Impact of vegetation mycorrhizal type on fungal community composition in arctic tundra

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Abstract

Compared to lower latitude ecosystems, the carbon storage in (sub-)Arctic tundra soils is high. Climate change is expected to alter tundra ecosystems, specifically concerning plant community composition. Plant symbiotic interactions with mycorrhizal fungi are an important factor in soil carbon storage capacity and biogeochemical cycling, and they depend on the plant species that are present. Shedding light on the effect of vegetation composition changes on their below-ground counterparts is, therefore, an important requisite towards understanding the effect and impact of climate change on these ecosystems. The thesis is part of the Abisko Long-Term Tundra Experimental Research (ALTER) project, a long-term field experiment in subarctic Sweden focusing on the effects of vegetation and associated changes on above- and below-ground processes in tundra soils. In a sub-arctic alpine tundra heath, vegetation composition was manipulated by removing plant species with certain mycorrhizal associations. The experiment will follow the effects of this manipulation on above and below-ground biogeochemical and ecological processes over the next decades. This thesis explores the links between fungal community composition and plant mycorrhizal type, plant community composition and soil chemistry. Analysis of soil and root-associated fungal DNA was used to relate the fungal community composition at the onset of the experiment (i.e. undisturbed baseline) to the fungal community composition one year after the first plant removal, as well as to soil chemical properties and vegetation observations. We found a strong relationship between plant mycorrhizal association type and root-associated fungal community composition of 28 plant species from the study site. Moreover, vegetation community composition explained a considerable part of soil fungal community composition (42 %), suggesting a systematic link between the two. Vegetation changes simulated by plant functional group removal, however, did not significantly affect the fungal community composition after one year. Changes could be expected in the longer term but there was no evidence for a quick turnover below-ground after rapid above-ground changes.

Popular-scientific summary

Compared to warmer ecosystems further towards the equator, the carbon (C) storage in (sub-)Arctic soils is high, current estimates are at about 1300 Gt of C. With climate change warming these regions faster than anywhere else on the planet, substantial changes are expected and already underway. These changes will potentially cause the C that is stored there to be released and therefore feedback into accelerating global warming. To be able to make sound and evidence-based policy decisions when it comes to climate change mitigation, it is thus vital to have accurate estimates of C cycles, especially in the Arctic. One specific effect of global warming in the arctic is a change in the plant community composition. Most plants form symbiotic interactions with mycorrhizal fungi. These mycorrhizal relationships are characterized by the fungus living partly closely connected to or inside the plant root tissue and partly extending its mycorrhizal network further out into the soil. Like this, the fungus can help the plant to access nutrients and water from the soil and in turn receives C that the plant fixes from the air above-ground. Different fungi thereby have different nutrient acquisition strategies and therefore also affect soil C and nutrient cycles differently. Furthermore, different plant species host certain types of mycorrhizal fungi. Changes in the vegetation composition might thus affect soil C storage through changes in the soil fungi that are present.

The thesis is part of the Abisko Long-Term Tundra Experimental Research (ALTER) project, a long-term field experiment in sub-arctic Sweden focusing on the effects of vegetation and associated changes on above- and below-ground processes in tundra soils. In a sub-arctic alpine tundra heath, vegetation composition was manipulated by removing plant species with certain mycorrhizal associations. Over the next decades, the experiment will follow the effects this manipulation has on the plant community above-ground and the fungal community below-ground as well as on carbon and nutrient dynamics in the soil. The thesis specifically explores links between fungal community structures and plant community composition, plant mycorrhizal type and soil carbon and nutrient content. Therefore, the fungal community composition at the onset of the experiment was characterized and then compared to the fungal community composition one year after the first plant removal. In addition, the fungal community was related to soil abiotic variables and the plant community composition.

We found a strong connection between the plant mycorrhizal association type and the fungal community it is hosting in and close to its roots, the presence of certain plant species can therefore be assumed to be highly influential for the root-associated fungal community composition. Consequently, also the plant species composition above-ground significantly affected the soil fungal community composition below-

ground. However, with only one year of the plant removal treatment, there was no significant effect measurable on the soil fungal community. It shows that the effect of very fast vegetation changes, even though there is a strong connection between the plant species and the fungal community composition, is not immediately translated into changes below-ground. These changes might become apparent in the future and will be followed by the ALTER experiment over time.

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List of Abbreviations

ACIA	Arctic Climate Impact Assessment
ALTER	Abisko long-term tundra experimental research
AM	Arbuscular mycorrhiza
ANS	Abisko naturvetenskapliga station (Abisko Scientific Research Station)
ASV	Amplicon sequence variant
C	Carbon
DSE	Dark septate endophyte
EcM	Ectomycorrhizal
ErM	Ericoid mycorrhizal
FCC	Fungal community composition
ITS	Internal transcribed spacer
N	Nitrogen
OM	Organic matter
OTU	Operational taxonomic unit
PCC	Plant community composition
PFG	Plant functional group
SLU	Sveriges lantbruksuniversitet (Swedish university for agricultural research)

1 Introduction

Arctic soils are currently an active carbon (C) sink and also storing huge amounts of C on a global scale (Hugelius et al. 2014; Huissteden and Dolman 2012; McGuire et al. 2009). Between one third and half of the terrestrial carbon ($\sim$ 1300 Gt), or about twice as much as in the atmosphere or terrestrial plants, is estimated to be stored within arctic soils (Hugelius et al. 2014; Huissteden and Dolman 2012; López-Blanco et al. 2019; Oechel and Billings 1992; Tarnocai et al. 2009; Zubrzycki et al. 2014). This is amongst others due to slow decomposition and low respiration rates in the cold climate (Oechel and Billings 1992). In general, however, estimates of C cycles in the arctic still contain large uncertainties about stock sizes as well as the implications of climate change and the possibility of positive feedbacks in arctic systems that would further accelerate the effects of global warming (Abbott et al. 2016; Huissteden and Dolman 2012).

Climate in the Arctic is warming more than twice as fast as in other parts of the world and profound changes to ecosystems in the area are visible already and also projected for the future (ACIA 2005; Callaghan et al. 2010; IPCC 2021). It is therefore vital to understand the effects and outcomes of climate change in these ecosystems in order to address current questions with regard to the global climate crisis. Here we focus on changes in the plant community composition and its effects on soil microbiota and biogeochemical cycles. Those vegetation changes are already visible and predicted to continue in arctic ecosystems, like the sub-arctic parts of northern Sweden (ACIA 2004; Åkerman and Johansson 2008; Mekonnen et al. 2021).

1.1 Soil and root-associated fungi

Plants should be regarded as holobionts that co-exist with a variety of microbial partners in varying composition in each plant-associated niche and that are substantially influenced in their functions by this microbiome (Cregger et al. 2018; Faure et al. 2018; Hacquard 2016; Vandenkoornhuyse et al. 2015). The plant's microbiome can be seen as an ecological facilitator that provides additional genetic possibilities to its host (Vandenkoornhuyse et al. 2015). Plant-microbe interactions are therefore essential to assess the effect of plants on an ecosystem. The arctic tundra soil food-web specifically, is highly influenced by fungi (Koltz et al. 2018; Zak and Kling 2006). Therefore, changes in fungal community structure and composition will likely have wide-reaching effects on biogeochemical cycles in arctic ecosystems.

Most terrestrial plants form mutualistic associations with mycorrhizal fungi in the soil, providing them

with simple C substrates (photosynthates) and benefiting in return from increased access to nutrients and help against abiotic and biotic stressors (Ostle et al. 2009; Read 1991; Tedersoo et al. 2020). Mycorrhizal fungi also mediate the plant's interaction with the soil microbiome. These below-ground interactions are also relevant for vegetation composition, as they are the drivers of plant below-ground traits, affect plant-plant interactions and influence ecosystem processes (Tedersoo et al. 2020). Therefore, and since it is difficult to directly link above- and below-ground processes in a consistent way, explicitly including below-ground processes in studies and models is necessary in order to gain a holistic understanding of ecosystem functioning (De Deyn and Van der Putten 2005; H. Li et al. 2015; Sulman et al. 2017).

Mycorrhizal fungi can be grouped into different types, arbuscular mycorrhiza (AM), ectomycorrhiza (EcM), ericoid mycorrhiza (ErM) and orchid mycorrhiza are the most common ones, that have substantial functional differences in nutrition acquisition for their host plant, soil carbon and nutrient cycling and in their capacity to protect their host from soil pathogens (S. E. Smith and F. A. Smith 2011; Tedersoo and Bahram 2019; Tedersoo et al. 2020). Worldwide, while most vascular plant species are associated with AM fungi (>70 % Brundrett 2009; Tedersoo et al. 2020), EcM are rarer (associated with 2% of plant species), ErM only appear in plants of the Ericaceae and Diaspensiaceae family and orchid mycorrhiza only in plants of the Orchidaceae family (Tedersoo et al. 2020). The different mycorrhizal types are not homogeneously distributed globally. AM are most abundant in temperate and tropical regions, whereas in the arctic they are mostly associated with graminoid species and only occasionally with shrubs (Iversen et al. 2015). ErM and EcM however, are more abundant in arctic and alpine ecosystems (Tedersoo et al. 2020). Ericaceous plant species are common in the arctic and ErM fungi therefore as well. EcM, mostly associate with woody evergreen and deciduous shrubs (Iversen et al. 2015). EcM and ErM are better decomposers than AM and help access N and phosphorus in nutrient-poor high-latitude environments (Read and Perez-Moreno 2003). The saprotrophic abilities of EcM are suggested to ensure nitrogen (N) supply for the symbiotic plants from organic sources in those soils (Kotilínek et al. 2017). One substantial difference is that ErM are suggested to increase C sequestration in the soil while EcM appear to cause faster decomposition and consequently might reduce C stocks (Clemmensen et al. 2015).

Not all root-associated fungi form mycorrhizal associations, among other fungal functional groups are endophytic fungi (Porras-Alfaro and Bayman 2011). Endophytic fungi, in opposition to mycorrhizal fungi, are not defined over their function but their location as colonizing internal plant tissues (Porras-Alfaro and Bayman 2011). However, endophytic fungi can have mycorrhizal-like functions and play a role in plant nutrient acquisition (Huusko et al. 2017; Newsham et al. 2009; Porras-Alfaro and Bayman

2011; Toju et al. 2013). One form of root endophytes with relevance in arctic ecosystems are the dark septate endophytes (DSE; Newsham et al. 2009). They are more abundant than mycorrhizal fungi and suspected to replace their functions in polar and alpine regions when especially AM are not abundant anymore. Nonetheless, they are only scarcely studied, especially with regard to their function for plant-soil interactions, and their role in arctic ecosystems remains unclear (Huusko et al. 2017; Newsham et al. 2009; Toju et al. 2013). Furthermore, soils are harbouring additional fungal functional groups like saprotrophs with varying substrate preferences (Vries and Caruso 2016).

