Linking root traits and plant-soil feedbacks to environmental change in the sub-arctic tundra

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Abstract

Plant community assembly processes shape the composition and abundances of species, and encompass functional traits and resource acquisition strategy of species, biotic interactions and abiotic filtering. Hence, an understanding of these complex processes requires disentangling the effects of multiple factors influencing plant community assembly. In this thesis, I investigated fine root trait associations with soil microorganisms, the resulting feedback effects from those interactions (i.e., plant-soil feedbacks), plant-plant interactions under warming, and the effects of temperature on fine root traits of plant communities in the Swedish sub-arctic tundra.

Here, the chemical root economics spectrum (i.e., tradeoff between acquisitive and conservative strategies) predicted the abundance of broad microbial groups, whereas individual fine root traits were associated with the relative abundances of fungal taxa. It also explained plant-soil feedback, with acquisitive trait values resulting in negative feedbacks. In addition, plant-plant interactions were altered under warming, but this was not related to resource-acquisition strategy. Further, community-level root trait responses to temperature were not necessarily related to root resource investment strategy.

Taken together, this thesis shows the importance of fine root traits for understanding plant community responses to global change. This has implications for plant community assembly, as well as carbon and nutrient cycling in a future warmer sub-arctic tundra.

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Länkar samman rötters egenskaper och växt-mark återkopplingar med miljöförändringar på den subarktiska tundran

Sammanfattning

De processer som formar sammansättningen och mängd arter i växtsamhällen innefattar arters funktionella egenskaper, resursförvärvande strategier, samt biotiska interaktioner och abiotisk filtrering. En ökad förståelse av dessa komplexa processer kräver därför att effekter av flera olika faktorer som påverkar växtsamhällens samansättning undersöks. I denna avhandling undersökte jag associationer mellan finrötters egenskaper och marklevande mikroorganismer och återkopplingseffekter mellan växter och mark som resulterar från dessa interaktioner. Jag undersökte också interaktioner mellan växter under uppvärmning samt hur temperatur påverkar finrötter i växtsamhällen på den svenska subarktiska tundran. Det kemiska ekonomiska spektrat för rötter, dvs. avvägningen mellan mer resursförvärvande och mer konservativa växtstrategier, förutsåg bredare mikrobiella gruppers olika mängd medan finrötters individuella egenskaper var associerade med den relativa mängden av olika svamptaxa. Det förklarade även återkopplingar mellan växterna och marken där resursförvärvande egenskaper resulterande i negativa växt-mark återkopplingar. Dessutom påverkades växternas interaktioner av ökade temperaturer men denna effekt var inte relaterad till växternas resursförvärvande strategi. Forsatt, varmare temperaturers påverkan på hela växtsamhällets rotegenskaper var inte relaterat till rötternas resursinvesteringsstrategi. Sammantaget visar denna avhandling på vikten av finrötters egenskaper för förståelsen av hur växtsamhällen svarar på globala miljöförändringar. Detta har implikationer på växtsamhällens sammansättning samt för kol- och näringsdynamik i en framtida varmare subarktisk tundra.

Nyckelord: Arktisk, finrötters egenskaper, svamp, växt-mark återkopplingar, växt-växt interaktioner, rhizosfär, root economic spectrum, variation i egenskaper, tundra.

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Dedication

To Cyril Ignatius Cyrus (†).

"*Think like a mountain*"
 Aldo Leopold

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Spitzer, C. M., Lindahl, B., Wardle, D. A., Sundqvist, M.K., Gundale, M.J, Fanin, N., Kardol, P. (2021). Root trait-microbial relationships across tundra plant species. New Phytologist, 229: 1508 -1520.

II. Spitzer, C. M., Wardle, D. A., Lindahl, B., Sundqvist, M.K., Gundale, M.J, Fanin, N., Kardol, P. Root traits and soil microorganisms as drivers of plant-soil feedbacks within the sub-arctic tundra (submitted manuscript).

III. Spitzer, C.M., Kardol, P. Warming alters plant-plant interactions of sub-arctic tundra species with contrasting resource acquisition strategies (manuscript).

IV. Spitzer, C. M., Sundqvist, M.K., Wardle, D. A., Gundale, M.J, Kardol, P. Fine root trait variation along a sub-arctic tundra elevational gradient (manuscript).

Paper I is reproduced with the permission of the publisher.

The contribution of Clydecia Melissa Spitzer to the papers included in this thesis was as follows:

I. Designed the study with co-authors, conducted field and greenhouse work, harvested the experiment, extracted DNA and prepared samples for sequencing, fungal annotations, all statistical analyses, and lead in the writing of the manuscript.

II. Designed the study with co-authors, collected soil and seeds in the field, conducted laboratory and greenhouse work, all statistical analyses, and lead in the writing of the manuscript.

III. Contributed to forming the idea, coordinated and participated in the fieldwork, designed the experimental setup, maintained the growth chamber study, harvested the plants, conducted all statistical analyses and lead in the writing of the manuscript.

IV. Designed the study with co-authors, conducted all field and laboratory work, performed data analyses, and lead in the writing of the manuscript.

1. Introduction

Plant community assembly refers to a set of processes that shape the composition and abundance of species in an ecological community. It can be influenced by biotic and abiotic factors, as well as by stochastic processes (Chase & Myers 2011; Dini-Andreote *et al.* 2015). A central aspect of plant community assembly involves the functional traits of the constituent species (*see* section 1.2) and their role in determining plant community composition (Shipley 2010; Kraft *et al.* 2015). Other important aspects include biotic interactions and abiotic filtering, which ultimately influence the species composition and abundance of plant communities (Kraft & Ackerly 2014). Therefore, because of the complexity of plant community assembly processes, research typically involves disentangling the effects of the various factors influencing plant community assembly, and at various scales.

To date, we understand little about plant community assembly in arctic ecosystems. At the same time, average air temperature is predicted to increase by about 4°C by the end of the century (IPCC 2018), which could influence plant community composition and species abundances. Hence, an understanding of plant functional traits, biotic interactions and community responses to elevated temperatures is urgently needed to enable predictions of future plant community dynamics in arctic ecosystems.

1.1 The sub-arctic tundra

Arctic ecosystems are characterised by harsh environmental conditions, including short growing seasons and cold temperatures, which affect productivity and species diversity (Murray 1998). The vegetated lowland of the arctic is the tundra. The word 'tundra' means treeless plain and originates from the Saami word "tundar". The sub-arctic tundra is generally classified

as high elevation tundra occurring above the tree line and between Northern latitudes 50° and 70°, but lower than the latitudinal limit for tree growth (Wielgolaski 1997), and with a growing season of approximately three months (Wielgolaski *et al.* 1981; Murray 1998). The low-statured vegetation in the sub-arctic tundra is typically meadow or heath. Meadow vegetation is dominated by graminoids and forbs, whereas heath vegetation is primarily characterized by ericaceous species, other dwarf shrubs, as well as some graminoids and forbs.

1.2   Plant functional traits

Plant functional traits are defined as, *"morpho-physio-phenological traits which impact fitness indirectly via their effects on grown reproduction and survival."* (Violle *et al.* 2007). The investigation of these traits and their values is useful for understanding the assembly of plant communities (Shipley 2010). This is because a trait-based approach is more useful for developing mathematical models for explaining and predicting plant community assembly and at several scales (Shipley 2010). Further, employing trait-based approaches in ecological models may have an advantage over species-based models, since they do not need to account for species extinctions or migration, e.g. in response to climate change.

1.2.1   The root of the matter: fine root traits

Plant trait research has generally focused primarily on aboveground traits (Díaz *et al.* 2016; Bruelheide *et al.* 2018), likely due to the ease of sample collection. However, there has been a recent shift towards investigating plant root traits and their implications for ecosystem functioning (Bergmann *et al.* 2017; McCormack *et al.* 2017; Valverde-Barrantes *et al.* 2017; Freschet *et al.* 2021). This recent development is critical for the advancement of plant ecology, especially since it has been shown that most above- and belowground traits are not necessarily mirrored (Kramer-Walter *et al.* 2016), probably because evolutionary pressures shaped the development of above- and belowground traits differently (Bergmann *et al.* 2017). Hence, the incorporation of only leaf traits in models may lead to an underestimation of the influence of plant communities on nutrient and carbon cycling, or the responses of plant communities to environmental change. Further, a large proportion plant biomass (up to 70%) is allocated belowground in alpine and

arctic ecosystems (Körner 2013; Iversen *et al.* 2015). Therefore, in these ecosystems roots and their traits may potentially be contributing more to plant survival or ecosystem functioning than aboveground traits.

Plant roots and their functions

The earliest fossil evidence of roots as multicellular plant organs appeared during the Devonian period, 416 to 360 million years ago (Kenrick & Strullu-Derrien 2014). There is strong evidence that roots of vascular plants co-evolved with mycorrhizae (Wang & Qiu 2006; Strullu-Derrien & Strullu 2007) and formed important symbiotic associations with mycorrhizal fungi from the outset with the exchange of plant metabolites for nutrients (Strullu-Derrien & Strullu 2007; Bonfante & Genre 2008). The cortex of plant roots (see Figure 1) hosts arbuscular mycorrhizal symbionts, which are essential for plant growth in nutrient-poor soil (Genre *et al.* 2008). Fine roots have the primary function of water uptake (Comas *et al.* 2013) and nutrient uptake (Guo *et al.* 2008), with the latter also being accomplished without dependence on mycorrhizal fungi (Wang *et al.* 2006). These nutrients are important for supporting plant photosynthesis, growth and maintenance (McCormack *et al.* 2015).
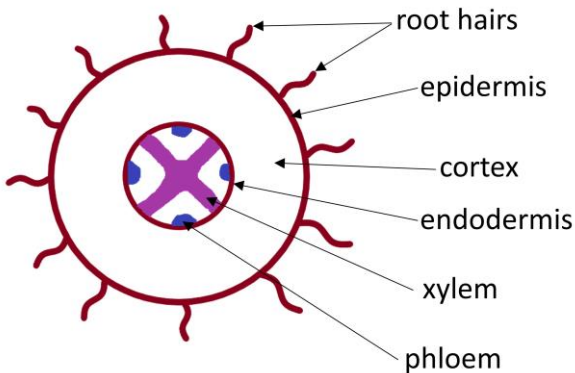

Figure 1. Simplified drawing of the cross section of a root

The root economics spectrum

The root economics spectrum has recently been incorporated into plant ecological research. It generally represents a trade-off axis, where plants

either invest in rapid growth of short-lived roots for fast nutrient uptake (i.e., acquisitive strategy) (Freschet *et al.* 2010; Reich 2014), or in slower growth of well-defended roots, but with a stronger dependence of plants on mycorrhizal symbionts for nutrient uptake (i.e., conservative strategy) (Cortois *et al.* 2016). However, there is increasing evidence that root traits are multidimensional (Kramer-Walter *et al.* 2016; Weemstra *et al.* 2016), and that there may be several root trait spectra (i.e., tradeoff axes) (Kong *et al.* 2019; Bergmann *et al.* 2020). For example, Bergmann *et al.* (2020) suggest that there may be two primary root trait axes, one representing a collaboration gradient (i.e., root exploration vs. carbon investment for outsourcing via mycorrhizal partners) and the second representing a conservation gradient (long-lived dense tissue vs. fast growth with short lifespan). These root trait axes are useful for understanding the interactions of plants and soil organisms (Zhang *et al.* 2020a), as well as plant community effects on ecosystem carbon and nutrient cycling in response to environmental change.

