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MINIREVIEW

Dynamics of microbial communities and CO_2 and CH_4 fluxes in the tundra ecosystems of the changing Arctic

Min Jung Kwon[1], Ji Young Jung[1], Binu M. Tripathi[1], Mathias Göckede[2], Yoo Kyung Lee[1], and Mincheol Kim[1]*

[1]*Korea Polar Research Institute, Incheon 21990, Republic of Korea*
[2]*Max Planck Institute for Biogeochemistry, Jena 07745, Germany*

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Arctic tundra ecosystems are rapidly changing due to the amplified effects of global warming within the northern high latitudes. Warming has the potential to increase the thawing of the permafrost and to change the landscape and its geochemical characteristics, as well as terrestrial biota. It is important to investigate microbial processes and community structures, since soil microorganisms play a significant role in decomposing soil organic carbon in the Arctic tundra. In addition, the feedback from tundra ecosystems to climate change, including the emission of greenhouse gases into the atmosphere, is substantially dependent on the compositional and functional changes in the soil microbiome. This article reviews the current state of knowledge of the soil microbiome and the two most abundant greenhouse gas (CO_2 and CH_4) emissions, and summarizes permafrost thaw-induced changes in the Arctic tundra. Furthermore, we discuss future directions in microbial ecological research coupled with its link to CO_2 and CH_4 emissions.

Keywords: soil microbiome, CO_2 and CH_4 emission, permafrost thaw, climate change, Arctic tundra

Introduction

The Arctic tundra is characterized by treeless ecosystems exposed to low temperatures and short growing seasons, and the presence of permafrost. It covers nearly eight percent of the global land's surface (McGuire *et al.*, 1997), and can be categorized into four types depending on the soil moisture level: aquatic, wet, moist, and dry tundra (Walker *et al.*, 1980). Aquatic tundra is waterlogged, i.e., it has permanent water tables above the soil surface; wet tundra has water tables close to the soil surface (< 30 cm) during the growing season; moist tundra has no standing water for most of the growing season but the soil is saturated; and dry tundra has dry soil conditions throughout the growing season. Due to these different soil hydrology regimes, each type of tundra hosts distinct plant species (Walker *et al.*, 1980).

The current estimate of the soil organic carbon (SOC) stock within the circum-Arctic permafrost zone, integrated down to a depth of 3 m, is 885 to 1,185 petagrams (Pg, 1×10^{15} g; Hugelius *et al.*, 2014; Schuur *et al.*, 2015). In permafrost, i.e., the soil layer that remains frozen for more than two consecutive years, the decomposition of SOC is decelerated due to subzero temperatures and the associated low water availability. Also, within the active layer, which is the top soil layer that experiences seasonal cycles of thawing and freezing, the decomposition of SOC is hampered owing to the short growing seasons with low mean soil temperatures, often accompanied by saturated soil conditions due to the poor drainage of water which is blocked by the permafrost. Instead of having distinct and stable soil horizons that are parallel to the soil surface, pockets of organic soils with high carbon content can be found in the deeper layer due to cryoturbation in permafrost-affected soils (Ping, 2013). Since the atmospheric temperature in the Arctic is increasing faster than that in the lower latitudes (Kirtman *et al.*, 2013; Huang *et al.*, 2017), associated increases in the thaw depth during the growing season indicates that less decomposed SOC stored in the deeper layers may become more vulnerable to microbial decomposition, leading to the enhanced production of greenhouse gasses (GHGs), such as carbon dioxide (CO_2) and methane (CH_4; Schuur *et al.*, 2008; Strauss *et al.*, 2015; Ejarque and Abakumov, 2016). It is predicted that 5–15% of the currently stored permafrost carbon may be released into the atmosphere by 2100 under the current warming trajectory (Representative Concentration Pathway; RCP 8.5; Schuur *et al.*, 2015). In addition to the changes in temperature, other related warming-induced changes, such as modifications in geomorphology and soil moisture, may influence biota and the function of ecosystems, modifying the impact of the decomposition of SOC, the release of GHGs, and potentially reshaping the feedback processes within climate change (Schuur and Mack, 2018).

Diverse soil microbiomes play key roles in decomposing SOC and emitting GHGs in Arctic tundra ecosystems (Nemergut *et al.*, 2005). Since the Arctic region is rapidly warming and ecosystems are undergoing substantial changes, it is important to explore the community structure and ecological

*For correspondence. E-mail: mincheol@kopri.re.kr; Tel.: +82-32-760-5561; Fax: +82-32-760-5509

function of the soil microbiome in order to better understand its potential response to future changes in Arctic tundra ecosystems linked to climate warming. This review summarizes the key findings from recent studies on the soil microbiome and its functionality, and its influences on CO_2 and CH_4 fluxes in response to warming and the thaw-induced changes in the Arctic tundra. A particular emphasis has been placed on the current state of knowledge regarding the relationship between soil microbes and CO_2 and CH_4 emission in the Arctic tundra, and recommendations for the direction of future research in this field.