Root-associated fungal communities differ between soil habitats and host plants. They are less directly influenced by their hosts the less closely they are associated or connected with them. Therefore, the soil fungal community composition (FCC) is different from the FCC in the rhizosphere, rhizoplane or the root endosphere with increasing specificity as the link to the host plant gets more direct (Vandenkoornhuyse et al. 2015). Since different fungal species have different nutrient acquisition strategies, they access different parts of soil resources. This resource partitioning and dynamic interactions by microbiota, also between plant-associated niches of the same plant, may influence plant-plant interactions and plant performance (Fitzpatrick et al. 2018). The community composition with regard to fungal species fut also functional guilds (e.g. EcM instead of ErM) in a given habitat of niche could thus imply big differences when it comes to C and nutrient dynamics.

With the help of next-generation sequencing and metabarcoding technologies that are targeting fungal DNA sequences (Schoch et al. 2012) it is possible to extract DNA sequences of the entire fungal community from a sample in any ecosystem, habitat or niche fast and affordably. Thus, a comprehensive analysis of fungal communities targeting specific soil or root-associated habitats becomes feasible. Relating such fungal DNA datasets to taxonomic information, and subsequently, ecological trait information makes it possible to link fungal community characteristics of those specific habitats to ecosystem functions (Clemmensen et al. 2016; Porras-Alfaro and Bayman 2011).

1.2 Shrubification and Arctic greening - implications for plant-soil interactions

One aspect of changing vegetation that has been linked to the effects of climate change is the shrubification of arctic ecosystems. This describes a general increase in growth, abundance and biomass of tall deciduous shrubs like birch (*Betula* spp.) or willow (*Salix* spp.; Callaghan et al. 2013; Mekonnen et al. 2021). Those species were already a part of the plant community before, but as they appear to have a competitive advantage over smaller heath species under climate change conditions, they grow taller

than they used to, fill in patches that used to be dominated by other types of vegetation and grow at higher elevations. Consequently, shifting the vegetation type towards more productive shrub ecosystems (Mekonnen et al. 2021). Greening, which is used as a proxy for shrubification and describes an increase in biomass of deciduous vegetation, occurred in 27 % of the arctic with an average increase of 3.9 % in the 20 years leading up to 2020. This can be observed heterogeneously, but still forms a consistent trend throughout the circum-arctic (Mekonnen et al. 2021).

This change in vegetation composition is likely to also cause changes in the root-associated microbial community. With regard to the soil fungal community, plant species dominant in heath ecosystems have predominantly ErM associations and the advancing deciduous shrubs are more commonly associated with EcM (Read 1991; Tedersoo et al. 2020). A shift from ErM towards EcM in the fungal community would in turn have implications for biogeochemical cycles because of their different effects on C and nutrient cycling in the ecosystem (Clemmensen et al. 2021, 2015; McLaren et al. 2017; Parker et al. 2017, 2015).

However, in their recent review on shrubification Mekonnen et al. (2021) identify the role of soil microbiota and specifically potential changes in plant-fungal interactions as a research gap. Importantly, the impact of shrubification on the carbon source or sink status of the arctic is unclear (Mekonnen et al. 2018; Sørensen et al. 2018). On one hand, the increasing shrub communities sequester more C as they are more productive but on the other hand that also promotes soil respiration and therefore C losses (Mekonnen et al. 2021; Parker et al. 2015). This balance might in part be elucidated by better understanding the below-ground part of the ecosystem, specifically by assessing if and how fast soil fungal communities are altered by shrubification and whether this has downstream effects on biogeochemistry.

1.3 Plant functional group removal experiments

The ecosystem properties of plant communities can be simplified by functional traits (e.g. leaf traits or plant growth form) whereby these functional traits are used as a simple method to scale up from measurements on a plant individual level to ecosystem functions (Garnier et al. 2004). By definition of Violle et al. (2007) a plant functional trait indirectly influences plant fitness through its effect on plant performance. In that way, considering only the traits of a limited but dominating species subset in an ecosystem can be meaningfully used to assess ecosystem properties (Garnier et al. 2004). Chapin et al. (1996) showed that the use of growth form as plant functional trait in arctic systems allows predicting vegetation responses to and their effects on environmental changes and processes. Plant traits are not necessarily limited to the plant itself, as Soudzilovskaia et al. (2015) evidenced that plant mycorrhizal

association and colonization intensity can be considered a plant trait (inter-specific variability in fungal communities exceeds intra-specific variability e.g. site variation) that directly and indirectly affects C cycling.

By grouping plant species according to such functional traits, plant functional groups (PFG) can be established. PFG removal experiments are a useful tool in understanding the implications of shifts in species composition and local, non-random loss of species (Diaz et al. 2003; Wardle and Zackrisson 2005). McLaren and Turkington (2010) showed that in a grassland experiment it was the PFG removal that affected ecosystem properties and not the amount of biomass removed. PFG removal was furthermore found to affect soil abiotic properties (Wardle and Zackrisson 2005) as well as soil biota (Bender et al. 2021; Fanin et al. 2019).

Here a PFG removal experiment based on mycorrhizal association types was used to simulate shrubification in sub-arctic Sweden. More specifically, this experiment reproduces the shift in plant mycorrhizal type dominance expected from shrubification (from ErM to EcM) by selectively removing plant species associated with ErM or EcM, to observe its impacts on soil biotic (specifically FCC) and abiotic properties. After removing plant mycorrhizal groups, the remaining species should eventually compensate for the removed biomass, even if they were not the dominant species before the removal (Wardle and Zackrisson 2005).

For the thesis, metabarcoding of fungal DNA sequences was used to characterize the fungal community composition of soil and root samples from the experimental site. First, to confirm that relationship in our study system, we assessed whether root-associated fungal communities in the rhizoplane and root endosphere were shaped by the mycorrhizal type of their host plant. We then related the soil fungal community to the plant community composition (PCC) to elucidate whether distinct plant communities within a homogeneous ecosystem also host distinct soil fungal communities. This will also provide a baseline for future measurements within the ALTER experiment. By manipulation of PCC, we then tested whether removing host plants of ErM and EcM would change the soil fungal community composition within a short time frame of one year by e.g. favoring other fungal functional groups (notably DSE, suspected of replacing AM at high latitudes). Finally, the soil fungal community before and after the plant mycorrhizal group removal was related to soil chemical variables to reveal possible effects of a plant or fungal community composition shifts on geochemical processes.

2 Material & Methods

This thesis is part of the Abisko Long-Term Tundra Experimental Research (ALTER) project, a long-term field experiment in northern Sweden focusing on the effects of vegetation and associated changes on above- and below-ground processes in tundra soils. In a sub-arctic alpine forest-tundra ecotone, vegetation composition was manipulated by removing plant species with certain dominant mycorrhizal associations. The experiment will follow the effects of this manipulation on above and below-ground biogeochemical and ecological processes over the next decades. Here, specifically, the soil fungal community at the onset of the experiment and after one year of treatment was characterized by metabarcoding of the ITS2 region and related to soil chemistry data and the vegetation cover before the manipulation. In addition, the fungal colonization status of the vascular plant species in the experimental area was assessed.

2.1 The ALTER experiment

2.1.1 Site description

The study area is an alpine forest-tundra ecotone in the sub-arctic northern part of Sweden. It is located 3 km from the Abisko Scientific Research Station (ANS; 560 m a.s.l., 68°19021N, 18°50040E). The mean annual temperature in Abisko is 0.2 °C, July is the warmest month with a mean temperature of 11.9 °C and February is the coldest month with −10 °C respectively, annual precipitation averages at 337 mm (ANS 2021). The bedrock at the study site is schist with no continuous permafrost layer. The organic soil horizon is 8 - 15 cm deep (Rousk and Michelsen 2017) and the soil pH is slightly acidic but close to neutral (5.9 ± 0.5; measured in 2019). The experimental plots were established in an arctic-alpine mesic tundra heath near Báddosdievvá (Fig. 1; 516 ma.s.l., 68°1938N, 18°5100E) on a north-facing slope at the mountain birch treeline. The vegetation at the study site is dominated by evergreen dwarf shrubs with ericoid mycorrhizal association such as *Empetrum nigrum*, *Vaccinium uliginosum* and to a lesser extent *V. vitis-idaea*, *Andromeda polifolia* and *Cassiope tetragona*. Species with ectomycorrhizal association are deciduous small shrubs mostly represented by *Betula nana* and various *Salix* species. Below the treeline, forests in the ecotone are dominated by *Betula pubescens* with an undergrowth of *Vaccinium myrtilus* and *V. vitis-idaea*, *Cornus* sp. and *Equisetum* sp. Table 1 shows a list of the dominant plant species found in the vicinity of the experimental plots and their mycorrhizal type (i.e. most common type of mycorrhizal association for each species; Akhmetzhanova et al. 2012; J. L. Harley and E. L. Harley 1987; Öpik et al. 2010) as well as the cover for the species subject to removal within the experimental plots.

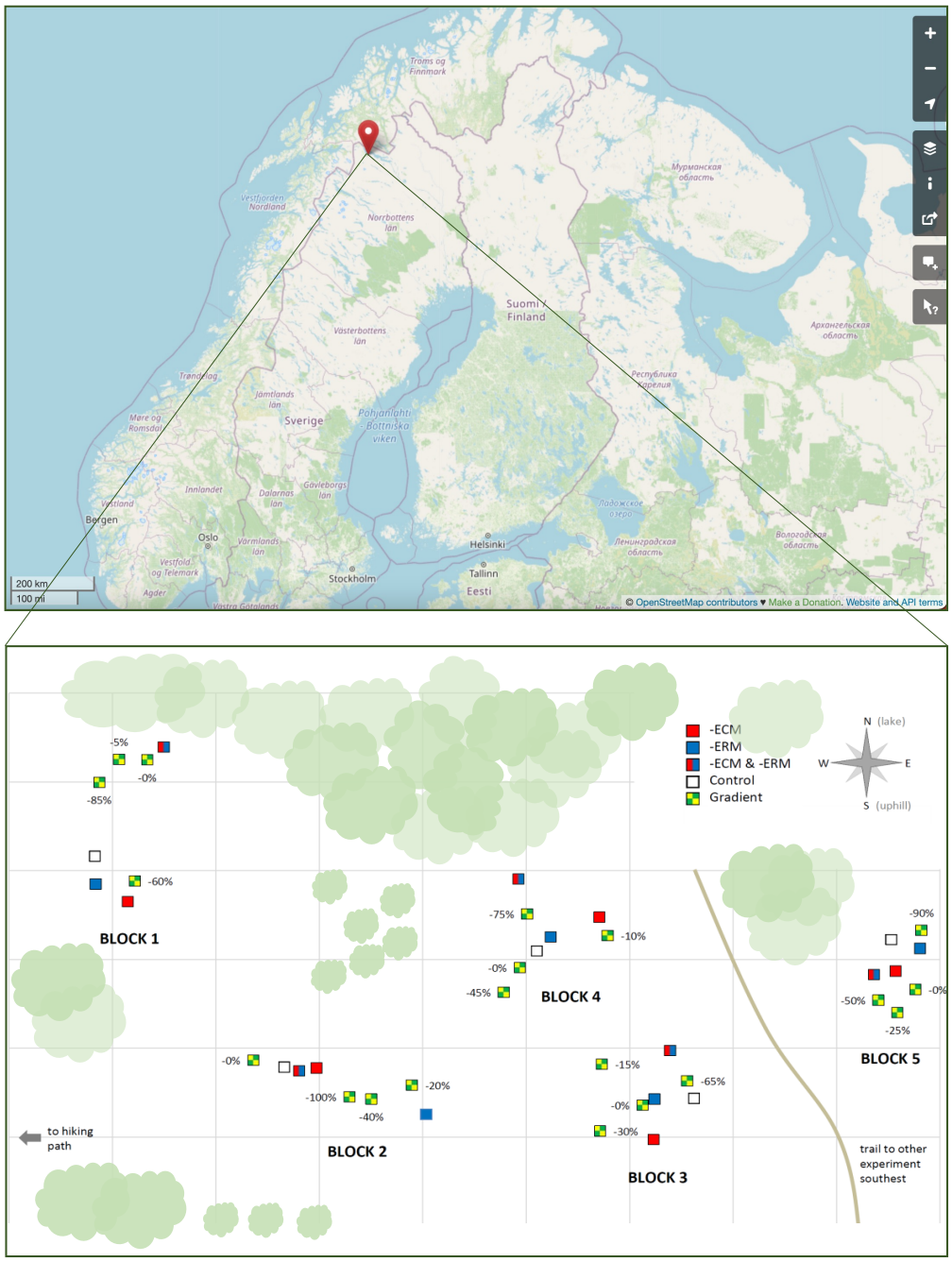

Fig. 1: The top panel depicts a map showing the location of the ALTER field site in Abisko in northern Sweden, north of the polar circle (*OpenStreetMap* 2021). The bottom panel shows a depiction of the experimental setup in the field. Each treatment plot, i.e. ericoid and/or ectomycorrhizal plant removal and gradient is replicated within five blocks.

