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The impact of climate change on fine roots and root-associated microbial communities in birch and spruce forests

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Department of Botany, Institute of Ecology and Earth Sciences,
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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications that are referred to in the text by Roman numerals:

I **Parts, K.**, Tedersoo, L., Lõhmus, K., Kupper, P., Rosenvald, K., Sõber, A., Ostonen, I., 2013. Increased air humidity and understory composition shape short root traits and the colonizing ectomycorrhizal fungal community in silver birch stands. Forest Ecology and Management 310, 720–728.

II Ostonen, I., Rosenvald, K., Helmisaari, H.-S., Godbold, D., **Parts, K.**, Uri, V., Lõhmus, K., 2013. Morphological plasticity of ectomycorrhizal short roots in *Betula* sp and *Picea abies* forests across climate and forest succession gradients: its role in changing environments. Frontiers in Plant Science 4, 335.

III Ostonen, I., Truu, M., Helmisaari, H.-S., Lukac, M., Borken, W., Vanguelova, E., Godbold, D.L., Lõhmus, K., Zang, U., Tedersoo, L., Preem, J.-K., Rosenvald, K., Aosaar, J., Armolaitis, K., Frey, J., Kabral, N., Kukumägi, M., Leppälammi-Kujansuu, J., Lindroos, A.-J., Merilä, P., Napa, Ü., Nöjd, P., **Parts, K.**, Uri, V., Varik, M., Truu, J., 2017. Adaptive root foraging strategies along a boreal-temperate forest gradient. New Phytologist 215, 977–991.

IV **Parts, K.**, Tedersoo, L., Schindlbacher, A., Sigurdsson, B.D., Leblans, N.I.W., Oddsdóttir, E.S., Borken, W., Ostonen, I., 2019. Acclimation of fine root systems to soil warming: comparison of an experimental setup and a natural soil temperature gradient. Ecosystems 22, 457–472.

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Author's contribution to each paper:

I The author is primarily responsible for field data collection and processing, data analysis and writing the manuscript.

II The author contributed to field data collection and processing.

III The author contributed to data collection and processing, and preparation of the manuscript.

IV The author is primarily responsible for field data collection and processing, data analysis and writing the manuscript.

LIST OF TERMS AND ABBREVIATIONS

FAHM	Free Air Humidity Manipulation experiment
D	absorptive root diameter (mm)
SRA	specific root area (m^2 kg^{-1}), absorptive root area per unit of root weight
SRL	specific root length (m g^{-1}), absorptive root length per unit of root weight
RTD	absorptive root tissue density (kg m^{-3})
L	absorptive root length (mm)
W	absorptive root weight (mg)
B_L	branching frequency per unit of absorptive root length (also RTFL – root tip frequency per unit of root length; no mm^{-1})
B_W	branching frequency per unit of absorptive root weight (also RTFW – root tip frequency per unit of root weight; no mg^{-1})
FRB/BA	total fine root biomass per stand basal area (kg m^{-2})
aFRB/BA	absorptive fine root biomass per stand basal area (kg m^{-2})
EcM	ectomycorrhizal

1. INTRODUCTION

1.1. Climate change and its impact on northern forests

Climate change scenarios forecast a 2–4 °C increase in air temperature and a 5–40% increase in precipitation in boreal and northern temperate regions of Europe by the end of this century (IPCC, 2013; Jaagus and Mändla, 2014; Jungqvist et al., 2014; Kjellström et al., 2018; Lindner et al., 2014). These changes impact soil temperature and moisture, which are governing factors in all belowground processes. The dynamics of soil organic matter (SOM) and nutrient cycles and the resilience of the surrounding forest ecosystems are highly dependent on developments in tree fine root systems and root-associated fungal communities (Adamczyk et al., 2019; Clemmensen et al., 2015; Courty et al., 2010; Jackson et al., 1997; Kieloaho et al., 2016). Therefore, gaining knowledge about tree root and rhizosphere community adaptations to soil warming and increased humidity is crucial for evaluating the resilience of different species to climate change and predicting forest carbon (C) and nutrient fluxes.

While changes in air temperature are predicted to be highest in the coldest months in high latitudes, largest increases in soil temperature occur during the vegetation period, when there is no insulating snowcover (Jungqvist et al., 2014). Predicted annual mean soil temperature increases for three Canadian boreal forests were 1.3 °C (by year 2050) and 2.3 °C (by 2080) for the forest floor and 1.4°C (by 2050) and 2.4 °C (by 2080) for mineral soil at 34 cm depth (predicted values are averaged for the three sites) (Houle et al., 2012). The same study predicts maximum increases as high as 5.2 °C for June in 2080 for mineral soil. Similar predictions have been made for Swedish boreal forests with an average increase of about 1.3–2.5 °C for most months of the year and a maximum increase of up to 4 °C in May in the northernmost area (Jungqvist et al., 2014; Oni et al., 2017).

The main growth-constraining factors in high-latitude and high-altitude forests are short growing season, low temperatures and for the former, low nitrogen (N) availability (Jandl and Schindlbacher, 2014; Ryan, 2013). Moderate warming could therefore initially benefit tree growth through prolongation of the growing season and mobilization of nutrients (Strömgren and Linder, 2002; Wu et al., 2011; Xu et al., 2012). However, excessive or long-term warming can cause depletion of soil water and nutrient supplies and result in retardation of growth and subsequently tree die-off. For Norway spruce, a threshold from a positive to a negative growth response has been recorded at a mean June air temperature of 12–14 °C (Andreassen et al., 2006; Sidor et al., 2015). Experimental soil warming has been shown to bring about deeper rooting, a decrease in fine root biomass or an increase in fine root mortality (Leppälammi-Kujansuu, 2014; Nishar et al., 2017; Wan et al., 2004). Accordingly, an increase in fine root turnover and decrease in fine root biomass has been exhibited to co-occur with increasing mean annual temperature in large-scale latitudinal studies (Gill and Jackson, 2000;

Leuschner and Hertel, 2003). Interestingly, it has been demonstrated for Norway spruce that the soil temperatures, where maximum root growth appears, are much higher than what they experience in either natural conditions or in warming experiments (Lahti et al., 2005; Lyr and Hoffmann, 1967). The negative warming effect on fine root biomass and lifespan that has been observed at higher temperatures in field experiments has been attributed to reduced soil moisture, enhanced root maintenance respiration, changes in soil fertility and chemical composition, or increased herbivore and pathogen activity (Nishar et al., 2017; Sidor et al., 2015; Wan et al., 2004). The size and direction of warming effects on root biomass, morphology and the EcM community depends largely on initial nutrient and water availability in the soil (Johnson et al., 2006; Leppälammi-Kujansuu, 2014). For example, in high-latitude N-limited ecosystems, warming has increased EcM mycelial production and community diversity (Clemmensen et al., 2006; Treseder et al., 2016) and caused a shift towards taxa characterized by abundant extramatrical biomass and large proteolytic capacity and a reduction in taxa with high affinities for labile N (Deslippe et al., 2011). On the other hand, in an alpine forest, where warming resulted in higher inorganic N availability, an increase in the relative abundance of species that are known to tolerate high levels of N was reported (Lilleskov et al., 2011; Solly et al., 2017).

Increases in air temperature co-occur with a rise in precipitation and air humidity at high latitudes (Dai, 2006; Willett et al., 2010). Over the recent decades (1976–2004), an increase in specific air humidity (g kg^{-1}) of 1.5%–6.0% decade^{-1} has taken place over Eurasia (Dai, 2006). In the northern part of the Baltic Sea region, the largest increases in precipitation have been observed during the winter months and in June (Jaagus et al., 2018). Air humidity and precipitation are closely related to plant productivity, which has shown higher sensitivity to increased precipitation than to decreased precipitation (Wu et al., 2011). Higher air humidity may affect forests through a reduction in transpiration (Kupper et al., 2011) and thereby limit the mass flow of soluble minerals in the soil and nutrient uptake of roots (Cramer et al., 2009). Indeed, lower foliar concentrations of N and phosphorus (P) have been recorded for silver birches and hybrid aspens grown in conditions of elevated air humidity (Sellin et al., 2017). The reduction in transpiration also leads to an increase in soil moisture (Hansen et al., 2013), which directly affects the growth environment of roots and soil microorganisms. Excess soil water can cause hypoxia, which can impact membrane transport in roots and impair the uptake and root-to-shoot transport of N compounds (Kreuzwieser et al., 2009; Liu et al., 2015). Furthermore, increasing humidity has been shown to increase pathogen damage (Sellin et al., 2017). Studies of tree fine root biomass variation in relation to varying precipitation show that although dry conditions induce a more rapid fine root turnover, then the standing stock of fine root biomass and soil organic carbon (SOC) increases towards the humid end of the gradient (Leuschner and Hertel, 2003; Meier and Leuschner, 2010). Similar findings of increased fine root biomass and a higher proportion of absorptive root biomass have been observed for silver birches growing in elevated air humidity (Rosenvald et al., 2014).

1.2. Fine roots and ectomycorrhizal fungi

Fine roots (<2 mm in diameter) along with their ectomycorrhizal (EcM) symbionts are responsible for the water and nutrient uptake of trees. They are considered to be the most important component of below-ground C and nutrient fluxes, consuming up to 75% of fixed C and contributing up to 70% of the C stored in boreal forest soils (Clemmensen et al., 2013; Fogel and Hunt, 1983). Fine roots respond to changes in the growth environment with great plasticity, either through modifications in root biomass, root morphology or shifts in root-associated microbial communities (Ostonen et al., 2011; Richardson et al., 2009; Rosenvald et al., 2011b; Truu et al., 2017; Valverde-Barrantes et al., 2015).

Fine roots can be functionally divided into transport roots with secondary structure and absorptive roots with primary structure. Hereafter, I refer to the entire fine root compartment, which includes both absorptive and transport roots, as ‘fine roots’ and to the proportion of absorptive fine roots as ‘absorptive roots’. Absorptive roots, also known as short roots or ectomycorrhizal roots, are the first- to third-order roots (McCormack et al., 2015; Ostonen et al., 2007, 1999) that constitute the most active and predominant part of the fine root system, accounting for more than 75% of total fine root length and 60% of total fine root surface (Guo et al., 2004). In temperate and boreal forests, absorptive roots are prevalently (90–100%) colonized by ectomycorrhizal fungi (Kraigher et al., 2007; Taylor et al., 2009), which in turn are associated with rhizosphere bacteria (Frey-Klett et al., 2007; Marupakula et al., 2016).

Fine and absorptive roots exhibit several traits that determine nutrient uptake and root functioning, while providing information about root demographic patterns, soil fertility and plant stress status. A number of attempts have been made to incorporate these traits into frameworks of plant foraging strategies, although the results are far from conclusive. For example, high specific root length and area (SRL and SRA) have been thought to reflect the acquisitive or intensive strategy of enhanced resource uptake at lower biomass investments, high root cost efficiency and fast growth, which plants may employ either in conditions of soil resource scarcity or, on the contrary, in productive environments, where rapid acquisition of nutrients is essential to withstand competition (Comas and Eissenstat, 2004; de la Riva et al., 2018; Holdaway et al., 2011; Lõhmus et al., 2006; Ostonen et al., 2007; Weemstra et al., 2016). Depending on the circumstances, an increase in SRL and SRA can be viewed either as means of acclimation or serve as indication of plant stress (Rosenvald et al., 2011b). High SRL and SRA are achieved through a reduction in either root tissue density (RTD) or root diameter (D). Both D and RTD have been linked to root survivorship and age (Hajek et al., 2014; McCormack et al., 2012; Valverde-Barrantes et al., 2015; Weemstra et al., 2016; Wells and Eissenstat, 2001), but appear to vary independently from each other due to differing dependence on factors, such as soil structure and fertility, mycorrhizal colonization and phylogeny (Bergmann et al., 2020; de la Riva et al., 2018; Kramer-Walter et al., 2016; Valverde-barrantes et al., 2017). Another trait suggested to be of high importance in precision foraging and acclimation is branching frequency, which is largely influenced by mycorrhizal association (Kong et al., 2014; Liese et al., 2017). In addition to altering root morphology, plants respond to varying nutrient availability through shifts in root biomass allocation. For example, higher investment in fine and absorptive root biomass has been shown to be common in nutrient poor forests and associated with the extensive foraging strategy (Helmisaari et al., 2007; Lõhmus et al., 2006; Ostonen et al., 2011). In small-scale nutrient patches, extensive fine root biomass accompanied by increased RTD has been reported and associated with the conservative syndrome of forming long-living roots (Valverde-Barrantes et al., 2015).

