within a few hundred meters of established communities. The fact that these studies do not find a benefit of retention trees for recolonization might be because of the proximity of standing forests to the studied clearcuts. For isolated forest patches or larger clearcuts there might still be a benefit of retaining trees in terms of spore dispersal. It's also possible that the retention trees couldn't properly preserve the ECM community, as Kranabetter et al. (2013) found that forest patches larger than 20m were necessary to support ECM similar to mature forests. Since all reviewed studies analyzing seedling colonization alongside retention trees only utilized dispersed tree retention, they might not encompass the

benefits of retaining larger patches regarding ECM recolonization. Churchland et al. (2021) did include forest patches alongside dispersed retention trees, although sampling ECM via soil cores instead of seedlings. Supporting previous studies relative ECM abundance declined significantly in clearcut and dispersed tree retention, but was not impacted within the retained forest patches.

The study by Lazaruk et al. (2005) also used soil core samples, highlighting the negative effects of soil compaction by harvesting machines on active root tips and ECM diversity. As a majority of active ECM resides in the top 4 cm of the soil (Harvey, et al. 1986), extensive soil compaction from heavy machinery or soil preparation practices that disturbs this layer could damage mycorrhizal inoculum (Lazaruk, et al. 2005, 2008). Page-Dumroese et al. (1998) found that soil compaction and stump removal negatively affected amount of ECM root tips, morphological types and seedling growth. However this could in part be explained by seedlings forming shorter and fewer roots in the two treatments. Kranabetter et al. (2017) studied clearcut plots with different levels of disturbance and found that ECM species richness and community composition was negatively impacted by both soil compaction and removal of forest floor, with noticeable effects remaining after 20 years. Most of the reviewed studies used machine harvesting during clearcutting which inevitably causes soil compaction, and as such some of the reduced species richness could be explained by this factor alone. Using lighter machinery and strategies to avoid soil compaction could therefore limit the loss of ECM species richness after clearcutting.

In summary, clearcutting has a large negative impact on ECM diversity and abundance, and while dispersed tree retention can counteract the negative effects of clearcutting on soil nutrient turnover, it does not sufficiently preserve the ECM community. Utilizing retained forest patches will locally preserve the ECM community, but at least in the short term it does not seem to speed up recolonization of new seedlings.

Correlation between ECM community and tree growth

The results from Kranabetter et al. (2004) and Heinonsalo et al. (2007) both found a correlation between lower ECM diversity for seedling growth under post-clearcut conditions. The disturbed site seedlings Kranabetter et al. (2004) transplanted came from the side of a road, and likely harbored broad generalist ECM species better suited to the clearcut environment than the mature forest seedlings. While the lower ECM diversity seedlings promoted slightly higher growth rates, this could be related to the specific species composition rather than the lower diversity. The ECM composition of the mature forest seedling also became more similar to the disturbed site seedlings over time, supporting the idea that they initially had a less favorable species composition for clearcut conditions. The findings of Heinonsalo et al. (2007) showed much greater seedling growth in the lower ECM diversity clearcut plot, although interestingly only when seedlings were planted before harvesting. As noted by the researchers the proximity of the control forest seems to somewhat preserve the forest-type ECM community of the interface seedlings, stopping it from adapting to the clearcut conditions. However seedlings planted before and after clearcutting did not show much difference in growth in the clearcut plot, so it was more about a stunted growth effect in the interface seedlings with a more forest-like ECM community.

Despite disturbance adapted species seeming important for early growth, the *Thelephoraceae* and *Russulaceae* family have been correlated with slow growth (Anthony et al., 2022) while also being found in high relative abundance by Byrd et al. (1999), see table 2 and 1, respectively. As a family can contain very different species, this does not conclude a connection, but is an interesting indication. The *Russula* genus was also much more common in older stands (Twieg et al., 2007, Kyashenko et al., 2017, Rodriguez-Ramos et al., 2021) while the species *Russula ochroleuca* was found to be an indicator species for fast growth (Anthony et al., 2022). Species from this genus have a hard time surviving in the post-clearcut environment, but using less intensive harvesting methods could allow for earlier colonization by *Russula ochroleuca*. Varenius et al. (2017) also note that the *Cortinarius* genus, which is adapted to accessing complex nutrient pools and increasing turnover of organic carbon and nitrogen pools (Lindahl et al., 2021), was much more prevalent in old natural stands than regenerated stands.