2.1.2 The experimental setup and treatments

In August 2018, five spatially replicated blocks were established to host the experimental plots. The blocks are situated within an area of approximately 4 ha and located between 20 and 100 m apart from each other. Within each block, 8 plots (2 x 2 m area, n = 40) were placed $\geqslant$ 1 m apart from each other. While the blocks were chosen to represent vegetation variability of the ecosystem, the plots within each block were chosen to have similar vegetation composition and topography. Each plot was then further divided into 4 subplots (1 x 1 m) and geographical coordinates (latitude, longitude and altitude) were recorded (Trimble, RS8 GNSS System, Raunheim, Germany).

Four plots in each block were randomly assigned one of the mycorrhizal type removal treatments. Those were control (CTL, no plant removal), ectomycorrhizal plant species removal (ECM), ericoid mycorrhizal plant species removal (ERM) and combined removal of ecto- and ericoid mycorrhizal plant species (EE, see Tab. 1 for a list of the respective species). Plant removal consisted of pulling up the plant stems, including their below-ground stem and roots for small individuals, and clipping the above-ground biomass for larger, woody individuals. The biomass was collected separately for each plant species, and dried (40°C) until constant weight before weighing.

The removal of plants is destructive, particularly so when removing ericoid mycorrhizal plants from an ericaceous-dominated heath. A biomass removal gradient was therefore designed to assess the effect of the removal and control for the entailing disturbance to the ecosystem. The removal levels were divided into no removal (0 %), moderate removal with low disturbance (5 - 25 %, see exact removal level per block in Tab. S1), medium removal and disturbance (30 - 60 %, Tab. S1) and high removal and disturbance (65 - 100 %, Tab. S1). One level of each group was randomly assigned to one of the remaining four plots in each block. A 2 x 2 m grid with 20 x 20 cm cells was used, where one cell represents 1 % of the plot surface. The number of cells corresponding to the respective removal level was quasi-randomly distributed in the plot (ensuring homogeneous distribution over the four sub-plots) and all vascular plants were removed in the respective cells. The biomass was collected without separating per species, and dried and weighed as described above.

Block 1 and 2 were established in late August 2018 at the very end of the growing season. Blocks 3, 4 and 5 were established in July 2019. At this time blocks 1 and 2 were also clipped a second time. Since the initial clipping in blocks 1 and 2 took place right at the end of the growing season and not much growth occurred until then, July 2019 will be considered as the onset of the experiment. All plots were clipped a second time in August 2019, and again one year later in 2020 to eliminate regrowth.

Table 1: List of species present at the study site and their type of mycorrhizal association. Mycorrhizal association was assigned via literature (Akhmetzhanova et al. 2012; J. L. Harley and E. L. Harley 1987; Öpik et al. 2010) and confirmed with microscopy of stained roots. Percentage cover of the to be removed species was assessed using a frame (1 x 1 m) with 10 x 10 cm grids in each plot and calculated as $\mathrm{cover}\% = \#\ \mathrm{grids\ present}/400\mathrm{grids} \times 100\%$. Values presented in the table are averaged over all plots.

Mycorrhizal type	Species	Cover in experimental plots [%]
Ectomycorrhiza	*Betula nana* L.	32.3
	Dryas octopetala L.	3.18
	Polygonum viviparum (L.) Delarbre	4.44
	Salix glauca L.	0.25
	Salix hastata L.	0.90
	Salix myrsinites L.	2.05
	Salix phylicifolia L.	2.69
	Salix reticulata L.	3.48
Ericoid mycorrhiza	*Andromeda polifolia* L.	67.6
	Cassiope tetragona D.Don	34.2
	Empetrum nigrum L.	96.2
	Rhododendron lapponicum (L.) Wahlenb.	6.80
	Vaccinium uliginosum L.	90.7
	Vaccinium vitis-idaea L.	27.7
Arbuscular mycorrhiza	*Astragalus frigidus* Bge.	
	Bartsia alpina L.	
	Calamagrostis lapponica (Wahlenb.) Hartman	
	Festuca ovina L.	
	Nardus stricta L.	
Arbutoid mycorrhiza	*Arctostaphylos alpina* (L.) Nied.	
	Pyrola rotundifolia L.	
	Silene acaulis (L.) Jacq.	
No mycorrhiza	*Carex bigelowii* Torr. ex Schwein.	
	Carex vaginata Tausch	
	Equisetum pratense Ehrh.	
	Pinguicula villosa L.	
	Rubus chamaemorus L.	
	Tofieldia pusilla (Michx.) Pers.	

Experimental plots were trenched at the onset of the experiment and twice the year after that, to cut off plant roots and inhibit the growth of roots and mycorrhiza into the experimental plots. Trenching was carried out each time by cutting at the edges of the plots, once with a spade and then twice with a breadknife.

2.1.3 Root fungal community assessment

At the start of the experiment in 2018, a dozen individuals of each species listed in Table 1 were collected outside the experimental plots with as much of their below-ground biomass as possible. The roots of these were divided between three activities. A part of the roots was stained with ink (Phillips and Hayman 1970) and microscopically analyzed for their mycorrhizal or endophytic partners. Colonization with ecto-, ericoid, arbuscular or arbutoid mycorrhiza was recorded as well as dark-septate or fine endophyte presence. The rest of the root biomass was prepared for fungal ITS sequencing as described in section 2.2 whereby part of the roots was washed with ddH_2O and the other half additionally dipped in bleach (5% NaClO) before being freeze-dried. The ddH_2O samples depict the fungal community present both in the root endosphere (i.e. within root tissue) and the rhizoplane (i.e. directly on the root surface) of the respective plant species, whereas the bleached samples represent only fungal sequences that are present in the root endosphere.

2.1.4 Plant species cover in the experimental plots

Before beginning the plant removal treatment, the cover of the species of interest (i.e. the species targeted by the removal treatment) in the ECM, ERM and EE treatment plots was assessed (see Tab. 1). To that end, a frame (1 x 1 m) with a 10 x 10 cm grid was placed on each sub-plot and presence or absence of the targeted species in each grid was recorded. An index for the total cover of each species per sub-plot was calculated with: $\mathrm{cover}\% = \#\ \mathrm{grids\ present}/400\mathrm{grids} \times 100\%$. EcM plant cover was on average 13.1 % (σ 5.5) and ErM plant cover 86.9 % (σ 5.5), the most abundant ones being *Betula nana* (EcM) and *Empetrum nigrum* (ErM) appearing in 32 % and 96 % of the total plot area respectively. Results for each species averaged over all plots, are presented in Table 1.

2.1.5 Soil sampling for fungal DNA and abiotic variables

Soil samples were taken from all experimental plots on July 18, 2019 (except gradient plots in the zero removal group) and August 21, 2020. Sampling for soil chemistry was carried out with apple corers

(∅ 1 cm) in the organic layer to a depth of 5 - 8 cm once in the middle of each subplot in both years (4 cores in total per plot and sampling). Soil from the edges of these four holes per plot was then sampled for the fungal DNA analysis with bleach- and ethanol-cleaned tweezers into a single 1.5 ml microcentrifuge tube, which was snap-frozen in dry ice and kept at -80 °C until DNA extraction. The four cores for soil chemistry analysis were homogenized by hand, and a sub-sample was assessed for soil moisture (oven drying at 105°C for 48 h) and organic matter content (weight loss on ignition at 475°C for 4 h). Water extractions (3 g of soil into 75/ 42 ml ddH2O, orbital shaking at 250 rpm for 2 h, filtering on Munktell (Ahlström-Munksjo 3hw 8-10µm)/ Whatman (Whatman 201 7-14µm) filters, for 2019 and 2020, respectively) of other sub-samples were used for measuring pH (Mettler-Toledo, SevenCompact for 2019 and MP220 for 2020 samples, Greifensee, Switzerland) as well as nitrate (NO3) and nitrite (NO2) and ammonium (NH4) content with a Lachat Flow Injection Analysis System (Hach, Loveland, United States) at Oulanka research station. Total organic carbon (TOC) and total nitrogen (TN) in the water extracts were measured after filtering and acidifying (0.45 µm Filtropur S, Sarstedt AG & Co., Germany; 50 µl 20 % HCl to 20 ml filtrate) by high-temperature catalytic oxidation (HTCO) using a Shimadzu TOC-V CPH analyzer with a TN unit (Shimadzu Corporation, Japan).

2.2 Fungal metabarcoding

In summary, DNA was extracted from soil and root samples and the ITS2 barcoding region was targeted by PCR and sequenced on a PacBio Sequel RS1 system. Fungal 'species' (amplicon sequence variants, ASVs) were inferred using the DADA2 pipeline, taxonomy assigned based on the UNITE 8.2 database, and quality control was carried out based on positive and negative controls.

2.2.1 DNA extraction and molecular work

For 2019 samples, DNA was extracted (DNeasy Power Soil Kit (Qiagen, Venlo, The Netherlands) once for each plot from the homogenized soil sample (c. 100 mg FW frozen soil) described in section 2.1.5 and from freeze-dried roots. Fungal ITS2 amplicons were generated at WSL Birmsensdorf in spring 2020 from root samples of all plant species present in the experiment and for 2019 soil samples from all experimental plots (except gradient plots with zero removal) and afterwards sequenced at SciLifeLab Uppsala. This was finished before the start of the thesis.

For 2020 soil samples, I extracted DNA and generated fungal ITS2 amplicons in February 2021 at SLU in Uppsala in two technical replicates for each plot. These technical replicates were kept separated

throughout the whole preparation from DNA extraction to sequencing. Frozen soil samples from 2020 were freeze-dried because of practical constraints (for DNA analysis after freeze-drying see Castaño et al. 2016) and homogenized by bead-beating in Precellys 15 ml dry hard tissue grinding tubes, after which DNA was extracted from c. 100 mg freeze-dried soil using the DNeasy Power Soil Kit. Past this initial difference in DNA extraction, the sample preparation for amplicon sequencing for 2019 and 2020 samples followed the protocol by Clemmensen et al. (2016).