The identity of the fungal colonizer has a considerable effect on EcM absorptive root diameter, length and weight, thereby also influencing SRA and SRL (Makita et al., 2012; Ostonen et al., 2009; van der Heijden and Kuyper, 2003), which is why changes in root morphology should not be addressed separately from developments in the EcM fungal community. Besides differing in their influence on root growth and shape, EcM fungal taxa exhibit contrasting foraging strategies with varying capacities of enzymatic activities, nutrient uptake and translocation, and maintenance costs to the host plant (Gorissen and Kuyper, 2000; Lilleskov et al., 2002; Tedersoo et al., 2012; van der Heijden and Kuyper, 2003; Velmala et al., 2014). The different ecological strategies of EcM fungi have been associated with exploration type and hydrophobicity (Lilleskov et al., 2011; Unestam and Sun, 1995). Hydrophilic morphotypes (prevalently concurring with contact-, short-distance and medium-distance smooth exploration types) have lower proteolytic capabilities and depend on the availability of labile N forms, thus representing the exploiting ruderal strategy (Hobbie and Agerer, 2010; Lilleskov et al., 2011; Tedersoo et al., 2012). These morphotypes prosper in humid environments and have been shown to tolerate waterlogging and oxygen deficiency better (Bakker et al., 2006; Stenström, 1991). On the other hand, hydrophobic morphotypes that form rhizomorphs and produce high extramatrical biomass characterize environments, where labile N is scarce and insoluble organic N-sources are widely dispersed and spatially concentrated. Hydrophobic rhizomorphs facilitate effective long-distance water transport, prevent leakage of solutes and are characteristic for stress tolerant species in cases of drought and consequent nutrient limitation (Hobbie and Agerer, 2010). In such conditions, the costly formation of high extramatrical biomass and exudation of extracellular enzymes, capable of decomposing complex organic substrates, is advantageous. Producing extensive hydrophobic hyphal mats may also drive out other microorganisms and thus render a competitive quality (Unestam and Sun, 1995). Undoubtedly, the effectiveness of a morphotype, whether hydrophilic and forming low extramatrical biomass or hydrophobic and forming high biomass, depends on the specific conditions and limiting resources.

Extending the above-described inter-relatedness even further, shifts in root traits and fungal communities are reciprocally associated with changes in rhizosphere bacterial communities (Friesen et al., 2011; Marupakula et al., 2016), the effect of which on plant performance and root traits has been shown to vary largely on climatic gradients (Rutten and Gómez-Aparicio, 2018). Additionally, elevated air humidity has been shown to affect the rhizosphere microbial community directly via changes in soil moisture and pH, but also through changes in absorptive root D, branching frequency and SRL (Truu et al., 2017). For example, higher SRL and branching frequency indicate larger number of young metabolically active root tips, which may create better substrate supply and benefit specific groups of rhizosphere bacteria.

1.3. Different approaches to studying the effects of climate change

Different approaches are available for studying the effects of climate change, which all have their advantages and restrictions: field manipulation experiments, natural small-scale environmental gradients and large-scale latitudinal gradients.

Field manipulation experiments enable us to study the ecosystems, species or genotypes of interest and identify causal effects, while maintaining a high degree of control over unwanted sources of variation. At the same time, the amount of treatment levels and the spatial and temporal span are usually limited, although exceptions do exist (Deslippe et al., 2011; Ryan, 2013; Schindlbacher et al., 2015). The short duration of most experiments increases the risk of under- or overestimating ecosystem responses (Walker et al., 2020), making it difficult to provide reliable predictions of long-term climate change effects. Underestimation of manipulation effects may arise from a delayed reaction of the ecosystem (especially regarding slow processes, such as changes in soil structure or shifts in community composition of long-lived species), while overestimation may occur when the studied system responds in a logarithmic or overshoot manner (Beier et al., 2012; De Boeck et al., 2015; Romero-Olivares et al., 2017). The spatial limitation of manipulation experiments also increases the chances of misinterpreting the results, because only parts of the plant or studied system are exposed to the manipulated conditions, which enables unmanipulated parts of the system to compensate for any resource imbalances and environmental changes, or more broadly, due to the 'island effect' (Leuzinger et al., 2015). The small number of treatment levels of manipulation experiments is also problematic as it prevents the detection of more complex responses, thresholds and tipping-points (Kreyling et al., 2014). In addition, the treatment intensity employed by manipulation experiments is rarely allowed to reach such extremes that lead to mortality (Beier et al., 2012).

Small-scale natural gradients offer solutions to some of the above-mentioned limitations. They allow us to investigate large and gradual changes over relatively small distances, while keeping other environmental factors (climate, elevation, soil type, photoperiodicity) unchanged. In case of natural geothermal temperature gradients, their large temperature ranges encompass the entire set of climate change predictions, which helps to reveal the shape of the warming response and potential thresholds in acclimation ability (Leblans et al., 2017). However, geothermal studies are confined to volcanic environments. Also, although they may be long-persisting, which allows long-term observations, they are still created by an abrupt change in temperature, acting as a disturbance. The main limitation of both manipulation experiments and small-scale natural gradients is that they both act as 'islands' in ambient surroundings, which may obscure treatment effects. Regarding soil warming experiments, they do not imitate global warming in full, as heat originates from the ground, leaving the air mostly unwarmed (Leblans, 2016; O'Gorman et al., 2014). More generally, results from single-factor treatments should be extrapolated cautiously, as it has been shown that combinations of environmental factors can interact synergistically or antagonistically (Leuzinger et al., 2011; Wu et al., 2011). Nevertheless, single-factor studies allow us to identify causes behind the observed changes by reducing complexity (De Boeck et al., 2015).

A valuable alternative to the small-scale manipulation and natural gradient experiments is studying latitudinal or altitudinal gradients as a proxy for climate change, i.e. the space-for-time approach. The advantage of using latitudinal gradients is their experimental realism and absence of the 'island effect', the lack of the initial abrupt change in temperature, and most importantly, their long-term character, which enables us to witness persistent changes and equilibrium states. At the same time, latitudinal gradients encompass different populations and cover a wide range of climates, soil types and other environmental factors that also significantly influence ecosystem functioning, making it harder to isolate causal effects and distinguish phenotypic plasticity from genetically determined differences. Still, large-scale latitudinal studies facilitate predicting the direction in which our studied ecosystems could evolve in a warmer world, identifying the natural endurance limits of species and ecosystems of interest and discovering generality in ecosystem responses. Altogether, it is recommended to apply and compare the results of all the different types of experiments to make reliable predictions and generalisations about climate change outcomes.

In this thesis, all three above-discussed approaches have been used to study the effects of soil warming and elevated air humidity on the fine roots and root-associated microbial communities of spruce (*Picea sitchensis* Bong. Carr and *Picea abies* (L.) Karst.) and birch (*Betula pendula* Roth.). Spruce and birch were chosen for investigation because of their economical importance and wide distribution in temperate and boreal European forests (Caudullo et al., 2016; Houston Durrant et al., 2016; Hynynen et al., 2010), spruce species representing common late-successional and birch a pioneer tree species.

1.4. Aims of the thesis

The overall objective of this doctoral thesis was to analyse the effects of elevated air humidity and soil warming on the acclimation processes of fine roots and root-associated microbial communities of birch and spruce, and compare these findings to patterns witnessed on latitudinal gradients with particular emphasis on root-EcM fungi-bacteria interactions. In addition, latitudinal gradient studies were used to distinguish root traits that respond most plastically in the studied tree species.

The specific aims were:

1) To examine whether and how elevated air humidity affects silver birch absorptive root morphology and the root-colonizing EcM community in relation to different understory types; and whether the morphological reaction shows any temporal change (**I**).
2) To find out whether and how soil warming affects spruce fine and absorptive root biomass allocation, absorptive root morphology and the root-colonizing EcM community; whether the response is similar in a man-made experiment and on a natural soil temperature gradient; and to analyse the response curves of the root traits up to the die-off edge of the trees (**IV**).
3) To investigate spruce and birch fine root-rhizobiome acclimation patterns on latitudinal gradients and identify the absorptive root traits that are most responsive in acclimation for both genera (**II, III**).

The main hypotheses were:

1) Elevated air humidity causes a morphological stress response in absorptive roots and a shift in root-colonizing EcM fungal community composition.
2) Soil warming induces a decrease in fine and absorptive root biomass allocation, which concurs with an increase in specific root area and length, and a shift in the community structure of EcM colonizers; root response to warming is similar in the man-made experiment and the natural soil temperature gradient.
3) There are root traits, such as absorptive root biomass, that change similarly in both tree species along the latitudinal gradient and are driven primarily by environmental factors, while spruce and birch also show distinctive morphological acclimation patterns.

2. MATERIALS AND METHODS

2.1. Description of study sites

The effect of elevated air humidity on silver birch absorptive root morphology and the root-associated EcM community was studied on the FAHM (Free Air Humidity Manipulation) experimental site, which is situated at Rõka village in south-eastern Estonia (Kupper et al., 2011) (Table 1; Publication I). The effect of soil warming on spruce fine and absorptive root biomass and absorptive root morphology was studied on two sites: a man-made soil warming experiment in the Northern Limestone Alps, close to the village of Achenkirch, Austria (Schindlbacher et al., 2009); and a natural geothermal gradient (ForHot) close to Hveragerði in southern Iceland (Sigurdsson et al., 2016) (Table 1; Publication IV). At Achenkirch, we also identified the root-associated EcM community. The number and location of study stands on the latitudinal gradient are described in section 2.1.3.

For all the sites included in this doctoral thesis, there were comprehensive background data of climate variables, stand characteristics and soil chemical characteristics available, of which the relevant variables are presented in Tables 2 and 3. The full descriptions and references, how the measurements were conducted, are in the publications.

Table 1. Background information about the soil warming and air humidification study sites (Publications I and IV).

Site (tree species)	Achenkirch (*Picea abies*)	ForHot (*Picea sitchensis*)	FAHM (*Betula pendula)*
Location	47.581°N, 11.639°E	64.008°N, 21.178°W	58.4°N, 27.3°E
Elevation, m a.s.l.	910	83–168	40–48
MAT, °C	6.9[a]	5.2[b]	5.6[c]
MAP, mm	1506[a]	1457[b]	650
Stand age	130	50	3–5
Soil type[d]	Chromic Cambisol	Silandic Andosol	Endogenic Mollic Planosol
Stand basal area, m^2 ha^{-1}	35[e]	49	8
Stand density, trees ha^{-1}	487[e]	4461	10 000

[a] Measured between 1992 and 2012 at Achenkirch village (7 km away at similar altitude); data from Zentralanstalt für Meteorologie und Geodynamik (ZAMG); reported by Schindlbacher et al. (2015). [b] Measured between 2003 and 2015 at the closest synoptic station at Eyrabakki (9 km south of Hveragerði); data from Icelandic Meteorological Office; reported by Sigurdsson et al. (2016). [c] Measured between 2009 and 2011 at the closest synoptic station at Ahja village; data from the Estonian Environment Agency. [d] IUSS Working Group WBR 2015. [e] Including only spruce.

Table 2. Mean monthly values of meteorological parameters throughout the vegetation periods of the three study years (2009–2011) at the FAHM site (Publication I). Abbreviations: throughfall precipitation (TF; mm), soil water potential at the depth of 15 cm (SWP; kPa), soil temperature at the depth of 15 cm (ST; °C), air temperature (AT; °C) and relative humidity (RH; %); C – control, H – humidification.

	May		June		July		August		September		October	
	C	H	C	H	C	H	C	H	C	H	C	H
2009												
TF	14.4	23.7	107.0	105.0	71.4	97.4	35.2	42.5	56.5	63.8	70.8	67.7
SWP	–30.0	–9.8	–20.5	–12.0	–85.9	–12.0	–206.2	–3.8	–137.1	–5.7	–15.0	–1.5
ST	9.1	9.5	12.1	13.0	15.3	15.7	14.9	15.4	13.2	13.4	7.1	7.0
AT	11.5	11.2	14.1	14.0	17.0	16.6	15.2	14.7	12.7	12.2	4.0	3.8
RH	67.0	68.4	78.6	78.9	82.1	83.7	83.3	84.6	86.1	88.2	90.7	91.3
2010												
TF	38.0	45.0	93.7	85.1	33.4	25.6	103.4	104.8	93.9	108.0	41.5	41.4
SWP	–8.9	–13.6	–21.9	–36.0	–168.9	–132.4	–147.5	–97.0	–14.2	–17.2	–3.4	–12.6
ST	10.6	11.4	13.0	13.7	17.7	18.5	17.7	17.7	12.5	12.2	6.9	6.5
AT	12.5	12.5	14.8	14.9	22.1	21.7	18.2	17.9	10.9	10.7	3.9	3.8
RH	76.0	77.3	77.0	77.1	73.7	75.7	81.6	84.1	86.8	88.9	85.7	86.2
2011												
TF	39.2	38.0	28.3	24.6	17.7	15.3	38.6	37.9	32.8	29.5	42.9	45.8
SWP	–13.2	–20.8	–137.4	–104.1	–212.2	–154.4	–185.3	–185.6	–180.4	–189.5	–59.2	–92.8
ST	9.8	9.8	14.1	14.5	17.2	17.4	16.0	15.9	13.1	13.1	8.6	8.6
AT	11.2	11.4	17.3	17.1	20.7	20.4	16.7	16.3	12.4	12.4	7.0	6.9
RH	69.2	69.6	73.4	75.4	77.7	80.5	79.7	82.3	85.7	87.2	86.5	87.1

2.1.1. The free air humidity manipulation (FAHM)

The study site has been established on former agricultural land. One-year-old silver birch seedlings were planted in the experimental area in spring 2006. The site contains humidified (H) and control (C) plots (samples were taken from two H and two C plots). Humidification started on 1 June 2008 and has been carried out daily throughout all following growing seasons. Humidification took place if the ambient relative air humidity dropped <75% and wind speed was <4 m s^{-1}. The FAHM system enabled an average increase in relative air humidity of 7% (maximum 18%) over the ambient level.