1.3   Plant-soil feedback

Plant-soil feedback is the outcome of plant-microorganism interactions, where plants change the composition of the soil community (Bever 1994; Bever *et al.* 1997) and abiotic soil properties (Van der Putten *et al.* 2013), which in turn affects the growth rate of the plant (Van der Putten *et al.* 1993; Bever 1994). The net outcome of plant interactions with antagonistic and mutualistic microorganisms may be positive, negative or neutral (Bever *et al.* 2012). These interactions are important drivers of plant community assembly (Klironomos 2002; Kardol *et al.* 2007).

1.3.1   Root influences on soil microorganisms.

Plants have been shown to influence soil microorganisms via root exudation (Bais *et al.* 2006; Hu *et al.* 2018), and by influencing litter quantity and quality for decomposers (Sun *et al.* 2018; Veen *et al.* 2019). In addition, roots grow in close association with soil microorganisms within the rhizosphere, i.e., the millimetres of soil surrounding roots (Bais *et al.* 2006). Hence, the rhizosphere provides an environment for direct interactions between roots and soil microorganisms. These root-microorganism interactions have been shown to influence the abundance of both antagonistic (Philippot *et al.* 2013)

and mutualistic (Bonfante & Genre 2010) soil microorganisms. However, there remains a huge knowledge gap as to the extent to which fine root traits influence the abundance of various soil microbial functional guilds. Further, the relative importance of morphological and chemical traits for explaining these microbial functional guilds is not well understood.

The tundra is known to harbour a high abundance of cold-tolerant fungi (Margesin *et al.* 2009; Treseder & Lennon 2015) and mycorrhizal associations are commonly observed (Newsham *et al.* 2009). At the same time, there is a paucity of research on moulds, saprotrophic and pathogenic taxa in these cold ecosystems. Therefore, research in the tundra, aimed at understanding the importance of the large biomass of roots (and their associated traits) for influencing these various functional guilds is important for predicting ecosystem functioning, as well as plant community assembly.

1.3.2   Role of root traits in plant-soil feedbacks

Plant-soil feedback studies have increased over the past two decades, but the importance of root traits (and their interactions with soil organisms from various functional guilds) in driving plant-soil feedbacks is still not well understood. Indeed, the importance of root trait-mycorrhizal relationships has been shown to influence plant-soil feedback direction and strength (Cortois *et al.* 2016). Still, little research has been conducted into the importance of root trait interactions with saprotrophs, pathogens, and opportunistic fungi for driving these feedbacks. A recent study provided evidence that lower taxonomic richness of soil pathogens gave rise to negative plant-soil feedback (Semchenko *et al.* 2018). However, additional studies in other ecosystems and with a larger number of fine root traits, as well as other fungal functional guilds such as opportunistic fungi may be important for establishing general patterns. Further, there is a large knowledge gap regarding the role of the root economics spectrum in explaining the direction (i.e., positive, negative or neutral) and strength of plant-soil feedbacks. Recent studies have shown that species with a high specific root length and low percentage mycorrhizal fungi colonization were associated with negative plant-soil feedbacks (Cortois *et al.* 2016), while thicker root diameters resulted in positive plant-soil feedbacks (Semchenko *et al.* 2018). However, these studies were based in temperate grasslands with different nutrient dynamics (Rumpel *et al.* 2015; de Vries & Bardgett 2016). In the arctic tundra, there is a paucity of research related to plant-soil

feedbacks and the role of root trait-microbial interactions in driving these feedbacks. This presents a knowledge gap for understanding the mechanisms involved in plant community assembly in the arctic tundra.

1.4   Plant-plant competition under warming

Temperature increases in the tundra are already causing shifts in plant community composition (Edwards & Henry 2016) and plant functional group abundances (Elmendorf *et al.* 2012a; Bråthen *et al.* 2018). Species interactions may dictate the response of plant communities to these increasing temperatures (Suttle *et al.* 2007; Van der Putten 2012), but most research on community responses in the tundra has not examined plant-plant interactions. Plant-plant interactions can be either competitive or facilitative (Körner 2013). Specifically in the sub-arctic tundra, the outcomes of these plant-plant interactions could be driven by the root resource-acquisition strategy (i.e., resource acquisitive vs. resource conservative) of the interacting species, and may be determined by whether plants may be competing for a common limiting nutrient to support photosynthesis. For example, a substantial proportion of biomass is allocated belowground (Körner 2013; Iversen *et al.* 2015) in the sub-arctic tundra, which may result in increased competition for the low quantity of plant-available nitrogen and phosphorous (Thomas & Bowman 1998; Körner 2013).

1.5   Plant community responses to global warming

An increasing number of studies are being conducted to understand plant community responses to increasing temperatures within the tundra (Elmendorf *et al.* 2012b; Edwards & Henry 2016), but few studies have incorporated a trait-based approach (Read *et al.* 2014; Bjorkman *et al.* 2018). For example, Bjorkman *et al*. (2018) show that plant height increased with increasing temperature in the tundra. However, we have little understanding about root trait responses to increasing temperatures within the tundra. This is despite the potential for fine root traits to play a more important role than aboveground traits in plant responses to climate change in the arctic tundra, as a substantial proportion of plant biomass is allocated belowground (Körner 2013; Iversen *et al.* 2015). Elevational gradients are useful for increasing our understanding of responses of plant communities to global

warming. This is because plant communities at higher elevations experience lower temperatures relative to those at lower elevations (Sundqvist *et al.* 2013). Further, community-level changes in root trait values along elevational gradients can be influenced by plant species turnover (Descombes *et al.* 2017) and intraspecific trait variation (Albert *et al.* 2010; Messier *et al.* 2010). Therefore, exploring both intraspecific root trait variation and species turnover along elevational gradients allows for disentangling the drivers of community root trait variation.

1.6   Thesis objectives

The overall aim of this thesis is to understand root trait variation in the sub-arctic tundra and its ecological significance for plant community assembly in the context of climate change (Figure 2). This is done by conducting experiments on plant species interactions with soil microorganisms and the subsequent feedback effects (**papers I and II**), plant-plant interactions under warming (**paper III**) and root trait responses to temperature both at the plant species and community levels (**paper IV**). Hence, the thesis is structured to disentangle root-trait-related processes at various scales (i.e., trait scale, species scale, multiple species scale and community scale), which contribute to plant community assembly in the sub-arctic tundra under global warming. The study system for all research for this thesis is the sub-arctic tundra in Northern Sweden.

The main aim of each paper in this thesis is:
I.   To explore how fine root traits influence various soil fungal guilds and fungal to bacterial ratios in the sub-arctic tundra meadow (**paper I**).
II.   To investigate fine root traits and root trait-microbial relationships as predictors for the direction and strength of plant-soil feedback in the sub-arctic tundra meadow (**paper II**).
III.   To investigate the extent to which root resource-acquisition strategies influence plant-plant interactions under warming in the sub-arctic tundra meadow (**paper III**).
IV.   To determine root trait responses to temperature at the plant species and community levels in the sub-arctic heath (**paper IV**).
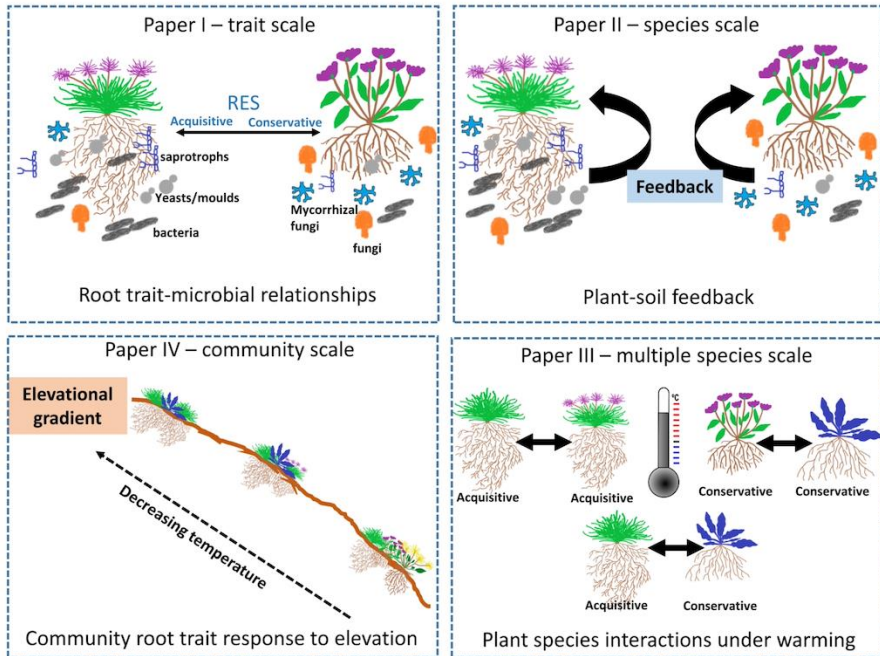
Figure 2. Overview of research conducted in this thesis (papers I – IV in a clockwise direction). RES refers to the root economics spectrum.

2. Methods

2.1 Study system: sub-arctic tundra

Two sub-arctic tundra sites (Figure 3) near Abisko (68°21′N 18°49′E) were utilized either for collecting soil and/or seed material (papers I, II, and III) or for conducting a field study (paper IV). Soil and seeds for papers I and II were collected approximately 27 km north-east of Abisko (68°21′N 18°49′E) (site 1), at the foothills of Mount Gearggečorrus (700 m a.s.l.). The soil is classified as cryorthents (Darmody *et al.* 2000) and has the following basic properties: moisture = 25.8 %; NH^{4+} = 0.009 mg g^{-1} dry soil; PO^{4+} < 0.000 mg g^{-1} dry soil, and pH 5.54 (Veen *et al.* 2015). The second site was located approximately 20 km south of Abisko on a well-described elevational gradient on the northeast-facing slope of Mount Suorooaivi (Sundqvist *et al.* 2011a;b) and was utilized for papers III and IV. Briefly, along the elevational gradient air temperature based on measurements in July decline by around 2.5°C from 450−1000 m, whereas precipitation does not vary (Sundqvist *et al.* 2011a). The treeline occurs at approximately 500–600 m and comprises of *Betula pubescens spp. czerepanovii*. The tundra landscape located above the treeline consists of a mosaic of meadow (is comprised mainly of herbaceous and graminoids species) and heath (consisting primarily of dwarf ericaceous shrubs and *Betula nana*) vegetation types (Figure 4). The bedrock at this site consists of salic igneous rocks and quartic phyllitic hard schists. The mean annual temperature from 2005–2017 at the Abisko Scientific Research Station was +13°C in July and -9.9°C in January and the mean precipitation for the corresponding period was 340 mm (the Swedish Meteorological and Hydrological Institute). The growing season length in this region is approximately 3 months (Björk *et al.* 2007).