Soil microbiome in the Arctic tundra ecosystems

Microbial community composition and functions

Studying the ecology of the soil microbiome has gained enormous importance worldwide in recent years (Fierer and Jackson, 2006; Lauber *et al.*, 2009; Griffiths *et al.*, 2011). However, the Arctic region has received relatively little attention. Based on the assumptions derived from a latitudinal diversity gradient of animal and plant taxa, the microbial diversity in Arctic tundra soil was considered to be low (Heal, 1999; Hodkinson and Wookey, 1999). However, recent studies using high-throughput DNA sequencing have found contrasting results: Arctic tundra soils host a similar level of microbial diversity to that of other biomes (Chu *et al.*, 2010; Bahram *et al.*, 2018). The microbial community composition and diversity were found to vary among tundra ecosystem types, e.g., the bacterial and fungal communities were different in dry and wet tundras (Wallenstein *et al.*, 2007; Chu *et al.*, 2011; Gittel *et al.*, 2014b; Shi *et al.*, 2015; Taş *et al.*, 2018); however, some studies found no difference among tundra ecosystems (Buckeridge *et al.*, 2010b).

Since the composition of the microbial communities in the permafrost varies widely with geographical locations across the Arctic, they are difficult to generalize even at the phylum level. For example, *Chloroflexi* was found to dominate in Alaskan permafrost but was one of the minor groups in Swedish and Canadian permafrost (Jansson and Taş, 2014), whereas another study from Alaska reported the dominance of *Chloroflexi* in the active layer but not in the permafrost (Tripathi *et al.*, 2018). The factors that generate this high variability in the composition of the microbiome in the permafrost across the Arctic are still poorly understood, but might be related to the age and history of the permafrost (Mackelprang *et al.*, 2017), and a combination of dispersal limitations and thermodynamic constraints within permafrost soils (Bottos *et al.*, 2018), as well as variations in geochemistry and mineralogy.

The presence of permafrost in Arctic tundra ecosystems strongly influences the abundance, diversity, composition, and function of the soil microbiome. Several studies have reported that the abundance and diversity of bacteria, archaea, and fungi decreases with soil depth (Gittel *et al.*, 2014a, 2014b; Deng *et al.*, 2015; Kim *et al.*, 2016; Müller *et al.*, 2018; Tripathi *et al.*, 2018), with a higher abundance and diversity reported in the active layer than in the permafrost. The composition of Arctic tundra soil microbiomes also differs between the active layer and the permafrost. For example, bacterial taxa such as *Acidobacteria*, *Alphaproteobacteria*, *Betaproteobacteria*, *Verrucomicrobia*, and *Cyanobacteria* have often been reported to dominate the active layer, whereas *Firmicutes*, *Actinobacteria*, *Bacteroidetes*, and *Chloroflexi* were usually abundant in permafrost (Gittel *et al.*, 2014a, 2014b; Deng *et al.*, 2015; Kim *et al.*, 2016; Müller *et al.*, 2018; Tripathi *et al.*, 2018). Poorly characterized bacterial phyla such as *Caldiserica*, AD3, TM7, and OD1 have also been found in the permafrost layer (Jansson and Taş, 2014; Taş *et al.*, 2014; Tripathi *et al.*, 2018). Similarly, the dominating archaeal groups differed between the active layer and the permafrost. In the active layer, the archaeal community was dominated by members of the phyla *Thaumarcheota* and *Bathyarchaeota*, whereas the permaforst harbored members of methanogenic archaea from the *Euryarchaeota* phylum (Tripathi *et al.*, 2018). A taxonomically diverse group of fungal species have been found to inhabit Arctic soil ecosystems. At the phylum level, *Ascomycota* has been reported to dominate both the active layer and permafrost soil microbiomes, followed by *Basidiomycota* (Bellemain *et al.*, 2013; Timling *et al.*, 2014).

The stratified taxonomic composition of the soil microbiome across the active layer and permafrost results in differences in microbial functions at different soil depths. The surface of the active layer has been shown to favor the metabolism of both polysaccharides and oligosaccharides (Yergeau *et al.*, 2010; Gittel *et al.*, 2014b). A recent meta-omics study suggested that various acidobacterial taxa (Woodcroft *et al.*, 2018) and *Actinobacteria*, *Bacteroidetes*, and *Verrucomicrobia* (Tveit *et al.*, 2015) are key players in polysaccharide degradation in Stordalen Mire and in Svalbard, respectively. The difference in the major decomposer groups between the two locations may be ascribed to soil pH since soils of the former are acidic (pH 4.0–4.2) favoring *Acidobacteria*, whereas soils of the latter are only moderately acidic (pH 5–6). Fungi are typically primary decomposers of organic matter in acidic soils of warmer biomes. However, in cold environments, the major decomposers are bacterial taxa which have successfully adapted to the acidic conditions of the Arctic tundra (Tveit *et al.*, 2013). This is in line with generally low fungal activities found in some permafrost-affected soils (Zak and Kling, 2006).