To investigate the impact of soil biota and understory species composition on ecosystem functioning, two different types of ground vegetation were established in the plots, representing either disturbed forest vegetation, such as that usually recorded in recent clear-cut areas, or early-successional vegetation with low diversity and a strong dominance of a few grass species, such as that in abandoned arable fields (Kupper et al., 2011). The 'forest' understory was dominated by *Ranunculus repens* L., *Lathyrus pratensis* L., *Festuca rubra* L., and *Veronica chamaedrys* L. and consisted of 67 species. The grass understory comprised only 31 species and exhibited strong dominance of *Elymus repens* (L.) Gould accompanied by *Aegopodium podagraria* L.

2.1.2. The soil warming experiments

The studied 130-year-old forest at the Achenkirch site was dominated by Norway spruce (*Picea abies*), inter-mixed with European beech (*Fagus sylvatica*) and silver fir (*Abies alba*). The amount of ground vegetation was negligible. In 2004, three spots were randomly selected on the site, where a warmed plot and an ambient plot were established, each with a size of 2×2 m. Warmed plots were equipped with resistance heating cables, which were buried in 3-cm-deep trenches and had a spacing of 7–8 cm. The soil temperature of each warmed plot was kept 4 °C above that of the adjacent ambient plot during the snow-free seasons, starting in spring 2005. The 4 °C warming level is in accordance with the soil temperature predictions made for the growing season in Canadian and Swedish boreal forests (Houle et al., 2012; Jungqvist et al., 2014).

In southern Iceland, an earthquake occurred on May 29, 2008, which affected geothermal systems close to its epicenter. One such system at Reykir moved to a previously unwarmed area (Sigurdsson et al., 2016; Þorbjörnsson et al., 2009), where the new geothermal bedrock channels caused increasing temperature in the soil above by radiative heating (O'Gorman et al., 2014). This recently warmed area is covered by an unthinned Sitka spruce forest that was planted in 1966–1967. In autumn 2012, twenty-five permanent experimental plots were established on five replicate transects in the stand (Figure S1 in IV). The transects were about 50 m in length and ranged from ambient soil temperature to about +10 °C. The location of the plots was chosen aiming for the long-term warming levels of about 0, +1, +3, +5 and +10 °C warming (hereafter called levels A (unwarmed ambient), B, C, D and E, respectively), although the realized annual temperature means were slightly lower (Table 3; Sigurdsson et al., 2016). Owing to the geothermal origin of soil warming, temperature also increased towards the deeper soil on average 2 °C per depth interval (0–5, 5–10 and 10–20 cm; Figures 1 and S2 in IV). Ground vegetation proliferated only starting from D or E plots, which was close to the warming-induced die-off edge in the spruce stand (Figure S1 in IV; O'Gorman et al., 2014).

Table 3. Main site and soil characteristics per treatment in the soil warming experiments in 2013 (Publication IV). Abbreviations: AK – Achenkirch warming manipulation; FH – ForHot geothermal gradient; A – ambient, W – warming at Achenkirch; B–E – warming levels at ForHot; NE – not estimated.

Site, treatment (mean 2013 warming levels [a], ΔT)	Average soil temperature during vegetation period [ab], °C (ΔT)	Soil temperature during sampling, °C (ΔT) [c]	Stand basal area, $m^2\ ha^{-1}$	Topsoil C:N ratio	Topsoil NO_3^- availability, µg $10cm^{-2}$ $89days^{-1}$ [d]	Volumetric water content, % [e]	pH_{H2O} [f]
AK A	10.5	8.0	35	14.9	NE	47.2	~7
AK W (+4)	14.6 (+4.1)	12.1 (+4.1)	35	16.0	NE	43.5	~7
FH A	8.2	5.8	48	17.3	0.58	31.2	5.3
FH B (+1)	8.9 (+0.7)	7.1 (+1.3)	56	22.3	0.98	31.2	5.1
FH C (+2)	10.2 (+2.0)	7.7 (+1.9)	50	19.5	1.22	31.3	5.1
FH D (+4)	11.7 (+3.5)	8.7 (+2.9)	35	17.1	2.84	30.7	5.0
FH E (+8)	15.9 (+7.7)	13.7 (+7.9)	27	16.6	82.2	45.0	5.2

[a] Soil temperature (for long-term averages) was measured at 10cm. [b] Vegetation period at Forhot from May to August, vegetation period at Achenkirch from May to October. [c] For Achenkirch, mean October 2013 soil temperature is given. [d] Measured from 0–10cm depth throughout the growing season. [e] Measured from 0-5cm depth from April to June 2013. [f] Measured from 0-10cm of mineral soil in July 2013.

2.1.3. The latitudinal studies

Root acclimation patterns were investigated in two latitudinal studies, with the first study focusing on morphological plasticity of Norway spruce and silver birch absorptive roots (Publication II), and the latter study viewing acclimation patterns of the whole fine root-rhizobiome, including root-colonizing EcM fungi and soil and rhizosphere bacteria (Publication III). In the first study (II), the spruce stands covered a latitudinal range from 48 to 68°N, including 5 temperate, 3 hemiboreal, and 6 boreal stands of ages from 30 to 140 years. The birch stands covered a latitudinal range from 53 to 66°N and a longitudinal range from 2°W to 51°E and included 6 native forest stands in boreal, 8 in hemiboreal, and 1 in the temperate zone (Figure 1 in II and Tables S1 and S2 in II). In the latter study (III), 10 silver birch and 15 Norway spruce forests covering a latitudinal range from 48 to 69°N were studied (Figure 1 in III and Tables S1 and S2 in III).

The study sites for both tree species display gradients in climate (e.g. mean annual temperature and precipitation, growing season length) as well as in N deposition. The different fertility of studied spruce sites was reflected by soil C:N ratio. In general, the southern stands displayed higher fertility. Silver birch stands on native forest land all belonged to the fertile forest site types.

2.2. Fine and absorptive root biomass and morphology: sampling and measurements

Root samples were collected at the end of the growing season (September-October) from the organic and 0–20-cm mineral soil layer. In the latitudinal studies, 10–15 soil cores (38 mm in diamater) were taken per site for fine root biomass (FRB; g m^{-2}) estimations and 8–10 samples per site to study absorptive root morphology, EcM community and birch rhizosphere bacterial community. At the FAHM site, 8 samples were taken per experimental plot for morphological studies in three consecutive years (16 samples per treatment, altogether 32 samples from the whole experimental site). Each plot comprised two quarters of different understory; four samples were collected from both quarters. At the ForHot site, one soil core (88 mm in diameter for 0–10-cm depth and 38 mm for 10–20-cm depth) was taken per plot for morphological analyses and FRB estimation (5 samples per warming level, altogether 25 samples from the whole experimental area). For morphological studies, the soil cores were further divided into three soil layers: 0–5, 5–10 and 10–20 cm, because of the approximately 2 °C increase in soil temperature per layer. At the Achenkirch site, 5 soil cores (50 mm in diameter) were taken per plot for morphological studies and an additional 3 soil cores per plot for FRB estimations, altogether 15 and 9 samples per treatment, respectively.

To determine the number of absorptive roots per m^2, the root tips of two or three fine root fragments (which accounted for at least 1/5 of a sample) were counted. Fine roots were then dried at 65 °C for 48 h to constant weight and weighed to ±0.05 mg accuracy. Absorptive fine root biomass (aFRB; g m^{-2}) was calculated by multiplying the mean absorptive root weight by the root tip number per m^2. The FRB and aFRB are presented per stand basal area (BA) to describe the functional relationship between the above- and below-ground parts of a forest stand and to facilitate comparison between sites with varying tree sizes and numbers.

For morphological analyses, 2–5 random subsamples of first-to-third-order absorptive roots were taken per sample (20–30 living root tips per subsample). All morphological parameters were measured and calculated for the subsample level. Absorptive root length, projection area and mean diameter (D; mm) of a subsample were measured using WinRHIZO Pro 2003b software. After measuring, absorptive roots were dried at 70 °C until constant weight and weighed with an accuracy of ±0.05 mg. The method for determining absorptive root morphological parameters: absorptive root length (L; mm), specific root area (SRA; m^2 kg^{-1}), specific root length (SRL; m g^{-1}), root tissue density (RTD; kg m^{-3}), and branching frequency (B_W and B_L; mg^{-1} and mm^{-1}) is given in detail in Ostonen et al., 1999.

2.3. Microbiological analyses

2.3.1. Ectomycorrhizal community analysis: sampling and identification

To determine the EcM community composition, the same amount of root samples were taken as described for root morphological sampling at the FAHM site (I), at the Achenkirch site (IV) and for all the sites in the latitudinal gradient (III). Root tips from three fine root fragments (5–7cm in length) were taken from each sample and subjected to morphotyping on the basis of mantle color, texture, and the presence of emanating hyphae and rhizomorphs. The relative abundance of each morphotype was estimated and all the morphotypes were assigned into exploration types (III, IV; Agerer, 2006) or classified as hydrophilic or hydrophobic (I). Two to three representative root tips of each morphotype per sample were subjected to DNA analysis. Fungal taxa were identified by use of sequence analysis of the nuclear rDNA Internal Transcriber Spacer (ITS) region (a detailed description is presented in Publication IV). Sequences were assigned to operational taxonomic units (OTUs) based on a 97.0% ITS barcoding threshold (Tedersoo et al., 2003).

Extramatrical mycelium biomass per EcM root tip (µg cm^{-1}) of each stand was calculated using biomass coefficients for different exploration types (calculations in Weigt et al., 2012, 2011) and the frequency of dominating EcM morphotypes (percentage of root samples colonized).

2.3.2. Bacterial community analysis

The abundance of bacterial communities in bulk soil was evaluated by bacterial 16S rRNA gene copy numbers, using a quantitative polymerase chain reaction (qPCR). Bacterial community profiling was performed by sequencing bacterial 16S rRNA gene fragments on the Illumina ® HiSeq 2000 (Illumina Inc., San Diego, CA, USA). The details about used primers, qPCR conditions, calculation method, the preparation of amplicons for sequencing and bioinformatic analysis can be found in Publication III.

2.4. Statistical Analyses

Statistical analyses were carried out using STATISTICA 7.1 (StatSoft, 2005), R (R Core Team, 2013), PERMDISP (Anderson, 2004), CANOCO (ter Braak and Šmilauer, 2002) and EstimateS 9.1.0 (Colwell, 2013) software. The significance level was set at $\alpha=0.05$ for all the analyses. Root variables were checked for normality using the Kolmogorov-Smirnov, Lilliefors and Shapiro-Wilk tests; homogeneity of variance was assessed using Levene's test.

The effect of soil warming on FRB, aFRB and absorptive root morphological traits was checked with the t-test (for the Achenkirch data) and using simple linear regression analysis and one-way ANOVA (for the ForHot data) (IV). The warming response of FRB/BA, aFRB/BA and RTD on the soil temperature gradient was modelled by the Gompertz function. To determine which soil properties influenced absorptive root morphology and fine root biomass in addition to soil temperature at ForHot, partial correlations were found and all soil parameters that correlated with a given root trait with a probability level of $p<0.1$ were included in forward stepwise multiple regression analyses. In the latitudinal studies (II, III), linear and non-linear modelling tools were used to analyse relationships between root traits, environmental variables and latitude. When assessing the effect of tree species and forest zone on root traits; climate, soil and stand characteristics were used as covariates (III). Student's t-test was applied to verify the differences in trait means and PI values between spruce and birch (II). Repeated measures ANOVA was used on repeatedly measured data to evaluate the influence of the study year and the effect of humidification and understory type over all years (I, II). Two-way ANOVA was employed to test the effect of humidification and understory type in each separate year (I).