The treeline of *Betula pubescens* ssp. *czerepanovii* at both sites within the mountainous landscape is found at approximately 500 – 600 m. The tundra vegetation, which occurs above the treeline, is generally comprised of mosaics of heath (comprised primarily of ericaceous dwarf shrubs and *Betula nana*) and meadow (comprised primarily of graminoids and forbs). The two vegetation types differ in their basic soil properties, with heath vegetation typically having a lower pH and mineral nitrogen and a higher phosphorous availability than the meadow (Björk *et al.* 2007; Sundqvist *et al.* 2011).
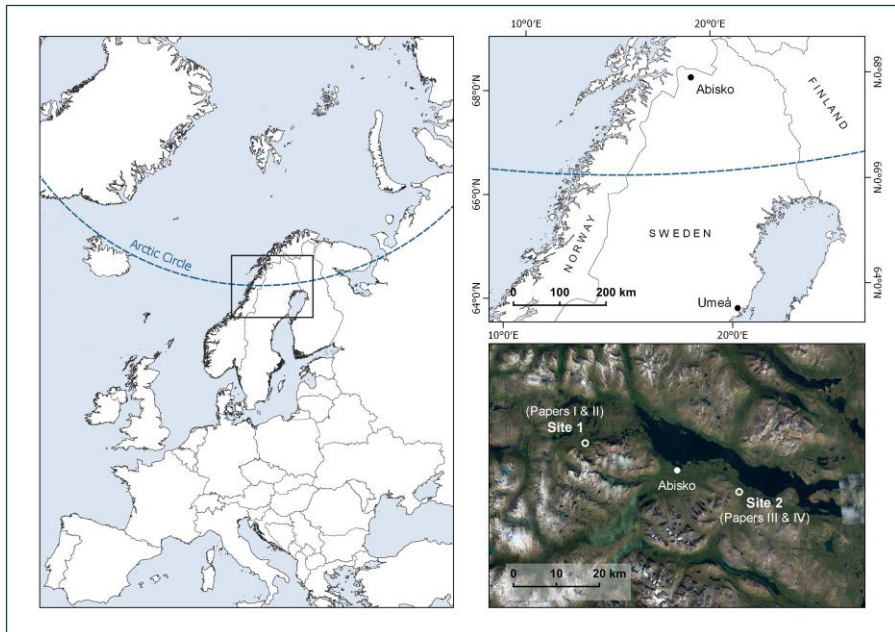

Figure 3. Map showing locations of field sites for various thesis chapters. Satellite image obtained from Google Earth ©. Map prepared by C. Fohringer.

Figure 4. Vegetation at field sites near Abisko. Photo: P. Kardol.

2.2 Greenhouse studies

Experiments for papers I and II were conducted simultaneously in the Wallenberg greenhouse at the University campus in Umeå. Prior to the greenhouse studies, we collected soil from the rooting zone (= upper 10 cm) of individuals of all visible graminoid and forb species at the end of the growing season in August 2016. Soil for both experiments was stored at 4°C, bulked and homogenized prior to the beginning of the experiment in February 2017. For paper I, we collected seeds from 17 meadow plant species, i.e., graminoids and forbs, at the field site in August 2016 and sourced seeds for three additional tundra meadow species from a local seed company (Pratensis, Lönashult, Sweden). For paper II, seeds were collected from 11 meadow plant species (i.e., 4 graminoids species and 7 forbs), and seeds for 7 additional plant species (i.e., 3 graminoids species and 4 forbs) were sourced from the local seed company (Pratensis, Lönashult, Sweden), resulting in a total of 18 species. The plant species used for paper II are a subset of those in paper I. Seeds were surface-sterilized in 1% sodium hypochlorite after soaking for 1 minute (De Long *et al.* 2015), and germinated on autoclaved sand according to the requirements of each species. Until the beginning of the experiment, germinated seedlings that reached a height of 3 cm were stored at 4°C with light (50%) to ensure that all seedlings were at a similar ontogenic stage at the time of planting. Field-

collected soil was sieved (10 mm mesh size) to remove stones and large roots, homogenized and mixed with autoclaved sand (soil:sand ratio: 3:1) to enable better drainage. Thereafter, the soil was left for 2 days at 20°C to facilitate the acclimatization of the soil microbial community to greenhouse conditions until time of planting. We reconstructed a soil depth of 10 cm in 1.4 L pots (9 × 9 × 20 cm), which was similar to the soil depth at the site where soil was collected. First, 0.4 L of warm-water-washed gravel was placed into each pot, followed by 1 L of homogenized bulk soil-sand mixture. In each pot, two seedlings of the same species were planted at the top right and bottom left. Conditions in the greenhouse were set to the following parameters: 18°C/13°C day/night temperature; 18/6 hour light/dark regime, and 80% humidity. Plants were watered every two days (Figure 5) and dead seedlings were replaced during the first two weeks of the experiment.

Figure 5. Greenhouse study for papers I and II. Photo: R. Spitzer.

2.2.1 Assessment of root-microbial relationships (paper I)

For paper I, plants were grown in six replicate blocks for 84 days, which is similar to the length of the growing season at the study site. This resulted in a total of 120 experimental units (i.e., 20 species × 6 replicates). At the end of the experiment, plants were harvested block-wise with harvested blocks being stored at 4°C in the dark for a maximum of three days. Plants were

removed from pots by gently tapping on the upturned pots over aluminium-foil-lined plastic trays. Rhizosphere soil (i.e., soil stuck to roots) was collected from roots by gently shaking plants (Saj *et al.* 2009). This method is commonly used to collect rhizosphere soil (Smalla *et al.* 2001; Carrillo *et al.* 2017). Soil not adhering to roots was considered bulk soil. We combined the rhizosphere soil from both plants within each pot into clean plastic bags and homogenized the combined sample by shaking the closed bags. Bulk soil was similarly homogenized. After homogenization, we immediately froze (-20°C) sub-samples (500 mg dry weight equivalent) of rhizosphere and bulk soils, freeze-dried, and ground samples using a roller grinder prior for the extraction of deoxyribonucleic acid (DNA) and phospholipid fatty acids (PLFAs). However, only the rhizosphere soil data were utilized for paper I, while both rhizosphere and bulk soil data were utilized in paper II.

Root-washing and trait measurements

Roots were washed over a sieve (4 mm mesh size), and the flow-through washed over a second sieve (2 mm mesh size) to recover any roots that were accidentally broken during washing. A spray bottle with water was used to remove any remaining soil particles on the roots after washing (Figure 6) and a representative fine root (≤ 1 mm) subsamples was collected from the larger of the two plants in each pot.

Figure 6. Using spray bottle to clean roots. Photo: N. Saavedra

We scanned root subsamples in transparent trays (15×20 cm) with cold tap water using WinRhizo 2016 software with a flatbed scanner (EPSON

Perfection V800/V850 1.9 V3.93 3.9.3.2). The following morphological characteristics were obtained from the WinRhizo software for each subsample: average diameter, number of root tips, root branching, total root length, and root surface area. The fresh weight of each subsample was recorded immediately after scanning. Samples were then dried at 60°C for 48 hours to obtain root biomass. The remaining roots were dried similarly and the biomass recorded. The biomass of each subsample was used to calculate the following traits: specific root length (cm mg^{-1}), specific root area (cm^2 mg^{-1}), specific root tip abundance (tips mg^{-1}), and root dry matter content (dry mass per unit fresh mass mg mg^{-1}). Chemical root traits were measured on manually ground fine root subsamples (approximately 150 mg dry weight) from the remaining roots of each sample that were not scanned. Total root phenol concentrations were measured from 50 ± 5 mg dry ground roots using the method of Stern *et al.* (1996). We obtained total root carbon and nitrogen concentrations by dry combustion using an elemental analyser (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany). This resulted in 11 fine root traits (see Table 1).

Table 1. List of root traits measured, their units and ecological relevance (paper I)

	Root trait	**Units**	**Ecological relevance**
Chemical	Carbon (C) content	%	Microbial C source
	Nitrogen (N) content	%	Nutrients for microbes
	C:N ratio	-	Tissue quality
	Total phenol	mg g^{-1}	Plant defence
	Phenol:N ratio	mg g^{-1}	Plant defence
Morphological	Average diameter	mm	Mycorrhizal colonization
	Specific root length	cm mg^{-1}	Soil exploration
	Specific root area	cm^2 mg^{-1}	Soil exploration
	Specific root tip abundance	tips mg^{-1}	Nutrient absorption
	Forks per root length	forks cm^{-1}	Soil exploration
	Dry matter content	mg mg^{-1}	Tissue density and quality

Soil DNA analyses

We sequenced the soil fungal community from 300 ± 10 mg ground rhizosphere and bulk soil using high-throughput sequencing of amplified ITS2 markers (Clemmensen *et al.* 2016) after extraction with the Nucleospin® Soil Kit (Macherey-Nagel, Düren, Germany). We performed

50 µl Polymerase Chain Reactions (PCRs) under the following conditions: 5 min at 95°C; 26–30 cycles of 30 secs at 95°C, 57 secs at 57°C, 30 secs at 72°C; 7 min at 72°C. After checking PCR products by gel electrophoresis, amplicons were purified using the Agencourt AMPure kit (Beckman Coulter, Beverly, MA, USA) and the concentrations measured fluorometrically (Qubit Fluorometer, Invitrogen, Carlsbad, CA, USA). We pooled equimolar mixtures of amplicons from each sample into three composite samples for sequencing, which was performed using the Pacific Biosciences Sequel Technology Platform (1 SMRT cell per composite sample) at SciLifeLab, Uppsala, Sweden. Sequences were processed using the bioinformatics pipeline SCATA (http://scata.mykopat.slu.se/). After filtering and quality control, this resulted in 1,648,502 high quality sequences, which were assembled into 7,474 Species Hypotheses (SHs; Kõljalg *et al.* 2013). We focused on the 100 most abundant SHs for papers I and II. Sequence annotations were conducted by comparing the UNITE Database and the annotated International Nucleotide Sequence Database (INSD) using the massBLASTer option (https://unite.ut.ee/) (Kõljalg *et al.* 2013; Nilsson *et al.* 2019).

Fungi with a well-known life form were classified into functional guilds according to published literature: saprotrophs and pathogens, ectomycorrhizal fungi, arbuscular mycorrhizal fungi, other root-associated (e.g. dark septate endophytes), yeasts and moulds, and other (e.g., mycoparasites), or unknown when there was insufficient information to enable classification. We merged saprotrophs and pathogens into one functional guild, since most pathogens and some saprotrophs are able to switch from one strategy to another (Olson *et al.* 2012; Zanne *et al.* 2020). Yeasts and moulds were also merged into one functional guild, since they both have limited capacity to utilise complex C substrates (Treseder & Lennon 2015), and therefore are functionally similar since they are both opportunistic fungi.

