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A song of ice and mud

Interactions of microbes with roots, fauna and carbon in warming permafrost-affected soils

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"I'm being quoted to introduce something, but I have no idea what it is and certainly don't endorse it"
Randall Munroe, xkcd.com

To my late grandfather, who loved peatland plants

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Author contributions

Chapter I
SM, GBW, JTW, MJ and ED designed the study.
SM, GBW and CO performed the fieldwork.
SM collected and analysed the data and wrote the manuscript with contributions from all authors.

Chapter II
SM, FK, SF, JTW and ED designed the study.
FK, SF, SM and SR performed the experiment.
SM collected and analysed the DNA data.
SM, FK and KG collected and analysed all other data.
SM wrote the manuscript with contributions from all authors.
SM and FK share equal author contribution.

Chapter III
SM, FK, JTW and ED designed the study.
SM performed the experiment, collected and analysed the data, and wrote the manuscript with contributions from all authors.

Chapter IV
SM, EK, JTW and ED designed the study.
SM collected and analysed the microbial data.
EK collected and analysed the fauna and environmental data, and wrote the manuscript with contributions from all authors.

Abstract

Permafrost-affected soils store a large quantity of soil organic matter (SOM) – ca. half of worldwide soil carbon – and currently undergo rapid and severe warming due to climate change. Increased SOM decomposition by microorganisms and soil fauna due to climate change, poses the risk of a positive climate feedback through the release of greenhouse gases. Direct effects of climate change on SOM decomposition, through such mechanisms as deepening of the seasonally-thawing active layer and increasing soil temperatures, have gathered considerable scientific attention in the last two decades. Yet, indirect effects mediated by changes in plant, microbial, and fauna communities, remain poorly understood. Microbial communities, which may be affected by climate change-induced changes in vegetation composition or rooting patterns, and may in turn affect SOM decomposition, are the primary focus of the work described in this thesis.

We used (**I**) a field-scale permafrost thaw experiment in a palsa peatland, (**II**) a laboratory incubation of Yedoma permafrost with inoculation by exotic microorganisms, (**III**) a microcosm experiment with five plant species grown either in *Sphagnum* peat or in newly-thawed permafrost peat, and (**IV**) a field-scale cold season warming experiment in cryoturbated tundra to address the indirect effects of climate change on microbial drivers of SOM decomposition. Community composition data for bacteria and fungi were obtained by amplicon sequencing and phospholipid fatty acid extraction, and for collembola by Tullgren extraction, alongside measurements of soil chemistry, CO_2 emissions and root density.

We showed that *in situ* thawing of a palsa peatland caused colonization of permafrost soil by overlying soil microbes. Further, we observed that functional limitations of permafrost microbial communities can hamper microbial metabolism *in vitro*. Relieving these functional limitations *in vitro* increased cumulative CO_2 emissions by 32% over 161 days and introduced nitrification. In addition, we found that different plant species did not harbour different rhizosphere bacterial communities in *Sphagnum* peat topsoil, but did when grown in newly-thawed permafrost peat. Plant species may thus differ in how they affect functional limitations in thawing permafrost soil. Therefore, climate change-induced changes in vegetation composition might alter functioning in the newly-thawed, subsoil permafrost layer of northern peatlands, but less likely so in the topsoil. Finally, we observed that vegetation encroachment in barren cryoturbated soil, due to reduced cryogenic activity with higher temperatures, change both bacterial and collembola community composition, which may in turn affect soil functioning.

This thesis shows that microbial community dynamics and plant-decomposer interactions play an important role in the functioning of warming permafrost-affected soils. More specifically, it demonstrates that the effects of climate change on plants can trickle down on microbial communities, in turn affecting SOM decomposition in thawing permafrost.

Keywords: microbial communities, permafrost, functional limitations, rhizosphere, SOM decomposition, soil fauna, climate change, carbon dioxide

Abbreviations

BCS: Bacterial community structure

DNA: Desoxyribonucleic acid

NSC: Non-sorted circle

OTU: Operational taxonomic unit

PCR: Polymerase chain reaction

PFT: Plant functional type

RCP: Representative concentrations pathway

RNA: Ribonucleic acid

SE: Standard error of the mean

SOM: Soil organic matter

Introduction

Although largely preserved from dense human populations, northern (boreal and Arctic) ecosystems undergo more rapid and severe effects of global warming than the rest of the world (Arctic Climate Impact Assessment, 2005; IPCC, 2014). The effects of this warming on northern soils are of interest, because they store approximately half of global soil organic carbon stock, equivalent to twice the amount in the atmosphere or in terrestrial plants biomass worldwide (Hugelius *et al.*, 2014; Tarnocai *et al.*, 2009). Unusually dramatic for scientific literature (Strauss *et al.*, 2017), the designations of 'Pandora's freezer' (Brown, 2013) or 'carbon bomb' (Treat and Frolking, 2013) denote the significant size of this carbon pool and the high stakes involved in determining its fate under higher temperatures. The disproportionately high amount of organic carbon stored in northern soils stems from the accumulation of soil organic matter (SOM) through three main mechanisms, partly co-occurring:

- peat accumulation: decomposition is hindered by peat chemical composition, acidity and often water-logging, inducing low oxygen availability, resulting in peatlands storing 28.6% of the permafrost region carbon (histosols and histels, 302 Pg-C; carbon stocks from Hugelius *et al.*, 2014);
- cryoturbation: the movement of soils due to repeated freeze-thaw cycles, which transfers organic-rich topsoil horizons deeper into the soil profile, where decomposition is slower due to absence of most faunal decomposers and lower temperatures, and potentially fast incorporation into the permafrost (turbels, 476 Pg-C);
- formation of permafrost soils, in which water has been frozen for at least two consecutive years, constraining decomposition through low temperatures, liquid water availability and oxygenation (cryosols also known as gelisols, 727 Pg-C).

Higher temperatures directly increase SOM decomposition rates due to the kinetic energy requirements of enzymatic breakdown of SOM (Lützow and Kögel-Knabner, 2009), at temperatures where it is not likely counteracted by enzyme denaturation (Alvarez *et al.*, 2018). Increases in temperatures may also reduce the rates and occurrence of cryoturbation (Becher *et al.*, 2013; Frost *et al.*, 2013), which could affect SOM decomposition rates by subtracting less organic topsoils from the surface where most soil faunal decomposers are found (Krab *et al.*, 2010; Setälä and Aarnio, 2002). In addition, permafrost soils thaw in response to warming, thereby increasing the thickness of the active layer – the upper layer of seasonally-frozen soil that thaws during warm periods. Because of active layer deepening, the hitherto permafrost layers will become

seasonally-thawing, reducing their freezing-associated constraints on SOM decomposition. Indeed, microbial activity in these newly-thawed layers will no longer be limited by the reduced availability of liquid water, nutrient or oxygen (Steven *et al.*, 2009). In addition, thawing permafrost soil may also subside due to the melting of ice layers, which may lead to the formation of ponds and to soil mixing events such as thaw slumps or active layer detachments (Inglese *et al.*, 2017; Segal *et al.*, 2016; Weiss *et al.*, 2016). During these soil mixing events, permafrost soils from below the active layer end up closer to or at the surface (Figure 1), directly exposed to higher temperature and oxygenation that further favour decomposition (Schuur *et al.*, 2015). Increasing decomposition rates in the permafrost-affected area as a result of these direct responses to higher temperatures is thus forecasted to result in considerable increases in emissions of greenhouse gases (CO_2, CH_4 and N_2O) from soils compared to current levels (Dorrepaal *et al.*, 2009; Knoblauch *et al.*, 2018; Schuur *et al.*, 2015; Voigt *et al.*, 2017). This increase may not be offset by increased plant growth and litter input (Abbott *et al.*, 2016) particularly without rapid climate change mitigation (i.e. RCP4.5, McGuire *et al.*, 2018), and the likely net positive release of greenhouse gases from permafrost areas under warming has been termed the "permafrost carbon-climate feedback" (Koven *et al.*, 2011). A better understanding of this climate feedback is one of the priorities of the sixth assessment of the intergovernmental panel on climate change to accurately predict climate change impacts at a global scale (IPCC, 2014).

While the direct physical effects of climate change on SOM decomposition in the permafrost area have been the focus of much scientific attention, indirect effects through biota are less well understood. Microbial communities may directly change upon thawing, but also be subject to colonization by overlying microorganisms, and changing microbial communities could in turn affect SOM decomposition. Moreover, changes in plant communities or rooting patterns upon warming, permafrost thaw, or decreased cryoturbation may also affect microbial communities and in turn SOM decomposition (Figure 2).

In deep soil layers, such as newly-thawed permafrost upon active layer deepening, microorganisms (bacteria, fungi, archaea and protists) are the main decomposers. During the last decade, advances in sequencing technologies and computing power have led to considerable progress in understanding the huge diversity and functioning of soil microorganisms. However, given this tremendous diversity (Thompson *et al.*, 2017) and the weak coupling between taxonomy and phenotypes (Bier *et al.*, 2015), as well as the high dispersal capacity of microorganisms, microbial community composition is often poorly descriptive of ecosystem processes rates (Graham *et al.*, 2016; Nunan *et al.*, 2017; Schimel and Schaeffer, 2012). Chapters **I** therefore assesses whether