To detect and visualize relationships between root traits, sites, treatments and environmental parameters, redundancy analysis (RDA) was used (I–IV). To evaluate the effect of treatments and environmental factors and illustrate the dissimilarities in EcM communities, the canonical correspondence analysis (CCA) was employed (I, IV). The significance of RDA and CCA results was tested with the Monte Carlo permutation procedure in CANOCO. At FAHM (I), the adonis function (vegan package in R) was used in addition to CCA to evaluate the effect of treatments, understory types and environmental factors on the fungal community species composition (whether a species appears in a sample or not). The difference in colonization percentages of hydrophilic and hydrophobic morphotypes between the treatments and understory types was checked by two-way ANOVA. For the EcM community analyses at Achenkirch (IV), OTU accumulation (rarefaction) curves and the minimum richness estimators, Chao1, Jackknife1 and ACE were calculated to evaluate the sufficiency of sample size and to estimate the proportion of unseen OTUs at the site. The differences in colonization percentages of dominant genera and exploration types, OTU richnesses and Shannon diversity indices between the treatments were checked using the Mann–Whitney U Test. The centroids and the dispersions of the two fungal communities were compared using PERMDISP. In the latitudinal study (III), Spearman rank correlation coefficients were used to describe the effects of root traits and environmental factors on EcM exploration types.

To analyse the trilateral relationships between tree roots, soil bacterial and EcM community structure across the latitudinal gradient of silver birch stands, phylogenetic molecular ecological networks (pMENs) based on bacterial OTU data were constructed for bulk soil and rhizosphere by application of the Molecular Ecological Network Analyses Pipeline (MENAP) (Deng et al., 2012). Kendall rank correlation coefficients were calculated to test the relationships between bacterial community diversity parameters and root morphology and soil parameters, as well as to test the relationship between the bacterial OTU abundances and stand geographical location (distance from the equator). Relationships between soil variables, root morphological parameters and the obtained network modules were analysed using RDA. In case of the network modules that were related to stand distance from the equator (Mantel test), the correlation of module OTU relative abundances to the stand distance from the equator was tested using linear regression analysis. Procrustes analyses, using ordinations of the bacterial (whole community and pMEN modules of the rhizosphere and bulk soil) and EcM fungal communities (at the functional group level), were applied to explore the relationships between bacterial and EcM fungal community structure in the studied forest soils.

3. RESULTS AND DISCUSSION

3.1. The effect of elevated air humidity on birch fine roots and ectomycorrhizal community

Humidification affected EcM root morphology significantly throughout the three study years (Figure 1). Within each study year, humidification had extensive influence in 2009 and 2010 (the second and third year of humidification); however, the number of morphological parameters that significantly differed between the treatments decreased greatly by 2011 (the fourth year of humidification) (Table 2 in I). Humidified birches reacted after the second year of humidification (in 2009) by forming absorptive roots with higher SRA and SRL, which was caused by lower values of RTD. This was especially pronounced in quarters with early-successional grasses, which seemed to have initially caused strong underground competition and additional stress for the roots of silver birch by producing the predominant proportion of the total fine root biomass in humidified plots (Kukumägi et al., 2014). Also, leaf N concentrations were significantly lower in humidified plots than in control in 2009, indicating malnutrition, although the experimental plantation was established on fertile abandoned arable land. Our observations are in good agreement with the results of Rosenvald et al. (2011a), where high SRL and SRA values were symptomatic of low leaf N, reflecting a decrease in the nutritional status of birches.

By 2010, after canopy closure, the biomass of understory vegetation dropped drastically, especially in the C plots, which were most disturbed by the mid-summer drought, and the effect of understory on root morphology disappeared. Inversely to 2009, the RTD of control plots was lower than that of humidified plots after the dry summer of 2010, indicating that humidification mitigated the impact of limited precipitation. Nevertheless, roots in humidified plots were longer, thinner and had higher SRL and less root tips per unit of length in 2010. By the fourth year of humidification, the differences between the treatments were evident only in root diameter and B_L – humidified birches were growing thinner roots with lower B_L.

Along with morphological studies, measurements of fine root biomass have been carried out on the FAHM experimental site. Four years of humidification resulted in significantly more fine root biomass and higher number of root tips per m^2 in humidified plots (Rosenvald et al., 2014), while in 2007, before humidification commenced, there were no differences between treatments (K. Lõhmus, unpublished). By 2011, leaf N concentrations had also risen to be significantly higher in humidified plots, compared to control plots (Rosenvald et al., 2014). The initial morphological response of absorptive roots in humidified plots was complemented by a subsequent increase in fine root biomass, which together seem to have eliminated the obstruction in nutrient uptake.

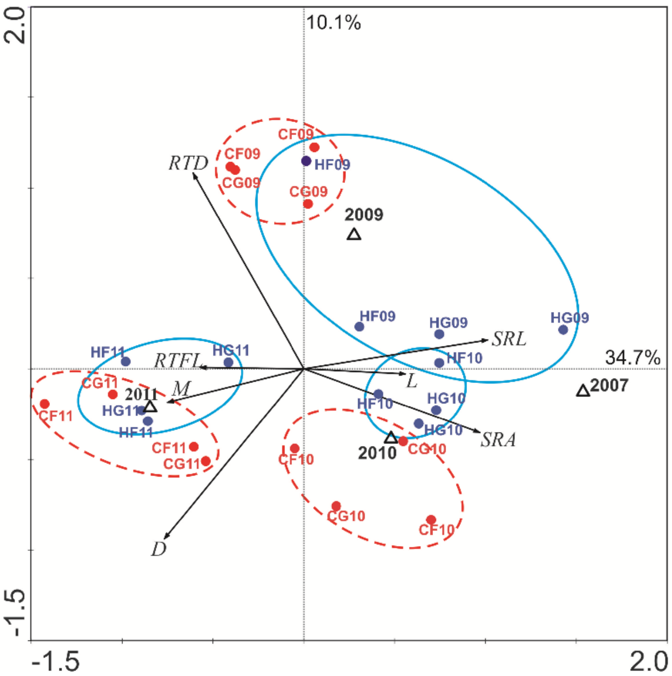

Figure 1. Ordination biplot based on redundancy analysis (RDA) of absorptive root morphological parameters of silver birch, indicating the effect of humidification throughout three study years. Open triangles depict the overall means of the study years. The blue continuous circles group samples from humidified plots; the red dashed circles surround samples from control plots of each year. The means of each experimental quarter (n = 214 to 404 analysed absorptive roots) are indicated by dots. Abbreviations: C – control, H – humidification, G – early-successional grass understory, F – diverse 'forest' understory. Figure from Publication I.

According to redundancy analysis, morphological parameters correlated significantly with air and soil temperature and moisture of July and October, SOM, soil Ca, Mg, N concentration and soil pH. Altogether, these factors accounted for 40.9% of the total variation in morphological root traits.

Sequence analysis revealed 64 fungal taxa (OTUs), of which 44 were singletons, (i.e. occurring in one sample). Among these 64 OTUs, species-level identification could be provided to 32 taxa from 16 lineages. Overall, the most frequent OTUs were *Paxillus involutus*, *Tomentella cinerascens* and *Tomentella sublilacina*. Quarters with diverse 'forest' understory exhibited a non-significant trend of having more OTUs identified. Three years of humidification caused a significant shift towards the dominance of hydrophilic morphotypes in the fungal community (Figure 2). The mean colonization percentages of the hydrophilic morphotypes were 33% in control plots and 72% in humidified plots. The most abundant colonizers of humidified plots were representatives of the /tomentella-thelephora lineage (*Tomentella* spp.), characterized by contact, short-distance, or medium-distance smooth exploration types and hydrophilic hyphae. This shift in

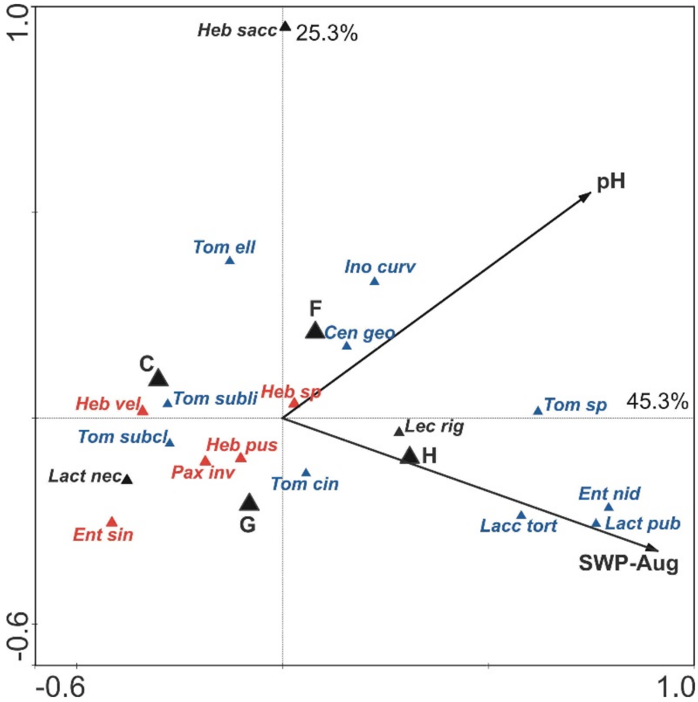

Figure 2. The species-environmental variables biplot of canonical correspondence analysis (CCA), which illustrates the shift in the EcM fungal community towards the dominance of hydrophilic morphotypes caused by humidification (Monte Carlo permutation test, $p<0.05$). Blue font color indicates hydrophilic morphotypes, red font color – hydrophobic morphoypes; black species produced both hydrophilic and hydrophobic morphotypes in different samples. Large triangles depict the treatments and the two understory types (C – control, H – humidification, F – diverse 'forest' understory, G – early-successional grass understory). Abbreviations: Cen geo – *Cenococcum geophilum*, Ent sin – *Entoloma sinuatum*, Ent nid – *Entoloma nidorosum*, Heb pus – *Hebeloma pusillum*, Heb sacc – *Hebeloma sacchariolens*, Heb sp – *Hebeloma* sp., Heb vel – *Hebeloma velutipes*, Ino curv – *Inocybe curvipes*, Lacc tort – *Laccaria tortilis*, Lact nec – *Lactarius necator*, Lact pub – *Lactarius pubescens*, Lec rig – *Leccinum rigidipes*, Pax inv – *Paxillus involutus*, Tom cin – *Tomentella cinerascens*, Tom ell – *Tomentella ellisii*, Tom subcl – *Tomentella subclavigera*, Tom subli – *Tomentella sublilacina*, Tom sp – *Tomentella* sp. Figure from Publication I.

community composition coincides with the notion of low extramatrical biomass producing hydrophilic morphotypes proliferating in humid environments (Unestam and Sun, 1995) compared to hydrophobic fungi, whose complex extramatrical systems can be extremely disturbed by even brief drenching (Stenström, 1991). *Tomentella* spp. have also been shown to have high functional plasticity, explaining their high abundance and disturbance tolerance (Rineau and Courty, 2011). Among other enzymes, these species have exhibited high activities of cellobiohydrolase, β-glucosidase and laccase, but also produce acid phosphatase and leucine aminopeptidase (Buée et al., 2007; Courty et al., 2005; Tedersoo et al., 2012). These enzymes are essential in fresh litter degradation, which could be beneficial, as humidification has also been reported to increase understory root turnover (Lõhmus et al., 2019).

When all environmental variables were analysed conjointly, the species composition of the EcM fungal community was significantly affected only by variation in soil pH and August soil water potential, so humidification influenced the species composition indirectly.

3.2. The effect of experimental soil warming on spruce fine roots and ectomycorrhizal community

At the ForHot site, soil warming reduced both FRB and aFRB significantly from 753±171 (mean±SE) and 100±28 g m^{-2} at the ambient level, respectively, to 50±27 and 8±7 g m^{-2} in the warmest plots (E; +8 °C), respectively. At Achenkirch, no significant temperature effect on neither FRB nor aFRB was revealed, although there was a similar trend of smaller biomass values in warmed plots. The sharp decline in FRB/BA started slightly below +4 °C (D plots), followed by a rapid decrease in aFRB/BA from +4 °C onwards and had reached a plateau by +6 °C (E plots) (Figure 3). This might partly explain the absence of a significant biomass response at the Achenkirch site, where the warming level was +4 °C above the ambient: at ForHot, there were also no significant differences in fine and absorptive root biomass between the ambient and D plots (+4 °C) yet. The other possible reason arises from differences in experimental setup: at Achenkirch, warming took place only during the growing season and only parts of the individual tree root system were exposed to it. At ForHot, spruces had to endure persistently warmer soils surrounding their whole root system throughout the year. Therefore, differences in the intensity, the seasonal duration and the spatial extent of warming may create the differences in the magnitude of the response of FRB and aFRB in different experiments. Nevertheless, a decrease in FRB or an increase in fine root mortality has also been documented in other soil warming studies (Majdi and Öhrvik, 2004; Nishar et al., 2017; Wan et al., 2004), agreeing with our findings. On absorptive root level, RTD followed a similar reduction as FRB and aFRB and could be indicative of faster root turnover as estimated by W. Borken et al. (unpublished data) for Achenkirch and P. Sigurðsson et al. (unpublished data) for ForHot. In respect of above-ground growth, stand basal area started decreasing from +3 °C onwards, which was due to increased tree mortality.