Phospholipid fatty acids (PLFA) analysis

The absolute abundance of PLFAs in each ground freeze-dried soil subsample was obtained after soil extraction using methods outlined in Frostegård *et al*. (1991). The following PLFA markers were used as indicators of bacteria: i14:0, 14:0, i-15:0, a-15:0, 15:0, i-16:0, 16:1ω9, 16:1ω7c, 16:1ω7t, i-17:0, a-17:0, cy-19:0, cy-17:0, 17:0, 17:1ω8, and 18:1ω7 (Frostegård & Bååth 1996), and 18:2ω6,9 was used as an indicator

for fungi (Kaiser *et al.* 2010). PLFAs i-17:0, i-15:0, a-15:0, i-16:0, and a-17:0 represented Gram-positive bacteria, and cy-17:0, 18:1ω7, and cy-19:0 Gram-negative bacteria (Wardle *et al.* 2013). We used the branched chained fatty acids 10me16:0, 10me17:0 and 10me18:0 as indicators of actinobacteria (Maaroufi *et al.* 2019). The data were used to calculate the ratios of Gram-positive to Gram-negative bacteria and fungi to bacteria.

2.2.2　Plant-soil feedback (paper II)

The plant-soil feedback study was conducted with 18 plant species in two phases and with five replicate blocks. The experimental design, as well as the length of each phase, are outlined in Figure 7. At the end of the conditioning phase, plants were removed from the pots as described above, but fine roots (≤ 1 mm diameter) were instead cut into smaller sections (approximately 1 mm) and homogenized in the soil collected from the respective pots. Soil from the duplicate pots from each block was then homogenized to create conspecific soil. After the feedback phase, plants were harvested and roots washed as described under section 2.2.1. Plants were dried (60°C for 48 hours) and the biomass of the larger of the two plants in each pot was recorded. The root traits, as well as bulk and rhizosphere soil data were used as explanatory variables in paper II. This is because plants from the soil conditioning phase were harvested simultaneously as those from the experiment in paper I from the same plant species.
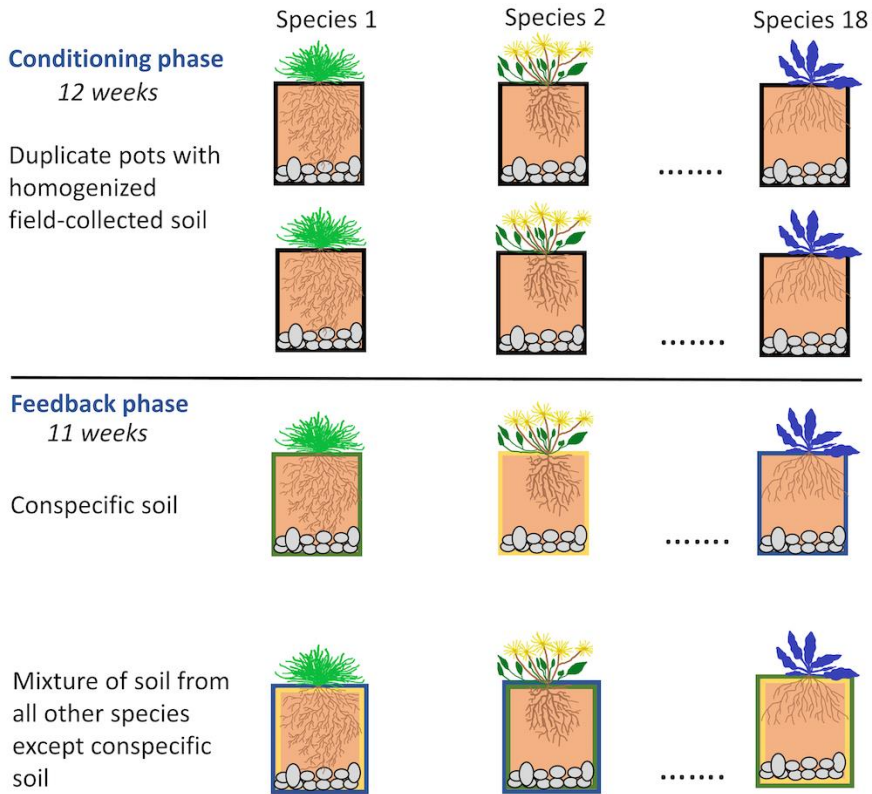
Figure 7. Experimental design of the plant-soil feedback study. Eighteen plant species were first grown on field-collected soil in a conditioning phase. In a subsequent feedback phase, the plant species were grown with conspecific soil and heterospecific soil. Plants were grown in 5 replicate blocks.

2.3 Growth chamber study (paper III)

Soil for this study was sourced (from the organic layer) from two sub-arctic tundra meadows located approximately 300 m apart at the Mount Suorooaivi site at approximately 700 m elevation. Two meadows were required to enable the collection of a sufficient volume of soil for our experiments. Seeds of one plant species, *Phleum alpinum*, were collected along the elevational gradient, and dried at 40ºC for 48 hours. Seeds for an additional 5 plant species were sourced from a local seed company (Pratensis, Lönashult,

Sweden). The six plant species were selected based on their resource-acquisition strategy from trait data in papers I and II, i.e., three resource-acquisitive species (*Phleum alpinum, Anthoxanthum odoratum and Festuca ovina*), and three resource-conservative species (*Saussurea alpina, Solidago virguarea and Ranunculus acris*). Soil was sieved (10 mm mesh size) to remove large roots and stones and homogenized and split into six equal blocks. Mesocosms were constructed by filling 1.5 L pots (11 × 11 × 17.8 cm) with the field-collected soil and by planting two seedlings each from two plant species (i.e., two acquisitive species, two conservative species, or one acquisitive and one conservative species). This resulted in 15 species combinations.

The experiment for paper III was conducted in two separate growth chambers, one at ambient temperatures and one at elevated temperatures (i.e., ambient + 4°C), as it provided the opportunity to precisely manipulate temperature and other micro-climatic variables. Mesocosms (15 species combinations × 2 temperature treatments × 6 blocks = 180 experimental units) were placed in a growth chamber for one week (16°C, 85% humidity, and 24 hours light) prior to the start of the experiment and watered every two days to enable plant establishment. At the beginning of the experiment, chamber settings were set and adjusted weekly to mimic ambient climatic conditions during one growing season in Abisko (Kardol *et al.* 2014). These settings were the maximum and minimum temperatures, photosynthetic active radiation, and day and night length each week. We set moisture in both chambers to 85% humidity and minimum temperatures lower than 5°C to 5°C, due to climate chamber constraints. After 12 weeks, all mesocosms were harvested block-wise. We washed roots over a sieve (2 mm) using a gentle spray tap and we collected any roots broken off during washing from the sieve. We separated the four plants in each pot into above- and belowground biomass and dried them at 60°C for 48 hours in paper bags.

2.4 Elevational gradient (paper IV)

The research for paper IV was conducted along the elevational gradient described above. Five plots were established at each of six elevations (500, 600, 700, 800, 900, and 1000 m) and the density of each plant species in each plot was measured in June 2018. These data were used to calculate relative abundances of plant species. We excavated the intact vegetation and soil in

each plot using a shovel to enable easier sampling of roots of each plant species. After removal of the mineral soil from the excavated vegetation we used our fingers to follow and disentangle the roots and/or rhizome, starting at the base of the shoot of each plant species. We placed roots of each plant species in each plot into separate plastic bags, along with a small part of the shoot to confirm species identification during the root-washing stage. We stopped sampling roots for each species after filling three 5-L Ziploc bags with roots, or until all roots of less abundant species were collected. We stored samples at 4°C until further processing. Roots from each sample were first carefully pre-washed in a 2 mm sieve over a 1 mm sieve under a showerhead tap and transferred to a tray filled with water. Large pieces of litter and/or mosses were removed from the root system followed by the smaller fragments of organic matter using tweezers. This method enabled easier washing of the remaining soil particles using a spray bottle. We scanned a sub-sample of fine roots ($\leq$ 1 mm) using WinRhizo 2016 software with a flatbed scanner (EPSON Perfection V800/V850 1.9 V3.93 3.9.3.2) in a large scanning tray (15 $\times$ 20 cm) with cold tap water. We used the same scanning parameters outlined above. We recorded the scanned subsamples fresh weights and dried them at 60°C for 48 hours and recorded their biomass. We ground the remaining roots that were not scanned using a ball mill (Retsch MM400) and analysed them for total carbon, and nitrogen, by dry combustion using an elemental analyser (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany) and phosphorus using the Kjeldahl method with acid digestion (Omni Process, Solna, Sweden).

2.5   Statistical analyses

Statistical analyses for all papers were performed using R version 3.4.0 (R Core Team 2018, Vienna, Austria). To test specific hypotheses in each of the papers in this thesis, multivariate statistical methods, generalized linear mixed models, general linear models, correlation analyses, phylogenetic analyses, path analyses and variance partitioning were used. For all studies conducted in the greenhouse or growth chamber, i.e., **papers I – III**, replicate blocks were included as random factors all linear mixed effects models to account for spatial heterogeneity.

Principal component analyses (PCA) were performed to establish, the fine root economics spectrum for **papers I , II and III**. Prior to the analyses,

data were log-transformed to fulfil the assumption of normality. In **paper I**, axes scores of the first two PCA principal components were also used as predictors in linear mixed models as conservative-acquisitive root economics spectra. In **paper III**, PCA was used to select plant species to include in the experiment and therefore the analysis was conducted using species averages. This is contrary to **paper I**, where the PCA and all other analyses were conducted using the total variation across all experimental units. In **paper II**, PCA was conducted as in paper III, i.e., with species averages. In addition, a second PCA was conducted using the absolute abundances of the fungal orders across all pots after square-root transforming the data. The first axes were then used as explanatory variables of fungal community effects on plant-soil feedback in a general linear model.

General linear mixed effects models were used for **papers I − III**. In **paper I**, it was used in two separate models to test for the effect of the fine root economics spectrum on the ratios of Gram-positive to Gram-negative bacteria and fungi to bacteria PLFAs, with the two PCA axis scores as explanatory variables. The final model was selected based on the lowest Akaike Information Criterion (AIC) and hence a larger model which included species as a random factor was excluded. In **paper II**, a multiple linear regression was conducted to test for the effect of the root economics spectrum on plant-soil feedback direction and strength. Similar to paper I, axis scores from the first two PCA components were used as predictors. Prior to the analyses average plant-soil feedback values were calculated for each plant species across all blocks. A second model was conducted using individual root traits as predictors of plant-soil feedback direction and strength, with the lowest AIC being used for selecting the best-fitting model. This resulted in root nitrogen content, root forks per root length and root dry matter content as explanatory variables in the final model. The effect of the fungal community on plant-soil feedback was tested using the first two fungal PCA axes as predictors. Additional individual models were conducted with each fungal order as an explanatory variable as predictors of plant-soil feedback. A multiple linear regression was also performed with the fungal functional guilds as of plant-soil feedback strength across all plant species. In **paper III**, general linear mixed effects models were performed with the total biomass of each plant species when grown with their neighbouring plant species as a response, the temperature treatment as a fixed factor and block

as a random factor. A similar model was used to assess the response of root to shoot rations to neighbour plant species and temperature.

In **paper IV**, the relationships between elevation and the fine root traits at each elevation were tested using weighted plot averages. These community weighted averages were calculated using the following formula:

$$\text{Weighted plot average } = \sum_{i=1}^{n}\left(\mathrm{p}_i \times \text{trait}_{i\_plot}\right),$$

where p_i is the relative abundance of the i-th species in a plot, n is the total number of species. Data were log-transformed or Tukey power-transformed prior to running the linear model and in cases where a linear model was inappropriate, second order polynomial models were tested. The model fits (i.e., linear vs. polynomial) were assessed using partial F-tests. The relationship between elevation and trait variation was also tested using weighted coefficient of variation for each plot that was calculated using the R package Weighted.Desc.Stat (Parchami 2016). Separate models were then conducted for each root trait, with elevation as an explanatory variable and the weighted coefficient of variation as a response variable. Type III ANOVAs were used to obtain p- and F values for the predictors of all models in all papers.