In deeper anaerobic horizons of the active layer, acetogenesis, and fermentation pathways become more important, facilitating the degradation of monosaccharides and the production of low-molecular-weight alcohols and organic acids together with hydrogen and CO_2 (Conrad, 1999; Ye *et al.*, 2012). These deeper active layers and permafrost soils have also been reported to contain a high genetic potential for methanogenesis (Lipson *et al.*, 2013), since methanogenesis is the terminal step in the anaerobic decomposition of organic carbon. Hydrogenotrophic methanogens (e.g., *Methanobacterium* and '*Ca.* Methanoflorens') that utilize H_2/CO_2 or formate as substrates have been reported to play a major role in methanogenesis in Arctic tundra soils (Mondav *et al.*, 2014; Taş *et al.*, 2018; Woodcroft *et al.*, 2018).

Methanotrophy is another important microbial metabolism found in Arctic tundra soils, which is mostly performed by bacterial methanotrophs that dominate in the active layer, but are present at lower levels in the permafrost (Lau *et al.*, 2015). The abundance of Type I versus Type II methanotrophs in the Arctic tundra varies according to the sampling

site, plant cover, and soil depth (Gittel *et al*., 2014b; Christiansen *et al*., 2015; Singleton *et al*., 2018). Recently, representatives of upland soil cluster alpha (USCα), known as atmospheric methane oxidizers, were found in a wide range of Arctic tundra (Lau *et al*., 2015; Singleton *et al*., 2018). Methane oxidation in permafrost-affected environments is known to occur largely by aerobic methanotrophs, whereas the anaerobic oxidation of methane (AOM) plays a relatively minor role in methane oxidation (Blazewicz *et al*., 2012). However, close relatives of '*Ca.* Methanoperedens nitroreducens', known to be anaerobic methane oxidizers that use nitrate as an electron acceptor (Haroon *et al*., 2013), were recently reported in permafrost-affected soils in Siberia (Shcherbakova *et al*., 2016) and Alaska (Tripathi *et al*., 2018), suggesting the potential activity of AOM in the deeper layers of the Arctic tundra.

Abiotic factors determining microbial community structure and functions, and CO_2 and CH_4 fluxes

A vertical gradient of soil physicochemical factors and seasonal freeze-thaw cycles in the active layer make Arctic tundra ecosystems highly heterogeneous. Similar to other biomes across the globe, the community composition and diversity of the Arctic tundra soil microbiome is reported to be strongly influenced by soil pH (Chu *et al*., 2010; Deng *et al*., 2015; Tripathi *et al*., 2018). For example, the relative abundance of some dominant bacterial (e.g., *Acidobacteria*) and archaeal (e.g., *Thaumarchaeota*) taxa have been shown to strongly correlate with soil pH (Lauber *et al*., 2009; Tripathi *et al*., 2013). The total organic carbon and soil moisture contents have also been reported to influence the composition of the Arctic tundra soil microbiome (Gittel *et al*., 2014a; Shi *et al*., 2015; Kim *et al*., 2016; Taş *et al*., 2018; Tripathi *et al*., 2018) and CO_2 emissions (Billings *et al*., 1977; Shaver *et al*., 2006; Nobrega and Grogan, 2008; Biasi *et al*., 2014; Eckhardt *et al*., 2018). Soil moisture content is especially important in determining CH_4 emission rates (Kutzbach *et al*., 2004; Høj *et al*., 2005, 2006; Vaughn *et al*., 2016), as methanogenesis occurs anaerobically, whereas methanotrophy occurs both aerobically and anaerobically, and thus the balance between methanogenesis and methanotrophy determines the direction of the net flux of CH_4. When methanogenesis dominates, CH_4 is emitted from soils into the atmosphere; when methanotrophy dominates, atmospheric CH_4 is taken up by soils (Reay *et al*., 2010; Singh *et al*., 2010). Since these ecosystem characteristics are spatially heterogeneous in tundra ecosystems (Suvanto *et al*., 2014), they are likely to affect the distribution of microbial communities in the Arctic. Even though these studies highlighted certain relationships among physicochemical parameters, the soil microbiome, and CO_2 and CH_4 fluxes, it is still unclear how these factors drive variations in the composition and diversity of the soil microbiome. Furthermore, additional factors that shape the soil microbiome in other ecosystems, including temperature, soil texture, and nitrogen and phosphorus availability, might influence the composition and activities of the soil microbiome in the Arctic tundra (Segal and Sullivan, 2014; Treat *et al*., 2014; Rime *et al*., 2015; Kim *et al*., 2017; Wang *et al*., 2018), however, the magnitude of their impact on the composition of the Arctic tundra soil microbiome is still not well understood.