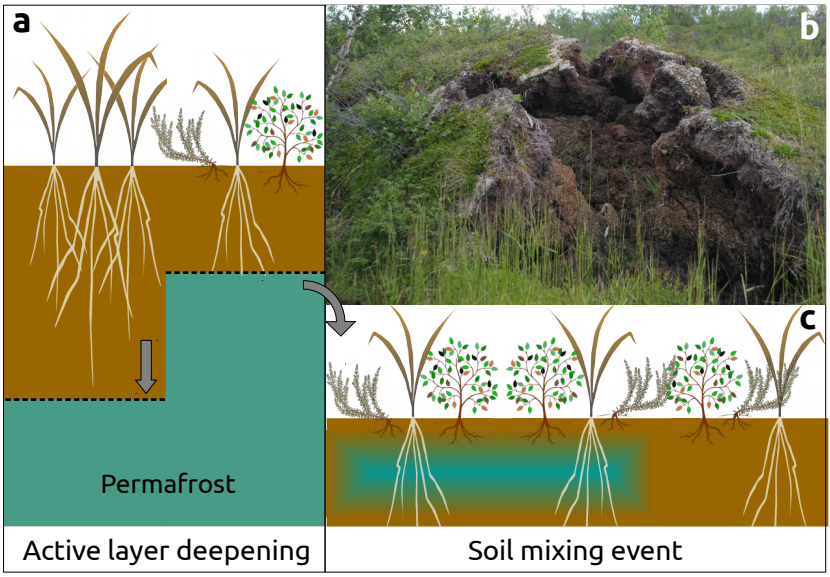

Figure 1: Summary of the two permafrost thaw scenarios discussed in this thesis. (a) Deep-rooting plants forage newly-thawed permafrost upon active layer deepening; (b) thermokarst collapse near Abisko, note the plants growing in the exposed soil; (c) all plants can root in newly-thawed permafrost upon soil mixing events

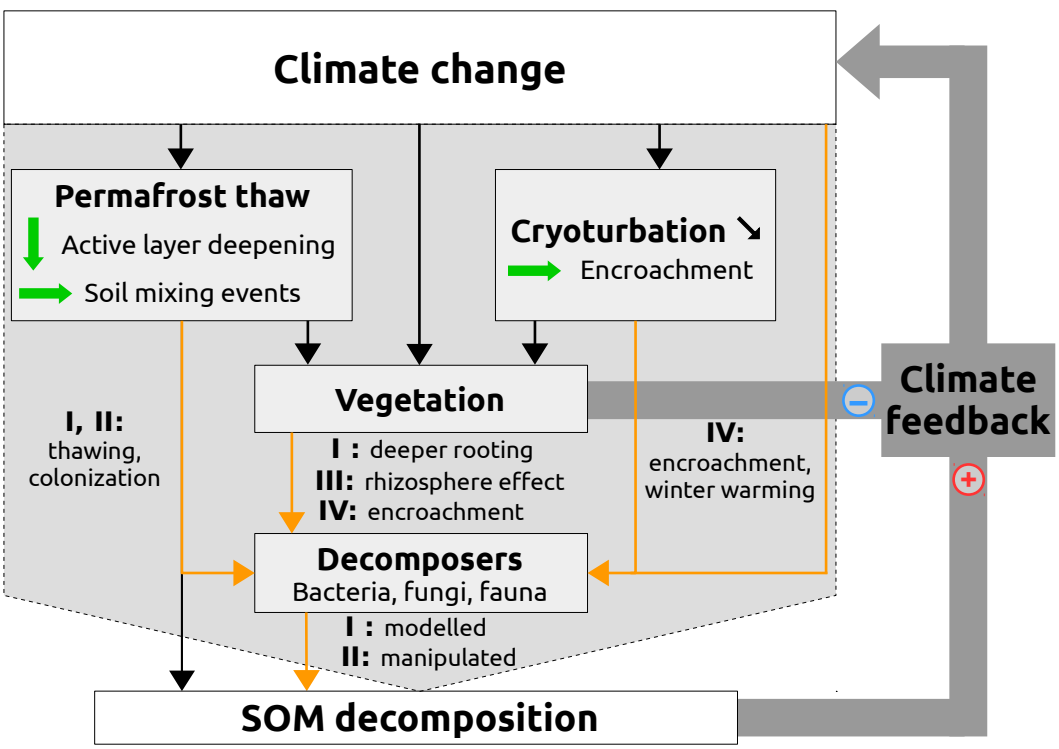

Figure 2: Conceptual diagram of the hypothesized indirect effects of climate change on SOM decomposition. Orange arrows indicate the mechanisms studied in this thesis. Black arrows indicate mechanisms addressed by existing literature, altogether representing the grey arrow in the background. Green arrows indicate plant development: horizontally into barren soil during soil mixing events (e.g. thermokarst) or with decreased cryogenic activity, vertically for deep-rooting species upon permafrost thaw inducing a thickening of the active layer.

bacterial community composition is associated with SOM decomposition rates in permafrost, using as a proxy aerobic respiration.

Long-term freezing in permafrost soils exerts strong constraints on microbial communities: limited water, nutrient and oxygen availability, high osmotic stress, as well as long-term exposure to radiation (Steven *et al.*, 2009). Together these constraints favour the development and/or selection of stress-tolerance strategies among microbial communities (Mackelprang *et al.*, 2017). In addition, the dispersal of microbial communities is limited in frozen soils (Bottos *et al.*, 2018), which results in large variation in communities found in frozen soils compared to communities in the active layer. In incubations, strong endogenous changes were observed in permafrost bacterial communities after thawing (Coolen and Orsi, 2015; Mackelprang *et al.*, 2011). Upon thawing in nature, these communities will likely be increasingly in contact with active layer microorganisms, through water infiltration or root growth, and might consequently undergo community coalescence (Rillig *et al.*, 2015, 2016), which may result in different changes than those observed in incubations. In chapters **I** and **II**, I therefore investigate whether permafrost bacterial and fungal communities are vulnerable to colonization *in situ* and *in vitro*.

Indirect effects of climate change on microbial community composition and functioning may also occur through plant encroachment into barren soil and changes in plant community composition. Plants are an important driver of microbial community composition and climate change induces both changes in plant communities (Myers-Smith *et al.*, 2015) as well as increased plant growth due to higher atmospheric CO_2 concentrations and temperatures. Although the latter could partly mitigate the permafrost carbon-climate feedback (Abbott *et al.*, 2016; McGuire *et al.*, 2018), plants can also stimulate microbial activity around their roots by rhizodeposition – the release of root exudates, mucilage and root cells into the rhizosphere (Jones *et al.*, 2009; Nguyen, 2003). These inputs can stimulate SOM decomposition through priming effects (Fontaine *et al.*, 2003, 2007; Kuzyakov, 2010), to which both peat, cryoturbated soils and permafrost soils are sensitive (Basiliko *et al.*, 2012; Wild *et al.*, 2016). The priming effects can depend on microbial community composition (Razanamalala *et al.*, 2018), and different plant species often harbour different rhizosphere microbial communities (Philippot *et al.*, 2013a). While the rhizosphere extent is relatively limited, it hosts a large fraction of the soil microbial activity (Kuzyakov and Blagodatskaya, 2015), and has been suggested as a part of the soil where microbial community composition is more likely to affect soil functioning (Nunan *et al.*, 2017; Schimel and Schaeffer, 2012). Plant communities may therefore affect subsoil functioning directly through rhizodeposition (e.g. Street *et al.*, 2018) but also indirectly by altering microbial communities.

Plant encroachment into barren soil will likely occur upon active layer deepening, soil mixing events, and decreased cryoturbation (Figure 2). Northern plants generally have very shallow rooting depths compared to plants in the rest of the world (Iversen *et al.*, 2015), and the extent of their influence on soil microbial communities may thus be limited to the shallow soil layers. Nonetheless, certain northern plant species can grow roots deep enough (e.g. > 50 cm) to forage newly-thawed permafrost upon active layer deepening (Blume-Werry, 2016; Keuper *et al.*, 2017), and might gain a competitive advantage from the nutrients it contains (Keuper *et al.*, 2012; Salmon *et al.*, 2018; Wild *et al.*, 2018). In contrast, during soil mixing events (Figure 1), when bare permafrost soil becomes exposed, even shallow-rooting plants could establish in it, benefit from its nutrients, and affect its microbial community composition. Further, higher air temperatures and increasing snow cover in Fennoscandia may reduce cryoturbation, allowing plant encroachment (Becher *et al.*, 2013, 2018). Upon plant encroachment on barren cryoturbated soil (non-sorted circles, also known as frost boils), the mineral soil will progressively see the formation an organic topsoil layer, similar to the surrounding soil which exhibits higher carbon and nitrogen pools and fluxes than the barren soil (Vaisanen *et al.*, 2017). Microbial communities may be affected by vegetation encroachment into barren cryoturbated soils directly, by rhizodeposition, but also in the longer-term by the changes in soil chemistry. Moreover, plant encroachment might not only affect microorganisms but also another important group of decomposers, soil fauna. Indeed, soil fauna can be strongly affected by plant presence (Eo and Nakamoto, 2008; Krab *et al.*, 2013), and may in turn affect both SOM decomposition and microbial community composition. Chapter **I** investigates the changes in bacterial community composition upon active layer deepening, while chapter **IV** assesses whether vegetation encroachment into barren cryoturbated soil affects bacterial and collembola community composition.

Rhizosphere microbial communities are largely unexplored in peat, cryoturbated and thawed permafrost soils, and likely result, as in other soils, from the interplay of plant species and soil type effects (Berg and Smalla, 2009; Philippot *et al.*, 2013a). Different plant species, in particular across plant functional types (PFT, Chapin *et al.*, 1996), affect microbial communities differently due to varying root traits, in particular root exudates (Bardgett *et al.*, 2014; Berg and Smalla, 2009; Philippot *et al.*, 2013a). Because different plant species are able to forage the newly-thawed permafrost in active layer deepening than in soil mixing events, species-specific rhizosphere effects could result in different microbial communities between permafrost thaw scenarios. While plants in cryoturbated and thawed permafrost soils may, as in most soils, develop rhizosphere communities distinct from the bulk soil and between plant species, this may not be the case in peat. *Sphagnum* spp. mosses are a major constituent of northern peat deposits due to their very slow decomposition

(Dorrepaal *et al.*, 2005; Mastný *et al.*, 2018; Ward *et al.*, 2014). The slow decomposition of *Sphagnum* peat results from its very acidic pH and its various secondary metabolites (Verhoeven and Liefveld, 1997), exerting strong chemical constraints on bacterial communities (Preston and Basiliko, 2016), which may override rhizosphere effects, but this has not been studied until now. Deeper, older, and more decomposed *Sphagnum* peat that has been incorporated into the permafrost might, in contrast, have lower concentrations of secondary metabolites and allow plants to more easily modify their rhizosphere chemistry and, in turn, microbial communities. In chapter **III**, I therefore compare how different plant species, differing in rooting depths and root traits, affect bacterial communities in shallow *Sphagnum*-dominated peat and in more decomposed, newly-thawed permafrost peat.