Two other multivariate statistical methods, besides PCA, were conducted in **paper I**. Canonical Correspondence Analyses (CCA) were performed to determine the relationships between the fine root traits and the the PLFA microbial groups, as well as for the fine root traits and the fungal functional guilds. Since both models were significant, posthoc Spearman's rank correlations were then conducted to assess the relationships between the fine root traits and the microbial groups. A partial Canonical Correspondence Analysis (pCCA) was performed to test for the effects of individual fine root traits on the relative abundances of the fungal orders, with block as a random variable (Ramette 2007). The fungal relative abundance data were square-root-transformed prior to the analysis to reduce the weighting of rare SHs in the ordination (Legendre & Gallagher 2001). Automated model selection from the vegan R package was utilised for the selection of explanatory variables to include in the final model. This resulted in the inclusion of root carbon content, root nitrogen content and root forks per root length as explanatory variables and block as a random factor. Permutation tests were used to test for model significance. In addition, Blomberg's K values (Adams

2014) were calculated and used to test for phylogenetic signal of any root trait that was associated with mycorrhizal fungi in the pCCA.

In paper I, generalized linear mixed effects models were used to test for the effects of the root economics spectra on the relative abundances of fungal functional guilds. Separate models were performed for each fungal functional guild (assuming a binomial distribution), with the axis scores from the two PCA axes as explanatory variables and block as a random factor.

In **paper II**, path analysis was used to assess how root-trait-microbial relationships are related to plant-soil feedback. The *a priori* assumption was that the second root trait axis would directly contribute to plant-soil feedback and indirectly via associations with the fungal orders Mucorales and Pleosporales. This is because the second root trait axis and the two fungal orders significantly predicted plant-soil feedback strength.

In **paper IV**, variance partitioning was used to assess the relative contributions of species turnover and intraspecific variation, following methods developed by Lepš *et al*. (2011).

3. Results and discussion

The results presented below are the main findings arising from the four papers contained in this thesis. I conclude with a general discussion based on the overall aim of the thesis, i.e., root trait variation and resource-acquisition strategies in the sub-arctic tundra and their ecological significance for plant community assembly under global warming.

3.1 Root-trait microbial relationships

The first two PCA root trait axes explained 66% of the total variation in root trait values, the first axis consisting primarily of morphological traits and the second axis primarily consisting of chemical traits and root dry matter content. The trait values on both axes aligned to form an acquisitive-conservative economic spectrum (Figure 8). These axes and their traits are similar to those recently shown in a meta-analysis conducted by Bergmann *et al*. (2020). On the first axis, the traits represent larger root diameters on the one hand, which are usually associated with higher abundances of mycorrhizal fungi (Ma *et al.* 2018). On the other hand, traits at the other end of the spectrum had thinner diameters and were associated with root exploration 'in search' of nutrients (Bardgett *et al.* 2014). The second axis represented a trade-off between the construction of dense roots associated with slower turnover rates and roots with higher nitrogen content that are associated with faster turnover rates (Bergmann *et al.* 2020). The rhizosphere fungal community was dominated by the composite fungal guild saprotrophs-pathogens, followed by opportunistic fungi (i.e., yeasts and moulds). Somewhat surprisingly, the relative abundance of mycorrhizal fungi was the lowest of all functional guilds (Figure 9). A higher abundance of cold-tolerant yeasts have been found in colder ecosystems (Treseder &

Lennon 2015), relative to temperate ecosystems (Margesin *et al.* 2009). At the same time, there is also a high relative abundance of "unknown" fungi, which could potentially be important for ecosystem functioning in the tundra.
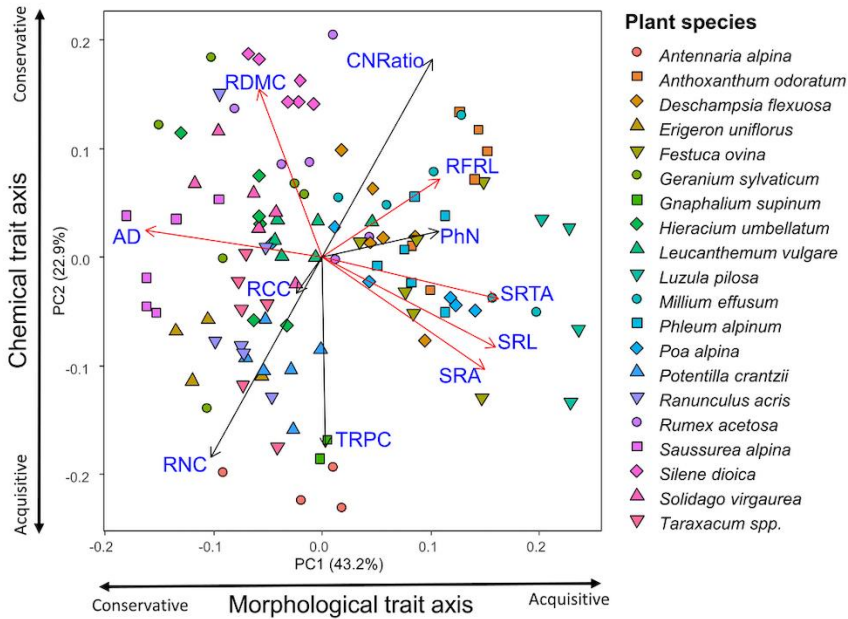

Figure 8. Principal Component Analysis of fine root traits across all species. Black arrows represent chemical root traits and red arrows represent morphological root traits. Fine root traits corresponding to the bi-plot arrows are shown in blue font: average diameter (AD), root carbon content (RCC), root nitrogen content (RNC), root phenol content (TRPC), specific root area (SRA), specific root length (SRL), specific root tip abundance (SRTA), root phenol to nitrogen ratio (PhN), root forks per root length (RFRL), root carbon to nitrogen ratio (CNRatio), and root dry matter content (RDMC) (paper I).

The chemical trait axis (but not the morphological) was found to be associated with the ratios of fungi to bacteria ($F = 4.497$; $p = 0.036$; coefficient = 0.004) and Gram-positive to Gram-negative bacteria ($F = 3.961$; $p = 0.049$; coefficient = -0.007). These findings were in line with our expectations, as lower values of tissue carbon to nitrogen ratios are expected to favour bacteria over fungi. Indeed, previous studies have shown that fungi have a broader suite of enzymes for decomposition (Strickland & Rousk 2010; Soares & Rousk 2019), as well as lower nutrient requirements (Fanin

et al. 2013). On the other hand, the observed negative relationship between higher values of carbon to nitrogen ratios and the ratio of Gram-positive to Gram-negative bacteria may be related to the higher demand of Gram-positive bacteria for nutrients to facilitate decomposition of more complex carbon forms (Orwin *et al.* 2018; Fanin *et al.* 2019). In addition, root dry matter content was negatively correlated with all PLFA biomarkers except Gram-negative bacteria, Gram-positive bacteria and actinobacteria (see Figure 2 in paper I). Hence, this trait may be important for predicting the biomass of broad soil microbial groups.
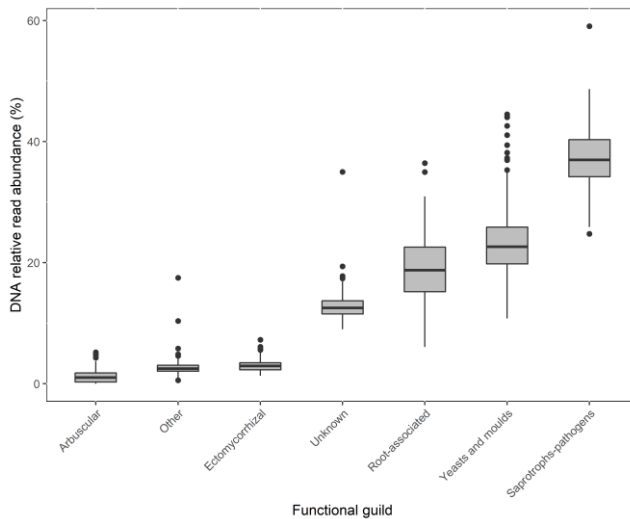

Figure 9. Relative abundances of various fungal functional guilds in the rhizosphere soil across all plant species. The line in each box is the median value and the box displays the 25th–75th percentile; whiskers represent the 1.5 inter-quartile range of the upper and lower percentile and outliers are shown as black circles (paper I).

No relationship was found between the root economics spectra and any of the fungal functional guilds. This was surprising because plant resource allocation to fine roots has been shown to be related to nitrogen allocation (Reich 2014), which is linked to fungal guilds involved in nutrient cycling. In particular, the morphological trait axis was expected to be associated with the relative abundance arbuscular mycorrhizal fungi. This finding indicates that the fine root economics spectrum may not be the 'holy grail' when investigating root-microorganism relationships, since it represents a

simplistic one-dimensional spectrum (i.e., acquisitive versus conservative). However, there may be several dimensions of resource use (Kong *et al.* 2019). On the contrary, some individual root traits were positively associated with some functional guilds. For example, the relative abundance of arbuscular mycorrhizal fungi was found to be positively associated with root carbon content and negatively with root forks per root length (Figure 10). The ordination analysis confirmed the relationships observed with the correlation analysis that the two arbuscular mycorrhizal orders Archaeosporales and Glomerales were positively associated with higher values of root carbon content. These observed associations are likely because conservative plants with a higher dependence on mycorrhizal fungi for nutrient uptake under nutrient-limited conditions also produce carbon-rich cellular structures (Li *et al.* 2015). The order Mucorales (moulds) had a positive association with root nitrogen content. This suggests that this order has a high nitrogen requirement for maintaining its rapid growth rates (Mehrotra 1967). On the other hand, the order Sporidiobolales (yeasts) was negatively associated with root nitrogen content, suggesting a lower reliance on freshly available plant-derived nitrogen. There is now some evidence that yeasts may have positive effects on nutrient cycling and plant growth (Botha 2011), and hence their interaction with plants should be further investigated.
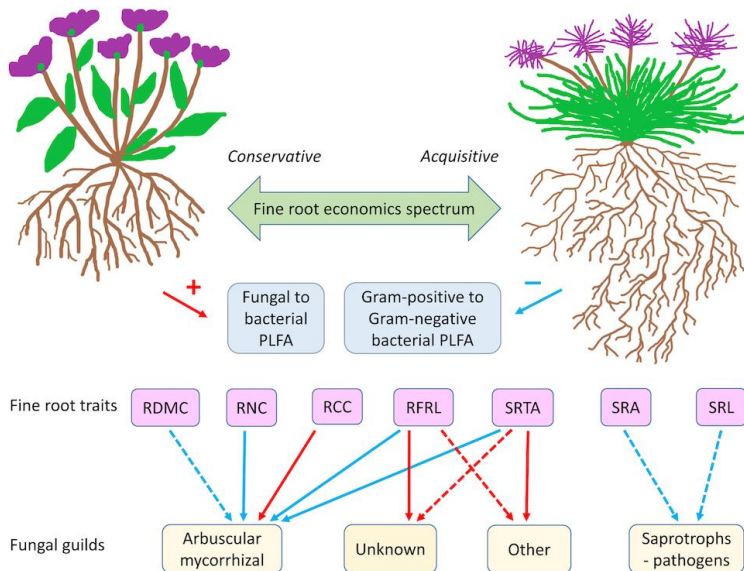
Figure 10. Summary of relationships between fine root traits and root economics spectra and various soil microorganisms. The fine root economics spectrum mainly consists of chemical root traits. Only fine root traits with significant or nearly significant relationships with any a fungal guild at α = 0.05 are included: root dry matter content (RDMC), root nitrogen content (RNC), root carbon content (RCC), root forks per root length (RFRL), specific root tip abundance (SRTA), specific root area (SRA), and specific root length (SRL). Red arrows indicate positive relationships and blue arrows indicate negative relationships. Solid arrows indicate significant associations and broken arrows a nearly significant associations at α = 0.05 (paper I).