Thaw-induced changes in microbial communities and CO_2 and CH_4 emissions

Changes in the landscape and soil upon permafrost thaw

Increasing atmospheric temperatures may lead to soil warming and permafrost thawing in the Arctic tundra. In turn, permafrost thawing may cause substantial changes in the hydrological conditions of the soil in tundra ecosystems. A huge amount of excess ice in the permafrost can initially slow down permafrost thawing due to the high energy requirement for the ice-to-water phase change, but once ice-rich permafrost starts thawing, the preferential degradation of ice-rich layers, including ice lenses and wedges, may change the geomorphology profoundly (Rowland *et al*., 2010; Schuur and Mack, 2018). As a consequence, the ground that has subsided or collapsed becomes wetter by collecting water from the surrounding areas, but further thaw may result in the drainage of water, making the soils drier (Yoshikawa and Hinzman, 2003; Smith *et al*., 2005; Jorgenson *et al*., 2006; Abbott and Jones, 2015; Liljedahl *et al*., 2016).

These thaw-induced soil hydrological changes may also affect microbial metabolism, the decomposition rates of SOC, and CO_2 and CH_4 emission rates. For example, Lee *et al.* (2011) showed that ground subsidence following permafrost thawing led to increased snow depth and winter warming, which ultimately enhanced SOC decomposition. In addition, improved soil drainage following permafrost thawing could enhance soil aeration, which increases SOC decomposition (Walvoord and Kurylyk, 2016) and the export of dissolved organic carbon to downstream aquatic ecosystems (Wrona *et al*., 2016). Permafrost thaw and the subsequent hydrological changes have also been shown to increase the availability of dissolved organic and inorganic nitrogen (Finger *et al*., 2016; Chen *et al*., 2018), which could affect carbon dynamics by changing the metabolic efficiency of the microbiome. Moreover, the mixing of soil materials due to thaw-induced soil erosion could change the soil pH (Pizano *et al*., 2014), which could alter the microbial community compositions and their functionality. To summarize, warming generally increases both CO_2 and CH_4 emissions by enhancing microbial activities and nutrient availability, however, transitions between aerobic and anaerobic conditions are critical to the effects on CO_2 and CH_4 emissions (Schädel *et al*., 2016), thus, soil hydrologic responses following permafrost thawing need to be taken into account when investigating and predicting carbon dynamics and the associated soil microbiome functionality. Furthermore, details of the links between changes in the tundra ecosystems and the microbial community composition and activity are still largely unknown, therefore, it is critical to uncover the relationship between them to project future scenarios.

Changes in microbial community structure and functions, and CO_2 and CH_4 fluxes upon permafrost thawing

Thaw-induced changes in landscape topology, hydrology, and soil geochemistry have been demonstrated to result in shifts in the abundance and composition of vegetation and microbes, and subsequently CO_2 and CH_4 fluxes. Increased microbial activity and CO_2 and CH_4 emissions constitute one

of the major concerns about increased permafrost thawing related to global warming. For example, the functional potential of the microbiome markedly changed even after a short-term thaw event, and cellulose degradation, sugar utilization, chitin degradation, as well as CH_4 consumption were significantly changed one week after permafrost soil thawed at 5°C (Mackelprang *et al*., 2011). Under natural conditions, the metabolic functions and the relative abundance of key genes involved in polysaccharide decomposition did not significantly change along the permafrost thaw gradient (Woodcroft *et al*., 2018). However, there was a change in the major microbial decomposers, with *Acidobacteria* becoming the main decomposer of both poly- and monosaccharides at the initial thaw stage, but being replaced by various other taxa (e.g., *Bacteroidetes*, *Ignavibacteriae*, etc.) at the later thaw stage. Similar results were found following temperature increases that altered the relative abundance of taxa and genes involved in anaerobic SOC decomposition that led to enhanced CH_4 production rates (Allan *et al*., 2014; Tveit *et al*., 2015). These findings suggest that there are three key steps in anaerobic soil organic matter (SOM) decomposition processes that are particularly temperature sensitive, namely syntrophic propionate oxidation, acetoclastic methanogenesis, and methanogenesis using formate as a substrate. In addition, runnels and polygonal ponds, formed by permafrost thawing, had higher CO_2 and CH_4 emissions than not-thawed areas, with acetoclastic methanogenesis being the dominant process, although both acetoclastic and hydrogenotrophic methanogens were found (Negandhi *et al*., 2013). Permafrost thaw increased potential CH_4 production as well as CH_4 fluxes, and these changes were related to alterations in the methanogenic community composition and the abundance of methanogenic genes in the community (Liebner *et al*., 2015).