DNA concentrations were measured with an ND-1000 spectrophotometer (NanoDrop, Thermo Fisher Scientific, Waltham, United States), then the extracts were diluted to 5 ng μl^{-1}. Polymerase chain reaction (PCR) conditions for amplification of the ITS2 region were optimized with regard to dilution and cycle number (see initial PCR conditions in Tab. S2). The goal after optimization was for the PCR product to only show a very weak band on the electrophoresis gel to minimize over-representation of short or more abundant sequences in the amplified sample (see optimized PCR conditions in Tab. S4 & S3). Individually tagged PCR ITS2 primers (Tab. S2), identified as the most universally applicable fungal DNA barcode marker by Schoch et al. (2012), were used for each sample to allow demultiplexing the fungal sequences per sample after sequencing the pooled sample (Clemmensen et al. 2016).

The PCR products for each sample were then cleaned of remaining PCR reagents and primer dimers with a magnetic bead solution (AMPure, Beckman Coulter, Indianapolis, United States) before measuring DNA concentration with a Qubit 1.0 fluorometer (Thermo Fisher Scientific, Waltham, United States). After that, the amplicons from each sample were equimolarly pooled into a sequencing library. The pooled library was then cleaned with the CyclePure Kit (Omega Bio-tek, Norcross, United States), and its DNA concentration, quality and size distribution were assessed by liquid electrophoresis on an Agilent 2100 BioAnalyzer (Agilent, Santa Clara, United States). Sequencing of the pooled amplicon library was carried out with the PacBio Sequel RS1 System at SciLifeLab Uppsala using one SMRT-cell for samples from 2019 and one for 2020.

2.2.2 Bioinformatics processing

Raw reads as received from the PacBio sequencing were run through the SCATA pipeline (Brandström Durling et al. 2011) in order to obtain tag mappings (i.e. which read belongs to which sample) for all the sequences in the pooled library, as other demultiplexing options resulted in higher data loss. These tag mappings were used to demultiplex the raw reads into separate FASTQ files with a Python script (Simone 2020). Afterwards, the reads were re-oriented to 5'-3' when necessary with seqkit (Shen et al.

2016) and the primers were removed with cutadapt (Martin 2011). Subsequent fungal 'species' inference and data cleaning followed the workflow as proposed by Callahan et al. (2016b) adapted for fungal ITS amplicons.

First, the R package DADA2 (Callahan et al. 2016a) was used for filtering, 'species' inference and chimera removal. Sequences were filtered with DADA2 *filterAndTrim* to remove those with more than one 'expected error' (maxEE=1) and trimmed whenever a low-quality base was encountered (truncQ=2). Sequences were not truncated to a certain length as in Callahan et al. (2016b) since fungal ITS sequences are biologically expected to vary in their length and the observed sequences did not exceed expected lengths (Clemmensen et al. 2016). Species inference in DADA2 (i.e. extracting biologically relevant sequences from the dataset) is based on a unique set of error rates calculated for the dataset which are used as a template for partitioning the amplicon reads. Compared to the construction of operational taxonomic units (OTU), which clusters sequences that are more similar than a certain dissimilarity threshold into an OTU, this process produces amplicon sequence variants (ASVs) on a single nucleotide difference level. Such ASVs can be compared across datasets and thus offer a more precise and ecologically comparable way of identifying 'species' through DNA sequencing (Callahan et al. 2017). The ASVs were then assigned taxonomy using the DADA2 implementation of the RDP naïve Bayesian classifier (Q. Wang et al. 2007) with the UNITE v8.2 general FASTA release (Abarenkov et al. 2020).

The dataset was then further processed with functions from the phyloseq R package (McMurdie and Holmes 2013), to assess the need for data normalization. First, the sequencing depth (i.e. number of reads per sample) was checked for correlations with the experimental design variables, or for the soil sequences with the abiotic soil variables. For the soil data, neither block nor treatment had a significant effect on the read length, i.e. sequencing depth was independent of the experimental design, but the interaction between block and treatment was significantly associated with the sequencing depth ($p = 0.012$, Tab. S5). There was a weak but significant ($p = 0.042$, $r = 0.198$, Tab. S6) correlation between sequencing depth and NO3 & NO2 per g dry soil but no correlation with any of the other soil variables. Sample origin of the root samples (i.e. endosphere or rhizoplane+endosphere) did not significantly influence the sequencing depth. Overall, the weak associations of sequencing depth with some variables were not sufficiently consistent to justify introducing additional variation into the dataset while controlling for it with e.g. rarefactions (Fig. S1), and the sample sizes were instead normalized by calculating proportional abundances within each sample (= reads of ASV in the sample/total number of reads in the sample; McMurdie and Holmes 2014).

2.2.3 Positive and negative controls

Prior to sequencing, a mock community with sequences of known lengths was added to the amplicon library to assess a potential bias in read lengths after the sequencing (based on Castaño et al. 2020). Within this mock community, there was a negative correlation (r = -0.88, p = 0.004) between abundance and length of the sequence. Read numbers were thus significantly lower for longer sequences. This read length bias fits what the authors found in their trial study for PacBio sequencing, although they also found that other sequencing technologies had an even bigger bias (Castaño et al. 2020). We decided against adjusting the abundance of ASVs based on their read length as such a procedure and its possible biases have not been thoroughly evaluated yet.

Non-fungal and unassigned sequences were filtered from the dataset as well as potential contaminants. This was carried out based on four extraction blanks for each extraction and two PCR blanks from 2020 and one blank from 2019. Blanks from 2020 had very low read counts, but the blank from 2019 did not (see Fig. S2). Potential contaminants from 2020 were identified *in silico* using the combined frequency and prevalence approach from the R package decontam (Davis et al. 2018) with the default threshold (0.1), identifying five contaminant taxa that were removed. The algorithm from decontam requires several negative controls and thus could not be used for 2019. Instead, contaminants in 2019 were identified as the most abundant ASVs in the blank (> 5 % of reads in the blank, as in Mackelprang et al. 2017 and Monteux et al. 2018). Six taxa (representing 1.4 % of the dataset) were identified and consequently removed from the whole dataset, overall removing 1.63 % of reads through the entire decontamination process.

2.2.4 Post-processing

To keep resolution at the species level while simplifying the dataset, ASVs that were assigned to the same fungal species were condensed into one entry. After assuring high correlation between the two technical replicates from 2020 using a mantel test (r = 0.9421, P = 0.001; R function *vegan*, Oksanen et al. 2012), they were merged to avoid pseudoreplication. This cleaned ASV or fungal 'species' dataset was then further processed in combination with the FungalTrait database to assign a functional guild (i.e. primary lifestyle) to the genera identified in the samples following the proposed workflow by Põlme et al. (2020).

2.3 Statistical analysis

Distance-based and multivariate methods were used to relate root-associated FCC to the mycorrhizal association type of their host plant, soil FCC to the species composition of the plant community, assess an effect of the plant mycorrhizal type removal treatment on FCC, and explore relationships between soil abiotic variables and the fungal community.

2.3.1 Root fungal community analysis

Using fungal sequences obtained from roots of plant specimen collected in the area of the experimental plots, plant species-specific fungal communities were analyzed. Principal coordinate analysis (PCoA) using Bray-Curtis distance (Bray and Curtis 1957) as a dissimilarity measure was carried out first with functions *cmdscale* and *vegdist*, respectively (R package *vegan*; Oksanen et al. 2012) to assess differences in FCC between the mycorrhizal association types and sampling origins (i.e. root endosphere or rhizoplane) respectively. Statistical relevance of these differences was assessed using a multivariate generalized linear model, implemented in the *manyglm* function of the R package *mvabund* (FCC $\sim$ Mycorrhizal Type + Sample Origin; Y. Wang et al. 2012), with negative binomial distribution and the default PIT-trap resampling (999 iterations) for ANOVA purposes. Abundances of functional fungal guilds (primary lifestyles; Põlme et al. 2020) for the 30 most abundant fungal genera in each plant species were calculated and visually compared.

2.3.2 Vegetation cover and soil fungal community analysis

Soil fungal communities and vegetation cover, as well as plot coordinates (representing a possible spatial effect), were related to each other using PCoA with Bray-Curtis distances for the fungal and plant community dissimilarity matrixes and euclidean distances for the plot coordinates. Quantification of block or treatment effects on the fungal community was done with permutational multivariate analysis of variance (PerMANOVA) using the *adonis* function in R package *vegan* (Oksanen et al. 2012). After checking for homoscedasticity (function *betadisper* in *vegan*), P values were obtained by using 999 permutations. Variances were homogeneous across blocks and treatments in 2019 and across treatments in 2020 but not blocks, this violation of PerMANOVA assumptions should not affect our conclusions.

To judge the role of spatial variation, one PerMANOVA (*adonis* function in *vegan*; Oksanen et al. 2012) was run with block and treatment as fixed factors (FCC $\sim$ Treatment + Block), while the treatment effect itself was tested using treatment as a fixed factor and constraining permutations within

blocks (*strata* argument in *adonis*; FCC ~ Treatment, strata = Block). Since the prerequisite of homoscedasticity was not met for PCC, relationships between that and the experimental design variables were assessed using a multivariate generalized linear model (*manyglm*: PCC ~ Treatment + Block; Y. Wang et al. 2012).

Correlations of the dissimilarity matrices of the fungal communities of 2019 and 2020 with the plant community from 2019, plot coordinates, and each other were calculated using mantel tests (Oksanen et al. 2012). Correlations between abiotic soil variables and the ordination spaces for soil fungal communities from both years and the initial plant communities were tested with the *envfit* wrapper (Oksanen et al. 2012). Relative abundances of functional fungal guilds (primary lifestyles, Põlme et al. 2020) within each treatment and year were calculated and visually compared.

To be able to rule out that effects of the mycorrhizal type removal treatment were only caused by the disturbance, PerMANOVA was used to also assess the effect of the amount of biomass removed in the first year (2019) on FCC in the next year (2020). To that end, the FCC in the removal gradient plots was related to the amount of biomass removed (i.e. removal gradient 0 - 100 %) and the removal category (i.e. none, moderate, medium, high; FCC ~ Removal Gradient + Removal Category; Oksanen et al. 2012).

All computational work, except the demultiplexing as described in section 2.2.2, was done in R version 4.0.4 (R Core Team 2021) and all plotting with the help of R package *ggplot2* (Wickham 2016). The respective scripts were stored and versioned in a git repository and will be made publicly available upon publication in a peer-reviewed journal.

3 Results

3.1 Initial condition - before treatment

3.1.1 Root associated fungi

The fungal community composition differs significantly between plant species associated with different mycorrhizal types and between the root endosphere and rhizoplane (*manyglm*: $P = 0.001$ and 0.013 respectively; Fig. 2, Tab. S7). The effect of plant species and interactions between the terms could not be tested for a lack of replicates and therefore degrees of freedom. Visual assessment of the ordination plot (Fig. 2) suggests that ectomycorrhizal plants host fungal communities that are distinct from fungal communities of plants associated with other mycorrhizal types. Furthermore, FCC between the root endosphere and rhizoplane on the one hand, and within the root endosphere only on the other hand are very similar for some species and quite different for others (Fig. 2).