3.2 Plant-soil feedbacks

Plant species had both positive and negative plant-soil feedbacks and the direction of feedback was unrelated to plant functional group (i.e., graminoid or forb) (Figure 11). We found a significant negative relationship between the second root trait axis and plant-soil feedback strength ($p = 0.004$, $F_{(1,14)}$ =11.79; overall $R^2 = 0.46$; *see* Figure 2a in paper II). In this study, similar traits contributed to the variation on the second axis as those in paper I. Here, plant-soil feedback became more negative as the root traits became more acquisitive (see Figure S3 in paper II). These findings show that within this nutrient-poor study system, some root traits that are related to nutrient conservation lead to positive plant-soil feedback. In addition, three of the individual root traits along this trait axis predicted plant-soil feedback ($p <$

0.001; r^2 adjusted = 0.64), i.e., root dry matter content, root forks per root length and root nitrogen content. Root forks per root length and root nitrogen content were negatively related to plant-soil feedback, while root dry matter content had a positive relationship. The negative relationship between plant-soil feedback and higher values of root forks per root length and root nitrogen is probably because the plant tissue was more attractive for parasites and fungal pathogens (Davison & McKay 2003; Mur *et al.* 2017) and root-feeding nematodes (Zhang *et al.* 2020b) that may negatively affect plant growth.

We found no significant relationship between plant-soil feedback strength and the first two PCA axes of the soil fungal community (i.e., based on absolute abundances of the fungal orders). The first axis (explaining 44.2% of the variation) consisted of arbuscular mycorrhizal fungal orders Archaeosporales and Glomerales at the one end and Diaporthales (order consisting of known saprotrophs, pathogens and endophytes) on the other end. This result was surprising, since arbuscular mycorrhizal fungi were found to be positively associated with root carbon content in paper I, which suggested a potential mutualistic relationship. However, it has been shown that arbuscular mycorrhizal fungi may sometimes result in negative plant-soil feedback (Bennett *et al.* 2017). The variation on the second axis was explained by Mucorales (moulds), Pleosporales (order consisting of saprotrophs, known parasites and endophytes) and Pezizales, which in our dataset consisted of saprotrophs-pathogens. Two of these orders (i.e., Pleosporales and Mucorales) were negatively related to plant-soil feedback in post-hoc tests with each of the individual orders, although these relationships were largely driven by *Antennaria alpina*, which had the strongest negative plant-soil feedback (Figure 11). Within this study, three of the six species hypotheses contained within these two orders are known pathogens (Mari *et al.* 2000), while others were either saprotrophic or could not be identified at a lower taxonomic level. Hence, it is plausible that the observed negative plant-soil feedback is as a result of pathogenicity.
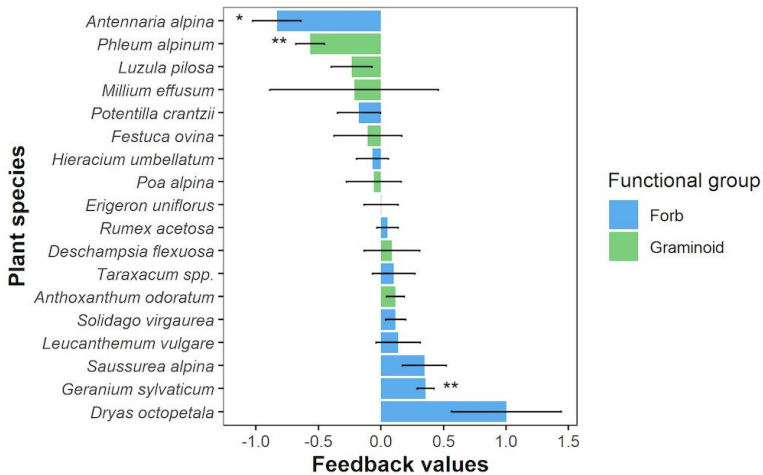
Figure 11. Bar plot showing plant-soil feedback for each plant species. Bars are mean values ± 1 SE (n = 5). Plant-soil feedback is log (plant biomass in conspecific soil) – log (plant biomass in heterospecific soil). Asterisks specify feedback values significantly different from zero at $p = 0.05$ (paper II).

Further, from the path analysis (Figure 12), we found that the second axis of the root economics spectrum directly explained plant-soil feedback ($p = 0.02$; Fig. 12a, and $p = 0.008$; Fig. 12b). However, it did not indirectly explain plant-soil feedback via effects on the fungal orders Mucorales and Pleosporales. This means that these fungal orders were not mediators between the fine root traits and PSF although they contributed to negative PSF. However it is possible that there may be other soil microorganisms or soil fauna that are stronger mediators between fine root traits and plant-soil feedback, such as root-feeding nematodes that have been shown to result in negative plant-soil feedback (Wilschut *et al.* 2019).
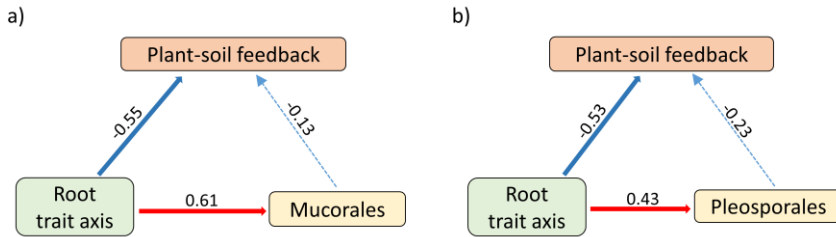
Figure 12. Path analysis of variables influencing plant-soil feedback. A) Second axis of the root economics spectrum and Mucorales. b) Second axis of the root economics spectrum and Pleosporales. Blue arrows indicate a negative relationship and the red arrows positive relationships. Solid one-directional arrows indicate a significant relationship ($\alpha = 0.05$), whereas dotted one-directional arrows indicate relationships that are not significant (paper II).

3.3 Plant competitive interactions under warming

At ambient temperatures, there was no statistical difference between the biomass of any of the plant species when grown with a neighbouring plant of the same or a different resource-acquisition strategy (Figure 13). This is likely because all plant species had small biomasses and therefore reduced competition, probably because ambient temperatures in this experiment were below the optimum temperatures required for photosynthesis and biomass production (Tieszen 1973; Chapin III 1983). Hence, plants were probably not large enough to compete for limiting nutrients in the soil, space or light. Indeed, at elevated temperatures, we found that the biomass of all plant species significantly increased.

At elevated temperatures (ambient temperatures + 4°C) the total biomass of the resource-acquisitive plant species was not consistently largest when grown with resource-conservative neighbours relative to resource-acquisitive neighbours. For example all plant species grew smaller with *Anthoxanthum odoratum* (a resource-aquisitive species) as a neighbour, which suggests that it is a strong competitor, including against other resource-acquisitive species. Further, the total biomass of *Festuca ovina* (a resource-acquisitive species) was not significantly different when grown with *Ranunculus acris* and *Solidago virgaurea* (resource-conservative species) and *Phleum alpinum* (a resource-acquisitive species). This shows that competitive interactions changed under elevated temperatures and that plant-plant interactions were typically species-specific rather than driven by

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plant resource-acquisition strategy. Indeed, there was a significant interaction effect between temperature and neighbouring species ($p < 0.001$) for all species except *Anthoxanthum odoratum*. Generally, resource-conservative species had a higher root to shoot ratio relative to the resource-acquisitive plant species at both ambient and elevated temperatures (*see* Figure 3 in paper III). However, the response of root to shoot ratios to elevated temperatures was not necessarily related to resource-acquisition strategy. For example, two resource-conservative species, i.e., *Ranunculus acris* and *Solidago virgaurea,* and *Anthoxanthum odoratum* (a resource-acquisitive species) had increased root to shoot biomass ratios at elevated temperature. These changes in root to shoot ratios may also influence how plants interact with their neighbour species under warming.
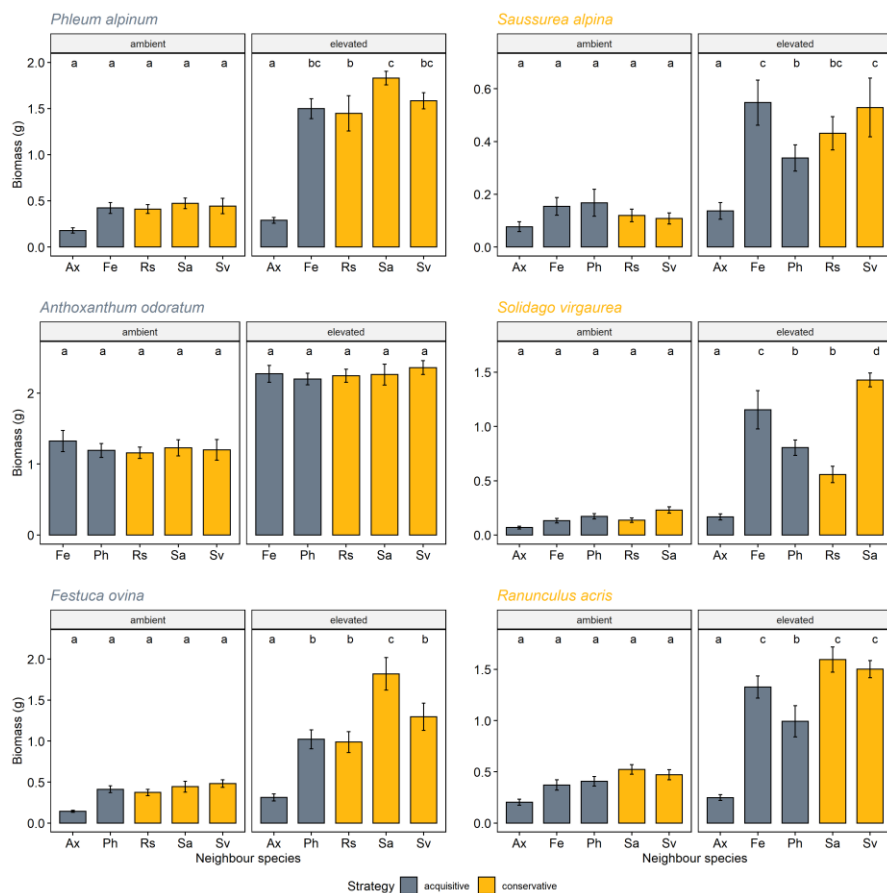
Figure 13. Total biomass of resource-acquisitive and resource-conservative plant species when grown with resource-acquisitive or resource-conservative neighbour species under ambient temperature or elevated (+4°C) temperature. Bars are mean values ± SE (n = 6). Letters above bars indicate statistical differences at α = 0.05 from general linear mixed models after posthoc pairwise comparisons using Tukey's method for p-value adjustment. The three acquisitive plant species are: *Phleum alpinum* (Ph), *Anthoxanthum odoratum* (Ax) and *Festuca ovina* (Fe), and the three conservative species are *Saussurea alpina* (Sa), *Solidago virgaurea* (Sv) and *Ranunculus acris* (Rs) (paper III).