The bacterial community composition has been shown to change as the temperature rises and the permafrost thaws, and the changing patterns in abundance differ by geographical region and thawing regimes. The relative abundance of *Firmicutes* and *Bacteroidetes* decreased with increasing temperature under anaerobic conditions (Tveit *et al*., 2015), and that of *Actinobacteria* increased after one week of thawing (Mackelprang *et al*., 2011). After 10 years of permafrost thawing, the bacterial community structure resembled that of the active layer, with the dominance of *Acidobacteria* and a decrease in *Firmicutes* due to the effect of oxygenation within the recently thawed active layer (Monteux *et al*., 2018). When the community shifts were investigated along a thawing gradient in Stordalen Mire, *Bacteroidetes*, *Chloroflexi*, *Chlorobi* (class *Ignavibacteridae*), and *Deltaproteobacteria* were found to become more abundant, whereas *Acidobacteria* and *Alphaproteobacteria* became less abundant in the initial stage of thawing, and the candidate phylum WPS-2 decreased in abundance along the thaw gradient (Mondav *et al*., 2017; Woodcroft *et al*., 2018). Similarly, *Bacteroidetes*, *Chlorobi*, and *Chloroflexi* became more abundant as the permafrost in Alaska thawed, and *Firmicutes* also became more abundant, which was not observed in Stordalen Mire (Hultman *et al*., 2015). The abundance of *Euryarchaeota* also increased along the thaw gradient, suggesting overall community shifts toward anaerobic microbial consortia (Hultman *et al*., 2015). A manipulation experiment that mimicked the enhanced drainage of water following permafrost thawing in Siberia showed opposite trends in phyla abundance to the reports cited above for the thawed and inundated sites in Sweden and Alaska; *Bacteroidetes* and *Chloroflexi* abundances decreased, whereas *Acidobacteria* and *Alphaproteobacteria* became more abundant following drainage, indicating the recovery of aerobic bacterial taxa in the drained locations (reanalysis of bacterial community data from Kwon *et al*., 2017).

Permafrost thawing also has significant impacts on the methanogenic communities. With increasing temperatures, the relative abundance of *Methanosarcinaceae* and *Methanosaetaceae* increased in the peaty active layer (Høj *et al*., 2008). Another study found that *Methanosaetaceae* increased in relative abundance with increasing temperature, but two contrasting patterns were observed for *Methanosarcinaceae* (Tveit *et al*., 2015). Such different responses to temperature by *Methanosarcinaceae* are attributed to the functional replacement of acetoclastic by methylamine-dependent methanogenesis among members of the *Methanosarcinaceae*. The proportions of hydrogenotrophic and acetoclastic methanogens were also changed by permafrost thawing; hydrogenotrophic methanogenesis is reported to be more common in the Arctic than in lower latitudes (Fey and Conrad, 2000; Glissman *et al*., 2004; Tveit *et al*., 2015), and the relative abundance of the hydrogenotrophic methanogens *Methanomicrobiales* generally increased with temperature (Høj *et al*., 2008; Tveit *et al*., 2015). In another study, the proportion of acetoclastic methanogenesis was higher following permafrost thawing, which was accompanied by an increased relative abundance of methanogenic groups and CH_4 emissions (McCalley *et al*., 2014; Mondav *et al*., 2014). During the initial stages of permafrost thawing, the relative abundance of hydrogenotrophic methanogen, '*Ca.* Methanoflorens', increased (McCalley *et al*., 2014; Mondav *et al*., 2014), and a H_2/CO_2 amended experiment showed that they were only found at low temperatures, suggesting that they are likely to be well adapted to cold niches in the Arctic and may lose methanogenic activity at higher temperatures (Blake *et al*., 2015).

The methane dynamics during thawing are also largely regulated by methanotrophs, which consume 20–60% of the methane produced in permafrost-affected soils (Moosavi and Crill, 1998; Popp *et al*., 2000). The abundance of Type II methanotrophs has been shown to increase in thawed permafrost and the active layer (Mackelprang *et al*., 2011; Stackhouse *et al*., 2015). The community composition and *in situ* activity of methanotrophs significantly changed along the permafrost thaw gradient. USCα, which oxidizes atmospheric CH_4, was one of the predominant methanotrophs until the initial stage of thaw, but not in fully thawed fens where CH_4 fluxes were the highest, confirming that they consume atmospheric methane (Singleton *et al*., 2018). This study demonstrated that the highest amount of methane oxidation occurred below the oxic-anoxic layer, suggesting that methanotrophs substantially oxidize methane under microaerobic or anaerobic conditions when bogs or fens are formed due to the thawing of permafrost.