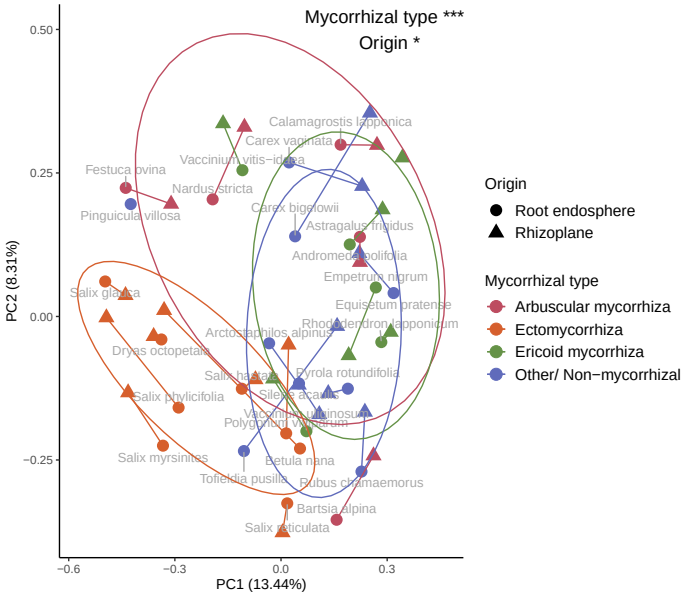

Fig. 2: PCoA with Bray-Curtis distances for the root associated fungal community. Pairs of symbols connected by a line represent the two sampling origins (i.e. root endosphere and/or rhizoplane) for a given plant species (n = 28). Ellipses represent 75 % confidence intervals. Results of a multivariate linear regression model for the effect of the plants mycorrhizal association type and origin of the sample on FCC is indicated in the top right corner (*** $P < 0.001$, * $P < 0.05$).

Visual comparison of the distribution of fungal functional groups and genera between plant species and mycorrhizal association types does not indicate a clear pattern related to the mycorrhizal type of the plant. Variation between plant species appears comparable to that between mycorrhizal association types (Fig. 3). Generally, fungal functional groups seem to not be restricted to plant species with their respective mycorrhizal association type. There are, however, more fungal genera identified as ectomycorrhizal in root material of ectomycorrhizal plants compared to other plants, particularly in the root endosphere

only, although the amount varies between plant species. Compared to ectomycorrhizal plants, arbuscular and ericoid plants appear to host more saprotrophic fungi. Here it is worth noting that FungalTraits does not attribute ericoid mycorrhizal fungi to a separate functional group but they are considered saprotrophs. Fungal genera do not appear to be distributed evenly between plant mycorrhizal types as well as species. Some fungal genera only appear in very few plant species (e.g. *Tylospora*) while others seem to be more ubiquitous (e.g. *Mycena* and the DSE *Phialocephala*; Fig. 3).

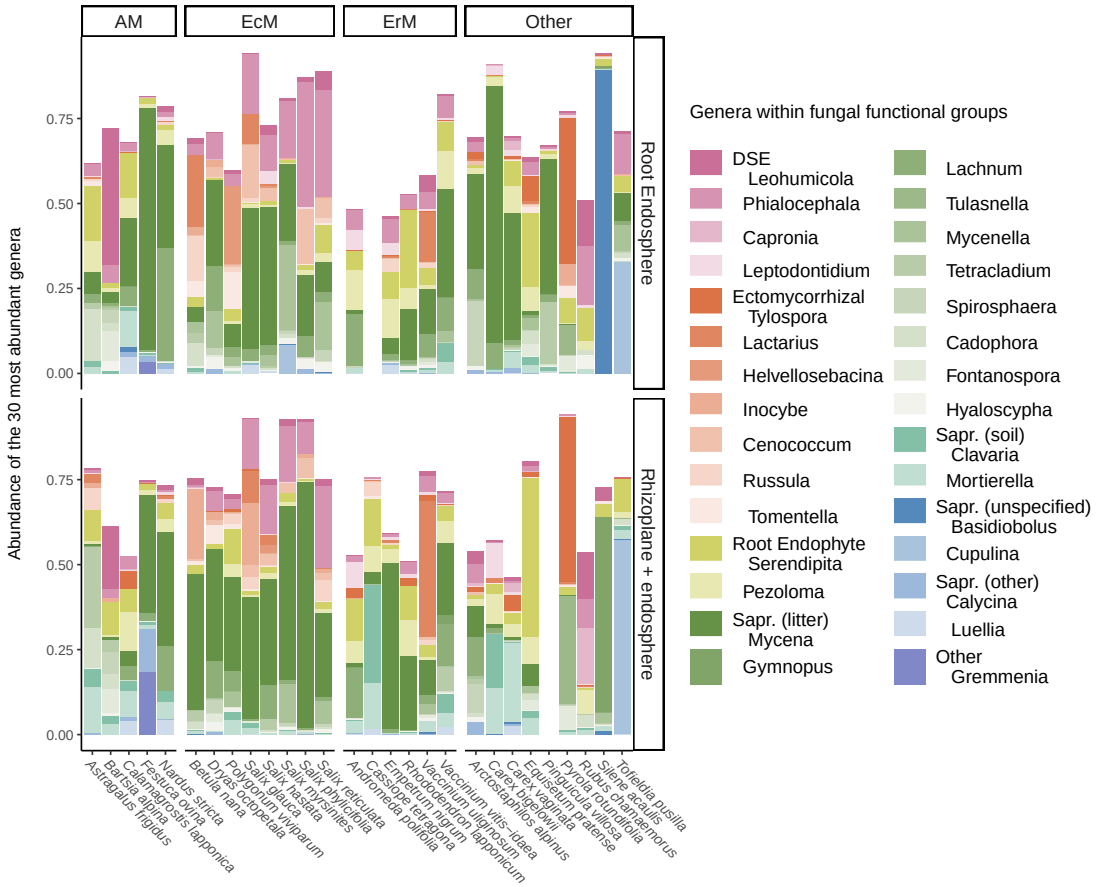

Fig. 3: Fungal functional groups (i.e. primary lifestyle; Põlme et al. 2020) per plant species (n = 28) and the respective fungal genera included in each group, based on the 30 most abundant fungal genera. The bars in the top and bottom panels show the abundance of lifestyles or fungal functional groups and genera in the plant root endosphere and rhizoplane + endosphere, respectively.

3.1.2 Plant and soil-fungal community composition

The plant community composition differs significantly between the blocks (*manyglm*: P = 0.002; Fig. 4; Tab. S7). Specifically, block 2 and 5 cluster away, reflecting that they have a different vegetation composition from blocks 1, 3 and 4 (Fig. 4). However, it does not significantly differ across treatments (*manyglm*: P = 0.941; Fig. 4; Tab. S7). Experimental plots, across treatments and within blocks, can thus be assumed to have homogeneous PCC before the onset of the experiment, reflecting the random treatment allocation within blocks with visually similar vegetation. PCC is furthermore significantly associated with pH, SOM and total N content of the soil (Fig. 4; Tab. S8).

Initial soil FCC, like PCC, does not associate with the mycorrhizal removal treatment (PerMANOVA: P >0.05, Fig. 5 A; Tab. S7), irrespective of whether block was included as a fixed factor or as to constrain permutation. When block was included as a fixed factor, it has a significant effect (PerMANOVA: F = 2.1, R^2 = 0.37, P = 0.001; Tab. S7). Fungal communities can thus be assumed to not differ between the plots that were assigned to different treatments before the start of the plant removal treatment, however like PCC they are heterogeneous between blocks. Correlation between the abiotic soil variables and FCC is significant for pH, ammonium and total N content (p < 0.05, Tab. S8; Fig. 5 A). The mantel test between the dissimilarity matrices for vegetation composition and the initial soil fungal community shows a positive and significant correlation (r = 0.42; P = 0.003, Tab. 2). Thus, 42 % of the variation in FCC can be explained with PCC. Correlation between spatial distribution (i.e. plot coordinates) and FCC is less pronounced (r = 0.25; P = 0.002, Tab. 2).

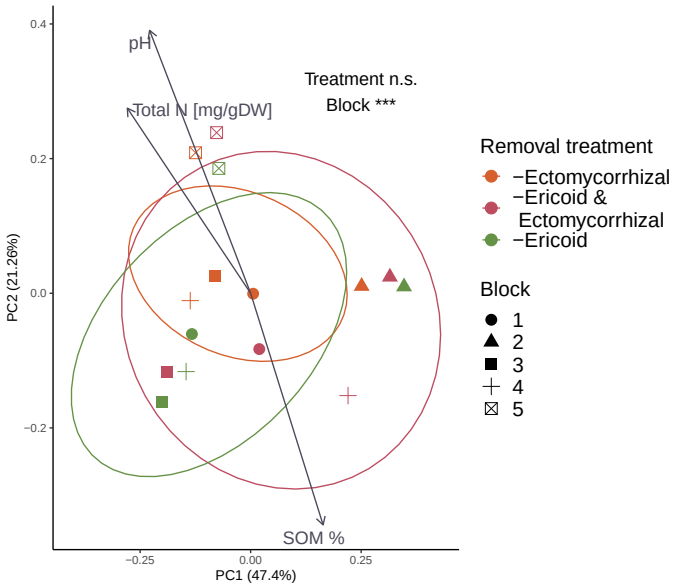

Fig. 4: PCoA with bray distances for the vegetation cover before the plant functional group removal. Each point represents the PCC at the respective location. Ellipses represent 75 % confidence intervals. *manyglm* results are indicated with asterisks (*** P <0.001, n.s. non-significant). Arrows show the relationship between the fungal community and soil variables. Only variables with a significant effect (p < 0.05) on PCC are shown.