3.4 Plant community traits relationships with temperature

Along the elevational gradient, four of the sixteen plant species were found at each elevation, with *Empetrum hermaphroditum* being the most abundant (56%), followed by *Betula nana* (20.2%) and *Vaccinium vitis-idaea* (13.4%). At the whole community level, five root traits had significant relationships

with elevation, however the direction of those relationships varied among root traits. For example, there were significant negative linear relationships between elevation, root carbon content, specific root area and root forks per root length (Figure 14). This indicates a shift to more conservative strategies. At the same time, the relationship between root phosphorous content and specific root length was quadratic, indicating an inflection point where the direction of the relationship changes. This suggests that at the community level there was no clear relationship between plant resource investment strategy and elevation. At the plant species level, the relationships between several root traits and elevation varied among the plant species. For example, root carbon to nitrogen ratios decreased linearly with elevation for *Vaccinium vitis-idaea* ($R^2 = 0.17$; $F = 6.38_{(1,28)}$; $p = 0.01$) and *Betula nana* ($R^2 = 0.22$; $F = 9.39_{(1,28)}$; $p = 0.005$). In contrast, root nitrogen content increased linearly with elevation for both species (*Betula nana*: $R^2 = 0.23$; $F = 8.46_{(1,28)}$; $p = 0.007$ and *Vaccinium vitis-idaea*: $R^2 = 0.17$; $F = 6.85_{(1,28)}$; $p = 0.01$, respectively). For these two plant species, this represented a shift towards more acquisitive trait values with increasing elevation. This could be associated with ammonium uptake, as higher root nitrogen content may be associated with a higher affinity for uptake of ammonium (Grassein *et al.* 2015). Along the elevational gradient ammonium is often low at the highest elevation (Sundqvist et al. 2011a), although another study found varying relationships between ammonium concentrations and elevation (Blume-Werry *et al.* 2018). Root carbon content decreased with elevation for *Betula nana* ($R^2 = 0.22$; $F = 9.34_{(1,28)}$; $p = 0.005$), suggesting a weaker relationship with its ectomycorrhizal symbionts at colder temperatures.

Across the elevational gradient, the community-weighted coefficient of variation either increased or remained constant for all fine root traits. There were significant positive relationships between elevation and the community-weighted coefficients of variation for average diameter, root carbon to nitrogen ratio, root nitrogen content and specific root length (*see* Figure 4 in paper IV). These observed relationships may be related to increased spatial heterogeneity of resources or microclimatic conditions at higher elevations, rather than temperature only. Indeed, both environmental means and environmental heterogeneity were found to drive the variation of aboveground traits within plant communities (Stark *et al.* 2017).
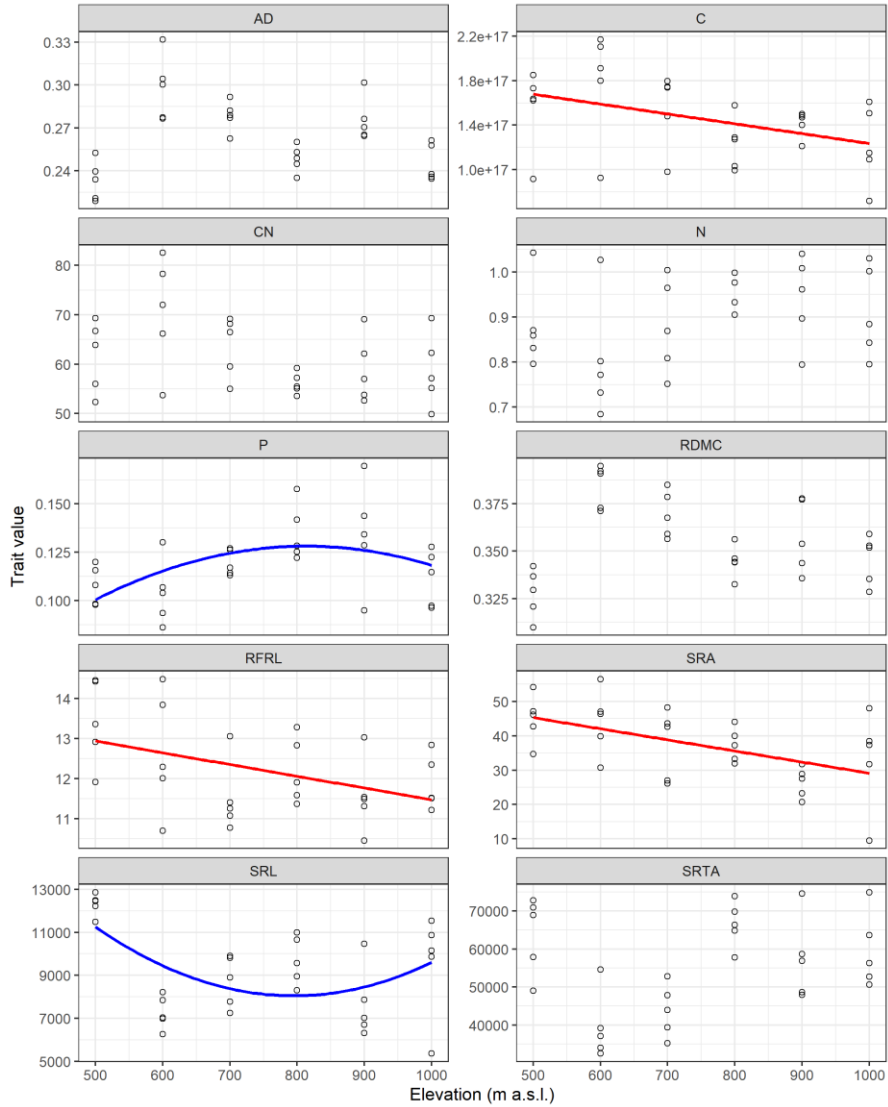
Figure 14. Community-level root trait relationships for subarctic heath vegetation with elevation. Coloured lines are significant relationships between root traits and elevation at α = 0.05. Red lines are linear model fits and blue lines are polynomial model fits. Circles are community-weighted average root trait values in each plot (n = 5). The fine root traits are: average diameter (AD) (mm), root carbon content (C) (%), root carbon to nitrogen ratio (CN), root nitrogen content (RNC) (%), root phosphorous content (P) (%), root dry matter content (RDMC) (g^{-1}), root forks per root length (RFRL) (forks cm^{-1}), specific root area (SRA) (cm^2/g), specific root length (SRL) (cm g^{-1}), and specific root

tip abundance (SRTA) (tips cm^{-1}). Data for root C content were transformed using Tukey's power transformation ($\lambda = 9.9$) (paper IV).

Intraspecific variation contributed more than species turnover to the variation explained by elevation for all fine root traits except for root N content (Figure 15). For example, for root dry matter content, intraspecific variation contributed 63.1% to the total variation explained by elevation (70.6%), while the contribution of species turnover was only 0.5%. This is probably because there was no replacement of dominant species along the elevational gradient, despite changes in species richness and relative abundances. Previous research has also found a large contribution of intraspecific variation for aboveground traits in plant community responses to elevation (Albert *et al.* 2010; Messier *et al.* 2010).Therefore, our results point to a strong role of intraspecific variability in arctic ecosystems for driving responses of plant communities to long-term climatic changes and plant community assembly.
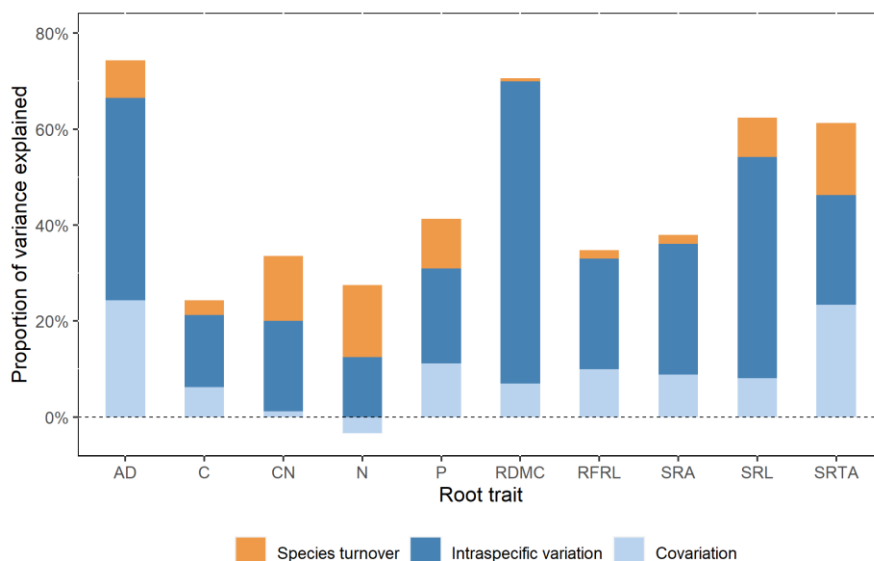
Figure 15. Variance partitioning of community-weighted means for each trait across an elevational gradient. Bars are variation explained by elevation for each root trait. The fine root traits are average diameter (AD), root carbon content (C), root carbon to nitrogen ratio (CN), root nitrogen content (RNC), root phosphorous content (P), root dry matter content (RDMC), root forks per root length (RFRL), specific root area (SRA), specific root length (SRL), and specific root tip abundance (SRTA) (paper IV).

3.5 General discussion

The findings in this thesis demonstrate that the chemical axis of the fine root economics spectrum is particularly important for explaining the abundance of broad soil microbial groups (paper I) and plant-soil feedbacks (paper II). Further, several chemical traits were shown to be strongly associated with the abundance of various fungal guilds. For example, root carbon content had a strong positive association with the abundance of arbuscular mycorrhizal fungi (paper I). In addition, root carbon content and root phosphorous content responded to elevation at the whole plant community level, as well as root nitrogen and the ratio of carbon to nitrogen content for some plant species (paper IV). Arctic ecosystems are nutrient-poor due to cold temperatures, short growing seasons and slow nutrient cycling (Chapin *et al.* 2011). It is therefore likely that chemical root traits may be more important than morphological traits for dictating plant-soil interactions and plant community responses to climate change in this ecosystem. For example, nitrogen deposition rates in Northern ecosystems are much lower (Forsmark *et al.* 2020) compared to temperate grasslands (de Vries & Bardgett 2016), and therefore the differences in plant-available nitrogen in these ecosystems may influence plant-microorganism interactions and the prevalence of the resource-acquisition strategies.