Whether or not microbial community composition is resistant to colonization or rhizosphere effects after permafrost thawing is relevant for better understanding of the permafrost carbon feedback because permafrost microorganisms may not be the most efficient decomposers. Indeed, shaped by two to two million years of life in a frozen environment, permafrost microbial communities may show functional limitations, in other words lack certain functions, some of which related to decomposition processes. Future permafrost SOM decomposition rates are, however, often estimated by incubating permafrost soil and its associated microorganisms *in vitro*, where such potential functional limitations may persist and cause underestimations of carbon and nitrogen cycling after colonization *in situ*. In chapter **II**, I test whether permafrost microbial communities have functional limitations that affect SOM decomposition, using as proxies nitrification and aerobic respiration.

Aims

The overarching aim of this thesis was to investigate direct and plant-roots driven indirect effects of climate change on decomposer (fauna and primarily microbial) communities in northern permafrost-affected environments, and their potential implications for SOM decomposition (Figure 2). I focussed my efforts on three soil types important for carbon storage in the Arctic: permafrost, peat and cryoturbated soils. More specifically I investigated:

A) Whether microbial communities in newly-thawed permafrost are vulnerable to colonization by exogenic microorganisms (chapters **I** and **II**).
B) Whether vegetation encroachment into barren soil, after a decrease in cryoturbation or permafrost thaw, modifies microbial and fauna communities (chapters **I** and **IV**).
C) Whether the presence of roots from different plant species affect

bacterial communities in fresh *Sphagnum* peat and in older permafrost peat (chapter **III**).

D) Whether changes in permafrost microbial communities are associated with decomposition, in particular heterotrophic respiration (chapters **I** and **II**) and nitrification (chapter **II**).

Materials and Methods

Study sites

The experiments described in chapters **I**, **III** and **IV** took place in the Abisko area, in northern Sweden. The region is characterized by a sub-arctic climate, mean annual air temperatures have risen by 2.5 °C since 1913 and were on average 0.6 °C in the lowlands (350 m) between 1995 and 2006 (Callaghan *et al.*, 2010). Although this is unfavourable to permafrost formation, permafrost can still be found at low elevation in palsa peatlands. Palsa peatlands are ombrotrophic *Sphagnum* peat plateaus uplifted by their glacial and lacustrine silty permafrost core, including segregated ice layers, and usually surrounded by lower fens or ponds without permafrost (Klaminder *et al.*, 2008). The uplifting (1-3 m), strong winds and the absence of trees on palsas result in a very thin snow layer during the cold season, when *Sphagnum* peat is moist and effectively conducts heat, thus allowing the soil to lose large amounts of heat to the air. In the warm season, the upper *Sphagnum* peat layers become drier, insulating the soil from the warmer air (Kettridge and Baird, 2007). The combined effects of thin snow cover in the winter, and varying insulation by *Sphagnum* peat between summer and winter explain the subsistence of permafrost in palsa peatlands in the Abisko area, which can therefore be classified as "environment-protected permafrost" *sensu* Shur and Jorgenson (2007). Permafrost temperatures have risen by 0.4-1 °C between 1980 and 2002 and are now just below 0 °C, and in the same interval the permafrost thickness has decreased by ca. 50% in the same interval (Johansson *et al.*, 2011). Further, thermokarst is a commonly observed feature in this area (Figure 1), likely suggesting a complete permafrost thaw within the coming decade(s) (Åkerman and Johansson, 2008). The long-term experiment used in chapter **I** was located in the Storflaket palsa peatland (6 km east of Abisko, Johansson *et al.*, 2013) and the plants and soils used in chapter **III** were collected in the same peatland.

At higher elevations, alpine permafrost covers a large extent of the Abisko area, although data on soil depth are scarce and the active layer often reaches the underlying bedrock. Ridges and mountain tops exposed to strong wind accumulate little snow, and consequently undergo frequent freeze-thaw cycles

in the autumn and spring. Freeze-thaw cycles induce strong cryogenic activity, and a substantial fraction of the alpine tundra harbours signs of cryoturbation, such as non-sorted circles, also known as frost boils (Becher *et al.*, 2013). Non-sorted circles (NSC) in the Abisko area consist of patches of barren soil within densely vegetated tundra heath (dominated by *Empetrum nigrum* ssp *hermaphroditum* L.). The area of barren soil has decreased by 10% between 1958 and 2008, which was attributed to decreased cryoturbation allowing vegetation to encroach (Becher *et al.*, 2013). Vegetation encroachment within the NSCs thus provides a proxy for longer-term climate change effects, which we utilized in chapter **IV**.

Microbial community characterization

In all chapters, we characterized bacterial (as well as fungal, in chapter **II**) communities by amplicon sequencing, sometimes referred to as 'metabarcoding'. This approach takes advantage of short variable regions of DNA embedded within the very conserved ribosomal RNA gene, allowing them to be targeted by PCR using 'universal' primers, and to provide phylogenetic information without the need for sequencing the entire ribosomal gene. Consequently, short sequencing reads technology such as Illumina sequencing by synthesis can be used on these regions to obtain high-throughput, semi-quantitative (i.e. relative and not absolute abundances) information about which microbial taxa are present in a given DNA pool (Bartram *et al.*, 2011), here extracted from soil samples. The software and parameters used for analysis of sequencing data varied slightly between chapters, but followed the same major steps of merging paired-end sequencing reads (for bacterial data only), quality filtering, open-reference clustering of operational taxonomic units (OTUs), chimeric OTUs removal, mapping original sequences to OTUs, removing OTUs abundant in extraction- or PCR-blanks, and assigning taxonomy to each OTU. The resulting information was then summarized as abundance tables of OTUs, on which a suite of community ecology tools were used, such as computing within-sample diversity (α-diversity) and between-samples diversity (β-diversity, using Bray-Curtis distance for fungi and phylogeny-informed UniFrac metrics for bacteria; Lozupone and Knight, 2005; Lozupone *et al.*, 2011). Multivariate statistical analyses were applied to visualize β-diversity by ordinations – principal coordinates analysis (PCoA) or non-metric multidimensional scaling (NMDS) – or to assess the effects of different factors on β-diversity – permutational multivariate analysis of variance (PERMANOVA) or correlation of variables with ordination axes (*envfit*, Oksanen *et al.*, 2017). The overall effects of factors on community composition were also assessed using generalized linear models (GLM, negative-binomial distribution) fitted on the abundance of each OTU (*manyglm*, Wang *et al.*, 2012; Warton *et al.*, 2012), and a GLM approach was also used to assess which

OTUs had a different abundance between two given sets of samples (Love *et al.*, 2014).

Experiments

In chapter **I**, we used a long-term passive snow addition experiment set up in 2005 in the Storflaket peatland close to Abisko. Passive snow addition utilizes the insulating capacity of snow to prevent heat loss from the (permafrost) soil during the snow-cover season, and is very efficient in thawing the upper permafrost in areas with a low ambient snow cover such as this palsa peatland. Over 10 years, the manipulation has increased soil temperatures and resulted in a substantial increase in active layer thickness at that site (Johansson *et al.*, 2013), which increased from ca. 69 cm in control plots to ca. 100 cm in snow addition plots. We sampled soil cores down to 1.50 m in the control plots and in manipulated plots (in parts where active layer thickness was ca. 80 cm), and compared the bacterial communities between treatments at 50, 70 and 90+ cm depths. This allowed comparison of bacterial communities in the active layer (50 cm), in the permafrost (90+ cm) and in the intermediate layer which was still permafrost in the control plots but had become part of the active layer in the snow addition plots (70 cm). Further, we incubated soil from these three depths at 11 and 21 °C, and used multiple linear regressions to relate the variation in aerobic respiration rates to variation in root density and multivariate summaries of soil chemistry and bacterial community composition.

In chapter **II**, we incubated Yedoma permafrost soil from the CRREL (Cold Research Regions Engineering Laboratory) tunnel in central Alaska (Long and Péwé, 1996; Shur *et al.*, 2004). Yedoma permafrost is a loess-like, Holocene fine silt deposit containing massive ground ice (ice wedges) formed in areas that were not ice-covered during the last glaciation. In some places, yedoma deposits can reach a thickness of up to several hundred meters and it therefore contains a large part of the permafrost carbon pool (Strauss *et al.*, 2017). To test the permafrost microbial community for vulnerability to colonization and for functional limitations, we incubated this soil with and without addition of a 'test of principle' inoculum, consisting of soil with a functionally-diverse microbial community from an experimental grassland in central France (Fontaine *et al.*, 2007; Patra *et al.*, 2005; Wertz *et al.*, 2006). We then measured respiration rates, bacterial and fungal community composition and soil chemistry at five time points along a 161-days incubation.

In chapter **III**, we grew five regionally-important and locally-dominant peatland plant species in microcosms, placed in a common garden at the Abisko Naturvetenskapliga Station. The plants were grown for 14 months in either fresh *Sphagnum* peat or in newly-thawed permafrost peat. We then sampled

rhizosphere soil from each of the five species and compared the total (DNA) and active (RNA) bacterial communities with those found in non-planted controls, and between the plant species.

In chapter **IV**, we used insulating gardening fleeces or passive snow addition to simulate winter warming in a cryoturbated tundra site with non-sorted circles (NSC) in the Abisko area (860 m a.s.l.) over three winters. We assessed the responses of the composition of bacterial and collembola communities to the short-term experimental warming across a gradient in longer-term vegetation encroachment from the centre to the surrounding area of NSCs (space-for-time substitution, Figure 3).