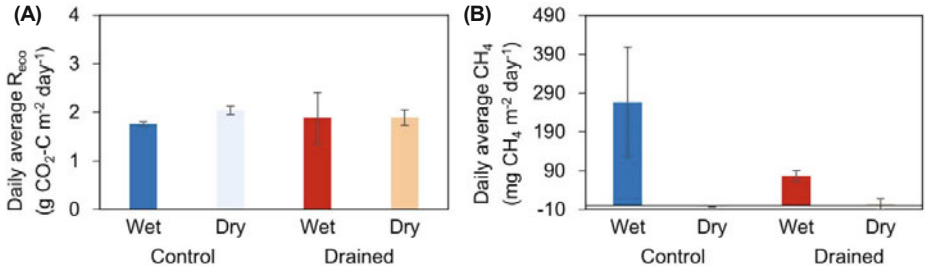

Fig. 1. A case study of (A) ecosystem respiration (R_{eco}; CO_2 emission) and (B) CH_4 fluxes in Chersky. R_{eco} and CH_4 fluxes were measured *in situ*. Flux rates (± SE) and their components are compared between naturally and artificially wet and dry locations.

Case study–Chersky, Russia

To estimate the CO_2 and CH_4 exchange rates between permafrost ecosystems and the atmosphere in Arctic wetlands, an observation site was set up in northeastern Siberia near Chersky, Russia (latitude: 68.6163, longitude: 161.3497). CO_2 and CH_4 fluxes were measured at 20 sampling locations within two different treatment areas; there were 10 sampling locations in the drained treatment area where a long-term ditch system had substantially drained the tundra since 2004, and the other 10 were in the control treatment area with undisturbed conditions. The control and drained sites were located approximately 600 m away from each other, and the sampling locations were selected at 25 m intervals along each 225 m-long transect. Since wet and dry sampling locations existing in both treatments, four hydrological regimes were monitored: control_wet (naturally wet), control_dry (naturally dry), drained_wet (partially drained since 2004), and drained_dry (substantially drained since 2004; Kwon *et al.*, 2016, 2017).

Ecosystem respiration (R_{eco}; total CO_2 respiration by heterotrophs and autotrophs under light exclusion) and CH_4 fluxes were measured using the following method; a dark chamber was placed on permanently inserted collars and the changes in CO_2 and CH_4 concentrations ([CO_2] and [CH_4]) within the chamber headspace were measured *in situ* at a frequency of approximately 1 Hz using an Ultraportable Greenhouse Gas Analyzer (Los Gatos Research). R_{eco} and CH_4 flux rates were calculated taking into account the within-chamber measurement of air temperature and air pressure, as well as the volume and area of the chamber, which were measured in parallel with [CO_2] and [CH_4] (Rochette and Hutchinson, 2005). Using the flux rates measured in 2013, half-hourly R_{eco} was calculated using an empirical Q_{10} model ($R_{eco} = \alpha \times e^{kT}$; where T is air temperature, and α and k are empirically-calculated constants). In the final step, daily averaged R_{eco} was calculated for the peak growing season of 2013 (Fig. 1), which is the same period during which the soil samples were collected to study the effect of drainage on the microbial community structure. The contribution of microbial respiration to R_{eco}, which is closely related to SOC decomposition, was estimated using the natural abundance of ^{14}C in R_{eco}, as well as that of respired CO_2 from soil and plant sources, following Hicks Pries *et al.* (2013). The daily CH_4 flux was calculated by linearly interpolating the measured flux rates. This simple interpolation was possible since no diurnal variation was observed. More detailed information on the R_{eco} measurement can be found in Kwon *et al.* (2016) and Kwon *et al.* (2017).

Soil cores were taken from the sampling locations representing the four hydrological regimes listed above, and subsequently divided into vertical sections of 7.5 cm each. The genomic DNA was extracted from these samples, and the V4 region of the 16S rRNA gene was sequenced on an Illumina MiSeq platform using the universal primer set (F515/R806) which covers a broad range of bacterial and archaeal groups (Bates *et al.*, 2011). Raw reads were processed using the program MOTHUR, which enabled the bacterial and archaeal community structures to be drawn for each sample (Fig. 2). A total of 1,903,891 high-quality sequences were obtained and 50,793 sequences (on average 2.7% of all sequences) represented lineages from archaea after SILVA-based taxonomic assignment. Further information can be found in Kwon *et al.* (2017).

Although there was no significant difference in R_{eco} between the control and the drainage treatments, R_{eco} was found to be 16% higher in the dry locations compared to the wet locations within the control treatment (Fig. 1A). Detailed analyses of the fractional contributions to R_{eco} revealed that the microbial contribution to R_{eco} was 28% and 31% higher in the dry than in the wet locations in the control and the drainage treatments, respectively (Kwon *et al.*, unpublished data), suggesting that the increase in R_{eco} at dry locations is mostly due to enhanced microbial respiration. CH_4 fluxes were substantially lower in the dry locations than the wet locations, both in the control and the drainage treatments (Fig. 1B). The dry locations in the control treatment even showed a negative net CH_4 flux, suggesting that the CH_4 oxidation exceeded the