From some of the studies lower ECM diversity has been correlated with greater seedling growth, but it is also possible that the benefit of greater ECM colonization on visible plant growth comes at later stages, as one study by Holste et al. (2017) found that ECM colonization increased seedling root growth, but not above-ground plant growth. Colonized seedlings might as such initially divert more nutrients to the roots and ECM community in order to maximize potential growth over time through more efficient nutrient uptake, especially under conditions where soil nutrients are more limiting than photosynthesis. One example by Nasholm et al. (2013) shows that under nitrogen limited conditions, the ECM community allocates less nitrogen to the plant, inhibiting tree growth. This prioritization of the ECM community could potentially lead to a greater increase in plant growth over longer time frames not captured by studies only looking at the early stages of growth.

Karst et al. (2011) did find a positive correlation between ECM species composition and plant growth. The ECM diversity was generally low, with dominating species of *Wilcoxina*, similar to those commonly found after disturbances. This suggests that at least while ECM diversity is low, increased diversity can promote plant growth.

Anthony et al. (2022) was the most comprehensive study that was analyzed, and best fit the objective of finding a correlation between different ECM communities and plant growth, as the study included different environmental conditions across all of Europe. The strongest correlator to tree growth was a community composition adapted to metabolizing nutrients, indicating that nutrient turnover-rate often is the most limiting factor regarding tree growth. The researchers do note that the lack of correlation between ECM species richness and diversity and tree growth could be the result of diminishing returns following saturation of ECM species richness, as the study spans large scale forests with very diverse ECM communities. They further imply that in a more localized context, for example with low diversity (clearcut site), the ECM species diversity might have a larger impact on growth rates. It is also to be considered that this study looked at tree growth of mature permanent forests, as opposed to the previous studies looking at seedling growth. It may therefore not accurately represent the optimal ECM structures for seedlings to young trees, which is an important phase for survival rate and future growth, as well as accounting for the specific conditions following a harvesting disturbance.

The effect of ECM diversity and composition on tree growth is highly dependent on the circumstances, but composition seems to be the most important factor. Conditions that allow for species adapted to nutrient turnover to thrive would likely have the highest impact on seedling growth, but some of these species have a hard time surviving post-clearcut. There are indications that ECM diversity could positively influence tree growth, but such a conclusion cannot be drawn from the reviewed literature.

The benefits of ectomycorrhizal preservation in timber production

From the combined studies there is no clear indication that efforts to retain a diverse ECM community would have a positive effect on timber production. The changed soil environment following the reviewed types of harvest seem to make it hard for most ECM species to reestablish, or alternatively only certain species are necessary and best suited for the early growth of seedlings and so do not allow other species to take hold. Harvesting also produces more favorable conditions for other types of microorganisms, and competition for resources could be the cause for delayed ECM diversification rather than a lack of potential colonizing species. This scenario does however rely on the larger landscape always retaining areas with established ECM communities. Based on the reviewed studies it is also not clear that an earlier ECM diversification would benefit tree growth. Additionally, one study by Jones et al. (2010) looked at the enzyme activity of ECM fungal communities after clearcutting and found that while enzyme profiles of individual ECM species changed following disturbance, the community wide enzyme profile stayed similar to control. These findings suggest that there is functionally complementary enzyme activity between different taxa and community structures. This provides additional evidence of the adaptability of ECM communities following disturbances. While the species diversity suffers from the intense disturbance of clearcutting, the enzymatic profile necessary for efficient nutrient turnover remains similar to that of undisturbed forests, as species

surviving in the post-clearcut conditions alter their enzyme profile to fill in the gaps. While this might be true for clearcut environments, Anthony et al. (2022) argues that the functional advantages of the overall ECM community composition is a far greater contributor to tree growth than the complementary effects of different species.