Soil warming significantly affected absorptive root morphology at both sites and in the same direction: in warmer soils, spruces formed longer and less-branched absorptive roots with higher SRL and SRA, and lower RTD. In contrast to RTD, which had significantly decreased at +4 °C at Achenkirch and started declining from +6 °C onwards at ForHot, significant changes in the other

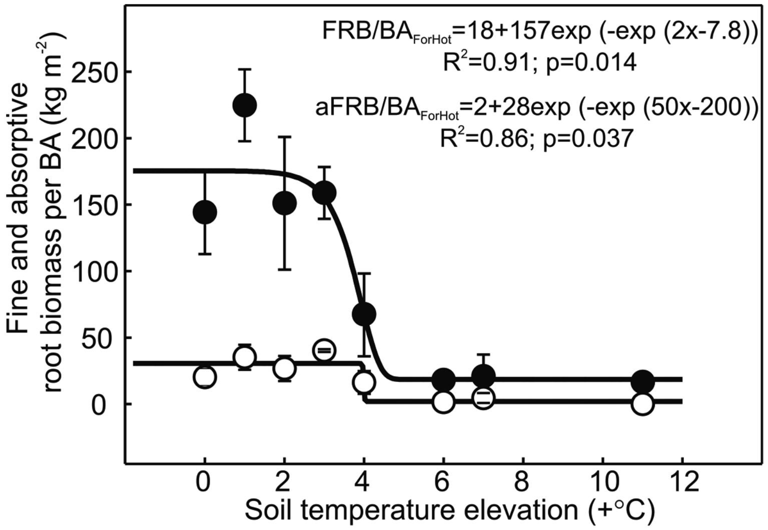

Figure 3. The effect of soil warming on fine (filled circles) and absorptive root biomass (open circles) per stand basal area at the ForHot soil temperature gradient (means ± SE). Figure from Publication IV.

morphological parameters (SRL, SRA, L and B_L) appeared already from lower warming levels (+3 °C onwards). The decrease in B_L and increase in L can be attributed to a shift from root tip formation to root elongation, which may partly be indicating a change in the fungal colonizer (Makita et al., 2012; Ostonen et al., 2009; van der Heijden and Kuyper, 2003), while the reduction in RTD suggests reduced lifetime of absorptive roots, but also higher metabolic activity (Hajek et al., 2014; Ostonen et al., 2011; Wahl and Ryser, 2000). Whether the main driver of changes in root morphology is a shift in root colonizers or changes in root tip production and longevity is indistinguishable, as the former also affects the latter (Guo et al., 2008).

RTD was distinct from the other morphological traits as it was extensively influenced by soil fertility, decreasing towards lower C:N (Table S2 in IV), and such a strong association has also been shown on the latitudinal gradient (III).

At both sites, branching, absorptive root length and weight (W) experienced the largest variation among the morphological traits (CV varied from 27 to 47), followed by SRL and SRA (CV from 16 to 29). RTD and D varied the least (CV from 14 to 15). This coincides with observations from the latitudinal study (II), where branching, L and W displayed highest plasticity for Norway spruce (CV varied from 25 to 31; PI varied from 0.60 to 0.68) and are proposed to reflect high relevance in the acclimation process.

The +4 °C increase in soil temperature at the Achenkirch site led to the formation of a more varied EcM community and a significant increase in the colonization of *Tomentella* spp. in warmed plots – a genus specialized for nutrient uptake in close vicinity of the roots and an affinity towards labile inorganic forms of N (Agerer, 2001; Cox et al., 2010; Kranabetter et al., 2015) (Figure 4).

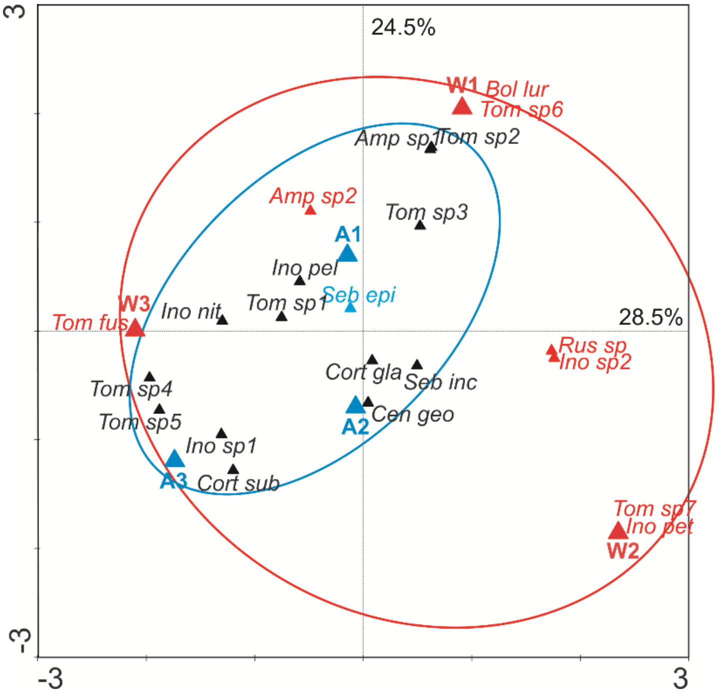

Figure 4. The species-environmental variables biplot of canonical correspondence analysis (CCA), which illustrates the effect of warming on the EcM fungal community (singletons excluded) (Monte Carlo permutation test, p<0.01). Altogether, the plots explained 87% of variation in the EcM community structure. Red font color signifies OTUs that were found only in warmed plots, and blue font color represents OTUs present only in the ambient plots. The black OTUs were present in both treatments. Large triangles depict the experimental plots. W – warming, A – ambient, Cen geo – *Cenococcum geophilum*, Ino pet – *Inocybe petiginosa*, Ino pel – *Inocybe pelargonium*, Ino nit – *Inocybe nitidiuscula*, Ino sp – *Inocybe* sp., Bol lur – *Boletus luridus*, Tom fus – *Tomentella fuscocinerea*, Tom sp – *Tomentella* sp., Cort sub – *Cortinarius subsertipes*, Cort gla – *Cortinarius glaucopus* var *olivaceus*, Seb epi – *Sebacina epigaea*, Seb inc – *Sebacina incrustans*, Amp sp – *Amphinema* sp., Rus sp – *Russula* sp. Figure from Publication IV.

Because Achenkirch is a N-rich site, soil warming did not result in any significant differences in soil N availability (Schindlbacher et al., 2015; Schnecker et al., 2016). Instead, the need for other nutrients (P, K) might have been driving the changes in the EcM community. Nutrient cycling was presumably faster in the warmed plots at Achenkirch because of intensified fine root turnover and *Tomentella* spp. have been demostrated to exhibit high activities of enzymes that are essential in fresh litter degradation and P acquisition (Buée et al., 2007; Courty et al., 2005; Tedersoo et al., 2012). In addition to the increase in *Tomentella* spp. colonization, morphotypes forming long-distance exploration type (represented by *Boletus luridus*) were present only in the warmed plots, although in low abundance. Fungi characterized by long-distance exploration type have been generally associated with great enzymatic capabilities required to access nutrients from SOM and fresh litter (Tedersoo et al., 2012). In addition, long-distance exploration types display higher drought tolerance (Lilleskov et al., 2009; Morgado et al., 2015; Wiklund et al., 1995), which may be especially beneficial as the frequency of dry spells is predicted to increase in the Alps (Gobiet et al., 2014).

On the ForHot site, an investigation of the EcM fungal community (determined from meshbags) revealed an increase in the abundance of ascomycetes driven by *Wilcoxina rehmii*, a species that has been commonly observed after fire or logging and is suggested to possess elevated potential for necrotrophy and facultative saprotrophy (Rosenstock et al., 2019). Soil warming likely increased fine root turnover and mortality, creating favorable substrate for such taxa. Since the use of ingrowth mesh bags discriminates against fungi that do not produce abundant extramatrical mycelium, such as species of the contact exploration type, these results are not directly comparable to results obtained by sampling root tips. Also, the fungal community exhibited very low diversity, probably due to the scarcity of forest in Iceland and the non-native host species (Rosenstock et al., 2019).

3.3. Patterns in tree root morphology, biomass and soil microbial community along the latitudinal gradient

On the latitudinal gradient, both the proportion of aFRB of the total FRB and aFRB per stand BA increased towards the northern boreal forests for both spruce and birch, agreeing with findings from other latitudinal studies (Ostonen et al., 2011; Zadworny et al., 2016). Even when the faster fine root turnover in temperate forests is taken into account, the investment to aFRB/BA is still more than four times higher in boreal forests (III). The absorptive roots of birches growing in the North were significantly thinner and had higher values of SRL, which was the root trait that exhibited highest plasticity for birch (Table 4 in II). Spruces growing in the North formed longer absorptive roots with higher RTD and lower B_W, which was the trait that displayed highest plasticity for spruce. Also, spruce fine root longevity was significantly higher in the North.

These results imply that tree species have different acclimation-indicative root traits in response to changing environments. Birch ensures morphological acclimation across forest zones by changing SRL of the absorptive roots, which is mainly (61%) determined by the variation in root diameter. Similarly, higher values of SRL and smaller root diameter were recorded for birches growing in mine areas in comparison to native birch forests (II). The sensitivity of SRL to the tree nutrient status and environmental stress has been shown for birch also in earlier studies (Rosenvald, 2011). The acclimation of spruce absorptive roots is based mainly on the variation of B_W, which is chiefly (41%) determined by the variation of L (II).

Silver birch as a pioneer species must have a broader tolerance to environmental conditions across multiple environments; however, the mean PI of all morphological traits did not differ between early-successional birch and late-successional spruce. In addition, the morphology of the studied tree species became more similar towards southern forests (Figure 5), which can be explained by more fertile and closer to optimal growing conditions in the temperate forests (II).

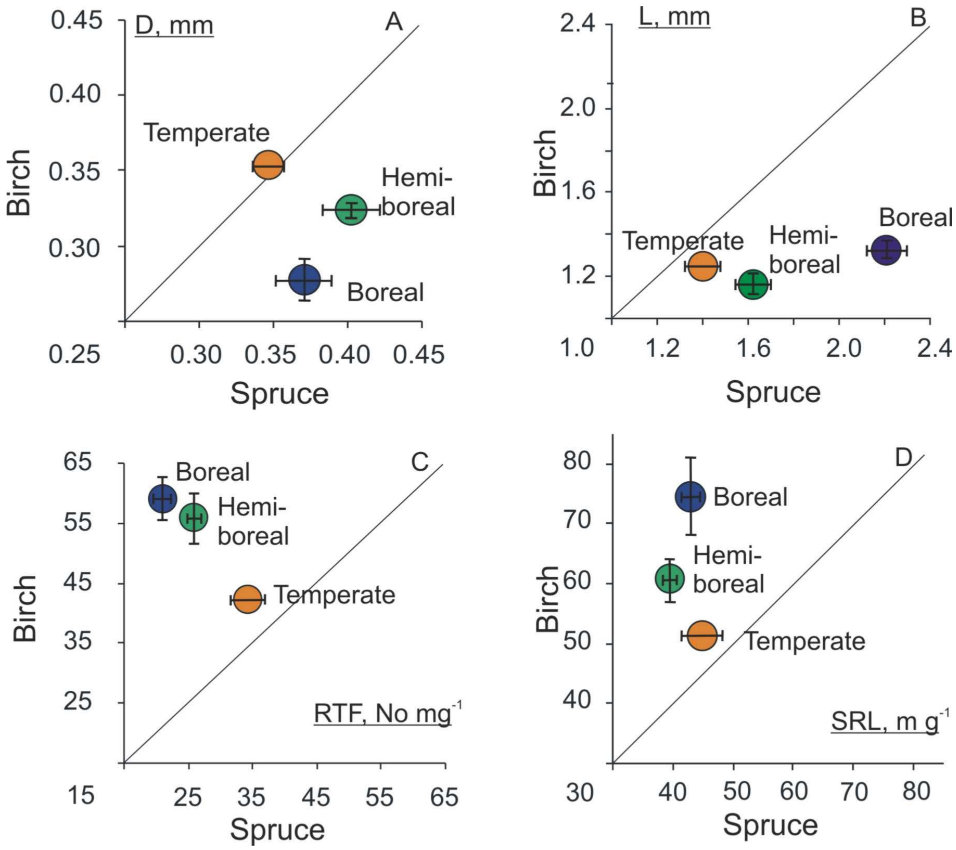

Figure 5. Mean values of (A) the diameter, (B) length, (C) branching frequency (root tip frequency per unit of weight – RTF) and (D) specific root length of birch and spruce in three forest zones: boreal, hemiboreal, and temperate. Average values and standard errors of the sample are shown. For birch forests, only stands that were older than 10 years and growing on native forest land were included and only one stand from the temperate zone was included. Figure from Publication II.