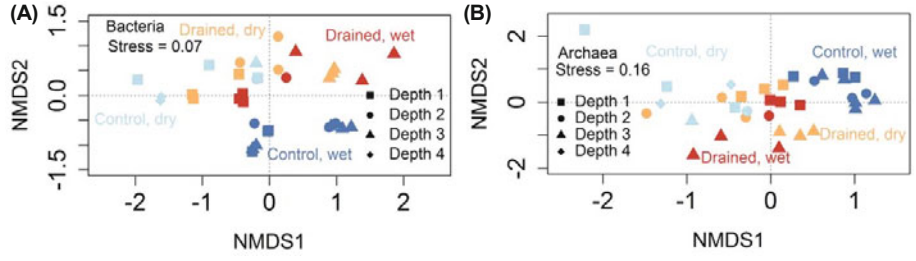

Fig. 2. A case study of (A) bacterial and (B) archaeal community structure in Chersky. The V4 variable region of the 16S rRNA gene was sequenced and non-metric multidimensional scaling analysis (NMDS) plots of Bray-Curtis dissimilarity values were drawn at the OTU level. Community composition was compared between naturally wet and dry locations as well as soil depths (depth 1 to 3, organic soil layers at 7.5 cm intervals; depth 4, mineral soil layer).

CH_4 production (Fig. 1B). These results suggest that when the naturally wet tundra is drained due to permafrost thawing, CO_2 emissions–especially from microbes–might increase, but CH_4 emissions might decrease. The archaeal and bacterial community structures at control wet locations were significantly different from the rest of the locations (ANOSIM: archaea; $R = 0.48$, $P < 0.001$, bacteria; $R = 0.34$, $P < 0.001$; Fig. 2), implying that decade-long drainage in wet tundra ecosystems holds the potential to change the bacterial and archaeal communities that influence CO_2 and CH_4 fluxes. For this disturbance experiment, the relative abundances of CH_4 producing and oxidizing microorganisms were found to be correlated with CH_4 flux rates, considering both the amount of CH_4 emission as well as the net balance between CH_4 production and oxidation (Kwon *et al.*, 2017).

Linking CO_2 and CH_4 emissions to microbial community dynamics

Methodologies in Arctic soil microbiome studies

Traditionally, Arctic microbiome studies began with cultivation-dependent approaches, as was the case for other biomes. Culture-dependent approaches have been hindered by difficulties in isolating and enriching Arctic microorganisms, many of which are slow-growing psychrotolerant or psychrophilic (Vishnivetskaya *et al.*, 2000; Kim *et al.*, 2013; Mykytczuk *et al.*, 2013). The majority of Arctic microorganisms are able to grow only in media mimicking natural environmental conditions and often require optimum redox conditions and syntrophic taxa (Zhang *et al.*, 1999; Krivushin *et al.*, 2010; Dedysh *et al.*, 2012). Thus, researchers started using culture-independent molecular techniques, such as fingerprinting methods coupled with Sanger sequencing, to investigate the composition and function of Arctic microbial communities (Neufeld and Mohn, 2005; Ganzert *et al.*, 2007; Høj *et al.*, 2008). However, the information obtained from these approaches is still insufficient and inaccurate due to the technical limitation of its low taxonomic resolution.

Recent advances in DNA sequencing technologies and mass spectrometry have enabled researchers to look into the previously unseen diversity of the soil microbiome more in detail. In recent years, various meta-omics approaches have been used to advance the study of the diversity and the metabolic potential of the Arctic tundra microbiome. Metagenomics has been used to elucidate the functional potential of the microbiome and to discover unknown lineages (Yergeau *et al.*, 2010; Mackelprang *et al.*, 2011; Lipson *et al.*, 2013; Taş *et al.*, 2014, 2018; Hultman *et al.*, 2015; Johnston *et al.*, 2016), and the combination of metagenomics, metatranscriptomics, and metaproteomics has been used to investigate *in situ* microbial activity in relation to changes in soil geochemistry and metabolite profiles. The application of these techniques yields the following novel insights: the genetic potential of organic carbon degradation and CH_4 metabolism was revealed by combining metagenomics and metatranscriptomics (Tveit *et al.*, 2013, 2015); significantly increased levels of acetogenesis and acetoclastic methanogenesis were found in freshly thawed permafrost using metatranscriptomics (Coolen and Orsi, 2015); the population genome of a novel dominant methanogen ('*Ca.* M. stordalenmirensis') in thawing permafrost was newly assembled from metagenomic data, and its *in situ* activity was further verified using metaproteomics (Mondav *et al.*, 2014); Hultman *et al.* (2015) combined three types of omics approaches–metagenomics, metatranscrptomics, and metaproteomics–to identify dominant microbial processes and the metabolic interactions among them; and Woodcroft *et al.* (2018) used the same analytical strategy and revealed that *Acidobacteria* played key roles in the breakdown of various polysaccharides in Stordalen Mire.