Main results

In chapter **I**, bacterial communities in a palsa peatland differed strongly between perennially-frozen soils (i.e. intermediate layer in control plots and permafrost layer in both control and snow addition) and those that were seasonally-thawed (i.e. intermediate layer in the snow addition plots and active layer in both control and snow addition, Figure 4). With the active layer deepening, resulting from the *in situ* snow addition, the bacterial communities in the intermediate layer, which had become seasonally-thawed, converged to become strikingly similar from those found in the active layer. We observed a high density of roots in the intermediate layer, mostly belonging to *Eriophorum vaginatum* L., which harbour aerenchymae and thus can partly oxygenate the water-logged deep peat. Moreover, the abundant OTUs for which relative abundance differed between control and snow addition soils in the intermediate layer reflected increased oxygen availability. However, since *E. vaginatum* roots were also present in the active layer, the effects of root presence, endogenous changes from the communities present before thawing and colonization by active layer microorganisms were confounded. Further, we found that potential respiration decreased over depth, and was overall lower in the snow addition plots. Soil chemistry-based regression models of potential respiration were not improved by including root density, but were improved by including a summary metric of bacterial community. Bacterial community even explained more variation than soil chemistry-based models after accounting for differences in organic matter content (i.e., to indicate how 'decomposable' the SOM was). Our results thus indicate that permafrost thaw induced a shift in microbial community, which is possibly related to colonization or deeper root growth, and further suggest that there is a role of bacterial community composition in explaining measures of decomposition.

Figure 3: Winter and spring climate manipulation in cryoturbated tundra. Non-sorted circles in (a) summer, and (b) in late winter / spring. Snow fences and their effects are depicted in photographs (a) and (b). Crosses in (a) denote sampling locations used as space-for-time substitution for vegetation encroachment: from left to right vegetated heath, cryoturbated soil with encroached vegetation, barren cryoturbated soil.

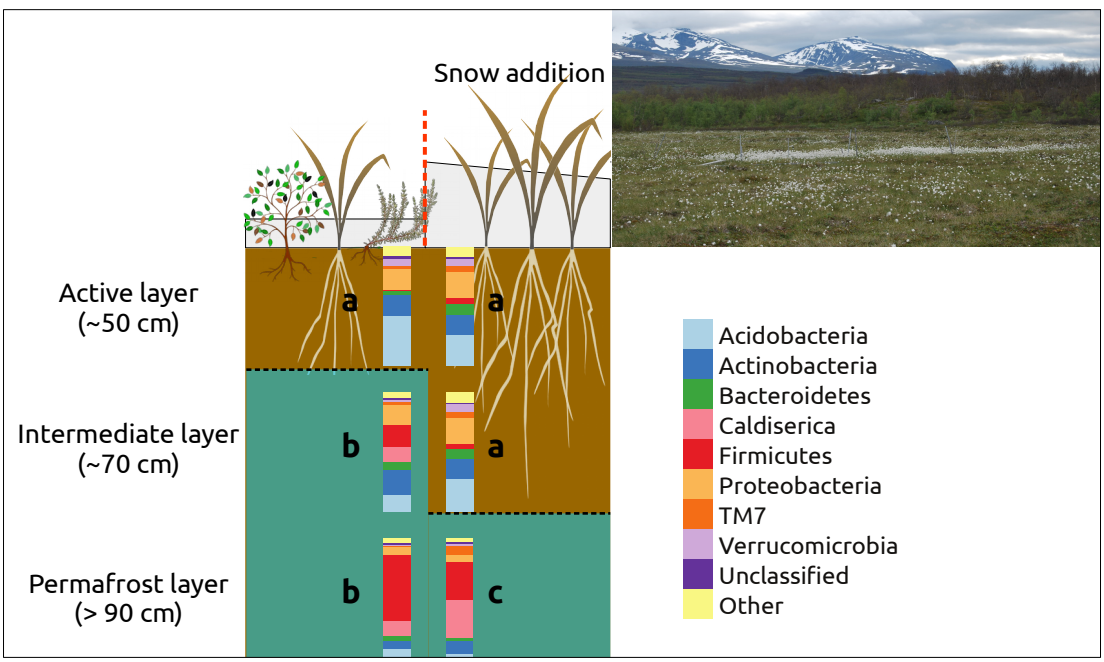

Figure 4: Effects of long-term snow addition in a permafrost peatland on soil, plants and bacterial communities. The black dashed line indicates the active layer depth, the stacked coloured bars indicate average relative abundances of bacterial phyla at each depth (n=6, except snow addition intermediate layer where n = 5) and different letters denote significantly different bacterial communities. The picture in the top-right corner illustrates the effect of snow addition on vegetation: the white area is a snow addition plot, denoting increased density of *E. vaginatum* flowers (picture credits Gesche Blume-Werry).

In chapter **II**, we tested the vulnerability to colonization of newly-thawed Yedoma permafrost bacterial community, and whether these communities were functionally-limited. Inoculating newly-thawed permafrost with small quantities of an exotic soil with functionally-diverse microorganisms induced strong and consistent changes in bacterial and fungal communities, without increasing microbial biomass, confirming that microbial communities found in permafrost soils are vulnerable to colonization by other microorganisms upon thawing. After 161 days, inoculation increased cumulative heterotrophic respiration by 32 %. Further, 54 % of the large ammonium pool had been oxidized to nitrates or nitrites in the inoculated soils, while the ammonium pool remained intact in the control soils. The profound changes in soil functioning and microbial communities after inoculation, along with the absence of increase in microbial biomass and similar initial soil chemistry measures demonstrate the existence of functional limitations of permafrost microbial communities.

I tested in chapter **III** whether different plant species can alter soil bacterial communities in their rhizosphere, both in fresh *Sphagnum* peat and in older, deeper, newly-thawed permafrost peat. I did not find any difference between bacterial communities in bulk *Sphagnum* peat and rhizosphere for three out of five plant species (*Betula nana* L., *Empetrum nigrum* ssp *hermaphroditum* L., *Eriophorum vaginatum* L.). However, rhizosphere communities of *Andromeda polifolia* L. and *Rubus chamaemorus* L. differed from communities in bulk *Sphagnum* peat and from each other. In contrast, all five plant species had rhizosphere communities distinct from those in the bulk newly-thawed permafrost peat. Further, there were plant species-specific differences in the permafrost peat, with rhizosphere bacterial communities of *B. nana* and *E. vaginatum* differing from those of all other species in their total (DNA) and active (RNA) fractions, respectively. Across species there was a similar but stronger rhizosphere effect in the most differing species (i.e. *B. nana*, *E. vaginatum* and to a lesser extent, *A. polifolia*), with a larger fraction of the community being affected and a larger relative replacement of OTUs within phyla, although the phylum-level composition remained relatively similar. The overall rhizosphere effect found for all plant species in the permafrost suggests increased oxygenation in the rhizosphere, which seemed more pronounced in the aerenchymatous *E. vaginatum*. We therefore found that rhizosphere effects on bacterial communities were limited to certain plant species in fresh *Sphagnum* peat but widespread in newly-thawed permafrost peat.

In chapter **IV** I looked at short-term, direct effects of winter warming and longer-term, indirect effects of vegetation encroachment on bacterial and collembola communities in cryoturbated NSC tundra. For both bacteria and collembola, winter warming by snow addition or winter and spring warming by using gardening fleeces had no measurable effects on summer community

composition. However, I observed strong effects of vegetation encroachment, particularly on collembola communities. Bacterial communities seemed to respond more to changes in soil chemistry associated with plant presence and should therefore be more affected by plant encroachment into barren mineral soil in the longer-term, after a more acidic and more organic soil has formed.

Discussion

Colonization of permafrost microbial communities

My first aim **(A)** was to assess whether microbial communities in newly-thawed permafrost are vulnerable to colonization by exogenic microorganisms. In a realistic permafrost thaw scenario such as induced in chapter **I**, I observed convergence of bacterial communities in the newly-thawed permafrost towards those found in the active layer, suggesting a strong effect of colonization. However, roots were also present within this newly-thawed permafrost soil and could have played a role in explaining the changes in bacterial communities. Moreover, permafrost bacterial communities are known to quickly undergo endogenous changes upon thawing without any colonization involved (Coolen and Orsi, 2015; Mackelprang *et al.*, 2011), which could also explain part of the changes we observed. In chapter **II**, I observed such endogenous changes along a 161-day incubation, but also found that bacterial and fungal communities rapidly underwent community coalescence – i.e. they changed in a different way – when they were inoculated with a small quantity of exotic soil microorganisms. I therefore demonstrate that permafrost microbial communities upon thawing are vulnerable to colonization by exogenic microorganisms. If the changes in community composition upon colonization are associated with a different microbial functioning, a large part of our understanding of permafrost microbial ecology – that is, derived from incubations of permafrost cautiously sampled in a near-aseptic way – could be omitting an important indirect effect of thawing.

Effects of vegetation encroachment on decomposer communities

My second aim **(B)** was to look at the sensitivity of bacterial and collembola communities to vegetation encroachment into non-vegetated soil. I assessed both deeper rooting into newly-thawed permafrost in chapter **I** and vegetation establishment into previously-barren cryoturbated soil in chapter **IV**. The strong changes in bacterial communities observed in chapter **I** upon permafrost thaw could be linked to root colonization, although not exclusively as discussed above. We observed *E. vaginatum* roots, known to harbour aerenchymae, in the

newly-thawed permafrost layer, and interpret the changes in the relative abundance of aerobic and anaerobic OTUs as an indication of increased oxygenation in this deep soil layer. Concomitantly, we observed lower potential respiration rates in the soil from plots manipulated with snow addition to induce permafrost thaw. We attribute this lower respiration to gradual labile SOM depletion under higher temperatures, which had been proposed to explain similar findings in Svalbard (Semenchuk *et al.*, 2016) and later supported by further analyses (Semenchuk *et al.*, 2019). Nonetheless, increased oxygen availability might have not only altered bacterial communities but also allowed a higher activity of phenol oxidase (Freeman *et al.*, 2001), which is impaired by anaerobic conditions and important for peat decomposition (Brouns *et al.*, 2014). Vegetation encroachment, by deeper-rooting, into newly-thawed permafrost therefore not only contributes to altering microbial communities but also likely affects microbial functioning in deep soil layers.