The community structure of the dominating EcM fungi explained 47% of the variation in spruce and 57% of the variation in birch absorptive root morphology (III). For spruce, it has been shown that RTD decreases and SRA increases from contact- to long-distance exploration type and the proportion of morphotypes forming long-distance exploration type is higher in temperate forests compared to boreal forests (Ostonen et al., 2011). Although the estimations for extramatrical mycelium biomass per unit of absorptive root length were higher in southern forests, taking into account the higher number of longer root tips in the North, the estimated extramatrical mycelium biomass was 2–4 times higher in the North.

Regarding the structure and diversity of the bacterial community in the bulk soil and rhizosphere of silver birch forests, a latitudinal effect was found for one bulk soil module, where four bacterial phylotypes were negatively related to the distance from the equator. Soil characteristics had a strong effect on bacterial community structure, describing 48% of the bulk soil and 51% of the rhizosphere bacterial community variation. The driving soil factors were pH and P content. Soil C:N ratio was negatively correlated to the number of OTUs in the rhizosphere, with a bacterial consortium (module H) containing *Fluviicola* gaining predominance in soils with higher N content. Bacteria from this genus prefer rich soils and are able to degrade persistent organic molecules in the rhizosphere (Song et al., 2016).

Strong relationships were found between absorptive root morphology, EcM fungal community structure and bacterial community structure in the bulk soil and rhizosphere in birch stands. Out of root morphological traits, bacterial community structure and diversity were most related to variation in root weight, RTD and branching frequency, which suggests that a larger number of bacterial species were more evenly distributed around younger root tips, probably because of better substrate supply from the root (Folman et al., 2001).

Overall, soil C:N ratio was found to explain most of the variability in absorptive root and extramatrical mycelium biomass, RTD, root N concentration and rhizosphere bacterial community structure.

3.4. Possible sources of stress regarding soil warming, humidification and growing in the North

The study sites for both tree species between latitudes 48 and 68°N displayed gradients in climate (e.g. mean annual temperature and precipitation, growing season length) as well as in N deposition. The varying fertility of the studied spruce sites was reflected by differences in soil C:N ratio. In general, the southern stands displayed higher fertility. Silver birch stands on native forest land belonged all to the fertile forest site types, so for this species other climate factors (low MAT, short growing season length) must have been limiting in the North. Both soil warming experimental sites exhibited optimal C:N values and sufficient soil water content, ruling N or water availability out as growth limiting factors. Thus, the possible sources of stress for spruces growing in warmed soils might have been soil nutrient imbalance, enhanced root metabolism and maintenance respiration, or higher pathogen and herbivore activities (Gill and Jackson, 2000; McCormack and Guo, 2014; Schindlbacher et al., 2009). At the FAHM site, elevated air humidity has been shown to affect trees through a number of concurrent mechanisms, such as impaired nutrient uptake, nutrient imbalance, increased soil moisture that may lead to hypoxia and metabolic stress, and higher frequency of fungal pathogen damage (Sellin et al., 2017). In addition, the impact of higher air humidity was initially amplified by early-successional grass understory, which caused strong below-ground competition.

3.5. General acclimation mechanisms to limiting growing conditions

All studied species reacted to nutrient limitation or otherwise suboptimal growing conditions by actively modifying their absorptive root morphology, which was the first response both temporally (I) and in terms of treatment intensity (IV). At the FAHM site, morphological differences were largest in the first two study years (second and third year of treatment), being replaced by an increase in FRB by the third study year (fourth year of treatment). On the geothermal soil temperature gradient, root morphology responded to smaller temperature increases, while FRB and aFRB decreased significantly at larger warming levels. At the same time, morphological changes proved to be persistent even after 9 years of warming in a 130-year-old forest (IV) and on the latitudinal gradient (II, III).

A general morphological reaction to environmental stress was forming longer and less-branched absorptive roots with higher SRL and SRA (Figure 6). This was observed for all the species included in this thesis and also for Scots pine, which has been analysed thoroughly in Publication III, but omitted from this thesis. Also, thinner absorptive roots were produced in the North by birch and pine and in relation to humidification by birch. A similar acclimation pattern of forming thinner roots with higher SRL in cold habitats and in infertile growing conditions has been demonstrated to occur globally across a large number of species (Freschet et al., 2017; Holdaway et al., 2011; Kramer-Walter et al., 2016), which permits us to to conclude that the observed responses reflect general acclimation patterns to environmental stress and nutrient deficiency. Higher values of SRL and SRA have been shown to be indicative of malnutrition (Rosenvald, 2011) and are thought to reflect enhanced resource uptake at lower biomass investments, high root cost efficiency and fast growth (Comas and Eissenstat, 2004; Ostonen et al., 2011; Weemstra et al., 2016). Kramer-Walter et al. (2016) and Holdaway et al. (2011) reason that producing thinner roots with higher SRL may be useful when foraging for nutrients, which are spatially dispersed or display poor diffusivity, such as P, while forming thicker roots with lower SRL in productive environments may be beneficial as a thicker root cortex might support higher metabolic rates in fertile soils and have enhanced pathogen resistance, also necessary for growing in the warmer southern soils of our studied latitudinal gradient. Longer and less branched roots imply a shift from root tip formation to root elongation, increased soil exploration and a change in the EcM colonizers.

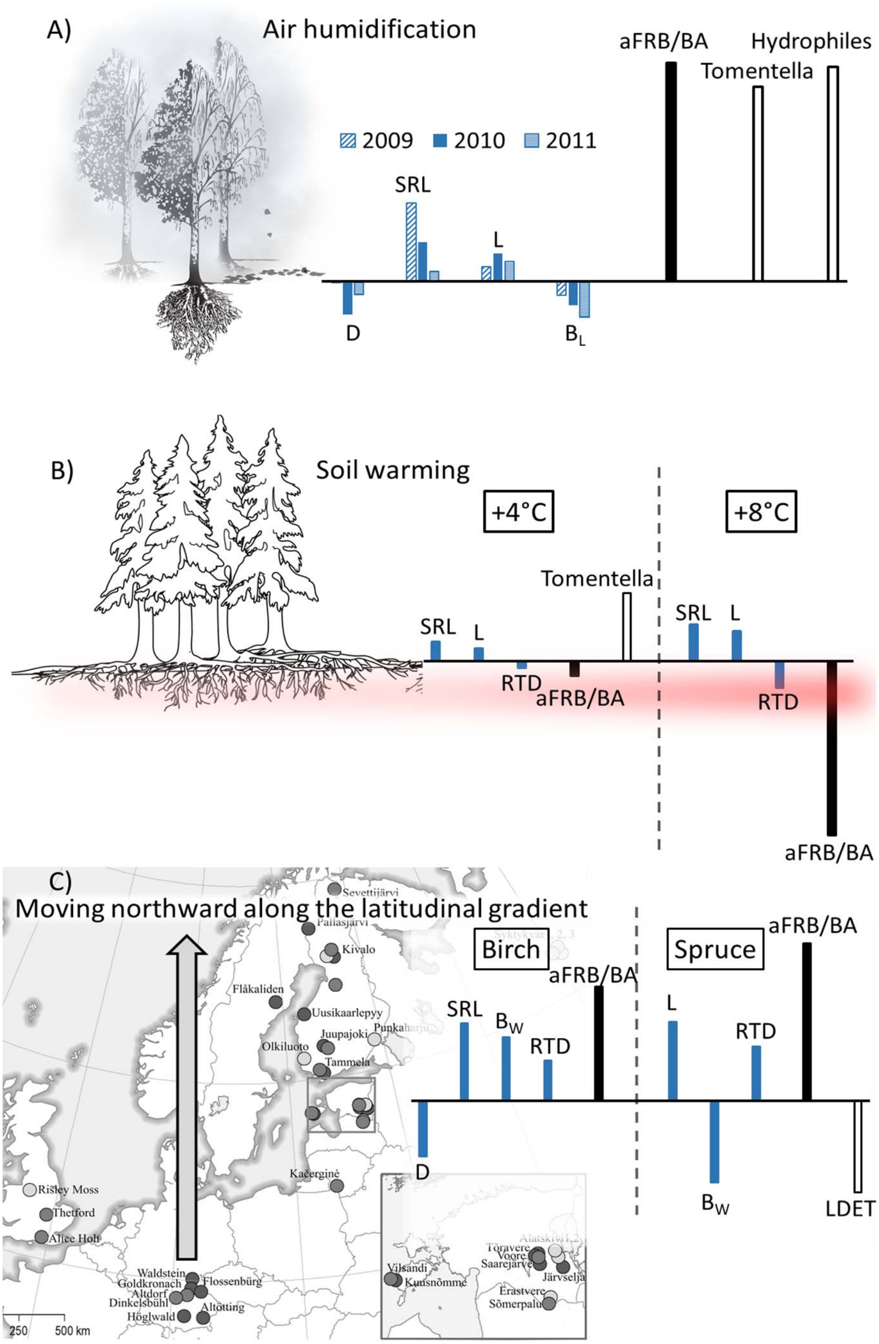

Figure 6. Main changes in absorptive root morphology (blue columns), absorptive root biomass (black columns) and the EcM fungal community (white columns) in A) the air humidification experiment, B) the soil warming experiments and C) northwards along the latitudinal gradient. Abbreviations: D – absorptive root diameter (mm), SRL – specific root length (m g^{-1}), L – absorptive root length (mm), B_L – branching per length (no mm^{-1}), B_W – branching per weight (no mg^{-1}), RTD – root tissue density (kg m^{-3}), aFRB/BA – absorptive root biomass per basal area (kg m^{-2}), LDET – long-distance exploration type.

RTD stood out from the other morphological traits for its larger sensitivity to soil fertility, increasing towards soils with a higher C:N ratio both in the soil warming experiments (IV) and northwards on the latitudinal gradient (III), which is a shared response for a number of species (Kramer-Walter et al., 2016) and may reflect an alternatively advantageous strategy of forming longer-living roots in infertile and colder soils. On the other hand, experimental soil warming caused a reduction in tissue density, which indicates shorter lifespan in warmed soils. Shorter spruce fine root lifespan has also been reported in relation to experimental soil warming in Flakaliden and southwards along a latitudinal gradient in Finland (Leppälammi-Kujansuu et al., 2014b, 2014a).

Both silver birch and Norway spruce responded to obstructed nutrient uptake, whether in northern forests with high soil C:N ratio or induced by air humidification, by increasing FRB/BA and aFRB/BA (Rosenvald et al., 2014 and III). A proportional increase in root biomass, especially in the absorptive root fraction, has been shown to be a common pattern across a large number of species in colder conditions (Reich et al., 2014; Zadworny et al., 2016) and for Scots pine in our latitudinal gradient study (III).

The higher proportion of fine root biomass in colder climate seems to be largely genetically determined (Last et al., 1983; Reich et al., 2014; Zadworny et al., 2016). It has also been shown, that tree genotype influences the root-colonizing EcM community structure and absorptive root branching (Velmala et al., 2013). Although attempts have been made to evaluate the contribution of intraspecific heritability to variation in root morphology (Salmela et al., 2020; Senior et al., 2019), the extent to which root morphological responses are under genetic control and how much they reflect phenotypic plasticity remains unclear. Answering this question calls for the common-garden approach and using clone trees in climate change manipulation experiments. For example, the latter method has been employed at the FAHM-site.

The root associated microbial community – in the current work: EcM fungi and rhizosphere bacteria – showed high adaptability to changes in their growing environment. Regarding the EcM community, humidification led to an increase in the proportion of hydrophilic morphotypes and *Tomentella* spp. (I). In warmer soils, there was also a rise in the proportion of *Tomentella* spp. and fungi characterized by long-distance exploration type (species belonging to the /boletus lineage) (IV). These alterations in the EcM community could be related to increased root turnover concurring with both air humidification and higher soil temperatures. Both in the humidification experiment (Truu et al., 2017) and along the latitudinal gradient (III), multilateral relationships were observed between absorptive root morphology, functional types of colonising EcM fungi, and rhizosphere and soil bacterial community structure, which demonstrates that root-rhizobiome acclimation is characterized by strong inter-relatedness between plant traits and soil microbe communities.

3.6. Implications for forest below-ground processes in relation to climate change

It is possible that C allocation below-ground via fine roots will increase in a warmer world with elevated levels of air humidity and CO_2 (Litton and Giardina, 2008; Lõhmus et al., 2019; Rosenvald et al., 2014; Wu et al., 2011), but this does not necessarily implicate increased standing fine root biomass as root respiration and mortality is expected to increase alongside root production (Leppälammi-Kujansuu et al., 2014b; Majdi and Öhrvik, 2004; Pendall et al., 2004; Pumpanen et al., 2012). Regarding standing fine root biomass, the effects of multiple climate factors, such as increased temperature and humidity that are discussed in this thesis, may interact by cancelling each other out (Leuzinger et al., 2011; Wu et al., 2011).