Conclusions

The aim of this study was to determine how different harvesting treatments affect the ECM community, and explore any correlation between the ECM community and tree growth, in order to evaluate if forest management practices with a lower impact on the ECM community could yield higher timber production. From the reviewed studies it is clear that clearcutting has a significant negative impact on ECM communities, causing shifts in community composition and dominance hierarchies, along with decreased species richness and diversity. Harvesting methods utilizing green tree retention, in particular forest patches, did preserve the ECM community locally, but it is unclear if this provides a benefit compared to clearcutting in recolonizing newly planted seedlings. Regardless of harvesting treatment, the ECM community gradually recovered over the entire growing cycle of the forest.

There was conflicting evidence regarding the correlation between the ECM community and tree growth, but a community composition adapted to nutrient turnover seem to have a positive correlation. There is however very little literature in this specific area, mainly because of the difficulties designing such a study in a real ecosystem environment. As such the reviewed literature is not sufficient to draw conclusions about this. Some studies do show a benefit of less intensive harvesting methods on seedling growth, but does not specifically correlate this to a more diverse ECM community. More research would have to be done monitoring forest growth and ECM community composition over a long duration, preferably including different management practices.

To gain more precise insight, a study design should include clearcuts with no standing forests within 1 km, compared to an aggregated and dispersed tree retention plot with similar conditions, alongside replicate plots that utilize lightweight machinery to preserve the soil conditions. Seedling growth and ECM community development should then be monitored over a 20 year period. This would provide data on the benefit of green tree retention in terms of wind dispersal of ECM spores, potential benefits of a lower soil disturbance, and could show additional correlations between the ECM community and forest growth not seen during early seedling development. Data on the long-term changes of ECM community composition, over several growth cycles, in managed forests could also highlight potential negative effects that are not seen from just one cut, but this is hard to accomplish because of the long cycles of timber production.

Acknowledgement

Thanks to my handler Håkan Wallander and examiner Maria Hansson for valuable feedback contributing to this paper.

References

Introduction/Discussion:

Brockerhoff, E.G, Barbaro, L, Castagneyrol, B, Forrester, D.I, Gardiner, B, Gonzalez-Olabarria, J.R, Lyver, P.O, Meurisse, N, Oxbrough, A, Taki, H, Thompson, I.D, van der Plas, F, Jactel, H. (2017). Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodiversity and conservation*, 26(13), 3005-3035. DOI: <https://doi.org/10.1007/s10531-017-1453-2>

Brundrett, M.C, Abbott, L.K. (1995). Mycorrhizal fungus propagules in the jarrah forest .2. Spatial variability in inoculum levels. *New phytologist*, 131(4), 461-469. DOI: <https://doi.org/10.1111/j.1469-8137.1995.tb03083.x>

Churchland, C, Grayston, S.J, Bengtson, P. (2013). Spatial variability of soil fungal and bacterial abundance: Consequences for organic carbon turnover along a transition from a forested to clear-cut site. *Soil biology and biochemistry*, 63, 5-13. DOI: <https://doi.org/10.1016/j.soilbio.2013.03.015>

Cline, E.T, Ammirati, J.F, Edmonds, R.L. (2005). Does proximity to mature trees influence ectomycorrhizal fungus communities of Douglas-fir seedlings? *New phytologist*, 166(3), 993-1009. DOI: <https://doi.org/10.1111/j.1469-8137.2005.01387.x>

Dreischhoff, S, Das, I.S, Jakobi, M, Kasper, K, Polle, A. (2020). Local Responses and Systemic Induced Resistance Mediated by Ectomycorrhizal Fungi. *Frontiers in Plant Science*, 11. DOI: <https://doi.org/10.3389/fpls.2020.590063>