In chapter **IV** I investigated the effects of horizontal vegetation encroachment into previously barren soil in cryoturbated tundra on bacterial and collembola communities, as well as their response to short-term warming. I observed strong changes in both bacterial and collembola communities with vegetation encroachment. While collembola communities strongly responded to plant encroachment, bacterial communities seemed more associated with long-term effects of plant presence on soil chemistry and may further change with the development of organic soil horizons. Whether these changes in communities will result in altered biogeochemistry remains to be seen, although the surrounding vegetated soil generally exhibits higher pools and turnover of C and N (Vaisanen *et al.*, 2017). Moreover, it is unclear whether the decomposer communities will be affected differently depending on which plants colonize the barren soil. While the two short-term experimental warming scenarios (winter and spring warming with an insulating fleece and winter warming with snow addition) affected neither type of decomposer, plant species-specific responses to snow addition have been observed in this system (Krab *et al.*, 2018). Decreased cryogenic disturbance may also lead to different plant communities (Becher *et al.*, 2018), therefore, beyond the overall vegetation effect, understanding plant species-specific effects on decomposer communities is a logical next step.

Rhizosphere effects on bacterial communities

Our third aim **(C)** was to assess the role of roots of different plant species in structuring rhizosphere bacterial communities in fresh *Sphagnum* peat and in older, more decomposed, newly-thawed permafrost peat. In fresh *Sphagnum* peat, only two out of five plant species harboured rhizosphere bacterial communities distinct from the bulk soil, and those were also distinct from each

other. I suggest that the absence of rhizosphere effects on bacterial communities for most plant species was due to the acidity and various secondary metabolites in *Sphagnum* peat (Verhoeven and Liefveld, 1997), although the exact mechanisms remain a knowledge gap. My findings are in line with recent findings about *Sphagnum* peat imposing strong constraints on microbial communities (Preston and Basiliko, 2016). In contrast, Robroek *et al.* (2015) observed changes in microbial communities upon shrub or graminoid removal in an alpine bog. Although the changes observed by Robroek et al (2015) were not observed within the rhizosphere but instead at the aerobic-anaerobic interface, the contrast with the results presented in chapter **III** remains partly unexplained. Preston & Basiliko (2016) did not observe any association between microbial communities and functioning in peat, and I suggest that in the rhizosphere a similar situation may be observed, with perhaps increased microbial activity due to rhizodeposition but unchanged community composition. Warming-induced changes in plant communities (Buttler *et al.*, 2015) as well as growth responses at the plant level (Keuper *et al.*, 2011) have been observed in northern peatlands. While such changes will likely affect soil functioning by altering rhizodeposition (Proctor and He, 2017) or litter inputs (Dorrepaal *et al.*, 2005; Mastný *et al.*, 2018; Ward *et al.*, 2014), rhizosphere effects on bacterial communities will probably remain limited.

Contrary to the lack of plant impacts on the fresh *Sphagnum* microbial community composition, I found significant differences in bacterial communities between bulk newly-thawed permafrost peat and all five plant species I tested for, as well as species-specific differences. Based on consistent relative abundance decreases in anaerobic Firmicutes, I suggest that the overall rhizosphere effect shared among species reflects increased rhizosphere oxygenation (Armstrong, 1964; McLamore *et al.*, 2010). As discussed earlier for *E. vaginatum* specifically, this may have repercussions on the permafrost peat decomposition through increasing phenol oxidase activity as observed in non-permafrost peat (Brouns *et al.*, 2014). The plant species-specific differences imply that changes in aboveground plant communities will determine the composition of bacterial communities in permafrost after it thaws. Following an increase in the active layer thickness, only deep-rooting species (*E. vaginatum*, *R. chamaemorus*) will likely reach the newly-thawed permafrost (Keuper *et al.*, 2017), and topsoil conditions may determine which deep-rooting species will dominate and occupy the subsoil. For example, wet or water-logged conditions would be advantageous to aerenchymatous species such as *E. vaginatum* or *R. chamaemorus* (Rydin and Jeglum, 2006), which would drive the bacterial communities in a certain direction. In drier conditions, such as well-drained, sloping terrain, *B. nana* may be more abundant, therefore the subsoil rhizosphere communities would undergo different influences. In soil mixing permafrost thaw events, however, even shallow-rooting such as *A. polifolia* or *E.*

nigrum would be able to grow into barren newly-thawed permafrost. The aboveground assemblage of plant species colonizing the newly-thawed permafrost would therefore determine the composition of bacterial communities over depth. In the top 15 cm, the communities would be determined by all plant species present depending on their relative rhizosphere volume. Deeper down, the abundance of deep-rooting species would be the main driver of bacterial community composition. In addition to their better-known impacts through production of litter or rhizodeposits, changes in plant community composition with permafrost thaw will thus likely affect soil functioning by altering microbial communities in newly-thawed permafrost soil

Functional limitations of permafrost microbial communities

My fourth and last aim **(D)** was to assess whether the composition of permafrost microbial communities affects soil functioning. The association between bacterial community composition and potential respiration in chapter **I** suggests that bacterial communities partly determine soil functioning, as observed in non-permafrost systems (Graham *et al.*, 2016; Liu *et al.*, 2018). However, non-measured confounding factors may have constrained both respiration and bacterial community composition (see Nunan *et al.*, 2017). However, in chapter **II** the possible confounding factors were minimized, allowing to test for the role of microbial community composition on decomposition. Microbial community composition was crucial, as the absence of certain taxa hindered processes as phylogenetically-broad as respiration rates. These results demonstrate the strong impacts of long-term environmental filtering of microbial communities on their functioning, through the mechanism I here refer to as functional limitations. The existence of functionally-limited communities, which can be easily altered by addition of certain taxa, could be an interesting addition to the dilution-to-extinction methods often used to investigate associations between microbial diversity and functioning (e.g. Philippot *et al.*, 2013b; Wertz *et al.*, 2006).

Together, the vulnerability of newly-thawed permafrost microbial communities to colonization and rhizosphere effects, and their functional limitations, underline that the effects of climate change on microbial communities and plant-microbe interactions could have far-reaching consequences for the permafrost carbon-climate feedback. In chapter **II**, I observed a 32% increase in heterotrophic respiration as well as initiation of otherwise absent nitrification, simply by adding exogenic microorganisms to permafrost soil. In chapter **I**, I found a convergence of newly-thawed permafrost bacterial communities towards those found in the overlying active layer, and active layer microbial communities are similarly functionally-diverse than in the rest of the world (Bahram *et al.*, 2018; Fierer *et al.*, 2012; Malard and Pearce, 2018). The relief of

functional limitations of permafrost microbial communities upon colonization by active layer microorganisms through water infiltration or root growth and rhizosphere effects is therefore likely. Current estimates of the permafrost carbon-climate feedback largely rely on long-term *in vitro* incubations of permafrost soil, in which microbial communities may therefore remain functionally-limited. For instance, Knoblauch *et al.* (2018) did not observe methanogenesis in some samples for several years but could later initiate it by adding methanogens. The current estimates of the permafrost carbon-climate feedback, by not accounting for colonization and the relief of functional limitations, may therefore lead to underestimating the magnitude of the permafrost carbon-climate feedback. It would be premature to extrapolate the observed (32%) increase in respiration to the entire permafrost area, as functional limitations in permafrost may vary regionally or locally. Therefore, the prevalence and extent of functional limitations, and the consequences of their relieving upon colonization by active layer microorganisms, are issues that need to be urgently addressed.

In summary, in permafrost-affected soils plants modify microbial communities, which are also vulnerable to colonization, and microbial communities affect SOM decomposition (Figure 5). More specifically:

1. Microbial communities in newly-thawed permafrost soils are vulnerable to colonization by exogenic microorganisms;
2. Reduced cryoturbation rates and the subsequent establishment of tundra heath vegetation results in strong changes in collembola and bacterial communities;
3. Climate change-induced changes in vegetation composition in *Sphagnum* peatlands are unlikely to result in altered bacterial communities in the topsoil;
4. Bacterial communities in the deep, newly-thawed permafrost layers of *Sphagnum* peatlands are likely to respond to deep-rooting plant species favoured by climate change;
5. Microbial communities in newly-thawed permafrost soils can exhibit functional limitations, which can be relieved upon introduction of exogenic microorganisms and can have important consequences for CO_2 release and nitrogen cycling.

Further research

I suggest two main directions for further research about the indirect effects of climate change on SOM decomposition and soil functioning. First, more

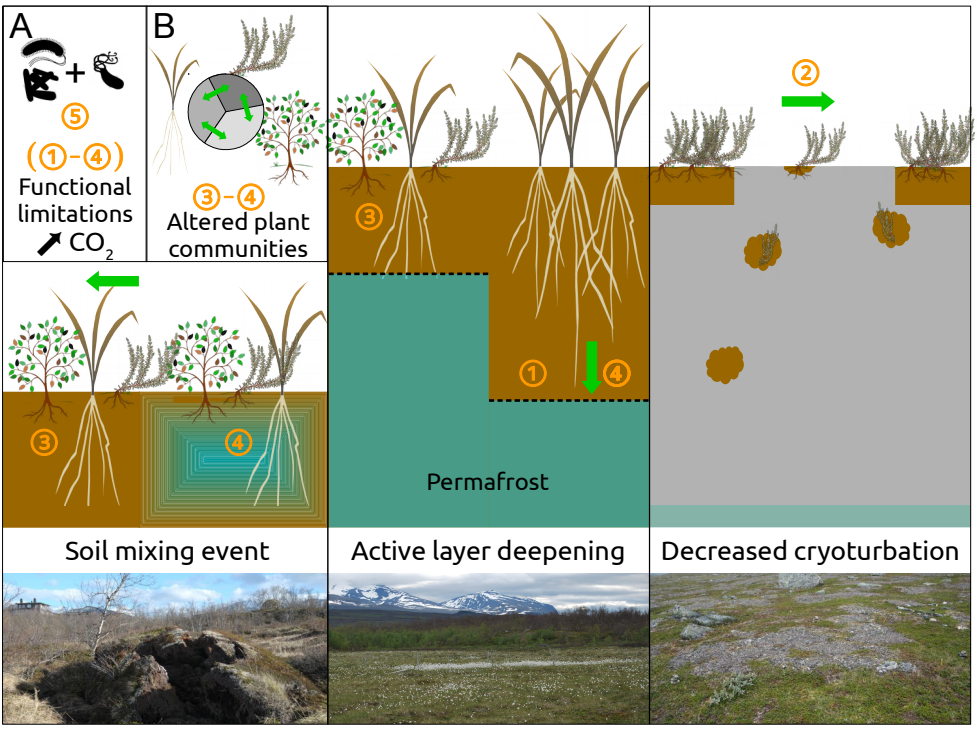

Figure 5: Conceptual diagram of the indirect effects of climate change on drivers of SOM decomposition identified in this thesis. Green arrows indicate changes in vegetation: box (A) changes in plant community composition; from left to right lateral encroachment into barren soil during soil mixing events, vertical encroachment for deep-rooting species upon active layer deepening, and lateral encroachment with decreased cryogenic activity.
1: upon permafrost thaw, microbial communities can change due to colonization by overlying soil microbial communities (community coalescence)
2: vegetation encroachment into barren cryoturbated tundra soil as a result of decreased cryogenic activity induces changes in collembola and bacterial communities.
3: the presence of roots of most plant species does not affect the composition of microbial communities in fresh *Sphagnum* peat
4: the presence of roots of different plant species induces rhizosphere communities distinct from the bulk soil and between plant species in newly-thawed permafrost
5 – box A: functional limitations of permafrost microbial communities may be relieved upon changes in microbial communities following permafrost thaw, either by coalescence (1) or by rhizosphere effects (4).
Box B, 3-4: climate change-induced changes in vegetation composition will affect soil microbial communities differently depending in different soil types.