In addition to fine root litter, an important source of soil C is the fungal mycelium (Godbold et al., 2006; Wallander et al., 2004). Warming has been shown to cause an increase in the proportion of taxa that form larger extramatrical mycelial biomass (Deslippe et al., 2011; Ostonen et al., 2011; III, IV), while intensified fine root turnover and elevated soil moisture may favor hydrophilic and low-mycelial-biomass-forming taxa, such as *Tomentella* spp. (I, IV). However, predicting the C input into soil based on the proportion of different exploration types should be conducted with caution as it has been shown that species known to produce large extra-matrical mycelial biomass may direct more assimilated C into respiration rather than mycorrhizal biomass (Heinonsalo et al., 2010). Also, differences in absorptive root biomass must be taken into account when assessing changes in fungal biomass. For example, it has been estimated that due to a larger amount of EcM root tips in the soil in humid conditions, the amount of C entering the soil as hyphae may still be almost twice as large compared to control, even with the larger proportion of low-biomass-forming hydrophilic morphotypes (Lõhmus et al., 2019).

Extending the uncertainty regarding future carbon flows even further, the potentially higher fine root and mycelial litter inputs may not result in increased C sequestration in the soil, as SOM decomposition is also expected to intensify with warming, when soil moisture is not limiting (Liu et al., 2017; Pendall et al., 2004; Walker et al., 2018). This may initially increase nutrient mobilization and enhance plant growth, but eventually result in the depletion of soil resources and lead to reduced plant and microbial growth (Andresen et al., 2016; Walker et al., 2018). Elevated humidity and temperature have been shown to affect the soil bacterial community in such a way that changes in C metabolism, P and N turnover, mineral weathering and shifts in SOC quality can be assumed (Liu et al., 2017; Truu et al., 2017; III). Possible nutrient imbalances may arise from these changes and inhibit plant growth, as has already been demonstrated for European forests (Penuelas et al., 2020).

In order to make more accurate predictions about the effects of future climate on forest ecosystems, manipulation studies need to be run and monitored for longer periods, as it has been shown that ecosystem responses often change in time (Andresen et al., 2016). Since most studies have focused on subsets of taxa, interactions or processes, there is still limited knowledge about how the ecosystems respond as a whole (Walker et al., 2020). Also, the interactive effects of different climate change factors need to be comprehensively analysed, as they may not always be additive (Dieleman et al., 2012; Leuzinger et al., 2011; Wu et al., 2011). Furthermore, the mechanisms through which climate change factors influence ecosystems are not completely understood. For this reason, for example, an additional irrigation treatment has been established at the FAHM site to decipher, whether the humidification effect was caused by an increase in soil moisture, reduction in transpiration or some other factor.

4. CONCLUSIONS

This thesis demonstrates how two climate-change factors – an increase in air humidity and soil warming – affect the fine roots and root-associated microbial communities of birch (*Betula pendula*) and spruce (*Picea abies* and *P. sitchensis*); and identifies root traits that change most plastically for both species. In this work, findings from field manipulation experiments and a small-scale natural soil temperature gradient are compared to patterns witnessed along latitudinal gradients.

Birches and spruces responded to increased environmental humidity and warming through alterations in a number of root traits as well as shifts in the rhizosphere microbial community, and these changes were strongly inter-related. Absorptive root morphology proved to be very sensitive to environmental change. Morphological responses were detected before changes in fine root biomass allocation, both temporally (I) and in terms of warming intensity (IV). The similar root reactions, irrespective of tree species, stand age and location, or experimental approach, permit us to conclude that the observed responses reflect general acclimation patterns.

A general morphological reaction to environmental stress (i.e. humidification, experimental soil warming, growing in the North) was forming longer and less-branched absorptive roots with higher SRL and SRA. Higher values of SRL and SRA have been shown to be indicative of malnutrition and are thought to reflect enhanced nutrient uptake at lower biomass investments, while longer and less-branched roots indicate a shift from root tip formation to root elongation and changes in the EcM colonizers. Both species responded to obstructed nutrient uptake, whether in northern forests with high soil C:N ratio or induced by air humidification, by increasing fine and absorptive root biomass. On the latitudinal gradient, the increase in root biomass was accompanied by an increase in root tissue density and fine root lifespan. Experimental soil warming, on the other hand, led to a decrease in root biomass and tissue density, indicating intensified root turnover.

Although Norway spruce and silver birch showed similar patterns in absorptive fine root biomass along the latitudinal gradient and similar overall morphological plasticity, the root traits with highest plasticity differed between the species. For birch, the most plastic root trait was SRL, which was determined by variation in absorptive root diameter. Birch absorptive roots were significantly thinner and had higher SRL in the North and the same response emerged in relation to air humidification. For spruce, branching frequency (both per length and weight), absorptive root length and weight displayed highest plasticity, which is suggested to reflect higher relevance of these characteristics in the acclimation process. Thus, the set of root traits that are relied on in the acclimation process is distinctive to tree species.

The EcM community showed high adaptability to changes in the environment. Humidification caused a shift towards the dominance of hydrophilic EcM morphotypes and an increase in the abundance of *Tomentella* spp. In warmer soils, there was also a rise in the proportion of *Tomentella* spp. and fungi characterized by long-distance exploration type. A similar increase in the proportion of long-distance exploration type was observed southwards along the latitudinal gradient for spruce. These shifts in the EcM community could partly be related to increased root turnover concurring with both air humidification and higher soil temperatures. The community structure of the dominating EcM fungi explained a large proportion of the variation in absorptive root morphology (47% for spruce and 57% for birch). For spruce, it has been shown that RTD decreases and SRA therefore increases from contact- to long-distance exploration type.

Strong multilateral relationships were also found between absorptive root morphology, EcM fungal community structure and bacterial community structure in the bulk soil and rhizosphere in birch stands. Out of root morphological traits, bacterial community structure and diversity were most related to variation in root tip weight, RTD and branching frequency, which suggests that a larger number of bacterial species were more evenly distributed around younger root tips, probably because of better substrate supply from the root. Regarding abiotic factors, soil characteristics, such as C:N ratio, pH and P content, had strongest influence on the bacterial community structure. Overall, soil C:N ratio was the factor found to explain most of the variability in a number of absorptive root traits and microbial community structure along the latitudinal gradient.

This thesis provides valuable knowledge about the prospective acclimation patterns of birch and spruce fine roots and rhizobiomes in relation to climate change and demonstrates the involvement of all the members and components of the root-rhizobiome complex in the forest acclimation process. Also, the novelty of the work is exploring the response curves of fine root traits along the soil warming gradient up to the die-off edge of the forest and the temporal dynamics of root responses to elevated humidity. The qualitative changes that we witness in the root-rhizobiome translate into quantitative changes in ecosystem nutrient fluxes and our results underline the need for future research to focus more on interactions within the root-rhizobiome, on the temporal dynamics in ecosystem responses and the interactive effects of different climate change factors. We emphasise the importance of studying the ecosystem in as much entirety as possible, since strong complementarity appears in the responses of different organism groups and plant traits to environmental change.

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SUMMARY IN ESTONIAN

Kliimamuutuste mõju kase ja kuuse peenjuurtele ning nendega seotud mikroobikooslustele

Käesoleva sajandi lõpuks ennustatakse Põhja-Euroopa jaoks 2–4-kraadist õhutemperatuuri tõusu ning 5–40% suuremat sademete hulka (IPCC, 2013; Jaagus ja Mändla, 2014; Jungqvist jt, 2014; Kjellström jt, 2018; Lindner jt, 2014). Sellest tulenevalt on oodata keskmiselt 1,3–2,5-kraadist mullatemperatuuri tõusu (suvel maksimaalselt 4–5 kraadi) (Houle jt, 2012; Jungqvist jt, 2014; Oni jt, 2017) ja ka mullaniiskuse suurenemist, mis mõjutab oluliselt kõiki mullaprotsesse. Mulla aineringed ning ümbritseva metsaökosüsteemi elujõulisus sõltuvad suuresti muutustest puude peenjuurestikes ning juuri koloniseerivates seenekooslustes, millest võib pärineda kuni 70% mullasüsinikust (Clemmensen jt, 2013). Seetõttu on oluline mõista, kuidas puude juured ning nende risosfääris elavate seente, bakterite ja teiste organismirühmade kooslused mulla soojenemise ja niiskuse tõusuga kohanevad, mis omakorda võimaldab hinnata erinevate liikide vastupidavust kliimamuutuste suhtes ning suurendada metsade süsiniku- ja toitainete voogude määramistäpsust.

Peenjuured (läbimõõduga kuni 2 mm) jagunevad funktsionaalselt puitunud juhtejuurteks ja esmase ehitusega imijuurteks. Boreaalsetes ja parasvöötmemetsades koloniseerivad imijuuri valdavalt (90–100%) ektomükoriisaseened (Kraigher jt, 2007; Taylor jt, 2009), mis on omakorda tihedalt seotud risosfääribakteritega. Peen- ja imijuurte iseloomustamiseks kasutatakse juureparameetreid, nagu eripind, eripikkus, juurte kudede tihedus, diameeter, harunemine ja juurte biomass basaalpinna kohta, mis mõjutavad ja kirjeldavad toitainete omastamist, andes ühtlasi teavet juuredemograafia, mullaviljakuse ja taimede stressiseisundi kohta. Näiteks iseloomustavad eripind ja eripikkus (ehk imijuure pindala ja pikkus massiühiku kohta) juurte biomassi jaotust imava juurepinna moodustamisel. Seega peegeldavad eripinna ja -pikkuse suured väärtused intensiivset toitainete omastamist väiksema juuremassi kohta ja kiiret kasvu. Taimed võivad juurte eripinda ja -pikkust suurendada nii toitainete vähesuse korral kui ka vastupidi, viljakates tingimustes, kus kiire toitainete omastamine on tugeva konkurentsi tõttu hädavajalik (Comas ja Eissenstat, 2004; de la Riva jt, 2018; Lõhmus jt, 2006; Ostonen jt, 2007; Weemstra jt, 2016). Suurt juurte eripinda ja eripikkust põhjustavad kas madal juurte kudede tihedus või väike juurediameeter. Mõlemat näitajat on seostatud juurte elueaga, kuid kuna neid mõjutavad tegurid, nagu mulla struktuur ja viljakus, mükoriisne kolonisatsioon ja fülogeneetiline taust, erineval määral, siis muutuvad nad enamasti üksteisest sõltumatult. Lisaks eelnevatele tunnustele, peetakse ebaühtlaselt paiknevate toitainete omastamisel oluliseks juureparameetriks ka harunemist, mis sõltub suuresti juuri koloniseerivast seeneliigist (Kong jt, 2014; Liese jt, 2017). Morfoloogiliste muutustega paralleelselt reageerivad taimed varieeruvale toitainete kättesaadavusele muutustega peen- ja imijuurte biomassis, mis üldiselt ressursipuuduse korral suurenevad (Helmisaari jt, 2007;

Lõhmus jt, 2006; Ostonen jt, 2011). Juurte kasv ja morfoloogia sõltuvad märkimisväärselt ka neid koloniseerivatest seeneliikidest, mis võivad üksteisest oluliselt erineda nii ensümaatilise aktiivsuse, toitainete omastamise ja jaotamise, kui taimepoolsete ülalpidamiskulude poolest (Gorissen ja Kuyper, 2000; Lilleskov jt, 2002; Tedersoo jt, 2012; van der Heijden ja Kuyper, 2003; Velmala jt, 2014).

Kliimamuutuste mõjude uurimiseks on mitmeid võimalusi: manipulatsioonikatsed, looduslikud väikeseskaalalised keskkonnagradiendid ja suureskaalalised laiuskraadigradiendid. Manipulatsioonikatsetes on võimalik uurida huvipakkuvaid ökosüsteeme, liike ja genotüüpe ning eristada põhjuslikke seoseid, hoides kaasneva ebasoovitava geneetilise ja keskkonnavarieeruvuse võimalikult madala. Samas on selliste katsete puhul töötluse tasemete hulk, katse ajaline kestvus ja ruumiline ulatus tavaliselt piiratud, mis tekitab „saare efekti", ei võimalda tuvastada ökosüsteemi taluvuspiire ning suurendab tulemuste põhjal ökosüsteemide tegelike reaktsioonide üle- või alahindamise riski (Beier jt, 2012; Leuzinger jt, 2015; Walker jt, 2020). Looduslikud väikeseskaalalised keskkonnagradiendid (näiteks geotermaalsed mullatemperatuurigradiendid) võimaldavad uurida suuri järk-järgulisi muutusi, mis toimuvad suhteliselt väikesel maa-alal, välistades samuti muude keskkonnafaktorite (kliima, aluskivim jne) samaaegse muutumise. See-eest tekivad sellised gradiendid järsult ning mõjuvad algselt häiringuna. Nii geotermaalsed gradiendid kui eksperimentaalne mullasoojendamine ei imiteeri kliimamuutusi täielikult, kuna ümbritsevat õhku ei soojendata ning ikkagi esineb „saare efekt" (Leblans, 2016; O'Gorman jt, 2014). Kahe eelneva katsetüübi puudujääke kompenseerivad mõnevõrra erinevatel laiuskraadidel tehtud uuringud (laiuskraadiuuringud), kus ajalisi muutusi prognoositakse ruumiliste seaduspärade põhjal. Laiuskraadiuuringute eelis on eksperimentaalne realism, „saare efekti" ja algse häiringu puudumine ning keskkonnatingimuste pikaajaline kestvus, mis võimaldab vaadelda püsivaid muutusi ja tasakaaluolekuid. Siiski esineb neilgi puudusi: laiuskraadigradiendil muutub korraga palju keskkonnafaktoreid (kliima, aluskivim, fotoperiodism jne), mis teeb põhjusliku seose eristamise keeruliseks. Ühtlasi on raske eristada, kuivõrd on täheldatud erinevused määratud geneetiliselt ja kuivõrd tuginevad fenotüübilisele plastilisusele. Kirjeldatud eripärade tõttu soovitatakse kliimamuutuste tagajärgede kohta usaldusväärsete ennustuste tegemiseks ülalkirjeldatud katsetüüpe kombineerida.