Dumais, D, Larouche, C, Raymond, P, Bedard, S, Lambert, M.C. (2018). Survival and growth dynamics of red spruce seedlings planted under different forest cover densities and types. *New forests*, 50(4), 573-592. DOI: <https://doi.org/10.1007/s11056-018-9680-2>

Garbaye, J. (2000). The role of ectomycorrhizal symbiosis in the resistance of forests to water stress. *Outlook on agriculture*, 29(1), 63-69. DOI: <https://doi.org/10.5367/000000000101293068>

Gauthier, S, Bernier, P, Kuuluvainen, T, Shvidenko, A. Z., Schepaschenko, D. G. (2015). Boreal forest health and global change. *Science*, 349(6250), 819-822. DOI: <https://doi.org/10.1126/science.aaa9>

Harvey, A.E, Jurgensen, M.F, Larsen, M.J, Schlieter, J.A. Distribution of active ectomycorrhizal short roots in forest soils of the inland northwest – Effects of site and disturbance. (1986). *USDA forest service intermountain research station*, 374, 1-8.

Holste, E.K, Kobe, R.K, Gehring, C.A. (2017). Plant species differ in early seedling growth and tissue nutrient responses to arbuscular and ectomycorrhizal fungi. *Mycorrhiza*, 27(3), 211-223. DOI: <https://doi.org/10.1007/s00572-016-0744-x>

Jørgensen, K, Granath, G, Strengbom, J, Lindahl, B.D. (2021). Links between boreal forest management, soil fungal communities and below-ground carbon sequestration. *Functional ecology*, 36(2), 392-405. DOI: <https://doi.org/10.1111/1365-2435.13985>

Kim, S, Axelsson, E.P, Girona, M.M, Senior, J.K. (2020). Continuous-cover forestry maintains soil fungal communities in Norway spruce dominated boreal forests. *Forest ecology and management*, 480. DOI: <https://doi.org/10.1016/j.foreco.2020.118659>

Klik, A, Rosner, J. (2020). Long-term experience with conservation tillage practices in Austria: Impacts on soil erosion processes. *Soil & tillage research*, 203. DOI: <https://doi.org/10.1016/j.still.2020.104669>

Kranabetter, J.M, De Montigny, L, Ross, G. (2013). Effectiveness of green-tree retention in the conservation of ectomycorrhizal fungi. *Fungal ecology*, 6(5), 430-438. DOI: <https://doi.org/10.1016/j.funeco.2013.05.001>

Kranabetter, J.M, Haeussler, S, Wood, C. (2017). Vulnerability of boreal indicators (ground-dwelling beetles, understory plants and ectomycorrhizal fungi) to severe forest soil disturbance. *Forest ecology and management*, 402, 213-222. DOI: <https://doi.org/10.1016/j.foreco.2017.07.008>

Lazaruk, L.W, Macdonald, S.E, Kernaghan, G. (2008). The effect of mechanical site preparation on ectomycorrhizae of planted white spruce seedlings in conifer-dominated boreal mixedwood forest. *Canadian journal of forest research*, 38(7), 2072-2079. DOI: <https://doi.org/10.1139/X08-035>

Lindahl, B.O, Taylor, A.F.S, Finlay, R.D. (2002). Defining nutritional constraints on carbon cycling in boreal forests - towards a less 'phytcentric' perspective. *Plant and soil*, 242(1), 123-135. DOI: <https://doi.org/10.1023/A:1019650226585>

Nasholm, T, Hogberg, P, Franklin, O, Metcalfe, D, Keel, S.G, Campbell, C, Hurry, V, Linder, S, Hogberg, M.N. (2013). Are ectomycorrhizal fungi alleviating or aggravating nitrogen limitation of tree growth in boreal forests? *New phytologist*, 198(1), 214-221. DOI: <https://doi.org/10.1111/nph.12139>