knowledge about the prevalence of functional limitations in permafrost microbial communities, and consequences of their relief, appears critical for accurately estimating the permafrost carbon-climate feedback. In addition, functionally limited microbial communities in a non-constraining environment open up opportunities for a better theoretical understanding of structure-function relationships in microbial communities. Secondly, as vegetation encroachment affects both microbial and faunal communities, how plants-fauna-microorganisms interactions affect SOM decomposition should be further studied, in cryoturbated soils but also in soil mixing permafrost thaw events. A precise depiction of the consequences of the rapid and severe climate change that northern soils undergo is critical for climate modelling, thus for elaborating climate change mitigation scenarios. This work shows that indirect effects of climate change, in particular through microbial communities, should no longer be neglected: the complexity they add is paramount to our understanding of the permafrost carbon-climate feedback.

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References

Abbott, B.W., Jones, J.B., Schuur, E.A.G., III, F.S.C., Bowden, W.B., Bret-Harte, M.S., Epstein, H.E., Flannigan, M.D., Harms, T.K., Hollingsworth, T.N., *et al.* (2016). Biomass offsets little or none of permafrost carbon release from soils, streams, and wildfire: an expert assessment. Environ. Res. Lett. *11*, 034014.

Åkerman, H.J., and Johansson, M. (2008). Thawing permafrost and thicker active layers in sub-arctic Sweden. Permafrost and Periglacial Processes *19*, 279–292.

Alvarez, G., Shahzad, T., Andanson, L., Bahn, M., Wallenstein, M.D., and Fontaine, S. (2018). Catalytic power of enzymes decreases with temperature: New insights for understanding soil C cycling and microbial ecology under warming. Global Change Biology *0*.

Arctic Climate Impact Assessment (2005). Impacts of a Warming Arctic-Arctic Climate Impact Assessment. Cambridge University Press: Cambridge *1*.

Armstrong, W. (1964). Oxygen Diffusion from the Roots of Some British Bog Plants. Nature *204*, 801–802.

Bahram, M., Hildebrand, F., Forslund, S.K., Anderson, J.L., Soudzilovskaia, N.A., Bodegom, P.M., Bengtsson-Palme, J., Anslan, S., Coelho, L.P., Harend, H., *et al.* (2018). Structure and function of the global topsoil microbiome. Nature *560*, 233–237.

Bardgett, R.D., Mommer, L., and De Vries, F.T. (2014). Going underground: root traits as drivers of ecosystem processes. Trends in Ecology & Evolution *29*, 692–699.

Bartram, A.K., Lynch, M.D.J., Stearns, J.C., Moreno-Hagelsieb, G., and Neufeld, J.D. (2011). Generation of Multimillion-Sequence 16S rRNA Gene Libraries from Complex Microbial Communities by Assembling Paired-End Illumina Reads. Appl. Environ. Microbiol. *77*, 3846–3852.

Basiliko, N., Stewart, H., Roulet, N.T., and Moore, T.R. (2012). Do Root Exudates Enhance Peat Decomposition? Geomicrobiol. J. *29*, 374–378.

Becher, M., Olid, C., and Klaminder, J. (2013). Buried soil organic inclusions in non-sorted circles fields in northern Sweden: Age and Paleoclimatic context. J. Geophys. Res. Biogeosci. *118*, 104–111.

Becher, M., Olofsson, J., Berglund, L., and Klaminder, J. (2018). Decreased cryogenic disturbance: one of the potential mechanisms behind the vegetation change in the Arctic. Polar Biology *41*, 101–110.

Berg, G., and Smalla, K. (2009). Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. FEMS Microbiol Ecol *68*, 1–13.

Bier, R.L., Bernhardt, E.S., Boot, C.M., Graham, E.B., Hall, E.K., Lennon, J.T., Nemergut, D.R., Osborne, B.B., Ruiz-González, C., Schimel, J.P., *et al.* (2015). Linking microbial community structure and microbial processes: an empirical and conceptual overview. FEMS Microbiology Ecology *91*, fiv113.

Blume-Werry, G. (2016). The hidden life of plants : fine root dynamics in northern ecosystems. Doctoral Thesis.

Bottos, E.M., Kennedy, D.W., Romero, E.B., Fansler, S.J., Brown, J.M., Bramer, L.M., Chu, R.K., Tfaily, M.M., Jansson, J.K., and Stegen, J.C. (2018). Dispersal limitation and thermodynamic constraints govern spatial structure of permafrost microbial communities. FEMS Microbiol Ecol *94*.

Brouns, K., Verhoeven, J.T.A., and Hefting, M.M. (2014). Short period of oxygenation releases latch on peat decomposition. Science of The Total Environment *481*, 61–68.

Brown, A. (2013). Permafrost carbon storage: Pandora's freezer? Nature Climate Change (Research highlight, doi:10.1038/nclimate1896)

Buttler, A., Robroek, B.J.M., Laggoun-Défarge, F., Jassey, V.E.J., Pochelon, C., Bernard, G., Delarue, F., Gogo, S., Mariotte, P., Mitchell, E.A.D., *et al.* (2015). Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland. Journal of Vegetation Science *26*, 964–974.

Callaghan, T.V., Bergholm, F., Christensen, T.R., Jonasson, C., Kokfelt, U., and Johansson, M. (2010). A new climate era in the sub-Arctic: Accelerating climate changes and multiple impacts. Geophysical Research Letters *37*.

Chapin, F.S., Bret-Harte, M.S., Hobbie, S.E., and Zhong, H. (1996). Plant functional types as predictors of transient responses of arctic vegetation to global change. Journal of Vegetation Science *7*, 347–358.

Coolen, M.J.L., and Orsi, W.D. (2015). The transcriptional response of microbial communities in thawing Alaskan permafrost soils. Front. Microbiol *6*, 197.

Dorrepaal, E., Cornelissen, J.H. c., Aerts, R., Wallén, B., and Van Logtestijn, R.S. p. (2005). Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? Journal of Ecology *93*, 817–828.

Dorrepaal, E., Toet, S., van Logtestijn, R.S.P., Swart, E., van de Weg, M.J., Callaghan, T.V., and Aerts, R. (2009). Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. Nature *460*, 616–619.

Eo, J., and Nakamoto, T. (2008). Spatial relationships between roots and soil organisms under different tillage systems. European Journal of Soil Biology *44*, 277–282.

Fierer, N., Leff, J.W., Adams, B.J., Nielsen, U.N., Bates, S.T., Lauber, C.L., Owens, S., Gilbert, J.A., Wall, D.H., and Caporaso, J.G. (2012). Cross-biome metagenomic analyses of soil microbial communities and their functional attributes. PNAS *109*, 21390–21395.

Fontaine, S., Mariotti, A., and Abbadie, L. (2003). The priming effect of organic matter: a question of microbial competition? Soil Biol. Biochem. *35*, 837–843.

Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B., and Rumpel, C. (2007). Stability of organic carbon in deep soil layers controlled by fresh carbon supply. Nature *450*, 277–280.

Freeman, C., Ostle, N., and Kang, H. (2001). An enzymic “latch” on a global carbon store. Nature *409*, 149–149.

Frost, G.V., Epstein, H.E., Walker, D.A., Matyshak, G., and Ermokhina, K. (2013). Patterned-ground facilitates shrub expansion in Low Arctic tundra. Environ. Res. Lett. *8*, 015035.

Graham, E.B., Knelman, J.E., Schindlbacher, A., Siciliano, S., Breulmann, M., Yannarell, A., Beman, J.M., Abell, G., Philippot, L., Prosser, J., *et al.* (2016). Microbes as Engines of Ecosystem Function: When Does Community Structure Enhance Predictions of Ecosystem Processes? Front. Microbiol. *7*.

Hugelius, G., Strauss, J., Zubrzycki, S., Harden, J.W., Schuur, E.A.G., Ping, C.-L., Schirrmeister, L., Grosse, G., Michaelson, G.J., Koven, C.D., *et al.* (2014). Estimated

stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps. Biogeosciences *11*, 6573–6593.

Inglese, C.N., Christiansen, C.T., Lamhonwah, D., Moniz, K., Montross, S.N., Lamoureux, S., Lafrenière, M., Grogan, P., and Walker, V.K. (2017). Examination of Soil Microbial Communities After Permafrost Thaw Subsequent to an Active Layer Detachment in the High Arctic. Arctic, Antarctic, and Alpine Research *49*, 455–472.

IPCC (2014). Climate Change 2013: The Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (Cambridge University Press).

Iversen, C.M., Sloan, V.L., Sullivan, P.F., Euskirchen, E.S., McGuire, A.D., Norby, R.J., Walker, A.P., Warren, J.M., and Wullschleger, S.D. (2015). The unseen iceberg: plant roots in arctic tundra. New Phytol *205*, 34–58.