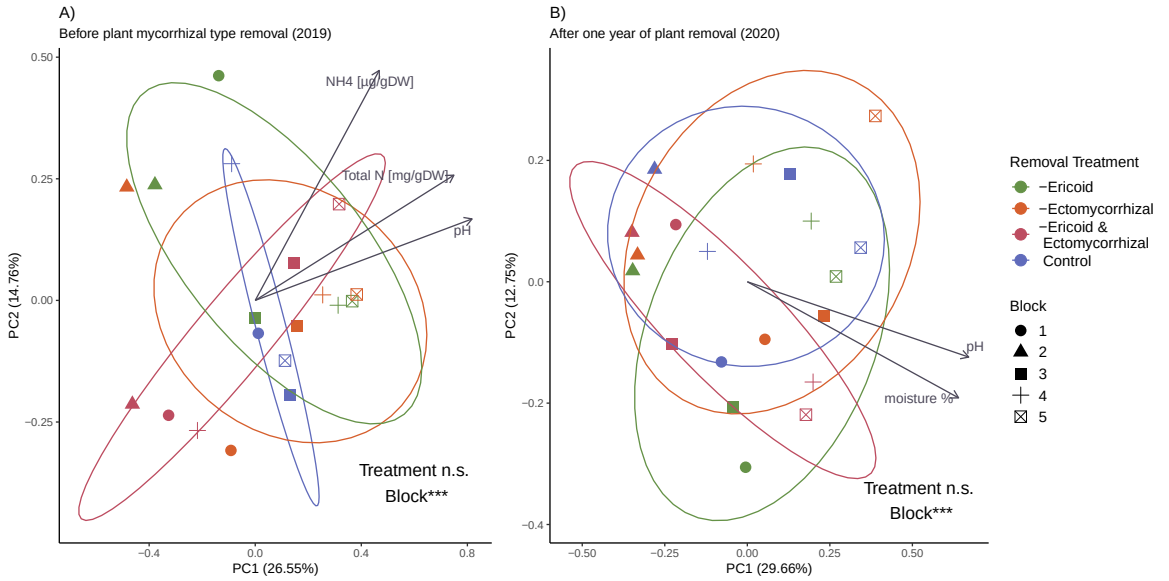

Fig. 5: PCoA with Bray-Curtis distances for the soil fungal community A) before and B) one year after the plant functional group removal. Each point represents the FCC at the respective location. Ellipses represent 75 % confidence intervals. PerMANOVA results are indicated in the down right corner (*** $P < 0.001$, n.s. non-significant). Arrows show the relationship between the fungal community and soil variables. Only variables with a significant effect ($p < 0.05$) on FCC in the respective year are shown.

3.2 Treatment effect on soil fungal community

To make sure that potential treatment effects are not merely artifacts of the disturbance caused by the plant removals, soil FCC in 2020 was related to the amount of biomass removed in 2019. There is no significant effect (PerMANOVA: $P > 0.05$, Fig. 6; Tab. S7), neither of the amount of biomass removed (removal gradient 0 - 100 %) nor of the removal category.

Like in 2019, in 2020 soil FCC does not associate with the mycorrhizal removal treatments (PerMANOVA: $P > 0.05$, Fig. 5 B; Tab. S7), irrespective of whether block was included as a fixed factor or as to constrain permutation. When block was included as a fixed factor, it has a significant effect (PerMANOVA: F = 2.4,

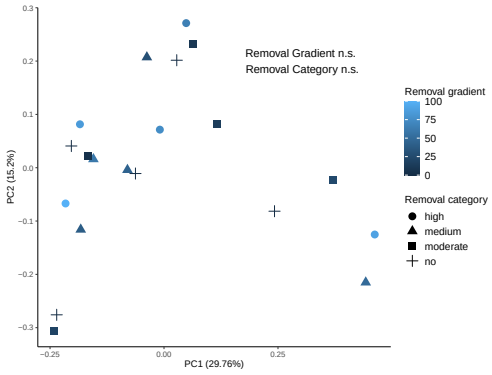

Fig. 6: PCoA with Bray-Curtis distances for soil fungal community composition in the removal gradient plots. PerMANOVA results are indicated in the down right corner (n.s. non-significant).

Table 2: Results of mantel tests relating the initial and the soil fungal community after one year of plant mycorrhizal type removal to the initial plant community distribution, spatial effects and to each other.

	r	*P*
Initial soil fungal community vs:		
Initial vegetation cover	0.42	0.003
Plot coordinates	0.25	0.002
Soil fungal community after plant removal vs:		
Initial soil fungal community	0.45	0.001
Initial vegetation cover	0.20	0.05
Plot coordinates	0.36	0.001

R^2 = 0.39, P = 0.001; Tab. S7). Correlation between the abiotic soil variables and FCC is significant ($P < 0.05$, Tab. S8) for soil moisture content and pH (Fig. 5 B).

Correlation between the dissimilarity matrixes for the initial soil fungal community and the fungal community after one year of treatment is positive and significant (r = 0.45; P = 0.001, Tab. 2), 45 % of the variation on the fungal community 2020 could be explained by the fungal community from before the removal treatment. Between the dissimilarity matrixes for the soil fungal community in 2020 and the initial vegetation cover, however, we found only a trend for a weak positive correlation (r = 0.20; P = 0.05, Tab. 2), with the P for this mantel test being above or below 0.05 depending on iterations. Thus, only 20 % of FCC one year after the removal treatment can be explained by the initial PCC compared to 42 % before the removal treatment (see section 3.1.2). The effect of spatial variability (i.e. plot coordinates) on the other hand is more pronounced than with the fungal community from before the plant removal treatment (r = 0.36 vs 0.25 in 2019; P = 0.001, Tab. 2).

When comparing fungal functional groups, a reduction in EcM fungi is observable. One year after the first removal treatment there appear to be fewer ectomycorrhizal fungi in the ectomycorrhizal removal and control plots than in the previous year. Due to our relative abundances data being semi-quantitative, it could instead be argued that the amount of litter saprotrophs increased in these plots as well as the combined removal plots, or that both increased or decreased in different proportions. In the ericoid and combined removal plots there appear to be fewer soil saprotrophs, while they increased in the control and ectomycorrhizal removal plots (Fig. 7).

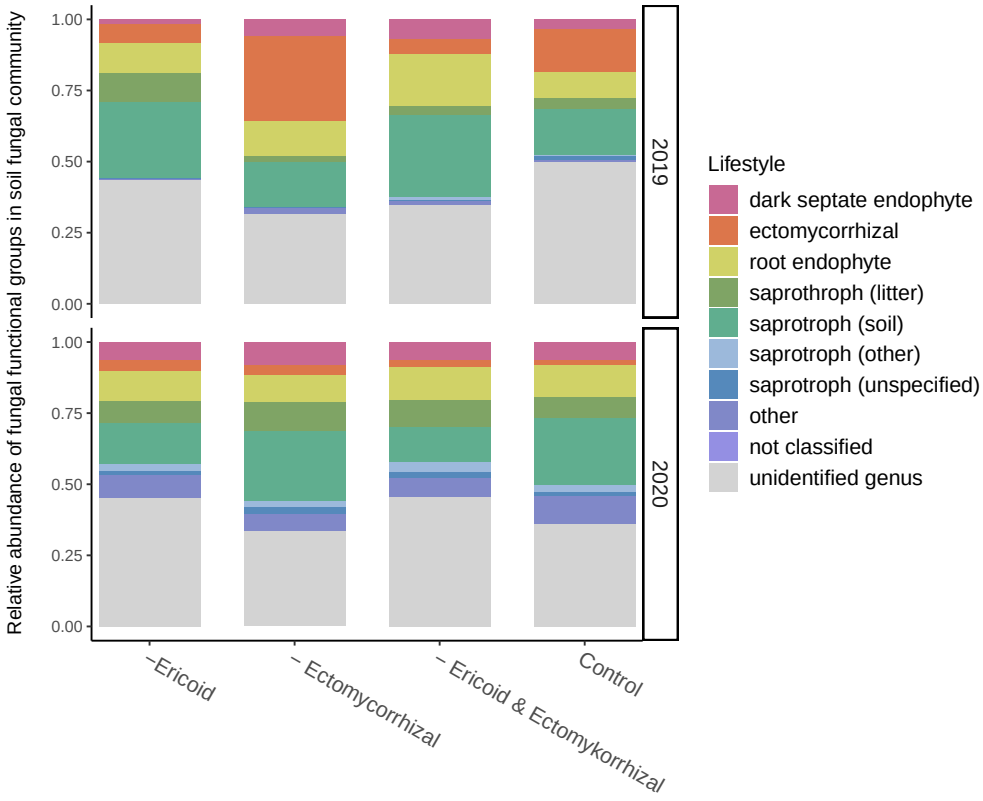

Fig. 7: Relative amount of fungal functional groups between Treatment Plots and years. Bars show the proportion of the respective fungal functional group (i.e. lifestyle; Põlme et al. 2020) in each of the treatment plots in the top and bottom panels for each year respectively.

4 Discussion

4.1 Plant mycorrhizal types and root-associated fungal community composition

By analyzing the fungal community composition in the rhizoplane and root endosphere of plant species typical in this sub-arctic tundra heath ecosystem, we could show that, as expected, the fungal communities of these plant species did differ significantly between the different mycorrhizal types and between the root rhizoplane and the root endosphere.

Generally, the importance of the host plant species in determining the microbial community structure, especially for the root endosphere (Fitzpatrick et al. 2018) is established in the literature, also specifically for the root-associated fungal community (Berg and Smalla 2009; Burns et al. 2015; Y. Li et al. 2018; Toju and Sato 2018; Toju et al. 2016). For example, Burns et al. (2015) showed that the plant species

identity was better in predicting fungal community composition in the rhizosphere (i.e. soil close to the roots that is directly influenced by their activity McNear Jr. 2013) and adjacent soil than soil chemistry, spatial location and plant relatedness. Grouping species into mycorrhizal types does not seem to mitigate this effect. Lugo et al. (2015) found that plant functional groups (growth form in this case) explained variation in fungal endophyte community (AMF and DSE) composition, especially for DSE, better or as well as phylogeny on different levels. A relationship between AM fungal colonization and plant functional traits was also described elsewhere (Davison et al. 2020, 2011; Neuenkamp et al. 2018). One explanation could be, that there are 'pools' of fungal species associated with certain plant mycorrhizal types and plant species differ in their fungal associations within these pools. Possible reasons for this species effect on FCC are that plants actively select for certain fungi via for example root exudates, that root nutrient uptake passively creates specific environments, effects of root structure, or that fungi and plants share habitat preferences (Burns et al. 2015).

The apparent difference between specifically rhizoplane and root endosphere fits well with studies showing marked differences between the fungal community in the soil and root endosphere (Cregger et al. 2018) as well as the rhizosphere and root endosphere (Fitzpatrick et al. 2018; Shakya et al. 2013). Although it should be pointed out that the fungal communities we sequenced from the unbleached samples represent a mixture of the rhizoplane and root endosphere. Vandenkoornhuyse et al. (2015) hypothesize that the plant-associated microbiome gets more host-specific the closer it is associated with the plant, the composition of the fungal community in the root endosphere can therefore be very different from the fungal community in the surrounding soil habitats which are less directly affected by the plant.

When fungal genera are grouped into functional types, differences between the plant mycorrhizal types but also on a species level become apparent as well, however less clearly. All the fungal functional groups show up in all the plant mycorrhizal types, for example, the presence of EcM fungi in the root endosphere and rhizoplane is not restricted to EcM categorized plant species. For most plant genera we only had one species represented, except within the EcM plants where a few *Salix* species are present. Looking at those it appears that variability is lower within the genus than within the mycorrhizal type. One conclusion could be that the distribution of fungal functional groups is more influenced by plant genus and/or plant species than the mycorrhizal type which would give leverage to the argument that also the 'species' composition of the fungal community is more influenced by the plant species or genus than its mycorrhizal type. There are, however, indeed more fungal species characterized as EcM in EcM plants than in other plant mycorrhizal types. Therefore, EcM fungi not only seem to have the most distinct FCC but also to be

most restricted to specific plant hosts. An increase in EcM plant species in an ecosystem would thus most likely also entail wide-reaching changes to the FCC.