Page-Dumroese, D.S, Harvey, A.E, Jurgensen, M.F, Amaranthus, M.P. (1998). Impacts of soil compaction and tree stump removal on soil properties and outplanted seedlings in northern Idaho, USA. *Canadian journal of soil science*, 78(1), 29-34. DOI: <https://doi.org/10.4141/S97-022>

Paul-Limoges, E, Black, T.A, Christen, A, Nesic, Z, Jassal, R.S. (2015). Effect of clearcut harvesting on the carbon balance of a Douglas-fir forest. *Agricultural and forest meteorology*, 203, 30-42. DOI: <https://doi.org/10.1016/j.agrformet.2014.12.010>

Pennock, D.J, van Kessel, C. (1995). Clear-cut forest harvest impacts on soil quality indicators in the mixedwood forest of Saskatchewan, Canada. *Geoderma*, 75(1-2), 13-32. DOI: [https://doi.org/10.1016/S0016-7061\(96\)00075-4](https://doi.org/10.1016/S0016-7061(96)00075-4)

Rosenvald, R, Lohmus, A. (2008). For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. *Forest ecology and management*, 255(1), 1-15. DOI: <https://doi.org/10.1016/j.foreco.2007.09.016>

Smith, S.E, Read, D. (2008). *Mycorrhizal Symbiosis*. (3rd ed.) London: Academic press. DOI: <https://doi.org/10.1016/B978-0-12-370526-6.X5001-6>

Suominen, M, Junninen, K, Heikkala, O, Kouki, J. (2015). Combined effects of retention forestry and prescribed burning on polypore fungi. *Journal of applied ecology*, 52(4), 1001-1008. DOI: <https://doi.org/10.1111/1365-2664.12447>

Van der Heijden, M.G.A, Martin, F.M, Selosse, M.A, Sanders, I.R. (2014). Mycorrhizal ecology and evolution: the past, the present, and the future. *New phytologist*, 205(4), 1369-1645. DOI: <https://doi.org/10.1111/nph.13288>

Literature reviewed:

Anthony, M.A, Thomas W. Crowther, T.W, van der Linde, S, Suz, L.M, Bidartondo, M.I, Cox, F, Schaub, M, Rautio, P, Ferretti, M, Vesterdal, L, De Vos, B, Dettwiler, M, Eickenscheidt, N, Schmitz, A, Meesenburg, H, Andreae, H, Jacob, F, Dietrich, H-P, Waldner, P, Gessler, A, Frey, B, Schramm, O, van den Bulk, P, Hensen, A, Averill, C. (2022). Forest tree growth is linked to mycorrhizal fungal composition and function across Europe. *The ISME journal*, 16(5), 1327-1336. DOI: <https://doi.org/10.1038/s41396-021-01159-7>

Byrd, K.B, Parker, V.T, Vogler, D.R, Cullings, K.W. (2000). The influence of clear-cutting on ectomycorrhizal fungus diversity in a lodgepole pine (*Pinus contorta*) stand, Yellowstone National Park, Wyoming, and Gallatin National Forest, Montana. *Canadian journal of botany*, 78(2), 149-156. DOI: <https://doi.org/10.1139/b99-171>

Churchland, C, Bengtson, P, Prescott, C.E, Grayston, S.J. (2021). Dispersed Variable-Retention Harvesting Mitigates N Losses on Harvested Sites in Conjunction With Changes in Soil Microbial Community Structure. *Frontiers in forests and global change*, 3. DOI: <https://doi.org/10.3389/ffgc.2020.609216>