Johansson, M., Akerman, J., Keuper, F., Christensen, T.R., Lantuit, H., and Callaghan, T.V. (2011). Past and Present Permafrost Temperatures in the Abisko Area: Redrilling of Boreholes. Ambio *40*, 558–565.

Johansson, M., Callaghan, T.V., Bosiö, J., Åkerman, H.J., Jackowicz-Korczynski, M., and Christensen, T.R. (2013). Rapid responses of permafrost and vegetation to experimentally increased snow cover in sub-arctic Sweden. Environ. Res. Lett. *8*, 035025.

Jones, D.L., Nguyen, C., and Finlay, R.D. (2009). Carbon flow in the rhizosphere: carbon trading at the soil–root interface. Plant Soil *321*, 5–33.

Kettridge, N., and Baird, A. (2007). In situ measurements of the thermal properties of a northern peatland: Implications for peatland temperature models. Journal of Geophysical Research *112*.

Keuper, F., Dorrepaal, E., Van Bodegom, P.M., Aerts, R., Van Logtestijn, R.S.P., Callaghan, T.V., and Cornelissen, J.H.C. (2011). A Race for Space? How Sphagnum fuscum stabilizes vegetation composition during long-term climate manipulations. Global Change Biology *17*, 2162–2171.

Keuper, F., Bodegom, P.M., Dorrepaal, E., Weedon, J.T., Hal, J., Logtestijn, R.S.P., and Aerts, R. (2012). A frozen feast: thawing permafrost increases plant-available nitrogen in subarctic peatlands. Global Change Biology *18*, 1998–2007.

Keuper, F., Dorrepaal, E., Bodegom, P.M. van, Logtestijn, R. van, Venhuizen, G., Hal, J. van, and Aerts, R. (2017). Experimentally increased nutrient availability at the permafrost thaw front selectively enhances biomass production of deep-rooting subarctic peatland species. Global Change Biology *23*, 4257–4266.

Klaminder, J., Yoo, K., Rydberg, J., and Giesler, R. (2008). An explorative study of mercury export from a thawing palsa mire. Journal of Geophysical Research: Biogeosciences *113*.

Knoblauch, C., Beer, C., Liebner, S., Grigoriev, M.N., and Pfeiffer, E.-M. (2018). Methane production as key to the greenhouse gas budget of thawing permafrost. Nature Climate

Change 1.

Koven, C.D., Ringeval, B., Friedlingstein, P., Ciais, P., Cadule, P., Khvorostyanov, D., Krinner, G., and Tarnocai, C. (2011). Permafrost carbon-climate feedbacks accelerate global warming. Proceedings of the National Academy of Sciences *108*, 14769–14774.

Krab, E.J., Oorsprong, H., Berg, M.P., and Cornelissen, J.H.C. (2010). Turning northern peatlands upside down: disentangling microclimate and substrate quality effects on vertical distribution of Collembola. Functional Ecology *24*, 1362–1369.

Krab, E.J., Berg, M.P., Aerts, R., van Logtestijn, R.S.P., and Cornelissen, J.H.C. (2013). Vascular plant litter input in subarctic peat bogs changes Collembola diets and decomposition patterns. Soil Biology & Biochemistry *63*, 106–115.

Krab, E.J., Roennefarth, J., Becher, M., Blume-Werry, G., Keuper, F., Klaminder, J., Kreyling, J., Makoto, K., Milbau, A., and Dorrepaal, E. (2018). Winter warming effects on tundra shrub performance are species-specific and dependent on spring conditions. Journal of Ecology *106*, 599–612.

Kuzyakov, Y. (2010). Priming effects: Interactions between living and dead organic matter. Soil Biol. Biochem. *42*, 1363–1371.

Kuzyakov, Y., and Blagodatskaya, E. (2015). Microbial hotspots and hot moments in soil: Concept & review. Soil Biology and Biochemistry *83*, 184–199.

Liu, Y.-R., Delgado-Baquerizo, M., Wang, J.-T., Hu, H.-W., Yang, Z., and He, J.-Z. (2018). New insights into the role of microbial community composition in driving soil respiration rates. Soil Biology and Biochemistry *118*, 35–41.

Long, A., and Péwé, T.L. (1996). Radiocarbon dating by high-sensitivity liquid scintillation counting of wood from the Fox permafrost tunnel near Fairbanks, Alaska. Permafrost and Periglacial Processes *7*, 281–285.

Love, M.I., Huber, W., and Anders, S. (2014). Moderated estimation of fold change and dispersion for RNA-seq data with DESeq2. Genome Biology *15*, 550.

Lozupone, C., and Knight, R. (2005). UniFrac: a New Phylogenetic Method for Comparing Microbial Communities. Appl. Environ. Microbiol. *71*, 8228–8235.

Lozupone, C., Lladser, M.E., Knights, D., Stombaugh, J., and Knight, R. (2011). UniFrac: an effective distance metric for microbial community comparison. ISME J *5*, 169–172.

Lützow, M. von, and Kögel-Knabner, I. (2009). Temperature sensitivity of soil organic matter decomposition—what do we know? Biol Fertil Soils *46*, 1–15.

Mackelprang, R., Waldrop, M.P., DeAngelis, K.M., David, M.M., Chavarria, K.L., Blazewicz, S.J., Rubin, E.M., and Jansson, J.K. (2011). Metagenomic analysis of a permafrost microbial community reveals a rapid response to thaw. Nature *480*, 368–371.

Mackelprang, R., Burkert, A., Haw, M., Mahendrarajah, T., Conaway, C.H., Douglas, T.A., and Waldrop, M.P. (2017). Microbial survival strategies in ancient permafrost: insights from metagenomics. ISME J.

Malard, L.A., and Pearce, D.A. (2018). Microbial diversity and biogeography in Arctic soils: Arctic microbial biogeography. Environmental Microbiology Reports.

Mastný, J., Kaštovská, E., Bárta, J., Chroňáková, A., Borovec, J., Šantrůčková, H., Urbanová, Z., Edwards, K.R., and Picek, T. (2018). Quality of DOC produced during litter decomposition of peatland plant dominants. Soil Biology and Biochemistry *121*, 221–230.

McGuire, A.D., Lawrence, D.M., Koven, C., Clein, J.S., Burke, E., Chen, G., Jafarov, E., MacDougall, A.H., Marchenko, S., Nicolsky, D., *et al.* (2018). Dependence of the evolution of carbon dynamics in the northern permafrost region on the trajectory of climate change. PNAS *115*, 3882–3887.

McLamore, E.S., Jaroch, D., Chatni, M.R., and Porterfield, D.M. (2010). Self-referencing optrodes for measuring spatially resolved, real-time metabolic oxygen flux in plant systems. Planta *232*, 1087–1099.

Myers-Smith, I.H., Elmendorf, S.C., Beck, P.S.A., Wilmking, M., Hallinger, M., Blok, D., Tape, K.D., Rayback, S.A., Macias-Fauria, M., Forbes, B.C., *et al.* (2015). Climate sensitivity of shrub growth across the tundra biome. Nature Clim. Change *5*, 887–891.

Nguyen, C. (2003). Rhizodeposition of organic C by plants: mechanisms and controls. Agronomie *23*, 375–396.

Nunan, N., Leloup, J., Ruamps, L.S., Pouteau, V., and Chenu, C. (2017). Effects of habitat constraints on soil microbial community function. Scientific Reports *7*, 4280.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., *et al.* (2017). vegan: Community Ecology Package.

Patra, A.K., Abbadie, L., Clays-Josserand, A., Degrange, V., Grayston, S.J., Loiseau, P., Louault, F., Mahmood, S., Nazaret, S., Philippot, L., *et al.* (2005). EFFECTS OF GRAZING ON MICROBIAL FUNCTIONAL GROUPS INVOLVED IN SOIL N DYNAMICS. Ecological Monographs *75*, 65–80.

Philippot, L., Raaijmakers, J.M., Lemanceau, P., and van der Putten, W.H. (2013a). Going back to the roots: the microbial ecology of the rhizosphere. Nat Rev Micro *11*, 789–799.

Philippot, L., Spor, A., Hénault, C., Bru, D., Bizouard, F., Jones, C.M., Sarr, A., and Maron, P.-A. (2013b). Loss in microbial diversity affects nitrogen cycling in soil. The ISME Journal *7*, 1609–1619.

Preston, M.D., and Basiliko, N. (2016). Carbon Mineralization in Peatlands: Does the Soil Microbial Community Composition Matter? Geomicrobiology Journal *33*, 151–162.

Proctor, C., and He, Y. (2017). Quantifying root extracts and exudates of sedge and shrub in relation to root morphology. Soil Biology and Biochemistry *114*, 168–180.

Razanamalala, K., Razafimbelo, T., Maron, P.-A., Ranjard, L., Chemidlin, N., Lelièvre, M., Dequiedt, S., Ramaroson, V.H., Marsden, C., Becquer, T., *et al.* (2018). Soil microbial diversity drives the priming effect along climate gradients: a case study in Madagascar.

The ISME Journal *12*, 451–462.

Rillig, M.C., Antonovics, J., Caruso, T., Lehmann, A., Powell, J.R., Veresoglou, S.D., and Verbruggen, E. (2015). Interchange of entire communities: microbial community coalescence. Trends in Ecology & Evolution *30*, 470–476.

Rillig, M.C., Lehmann, A., Aguilar-Trigueros, C.A., Antonovics, J., Caruso, T., Hempel, S., Lehmann, J., Valyi, K., Verbruggen, E., Veresoglou, S.D., *et al.* (2016). Soil microbes and community coalescence. Pedobiologia *59*, 37–40.

Robroek, B.J.M., Jassey, V.E.J., Kox, M.A.R., Berendsen, R.L., Mills, R.T.E., Cécillon, L., Puissant, J., Meima-Franke, M., Bakker, P.A.H.M., and Bodelier, P.L.E. (2015). Peatland vascular plant functional types affect methane dynamics by altering microbial community structure. J Ecol *103*, 925–934.

Rydin, H., and Jeglum, J.K. (2006). The biology of peatlands (Oxford; New York: Oxford University Press).

Salmon, V.G., Schädel, C., Bracho, R., Pegoraro, E., Celis, G., Mauritz, M., Mack, M.C., and Schuur, E.A.G. (2018). Adding depth to our understanding of nitrogen dynamics in permafrost soils. Journal of Geophysical Research: Biogeosciences.