To date, there appears to be a stronger focus on morphological root traits in root trait-based ecological studies. However, and interestingly, morphological root traits commonly incorporated into trait-based ecological studies, such as average diameter and specific root length, which are expected to be related to mycorrhizal association (Cortois *et al.* 2016; Bergmann *et al.* 2020), were not important for explaining plant-soil interactions and feedback in papers I and II. On the other hand, Sweeney *et al*. (2021) found a negative relationship between specific root length and the relative abundance of arbuscular mycorrhizal fungi in temperate grasslands. This thesis therefore points towards the importance of cautious selection of root traits for ecological studies by taking into consideration the ecosystem properties. For example, the relative abundance of arbuscular mycorrhizal fungi was low in our study system, relative to temperate grasslands (Sweeney *et al.* 2021), and in tropical ecosystems where arbuscular mycorrhizal associations are very common (Öpik *et al.* 2006; Davison *et al.* 2011). Therefore, morphological traits associated with mycorrhizal colonization may not be as important in the sub-arctic tundra as in other ecosystems. In

addition, architectural traits such as rooting depth or hydraulic conductance may be more important in temperate or tropical ecosystems than in arctic ecosystems, where soils are generally more shallow and plants take up shallow soil water (Amin *et al.* 2020).

Interestingly, both average root diameter and specific root length responded to elevation (Paper IV). For example, average root diameter was thicker at lower elevations for *Vaccinium vitis-idaea*, where the ambient temperature is higher (Sundqvist *et al.* 2011a). Although this relationship was not observed at the plant community level, it indicates that increased temperatures may result in thicker average root diameters of some species. Thicker root diameters are generally associated with higher mycorrhizal colonization rates and more foraging via mycorrhizal symbionts (Eissenstat *et al.* 2015). At the same time, elevated temperatures may increase mycorrhizal colonization rates in fine roots (Bennett & Classen 2020). Hence, there may be a more important role for average diameter and other morphological root traits at warmer arctic temperatures expected at the end of the century (IPCC 2018). This species-specific root trait response may also potentially influence plant-plant interactions and plant-soil feedback direction, i.e., should mycorrhizal colonization be more beneficial than a "do it yourself" strategy (root foraging for nutrients) (Bergmann *et al.* 2020) with global warming.

Although there was a strong association between some fine root traits and arbuscular mycorrhizal fungi, there were no strong associations between fine root traits and the relative abundances of yeasts and moulds, which in our study was a quarter of the total abundance of fungi (paper I). Hence, there remains a huge gap in knowledge as to which root traits drive the relative abundances of yeasts and moulds. However, it is likely that yeasts and moulds may respond to root carbohydrate content, which was not measured, as they rely on simple carbon compounds exuded by plant roots (Botha 2006; Pawłowska *et al.* 2019). Further, there is a high relative abundance of unknown fungi or fungi with unknown functions (papers I and II) that may potentially influence plant-soil feedback. This points to the need for soil taxonomic studies to better elucidate the identity and roles of these microorganisms, their roles in plant-soil interactions and ultimately plant community assembly in arctic ecosystems.

Finally, the tundra is predicted to warm by approximately 4°C by the end of the century (IPCC 2018), and shifts in plant community composition and

plant species abundances are already occuring (Elmendorf *et al.* 2012a; Myers-Smith *et al.* 2019). Few studies have investigated the role of plant-plant interactions in plant community assembly under warming. For example, Bråthen *et al.* (2018) show that the response of herbaceous plants to warming was reduced in communities where *Empetrum nigrum* was present. This suggests that dominant plant species may have an important role in determining the abundance of other interacting plant species under warming. Assessing the role of root resource-acquisition strategies could provide more additional insights into plant-plant interactions and the mechanisms involved in plant community assembly, as it incorporates belowground competition for nutrients. In paper III, we show that temperature does alter plant-plant interaction effects under warming, shifting interactions towards competition. However, there was no clear link to plant resource-acquisition strategy. This suggests that plant competition may become more species-specific, rather than related to resource-acquisition strategy (Kuijper *et al.* 2005) under warming, where nitrogen mineralization in colder ecosystems may increase (Salazar *et al.* 2020).

4. Conclusions and implications

Based on the results presented in this thesis, I conclude that:

- For sub-arctic tundra species, there are two distinct axes of fine root trait variation, i.e., a morphological root trait axis and a chemical root trait axis. The chemical root trait axis is important for predicting the abundances of broad microbial groups and plant-soil feedbacks. However, the fine root economics spectrum may not be the golden standard in ecological studies. For example, it was not useful for predicting the relative abundances of soil fungal taxa. In this regards, individual root traits were better predictors.
- Root forks per root length, root carbon content and root nitrogen content are potentially good predictors of the relative abundance of soil microorganisms, and useful response traits to temperature that can be included in future trait-based research in the sub-arctic tundra. In addition, root dry matter content is a useful trait for inclusion in plant-soil feedback studies, as it was positively associated with plant-soil feedbacks and negatively associated with most broad microbial biomarkers (as measured by phospholipid fatty acid biomarker concentrations).
- Not every fine root trait may be applicable for understanding plant-soil interactions across ecosystems. For example, average diameter and specific root length were not associated with any soil fungal guild. However, negative associations were found between specific root length and the relative abundance of arbuscular mycorrhizal fungi in temperate grasslands. The arctic tundra and temperate grasslands vary in terms of nutrient availability, growing season temperature and growing season length, all of which could affect mycorrhizal colonization rates.

- There is a high relative abundance of dark septate endophytes, yeasts and fungi with 'unknown' functions in the subarctic tundra. Our lack of knowledge about the functions of these microbial taxa may obscure our understanding of root-microorganism relationships in the sub-arctic tundra.
- Elevated temperature altered plant-plant interactions, but shifts in competitive interaction were not linked to plant resource-acquisition strategy in this study. However, the basis of the placement of plant species into a resource-acquisition strategy could potentially alter the results. For example, in this thesis plant species were selected based on morphological traits, based on an expected trade-off for nitrogen uptake either from mycorrhizal associations or via root exploration. However, chemical fine root traits appear to be more important in the sub-arctic tundra.
- Intraspecific variation in root trait values contributed more than species turnover to the variation explained by elevation in our study system. This points to the importance of not only focusing on trait means, but also including intraspecific variation in studies related to temperature effects on fine roots in plant communities.
- To understand plant community assembly under global warming, it is important to use a diversity of methods and at various scales. Both observational studies (e.g., along elevational gradients) and growth chamber studies or greenhouse studies are useful, but each method has advantages and disadvantages. Field studies enable a holistic experiment with all interacting variables in place. However, they simultaneously present a challenge for disentangling the effect of the explanatory variable(s) being studied. On the other hand, greenhouse and growth chamber studies allow for the manipulation of environmental and biotic variables, but may alter or exclude variables present in natural environments.

5. Future research

The work contained in this thesis has led to the following future research questions and/or identified remaining knowledge gaps:

- Which root traits predict the abundance of yeasts and moulds, as well as saprotrophs in arctic ecosystems?
- To what extent are shifts in root traits in response to temperature linked to associations with mycorrhizal fungi in the arctic tundra?
- How will the abundances of various fungal guilds change with warming, and what implications would this have for plant-microorganisms interactions and plant community assembly? For example, will the abundance of cold-tolerant opportunistic fungi decline under warming? If so, how would this influence plant-microbial interactions, soil food webs and nutrient cycles? Also, will there be an increase in all groups of mycorrhizal fungi (i.e., ericoid, arbuscular and ectomycorrhizal fungi) under warming and can this influence competitive interactions among plant species associated with the various mycorrhizal types?
- How are bacterial communities, nematodes and other soil fauna associated with fine root traits and how important are they for plant-soil feedback in the arctic tundra?
- To what extent do various global change factors interact to drive root trait-microbial relationships in the future? This is especially critical in arctic ecosystems, which are predicted to have increased precipitation and increased temperatures.
- Spatial heterogeneity may drive trait variation. To what extent does it play a role in the sub-arctic tundra? How important would this be for plant community responses to climate change?

- What is the generality of these studies herein in other ecosystems? For example, what is the relative importance of chemical root traits in other ecosystems, relative to the arctic tundra?

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Popular science summary

The arctic may be 4−7°C warmer by the end of this century. Scientists expect this to result in changes in the various types and quantities of plant species found there. This is because there has been a build-up of dead plant remains over time, since the generally low temperatures in the arctic are not ideal for the activity of the various kinds of fungi and bacteria to breakdown these plant remains. Only after plant material is broken down could nutrients be released and become available for plants to take up either directly by their roots or with the assistance of mycorrhizal fungi. Mycorrhizal fungi grow into and occupy the outer layers of plant fine roots and extend within the soil to search for and take up nutrients to share with plants in exchange for sugars. Not all plants prefer to depend on these associations with mycorrhizal fungi for nutrients and this is often reflected in the characteristics of the fine roots. For example, thinner roots are often associated with plants choosing a strategy to take up nutrients on their own using their roots. Plants with this type of strategy (called 'acquisitive' strategy) usually grow quickly and are effecient at taking up nutrients. On the other hand, plants with thicker fine roots grow slower and prefer to sacrifice the cost of producing sugars in exchange for gaining nutrients from the mycorrhiza fungi. They invest a lot of these nutrients in building complex chemicals that protect them from being attacked by microorganisms or soil-borne animals.

For this thesis, I wanted to find out what characteristics of fine roots (referred to as 'traits') occur in the arctic tundra, whether an understanding of these traits can help explain the types and quantities of fungi and bacteria in the soil. This is because some microorganisms in the soil, such as yeasts and mycorrhizal fungi prefer sugars from plants, harmful fungi (called 'pathogens') prefer roots with high quantities of nutrients, while other fungi responsible for breaking down dead plant remains prefer material with fewer

nutrients. Second, I was also interested in understanding the implications of the effects of fine root traits on the various types of microorganisms, and whether they would lead to positive or negative benefits for other plants of the same species. Third, I was interested in understanding how plants with the two types of strategies (acquisitive vs. conservative) compete with each other when temperatures are warmer. Fourth, I was interested in how different fine root traits change when temperatures increase. Altogether, this will help in gaining an understanding of what plant communities will be in the future in the arctic tundra, which is the part of the arctic where no trees occur and plants are generally short in height.

From my research, I found that fine root traits do influence the quantities of some of types of fungi, e.g. mycorrhizal fungi and a few types of yeasts. However, mostly chemical root characteristics, such as the quantity of carbon and nitrogen, as well as the amount of water in roots were important. These same characterisitics were also important for determining whether the effects on subsequent plants of the same species grew better or worse on the same soil. For example, fine roots with higher quantities of nitrogen led to poorer growth of the plants. I also found that some pathogens were harmful to other plants of the same species that were grown on the soil previously inhabited by plants with acquisitive strategies. Finally, I found that at warmer temperatures plants will compete more, with some species being better competitors than others. In addition, some fine root characteristics in plant communities may change, but we have not found any clear pattern to these changes that are related to plant strategies. Altogether, this helps to shed a light on the role of root traits in the arctic tundra and how this may result in changes within plant communities in the future.

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