In conclusion, there are significant differences in FCC between the plant mycorrhizal types but there is also considerable overlap and fungal functional guilds are not restricted to their respective host plant species. Therefore, in this case, the connection between fungal traits and plant traits is not completely linear. This could either represent a true mismatch between plant and fungal functional groups when it comes to mycorrhizal associations or reflect the fact that defining fungal functional types is not straightforward. By only looking at the primary lifestyle on the genus level as defined by FungalTraits (Põlme et al. 2020) fungal functional groups are only represented at a very high level of synthesis. This is necessary to simplify fungal lifestyles and break down their functions into ecologically comparable categories but does not realistically reflect the plasticity of fungal lifestyles (Lindahl and Tunlid 2015; Selosse et al. 2018). The plant-fungal association seems to be not as niche dependent as historically assumed, on the contrary, some fungi evidently can take on various niches (Selosse et al. 2018). For example, ectomycorrhizal and saprotrophic fungi exist on a lifestyle continuum (Lindahl and Tunlid 2015) and AM fungi can colonize leaf litter and thus access organic nutrients from dead plant material (Bunn et al. 2019). Also, functional redundancy between EcM and saprotrophic fungi concerning phosphorus cycling has been shown (Müller et al. 2020). In general, there seems to be high redundancy in functions of soil fungal species, whereby some fungal species play a disproportionately important role in maintaining soil functions, even though overall diversity appears more important than certain species (Mori et al. 2016).

4.2 Plant community composition and soil fungal community composition

Considering this strong link between plant mycorrhizal type and FCC, it is not surprising that there was also a significant relationship between the composition of the plant community and soil FCC. Differences in FCC between the blocks could largely (42 %) be explained by the variation in PCC. Spatial variation on the other hand only explained 25 % of variation in the FCC, suggesting a systematic relationship between plant and soil fungal community composition.

Such a relationship between the soil fungal and plant community has been shown before (Chen et al. 2017; Mitchell et al. 2010; Nielsen et al. 2010; Vries et al. 2018; Zinger et al. 2011). PCC seems to be a more stable and stronger predictor for the soil FCC than soil abiotic factors (Chen et al. 2017; Mitchell et al. 2010; Zinger et al. 2011). This is different for other soil microbial communities like bacteria and archaea which are less directly linked to the plants and more closely connected to soil abiotic factors

(Fierer and Jackson 2006; Nielsen et al. 2010). Here we are now able to show that FCC and PCC are interrelated, not only on a big spatial scale and across different habitat types as previously observed (Chen et al. 2017; Nielsen et al. 2010; Zinger et al. 2011), but even within a fairly homogeneous ericaceous heath that is furthermore heavily dominated by a few species (*E. nigrum* and *V. uliginosum* have > 90 % cover, Tab. 1). Accordingly, FCC seems to be influenced on a very local scale by PCC and by minor variations in non-dominant plant species.

Some factors (e.g. soil chemistry, snow depth) likely explain a share of variation in both PCC and FCC, yet it remains reasonable to assume that species presence above as well as below-ground affect each other (Ma et al. 2019; Tedersoo et al. 2020) beyond those factors, and therefore that shifts in PCC, such as those expected by shrubification, would affect FCC. While they do not necessarily imply changes in below-ground ecological functioning, shifts in soil FCC, especially if they involve EcM fungi, may alter soil functioning (Clemmensen et al. 2015). It is still a question whether and how such alterations would also affect ecosystem-scale functions in their outcome (Mori et al. 2016).

4.3 Effect of plant mycorrhizal type removal on soil fungal community composition

Before assessing or interpreting the potential effects of the plant removal treatment, we could control that the disturbance from biomass removal itself would not be a confounding factor by using the biomass removal gradient plots (Fig. 6). Nonetheless, within only one year of plant removal treatments, we could not see a straightforward and significant effect on the soil FCC. Although we confirmed that the root-associated fungal community is significantly influenced by its host's mycorrhizal type and that there is a significant link between soil FCC and PCC, our hypothesis that removing plant mycorrhizal groups would modify the soil fungal community composition should be rejected. However, the strength of the link between PCC and FCC seems to have substantially decreased between the two years, with the significant correlation between initial PCC and FCC in 2019 becoming a half as strong trend in 2020 (Tab. 2). It is however important to mention that the PCR conditions in preparation for the fungal sequencing differed between the two years, therefore comparisons between the years for FCC have to be interpreted cautiously.

One possible explanation for this absence of treatment effect could be that there is a lag between the effects the plant removal treatment is having above-ground and the below-ground effects that follow. Above and below ground systems can be partially decoupled and only below-ground factors that are closely linked to plants will be strongly affected by above-ground changes (Fanin et al. 2019). Changes

are expected after a longer time of treatments, like in Fanin et al. (2019) where plant functional group removal did significantly affect soil biota in an experiment spanning 19 years. Here it can also be pointed out, that in our study fungal DNA sequences were targeted, which implies the possibility that fungal 'species' are represented that are no longer active or even dead since DNA is fairly stable in the cold conditions of arctic soils (Carini et al. 2016). One growing season, which is also very short in these circum-polar ecosystems, was thus not enough to trigger a systematic response detectable by our DNA metabarcoding approach. Using RNA sequences, which is more expensive and laborious, would instead give a picture of the fungi that are active and alive. However, we assume the trend towards a decoupling of PCC and FCC after the plant mycorrhizal type treatment to be relevant and suggest that it will probably increase over the next decades.

When comparing the presence of fungal functional groups between the treatments and years, it seems that EcM fungal species decreased in the EcM-removal plots. However, the same seems to be true for the control plots. It could also be argued that there appear to be fewer soil saprotrophs, which contain ErM fungi in the FungalTraits database, in the ErM and combined removal plots respectively. In general, when comparing relative abundances of semi-quantitative DNA data the interpretation of increases and decreases is not straightforward, as an increase in one part could also be a depiction of a decrease in another. An increase in saprotrophic fungi and decrease in EcM fungi can however be explained with the effects of the removal treatment. It creates not only dead plant roots but also dead mycelium in the soil after the respective plant's above-ground biomass has been removed. This can then form a new habitat for saprotrophic fungi. In a study by Lindahl et al. (2010) disrupting plant roots, reduced EcM fungi drastically within days while fungal biomass in general increased, due to an increase in saprotrophic fungi (Lindahl et al. 2010). And in another example, decaying mycelium was a hot spot of microbial activity in a temperate forest (Brabcová et al. 2016). The conclusion could be that the decomposing mycelium is a specific habitat with a specific fungal community (Brabcová et al. 2016). However, the fungal functional group composition also appears fairly different in the control plots between 2019 and 2020 and there the only explanation is a minor disturbance caused by the trenching. Confidently comparing between the two years will be easier after re-doing the sequencing with identical PCR conditions. Therefore it was not possible to statistically assess a treatment effect on fungal functional groups within the time scope of this thesis.

4.4 Relationship between fungal community composition and soil chemistry

The relationship between the soil fungal communities and soil abiotic factors changed between 2019 and 2020. The initial plant and fungal community were significantly correlated with pH, SOM and zotal N content and pH, ammonium, nitrite and nitrate and total N content of the soil respectively. The soil fungal community after the first year of plant removal treatment (2020) however, was significantly correlated with soil moisture and pH. One of the long-term goals of the ALTER project this thesis is part of is to show the effects of shrubification on soil carbon and nutrient dynamics, therefore these relationships mostly provide a baseline for measurements in later stages of the experiment. Nevertheless, it is interesting to see that relationships between soil abiotic factors and the soil fungal community seem to change after the removal treatment.

The significant link between soil moisture and FCC, in 2020 but not in 2019, could be explained by the fact that the extensive plant cover removal, leaving the soil barren where it was covered before, is likely to have an effect on evapotranspiration. Before the removal treatment, the typical heath vegetation on the study site was covering the soil evenly, this could cause the moisture conditions to not be different enough between the plots before the removal treatment to statistically correlate with the soil fungal community composition.

The impact of pH, soil nutrient and carbon content and soil moisture content in determining soil fungal community composition are known (Hackl et al. 2005; Högberg et al. 2006; Mitchell et al. 2010; Xiao et al. 2020). Especially when the abiotic conditions change along a steep gradient, their influence can outcompete the host identity (Erlandson et al. 2016). However, most studies come to the conclusion that a combination of biotic (i.e. plant host identity) and abiotic factors is driving the soil fungal community composition (Chen et al. 2017; Dumbrell et al. 2010; Grayston et al. 2001; Kivlin et al. 2014; Linde et al. 2018; Zinger et al. 2011). Here it now appears that by manipulating the vegetation composition, the influence of soil N content on the fungal community decreased. Since the removal treatment is likely to decrease the N demand in the host community because dead plants do not require nutrition anymore, the mycorrhizal fungi that acquire N for their plant hosts would be at a disadvantage and the N content of the soil might have less of an influence on FCC.

4.5 Implications for biogeochemical cycles

Within the scope of this thesis, the hypothesis that changing PCC will also trigger changes in FCC with regard to species and functions can not be confirmed. Considering, however, that we could show a close link between the root-associated fungal community and a systematic relationship between PCC and soil FCC, it seems very likely that over the course of the experiment changes in FCC will become apparent. Especially if and when the remaining species in each plot, i.e. the EcM species in the ErM removal plots and vice-versa, will have compensated for the removed biomass and completely taken over the plots. At this stage, the fungal communities in the soil and especially in the root-associated habitats are expected to be affected by those changes (see sec. 4.1 & 4.2). Vegetation changes as a consequence of climate change are probably less abrupt than our selective removal, and the associated fungal community could therefore be expected to gradually change along with that. More so, since in the case of shrubification EcM plants are pivotal and those seem to harbor the most distinct fungal communities. Furthermore, considering the importance of the fungal community for the arctic food web and therefore C and nutrient cycles, changes in the above-ground parts of the ecosystems can be assumed to trigger substantial effects in below-ground biotic and abiotic parts of the ecosystem (Koltz et al. 2018).

Clemmensen et al. (2021) found forests, that have a higher degree of EcM fungal associations than heath ecosystems, to have higher decomposition rates and thus decreased carbon stocks. Ericoid species dominated ecosystems (i.e. heath), on the other hand, were accumulating more C than was decomposing, leading to the build-up of soil organic matter stocks (Clemmensen et al. 2021; Sørensen et al. 2018). The same effect was seen by Friggens et al. (2020) who hypothesized that this was caused by changes in the soil and root-associated FCC. This could be connected with different nutrition acquisition strategies of EcM and ErM fungi and a difference in turnover of their biomass. ErM fungi are associated with the long-term build-up of carbon in the soil since their necromass is more resistant to decomposition by other microbiota (Clemmensen et al. 2015).

5 Conclusions

First, we were able to confirm in our study system that the root-associated, as well as the soil fungal communities, are significantly influenced by the mycorrhizal association type and community composition of the host plants. This is also well established in the literature and provides the baseline for the assumption that a change in the plant community composition will be followed by changes in the fungal community composition. By grouping fungal species into functional guilds, however, we see that the respective guilds are not restricted to a certain type of plant host. On the contrary, fungal functions appear to be a lot less restricted to a certain niche in the soil than historically assumed. This as well fits with the recent development in the literature. It is therefore not clear to which degree changes in FCC will also affect soil functions. Manipulation of the plant community composition according to their mycorrhizal association type, did not lead to a significant response in the soil fungal community, within only one year. However the link between soil and plant community composition that was apparent before the vegetation manipulation got less strong, we hypothesize this decoupling to be a significant trend showing a change in the fungal community composition. The long-term implications of the vegetation manipulation on the fungal community composition but also biogeochemical cycles and soil microbial functions will be followed by the observations within the ALTER project.