Käesoleva doktoritöö eesmärk oli hinnata eksperimentaalselt suurendatud õhuniiskuse ja nii eksperimentaalselt suurendatud kui looduslikult tõusnud mullatemperatuuri mõju kuuse (*Picea* spp.) ja arukase (*Betula pendula*) peen- ja imijuurtele ning neid koloniseerivatele seenekooslustele ja võrrelda saadud tulemusi laiuskraadigradientidel ilmnevate kohanemisstrateegiatega. Laiuskraadiuuringutes hinnati puuliigispetsiifilisi erinevusi peen- ja imijuurte reaktsioonides, pöörates tähelepanu ka samaaegsetele seene- ning bakterikoosluste muutustele. Õhuniiskuse tõusu mõju arukase imijuurte morfoloogiale ja neid koloniseerivale seenekooslusele uuriti FAHM-katsealal Eestis (I), kus õhuniisutusest tingituna oli suhteline õhuniiskus keskmiselt 7% kõrgem kui kontrollaladel. Mullasoojenemise mõju hariliku kuuse (*Picea abies*) ja sitka kuuse (*P. sitchensis*) peen- ja imijuurte biomassile ning imijuurte morfoloogiale uuriti kunstlikul mullasoojendamis-katsealal Achenkirchis Austrias ja looduslikul geotermaalsel mullatemperatuurigradiendil ForHot-katsealal Islandil (IV). Achenkirchi katsealal hoiti soojendatud katseringide mulda vegetatsiooniperioodi vältel 4 °C soojemana kui tavaoludes, ForHot mullatemperatuurigradiendi kõige soojemas katseringis oli mullatemperatuur ~10 °C soojem kui kontrollringis. Achenkirchi alal määrati ka imijuuri koloniseeriv seenekooslus. Laiuskraadiuuringud hõlmasid 14 kuusikut laiuskraadivahemikus 48–68°N ja 15 kaasikut laiuskraadivahemikus 53–66°N. Neil aladel hinnati muutusi imijuurte morfoloogias (II), peen- ja imijuurte biomassis, juuri koloniseerivas seenekoosluses ja mulla ning risosfääri bakterikoosluses (III).

Laiuskraadigradiendil kasvavates puistutes esinesid gradiendid aasta keskmises õhutemperatuuris ja sademete hulgas, vegetatsiooniperioodi pikkuses ning mullaviljakuses. Kuna kõik uuritud kaasikud kuulusid viljakatesse kasvukohatüüpidesse, siis nende kasvu võis põhjapool piirata pigem lühike vegetatsiooniperiood või madal temperatuur, erinevalt kuuskedest, mida võis mõjutada ka vähene lämmastiku kättesaadavus. Seevastu mõlemal mullasoojendamiskatsealal (Achenkirch, ForHot) oli mulla süsiniku-lämmastiku suhe (C:N) optimaalne ja mulla veesisaldus piisav, nii et lämmastiku või vee kättesaadavus ei saanud kuuskede kasvu pärssida. Kõrgem mullatemperatuur võis seevastu põhjustada suurema vajaduse teiste toitainete (fosfor, kaalium) järele, kiirendada juurte ainevahetust, võimendada juurehingamist või esile kutsuda suuremat patogeenide ja herbivooride aktiivsust (Gill ja Jackson, 2000; McCormack ja Guo, 2014; Schindlbacher jt, 2009). FAHM-katsealal, mis paikneb samuti viljakal mullal, on õhuniisutuse mõjul tuvastatud madalam ksüleemivoolu intensiivsus (Kupper jt, 2011), mistõttu väheneb toitainete massivool mullast juurteni ja raskendub toitainete omastamine juurte poolt. Seda võib omakorda võimendada tugevat konkurentsi pakkuv alustaimestu või funktsionaalne struktuurimuutus mulla ja risosfääribakterite kooslustes (Truu jt, 2017). Suurendatud õhuniiskuse tingimustes kasvanud arukaskedel on esialgu tõepoolest mõõdetud madalamat lehtede lämmastiku- ja fosforisisaldust (Sellin jt, 2013), millest võib järeldada puude kehvemat mineraaltoitainetega varustatust.

Nii kuused kui kased reageerisid raskendatud toitainete kättesaadavusele ja ebasobivatele kasvutingimustele aktiivselt imijuurte morfoloogiat muutes, mis oli esmane reaktsioon ajaliselt (õhuniisutuskatses) ning ilmnes juba madalamatel soojenemistasemetel (mullatemperatuurigradiendil). Õhuniisutuskatses olid morfoloogilised erinevused suurimad esimesel kahel katseaastal ning kolmandaks katseaastaks asendusid morfoloogilised erinevused niisutatud katseringides peenjuurte biomassi tõusuga. Geotermaalsel mullatemperatuurigradiendil olid olulised erinevused juuremorfoloogias välja kujunenud juba 3-kraadisel soojenemisel, kuid peen- ja imijuurte biomass langes märkimisväärselt alles alates 4-kraadisest soojenemisest. Samas nähtus Achenkirchi soojendamiskatsest ning laiuskraadiuuringutest, et morfoloogilised erinevused võivad olla vägagi püsivad. Üldine morfoloogiline reaktsioon keskkonnastressile (õhuniisutus, mullasoojendamine, põhjapoolsed suboptimaalsed kasvutingimused) väljendus pikemate, vähemharunenud imijuurte moodustamises ning omastava pinna suurendamises juuremassiühiku kohta (ehk suuremas eripinnas ja -pikkuses). Mullasoojenduskatsetes ning õhuniisutuskatse esimesel aastal kaasnes eelnimetatud muutustega ka juurte kudede tiheduse vähenemine, mis võib peegeldada juurte kiiremat elutsüklit ja lühemat eluiga. Laiuskraadigradiendil oli põhjapoolsete puistute juurte kudede tihedus seevastu suurem, korreleerudes pikema juurte elueaga. Juurte kudede tihedus eristus teistest parameetritest tundlikkuse poolest mullaviljakuse suhtes, suurenedes kõrgemate C:N väärtuste suunas nii soojenduskatsetes kui laiuskraadigradiendil. Nii kuused kui kased reageerisid madalale toitainete kättesaadavusele (nii põhjapoolsetes väheviljakates tingimustes kui õhuniisutusest tulenevalt) peen- ja imijuurte biomassi suurendamisega.

Kuigi kuusk ja kask reageerisid keskkonnamuutustele üldiselt samasuunaliselt, erinesid liigid kõige plastilisemate tunnuste poolest. Kase puhul tõusis kõige plastilisema parameetrina esile imijuurte eripikkus, mida mõjutas peamiselt juurte diameeter. Kase imijuured olid oluliselt peenemad ja suurema eripikkusega põhjapoolsetes puistutes ning sama reaktsioon ilmnes ka seoses õhuniisutusega. Peente suure eripinnaga juurte moodustamine võib olla vajalik hajutatult paiknevate ja väheliikuvate toitainete (näiteks fosforiühendite) efektiivsemaks omastamiseks, samas kui paksemate ja seetõttu väiksema eripinnaga juurte moodustamine viljakates lõunapoolsemates kasvukohtades võib olla kasulik, kuna paksem juurekorteks võimaldab intensiivsemat ainevahetust ning suuremat vastupanuvõimet patogeenidele (Holdaway jt, 2011; Kramer-Walter jt, 2016). Kuuse puhul varieerusid enim imijuurte harunemine, pikkus ja kaal. Pikemate vähemharunenud juurte moodustamine (nii põhjas kui ka soojendatud muldadel) viitab intensiivsemale mullaruumi hõivamisele, vähenenud juuretippude moodustamisele ja juuri koloniseeriva seenekoosluse muutumisele.

Juuri koloniseeriv seenpartner määras laiuskraadikatsetes 47% kuuse ja 57% kase imijuurte morfoloogilisest varieeruvusest. Kuuse puhul on näidatud, et juurte kudede tihedus väheneb ja eripind suureneb kontakt-mütseelitüübist (*contact exploration type*) kauglevi-mütseelitüübi (*long-distance exploration type*) suunas ning suurema hüüfimassiga kauglevi-mütseelitüüpi moodustavate seeneliikide osakaal on parasvöötme metsades suurem kui boreaalsetes metsades (Ostonen jt, 2011). Kuigi lõunapoolsetes metsades tekib seetõttu mulda juurte pikkusühiku kohta rohkem hüüfimassi, on põhjapool suurema juuretippude arvu tõttu mullas paikneva mütseeli biomass siiski 2–4 korda kõrgem. Kunstlik 4-kraadine mullasoojendamine kutsus imijuuri koloniseerivas ektomükoriisakoosluses esile perekond *Tomentella* ohtruse tõusu ning toetas kauglevi-mütseelitüüpi moodustavate liikide (*Boletus luridus*) esinemist. Õhuniisutus põhjustas nihke hüdrofiilsete morfotüüpide ja perekond *Tomentella* osakaalu suurenemise suunas. *Tomentella* liikidele on omane kõrge funktsionaalne plastilisus, mis seletab nende suurt ohtrust ja häiringutaluvust. Ühtlasi on nad võimelised tootma ensüüme, mis on vajalikud värske varise lagundamiseks. Sellised muutused ektomükoriisakoosluses võivad olla osaliselt seotud intensiivsema juurekäibega, mis ilmnes nii õhuniisutuse kui mullasoojenemise tingimustes.

Laiuskraadiuuringutes tuvastati olulised kolmepoolsed seosed juuremorfoloogia, juuri koloniseeriva ektomükoriisakoosluse ning mulla ja risosfääri bakterikoosluse vahel. Bakterikoosluse struktuur ja mitmekesisus seostusid morfoloogilistest parameetritest enim imijuurte keskmise tipumassi, kudede tiheduse ning harunemisega, mis viitab sellele, et noorte väikese tihedusega juuretippude ümber leidus rohkem bakteriliike, tõenäoliselt parema toitainete kättesaadavuse tõttu. Kõige tugevamalt mõjutasid bakterikooslust aga mullatingimused, nagu C:N suhe, pH ja fosforisisaldus. Üleüldse oli piki laiuskraadigradienti peamine imijuuri ja nendega seotud mikroobikooslusi mõjutav tegur mulla C:N suhe.

Antud doktoritöö pakub väärtuslikku uut teavet kuuse ja kase peenjuurte ja risobioomide oodatavate kohanemismustrite kohta ning näitab, et keskkonnamuutused kutsuvad esile komplementaarseid nihkeid kõigil peenjuurestiku tasemetel. Esmakordselt kirjeldati juureparameetrite muutusi piki temperatuurigradienti kuni puude suremispiirini ning jälgiti õhuniisutuse mõju ajalist dünaamikat imijuurte morfoloogiale. Käesolevalt on näidatud, kuidas suurenenud õhuniiskus ja soojem muld puude peenjuurestikke ja juuri koloniseerivaid mikroobikooslusi eraldiseisvalt mõjutavad. Süsinikuvoogude usaldusväärsemaks prognoosimiseks on aga praegusest enam teavet vaja koguda ka mitmefaktorilistest katsetest, kuna erinevate kliimamuutusetegurite mõjud ei pruugi olla aditiivsed. Ühtlasi on kliimamuutuste uuringuid vaja teostada pikaajalisemalt, kuna ökosüsteemide reaktsioonid on sageli ajas muutuvad, ning vaadelda tuleks võimalikult suurt osa ökosüsteemi komponentidest ja protsessidest korraga, sest nagu antud töös nähtub – erinevate organismirühmade ja taimeparameetrite reaktsioonid keskkonnamuutustele on omavahel tugevalt seotud.

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