Schimel, J., and Schaeffer, S.M. (2012). Microbial control over carbon cycling in soil. Front. Microbio. *3*, 348.

Schuur, E. a. G., McGuire, A.D., Schädel, C., Grosse, G., Harden, J.W., Hayes, D.J., Hugelius, G., Koven, C.D., Kuhry, P., Lawrence, D.M., *et al.* (2015). Climate change and the permafrost carbon feedback. Nature *520*, 171–179.

Segal, R.A., Lantz, T.C., and Kokelj, S.V. (2016). Acceleration of thaw slump activity in glaciated landscapes of the Western Canadian Arctic. Environ. Res. Lett. *11*, 034025.

Semenchuk, P.R., Christiansen, C.T., Grogan, P., Elberling, B., and Cooper, E.J. (2016). Long-term experimentally deepened snow decreases growing-season respiration in a low- and high-arctic tundra ecosystem. J. Geophys. Res. Biogeosci. *121*, 1236–1248.

Semenchuk, P.R., Krab, E.J., Hedenström, M., Phillips, C.A., Ancin-Murguzur, F.J., and Cooper, E.J. (2019). Soil organic carbon depletion and degradation in surface soil after long-term non-growing season warming in High Arctic Svalbard. Science of The Total Environment *646*, 158–167.

Setälä, H., and Aarnio, T. (2002). Vertical stratification and trophic interactions among organisms of a soil decomposer food web – a field experiment using 15N as a tool. European Journal of Soil Biology *38*, 29–34.

Shur, Y.L., and Jorgenson, M.T. (2007). Patterns of permafrost formation and degradation in relation to climate and ecosystems. Permafrost Periglacial Process. *18*, 7–19.

Shur, Y., French, H.M., Bray, M.T., and Anderson, D.A. (2004). Syngenetic permafrost growth: cryostratigraphic observations from the CRREL tunnel near Fairbanks, Alaska. Permafrost and Periglacial Processes *15*, 339–347.

Steven, B., Niederberger, T.D., and Whyte, L.G. (2009). Bacterial and Archaeal Diversity in Permafrost. In Permafrost Soils, P.D.R. Margesin, ed. (Springer Berlin Heidelberg), pp. 59–72.

Strauss, J., Schirrmeister, L., Grosse, G., Fortier, D., Hugelius, G., Knoblauch, C., Romanovsky, V., Schädel, C., Schneider von Deimling, T., Schuur, E.A.G., *et al.* (2017). Deep Yedoma permafrost: A synthesis of depositional characteristics and carbon vulnerability. Earth-Science Reviews *172*, 75–86.

Street, L.E., Subke, J.-A., Baxter, R., Dinsmore, K., Knoblauch, C., and Wookey, P.A. (2018). Ecosystem carbon dynamics differ between tundra shrub types in the western Canadian Arctic. Environ. Res. Lett.

Tarnocai, C., Canadell, J.G., Schuur, E. a. G., Kuhry, P., Mazhitova, G., and Zimov, S. (2009). Soil organic carbon pools in the northern circumpolar permafrost region. Global Biogeochem. Cycles *23*, GB2023.

Thompson, L.R., Sanders, J.G., McDonald, D., Amir, A., Ladau, J., Locey, K.J., Prill, R.J., Tripathi, A., Gibbons, S.M., Ackermann, G., *et al.* (2017). A communal catalogue reveals Earth's multiscale microbial diversity. Nature *551*, 457–463.

Treat, C.C., and Frolking, S. (2013). Carbon Storage: A permafrost carbon bomb? Nature Climate Change *3*, 865–867.

Vaisanen, M., Krab, E.J., and Dorrepaal, E. (2017). Carbon dynamics at frost-patterned tundra driven by long-term vegetation change rather than by short-term non-growing season warming. Biogeochemistry *136*, 103–117.

Verhoeven, J.T.A., and Liefveld, W.M. (1997). The ecological significance of organochemical compounds in *Sphagnum*. Acta Botanica Neerlandica *46*, 117–130.

Voigt, C., Marushchak, M.E., Lamprecht, R.E., Jackowicz-Korczyński, M., Lindgren, A., Mastepanov, M., Granlund, L., Christensen, T.R., Tahvanainen, T., Martikainen, P.J., *et al.* (2017). Increased nitrous oxide emissions from Arctic peatlands after permafrost thaw. PNAS *114*, 6238–6243.

Wang, Y., Naumann, U., Wright, S.T., and Warton, D.I. (2012). mvabund– an R package for model-based analysis of multivariate abundance data. Methods in Ecology and Evolution *3*, 471–474.

Ward, S.E., Orwin, K.H., Ostle, N.J., Briones, M.J.I., Thomson, B.C., Griffiths, R.I., Oakley, S., Quirk, H., and Bardgett, R.D. (2014). Vegetation exerts a greater control on litter decomposition than climate warming in peatlands. Ecology *96*, 113–123.

Warton, D.I., Wright, S.T., and Wang, Y. (2012). Distance-based multivariate analyses confound location and dispersion effects. Methods in Ecology and Evolution *3*, 89–101.

Weiss, N., Blok, D., Elberling, B., Hugelius, G., Jørgensen, C.J., Siewert, M.B., and Kuhry, P. (2016). Thermokarst dynamics and soil organic matter characteristics controlling initial carbon release from permafrost soils in the Siberian Yedoma region. Sedimentary Geology *340*, 38–48.

Wertz, S., Degrange, V., Prosser, J.I., Poly, F., Commeaux, C., Freitag, T., Guillaumaud, N., and Roux, X.L. (2006). Maintenance of soil functioning following erosion of microbial diversity. Environmental Microbiology *8*, 2162–2169.

Wild, B., Gentsch, N., Čapek, P., Diáková, K., Alves, R.J.E., Bárta, J., Gittel, A., Hugelius, G., Knoltsch, A., Kuhry, P., *et al.* (2016). Plant-derived compounds stimulate the decomposition of organic matter in arctic permafrost soils. Scientific Reports *6*, 25607.

Wild, B., Alves, R.J.E., Bárta, J., Čapek, P., Gentsch, N., Guggenberger, G., Gustaf Hugelius, Knoltsch, A., Kuhry, P., Lashchinskiy, N., *et al.* (2018). Amino acid production exceeds plant nitrogen demand in Siberian tundra. Environ. Res. Lett. *13*, 034002.

Appendix

Correction to reference list in Chapter I

Independently of our will, errors are present in the reference list and the main text of the current online and printed versions of the article "Long-term *in situ* permafrost thaw effects on bacterial communities and potential aerobic respiration". These errors have not yet been addressed at the time of printing this thesis, and this appendix may no longer be valid at the time of publication if a publisher correction has been issued in the mean time.

More specifically:

- Reference nr. 73 is cited in the wrong place, and should instead be cited where reference nr. 96 is now placed (after "[…] priming effects observed in peatlands")
- Consequently, reference nr. 74 should be cited where reference nr. 73 is now cited, reference 75 instead of 74, and so on until the end of the article
- References nr. 96 and 97 should be cited together with reference nr. 95 (after "[…] where microbial activity is less constrained")
- There should be no reference where reference nr. 97 is now cited (after "[…] from other consequences of thawing")

Tusen tack

Like many before me and many to come, I have stood on the shoulders of giants and have to thank them for that. There's a pretty good sight from up there, and I could see a great landscape of knowledge accumulated over countless years: a small mapped area beyond which lies the immensity of our collective ignorance (*hic sunt dragones*, also known as to-do research). The best tribute I could give to scientists who preceded me is to extend our map and its uncharted area, I am reasonably confident the work presented here did so, to some extent, and will do my best to continue doing so.

All of this would not have been possible without my supervisor, Ellen Dorrepaal, and although I doubt I will be able to express my gratitude with a few words I will at least try. So, thank you Ellen, for trusting me with carrying out this project, for allowing me such freedom in finding the questions and designing the experiments presented here and the ones being written, both freedom and trust were important and stimulating. Thank you for your never-sleeping, intransigent critical view, for your patience and many meticulous revisions on texts that were not even close to being ready enough to deserve such a treat, and more generally for your flawless research standards that make you the excellent supervisor and scientific mentor you are. Thank you for making my PhD such an exciting time, with many international conferences, courses and collaborations, and even some field work in Alaska (five years ago I would not have suspected that), for tolerating my excessively shifted working hours and for helping me when I needed it. Thank you also for the opportunity to live in this wonderful place that Abisko is, for taking me ice climbing with Christian, or ski-touring when it was -30 °C (that I definitely never would have guessed).

All of this would also not have been possible without my two co-supervisors, Frida Keuper and James Weedon (now I couldn't decide which one should come first so I had to do it alphabetically, and Frida wins both first and last names, sorry James. I could also disguise it with a sexist, but consensual, 'ladies first' but I'm not sure that'd be any better). So Frida, thanks first for showing me around in Abisko, helping me and eventually agreeing to become my supervisor, and then for being extremely funny, even in the middle of a serious call or a round of commenting, it breaks the build-up of dramatic tension and that's really good for my mental health (although I doubt my sanity for wanting another piece of text to be "smooth like an otter"). Thanks also for your absolute absence of remorse in killing my darlings or suggesting big structural changes, for the opportunity to fill gaps in my French geography / list of cities with Maroilles and a cathedral, and a lot for trusting me with parts of your Mammoth. James, thank you for teaching me so much about statistics and

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Someone in Wiseman said that scientists are like ground squirrels, as they only show up in the summer. There's no ground squirrel in Abisko, and it would probably be more rude to compare people with lemmings, however there are many people visiting Abisko after the sun is back and who deserve thanking. Jonas, thanks for all the good times, and for always being up for a chat, a beer and a sauna, if possible all at once. Reiner, thanks for being my co-supervisor at first, for your passion about science and teaching, and mushrooms. Adrian, Anne, Damian, Elin, Hannah, Jan & Kristel, Joachim, Johannes, Lluis, Mathias, Mia, Moira, Scott, Sky, Stefan, Tom, Nina, Jens and Phil, thanks for the good times.

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