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Data availability

All data used for this analysis as well as the respective scripts are versioned and available upon request and will furthermore be made public upon publication in a peer-reviewed journal.

Supplementary Material

Table S1: Distribution of exact biomass removal within each removal level and for each block in the gradient treatment plots.

	Removal Level [%]			
Block	No removal	moderate	medium	high
1	0	5	60	85
2	0	20	40	100
3	0	15	30	65
4	0	10	45	75
5	0	25	50	90

Table S2: Initial PCR conditions, primer sequences and reagent volumes for amplicon preparation

Initial PCR conditions			
Initial denaturation		94 °C	5 min
35 cycles of	Denaturation	94 °C	30 s
	Annealing	57 °C	30 s
	Elongation	72 °C	30s
final elongation		72 °C	7min

Primer sequences for amplicon preparation	
5' gITS7	CXXXXXXXXTGTGARTCATCGAATCTTTG
3' ITS4	CXXXXXXXTTCCTCCGCTTATTGATATGC
	Uppercase X are samples tags, see Clemmensen et al. 2016

PCR reagent volumes	
DreamTaq Green PCR Mastermix	25 µl
gITS7 & ITS4 primer mix	5 µl
Sample/ Template DNA	20 µl

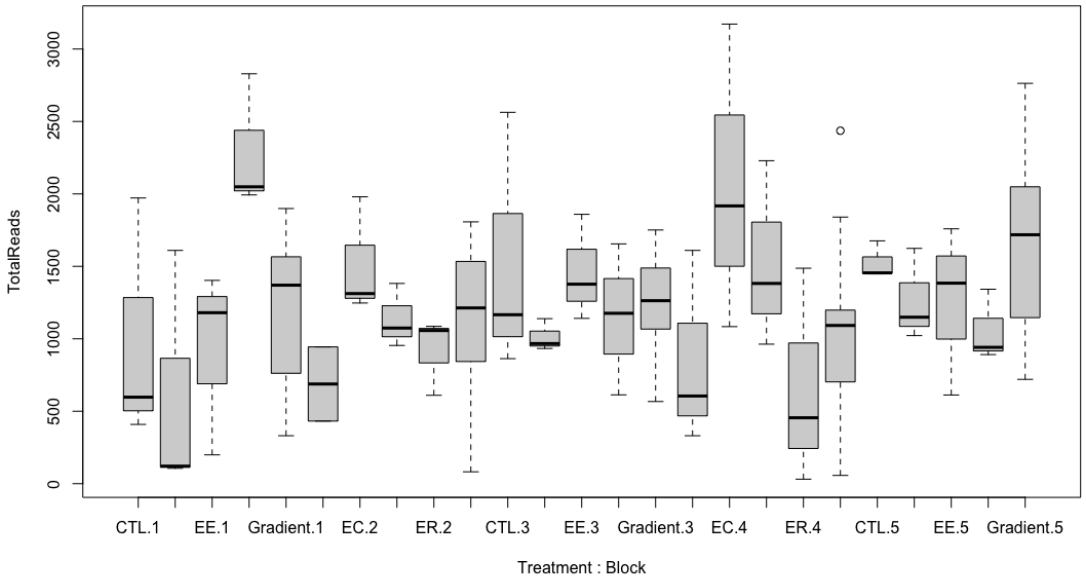

Fig. S1: Boxplots for relationship between design variables and sequencing depth

Table S3: Final PCR cycle numbers for root samples

	Bleach	ddH2O
Plant species	cycle number	cycle number
Andromeda polifolia	35	40
Arctostaphilos alpinus	37	37
Astragalus frigidus	29	29
Bartsia alpina	37	40
Betula nana	29	29
Calamagrostis lapponica	37	29
Carex bigelowii	35	35
Carex vaginata	33	
Cassiope tetragona	33	35
Dryas octopetala	37	37
Empetrum nigrum	40	
Equisetum pratense	35	35
Festuca ovina	33	33
Nardus stricta	33	29
Pinguicula	35	
Polygonum viviparum	33	31
Pyrola rotundifolia	31	29
Rhododendron lapponicum	29	31
Rubus chamaemorus	37	29
Salix glauca	35	35
Salix hastata	40	40
Salix myrsinites	35	35
Salix phylicipolia	35	35
Salix reticulata	40	
Silene acaulis	37	
Tofieldia pusilla	29	29
Vaccinium uliginosum	29	29
Vaccinium vitis ideae	29	29

Table S4: Final PCR cycle numbers and dilutions for soil samples

		2019		2020a		2020b	
Plot code	Treatment	cycle number	dilution	cycle number	dilution [ng μl^{-1}]	cycle number	dilution [ng μl^{-1}]
1A	Gradient	35		26	0.5	26	0.5
1B	Gradient	29		26	0.5	24	0.5
1C	Gradient			26	0.5	24	0.5
1D	Gradient			26	0.5	24	0.5
1CTL	CTL	29		26	0.5	24	0.5
1EC	EC	40		26	0.5	26	0.5
1EE	EE	29		26	0.5	24	0.5
1ER	ER			26	0.5	26	0.5
2A	Gradient			26	0.5	24	0.5
2B	Gradient	29		26	0.5	26	0.5
2C	Gradient	31		26	0.5	24	0.5
2D	Gradient	29		26	0.5	26	0.5
2CTL	CTL	40		26	0.5	26	0.5
2EC	EC	31		26	0.5	26	0.5
2EE	EE	31		26	0.5	26	0.5
2ER	ER	31		26	0.5	26	0.5
3A	Gradient			26	0.5	26	0.5
3B	Gradient	29		26	0.5	26	0.5
3C	Gradient			26	0.5	26	0.5
3D	Gradient	31		26	0.5	26	0.5
3CTL	CTL	31		26	0.5	24	0.5
3EC	EC			26	0.5	26	0.5
3EE	EE	31		26	0.5	26	0.5
3ER	ER	31		26	0.5	26	0.5
4A	Gradient	31		26	0.5	26	0.5
4B	Gradient			26	0.5	24	0.5
4C	Gradient	29		26	0.5	26	0.5
4D	Gradient			26	0.5	26	0.5
4CTL	CTL	31		26	0.5	26	0.5
4EC	EC	31		26	0.5	24	0.5
4EE	EE	29		26	0.5	24	5.0
4ER	ER	29		26	0.5	26	0.5
5A	Gradient	31		26	0.5	26	0.5
5B	Gradient			26	0.5	26	0.5
5C	Gradient			26	0.5	24	0.5
5D	Gradient	33		26	0.5	24	0.5
5CTL	CTL	29		26	0.5	24	0.5
5EC	EC			26	0.5	24	0.5
5EE	EE	31		26	0.5	26	0.5
5ER	ER	29		26	0.5	26	0.5

Table S5: Relationship between design variables and sequencing depth

Variable	Df	Sum Sq	Mean Sq	F	*P*
Treatment	3	169394	56465	0.1535	0.92622
Block	4	307353	76838	0.2089	0.93047
Year	1	273353	273353	0.743	0.39891
Treatment:Block	12	10257752	854813	2.3236	**0.04609**
Treatment:Year	3	2164435	721478	1.9611	0.15234
Block:Year	4	997090	249272	0.6776	0.61545
Treatment:Block:Year	11	2761620	251056	0.6824	0.73937

Table S6: Relationship between soil variables and sequencing depth

	P	r
SOM %	0.155	0.187
Moisture %	0.473	0.095
NO3 & NO2 [µg/gDW]	**0.042**	0.270
NH4 [µg/gDW]	0.142	0.198
TOC [mg/gDW]	0.603	0.070
TOC [mg/gOM]	0.896	-0.018

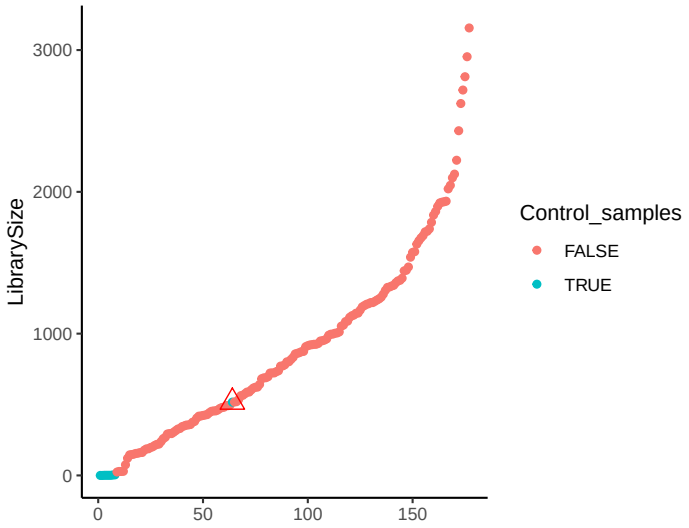

Fig. S2: Distribution of read numbers in the samples, negative controls (i.e. Blanks) are depicted in blue, the one blank from 2019 is specified with a red triangle.

Table S7: Results of the manyglm ANOVAs and PerMANOVAS

		manyglm ANOVA		**PerMANOVA**	
response variable	explanatory variable	*P*	F	R^2	*P*
root FCC	plant mycorrhizal type	0.001			
	sample origin	0.013			
PCC	block	0.002			
	treatment	0.941			
Initial soil FCC	block		2.1	0.37	0.001
	treatment		0.9	0.16	0.253
soil FCC after treatment	block		2.4	0.4	0.001
(mycorrhizal type removal)	treatment		0.8	0.13	0.289
soil FCC after treatment	removal gradient		0.4	0.02	0.992
(removal gradient treatment)	disturbance level		0.9	0.15	0.602

Table S8: Relationship between soil variables and fungal or plant community composition, correlation results with envfit wrapper after PCoA

	Initial soil fungal community		**Soil fungal community after plant removal**		**Initial plant community**	
	R^2	*P*	R^2	*P*	R^2	*P*
pH	0.70	**0.002**	0.47	**0.007**	0.82	**0.002**
SOM %	0.25	0.170	0.08	0.497	0.59	**0.017**
Dry matter %	0.10	0.499	0.45	**0.004**	0.20	0.319
Moisture %	0.10	0.499	0.45	**0.004**	0.20	0.319
NO3 & NO2 [µg/gDW]	0.31	**0.046**	0.06	0.595	0.36	0.092
NO3 & NO2 [µg/gOM]	0.31	**0.045**	0.02	0.869	0.37	0.083
NH4 [µg/gDW]	0.44	**0.029**	0.05	0.642	0.43	0.071
NH4 [µg/gOM]	0.45	**0.027**	0.05	0.690	0.43	0.068
TN [mg/gDW]	0.63	**0.004**	0.24	0.107	0.61	**0.011**
TN [mg/gOM]	0.63	**0.003**	0.15	0.257	0.63	**0.008**
TOC [mg/gDW]	0.01	0.914	0.05	0.649	0.16	0.419
TOC [mg/gOM]	0.03	0.844	0.03	0.788	0.16	0.440

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