- Guignabert, A, Delerue, F, Gonzalez, M, Augusto, L, Bakker, M.R. (2018). Effects of Management Practices and Topography on Ectomycorrhizal Fungi of Maritime Pine during Seedling Recruitment. *Forests*, 9(5), 245. DOI: <https://doi.org/10.3390/f9050245>
- Heinonsalo, J, Koskiahde, I, Sen, R. (2007). Scots pine bait seedling performance and root colonizing ectomycorrhizal fungal community dynamics before and during the 4 years after forest clear-cut logging. *Canadian journal of forest research*, 37(2), 415-429. DOI: <https://doi.org/10.1139/X06-213>
- Jones, M.D, Twieg, B.D, Ward, V, Barker, J, Durall, D.M, Simard, S.W. (2010) Functional complementarity of Douglas-fir ectomycorrhizas for extracellular enzyme activity after wildfire or clearcut logging. *Functional ecology*, 24(5), 1139-1151. DOI: <https://doi.org/10.1111/j.1365-2435.2010.01699.x>
- Karst, J, Hoeksema, J.D, Jones, M.D, Turkington, R. (2011). Parsing the roles of abiotic and biotic factors in Douglas-fir seedling growth. *Pedobiologia*, 54(5-6), 273-280. DOI: <https://doi.org/10.1016/j.pedobi.2011.05.002>
- Kranabetter, J. (2004). Ectomycorrhizal community effects on hybrid spruce seedling growth and nutrition in clearcuts. *Canadian journal of botany*, 82(7), 983-991. DOI: <https://doi.org/10.1139/B04-077>
- Kyaschenko, J, Clemmensen, K.E, Hagenbo, A, Karlton, E, Lindahl, B.D. (2017). Shift in fungal communities and associated enzyme activities along an age gradient of managed *Pinus sylvestris* stands. *The ISME journal*, 11(4), 863-874. DOI: <https://doi.org/10.1038/ismej.2016.184>
- Lazaruk, L.W, Kernaghan, G, Macdonald, S.E, Khasa, D. (2005). Effects of partial cutting on the ectomycorrhizae of *Picea glauca* forests in northwestern Alberta. *Canadian journal of forest research*, 35(6), 1442-1454. DOI: <https://doi.org/10.1139/X05-062>
- Parladé, J, Queralt, M, Pera, J, Bonet, J.A, Castaño, C, Martínez-Peña, F, Piñol, J, Senar, M.A, De Miguel, A.M. (2019). Temporal dynamics of soil fungal communities after partial and total clearcutting in a managed *Pinus sylvestris* stand. *Forest ecology and management*, 449. DOI: <https://doi.org/10.1016/j.foreco.2019.117456>
- Rodriguez-Ramos, J.C, Cale, J.A, Cahill Jr, J.F, Simard, S.W, Karst, J, Erbilgin, N. (2021). Changes in soil fungal community composition depend on functional group and forest disturbance type. *New phytologist*, 229(2), 1105-1117. DOI: <https://doi.org/10.1111/nph.16749>
- Twieg, BD, Durall, DM, Simard, SW. (2007). Ectomycorrhizal fungal succession in mixed temperate forests. *New phytologist*, 176(2), 437-447. DOI: <https://doi.org/10.1111/j.1469-8137.2007.02173.x>
- Varenus, K, Karen, O, Lindahl, B, Dahlberg, A. (2016). Long-term effects of tree harvesting on ectomycorrhizal fungal communities in boreal Scots pine forests. *Forest ecology and management*, 380, 41-49. DOI: <https://doi.org/10.1016/j.foreco.2016.08.006>
- Varenus, K, Lindahl, B.D, Dahlberg, A. (2017). Retention of seed trees fails to lifeboat ectomycorrhizal fungal diversity in harvested Scots pine forests. *FEMS microbiology ecology*, 93(9). DOI: <https://doi.org/10.1093/femsec/fix105>
- Wallander, H, Johansson, U, Sterkenburg, E, Durling, M.B, Lindahl, B.D. (2010). Production of ectomycorrhizal mycelium peaks during canopy closure in Norway spruce forests. *New phytologist*, 187(4), 1124-1134. DOI: <https://doi.org/10.1111/j.1469-8137.2010.03324.x>