Metagenomic sequencing enabled the discovery of novel microbial lineages in the Arctic tundra by assembling and binning metagenomic sequences into draft genomes. An unknown draft methanogen genome belonging to *Methanomicrobia* was first assembled from Alaskan permafrost soil (Mackelprang *et al.*, 2011). In a later study, a near-complete genome belonging to the uncultured euryarchaeal lineage 'Rice Cluster II' was assembled from northern Sweden (Mondav *et al.*, 2014). The recovered genome of this novel lineage ('*Ca.* M. stordalenmirensis') showed a high level of similarity to the Alaskan methanogen genome and included genes necessary for hydrogenotrophic methanogenesis. Hultman *et al.* (2015) binned three draft methanogen genomes belonging to *Methanomicrobia* from a thermokarst bog in central Alaska and these undescribed methanogen genomes showed very low sequence similarity to those of known methanogens. Recently, Woodcroft *et al.* (2018) reported 1,529 metagenome-assembled genomes from a permafrost thaw gradient in Sordalen Mire. The recovered genomes spanned 30 bacterial phyla including *Actinobacteria*, *Acidobacteria*, *Proteobacteria*, and *Chlorolflexi,* and three archaeal phyla mostly from *Euryarchaeota*. An in-depth metabolic analysis revealed the possibility of a novel syntrophic relationship between a hydrogenotrophic methanogen '*Ca*. M. stordalenmirensis' and facultative syntrophs belonging to '*Ca*. Acidiflorens', which contain genes encoding various hydrogenases with the potential for H_2 production and consumption. Metagenome-assembled genomes were also recovered for poorly described phyla including AD3, WPS-2, and FCPU426. Among them, a novel genus ('*Ca*. Changshengia') within the candidate phylum AD3 was found to have the metabolic potential for oxidizing glycerol, which is a cryoprotectant often found in organisms that live in cold environments.

Efforts to link the soil microbiome with CO_2 and CH_4 fluxes

There have been continuous attempts to relate microbial community dynamics to CO_2 and CH_4 emissions (Table 1). Many studies measured CO_2 and CH_4 emission rates first, and then tried to compare variations in microbial biomass (Larsen *et al.*, 2007; Buckeridge *et al.*, 2010a; Čapek *et al.*, 2015; Diáková *et al.*, 2016) or the composition of the microbial communities (Biasi *et al.*, 2005; Høj *et al.*, 2005, 2006; Liebner and Wagner, 2007; Lipson *et al.*, 2013; Christiansen *et al.*, 2015) to uncover the possible linkage between them. Occasionally, information on the microbial community structure was used to estimate the potential activity of GHG emissions in laboratory incubation studies (Müller *et al.*, 2018). Despite the substantial efforts, results often led to weak correlations between microbial communities and GHG emissions, especially for CO_2 emissions. For example, the carbon mineralization activity

Table 1. List of studies examining microbial community dynamics and the related CO_2 and CH_4 fluxes in the Arctic tundra

Reference	*in situ* or incubation	Site (country)	Method	Findings
Buckeridge *et al.* (2010)	*in situ*	Daring Lake, Northwest Territories (Canada)	Fumigation	CO_2 and CH_4 fluxes varied whereas microbial biomass was stable
Čapek *et al.* (2015)	Anaerobic incubation	Taymir peninsula (Russia)	Fumigation	CO_2 emission rates were high in organic soils where microbial biomass is high
Diáková *et al.* (2016)	Anaerobic incubation	Seida (Russia)	Fumigation	CO_2 emission rates were high in organic soils where microbial biomass is high
Larsen *et al.* (2007)	*in situ*	Abisko (Sweden)	Fumigation	Microbial biomass did not correlate with CO_2 emission rates
Biasi *et al.* (2005)	Aerobic incubation	Gdansky-Peninsula (Russia)	PLFA	Higher CO_2 emission was related to a shift in microbial community structure
Wagner *et al.* (2005)	Anaerobic incubation	Lena Delta (Russia)	PLFA	CH_4 emission and microbial community structure did not show correlations
Ganzert *et al.* (2007)	Anaerobic incubation	Lena Delta (Russia)	DGGE	Methanogenic community was shifted from mesophilic to psychrotolerant with soil depth, which affected CH_4 production rates
Høj *et al.* (2005, 2006)	*in situ*	Spitsbergen, Svalbard (Norway)	DGGE	Variations in CH_4 emissions were correlated with archaeal community structure
Steven *et al.* (2008)	*in situ*	Eureka, Nunavut (Canada)	DGGE	Variations in CO_2 emission were not correlated with microbial diversity and composition
Høj *et al.* (2008)	Anaerobic incubation	Solvatnet, Svalbard (Norway)	FISH, DGGE	Methanogenic abundance, diversity, and CH_4 production increased with rising temperature
Liebner and Wagner (2007)	*in situ*	Lena Delta (Russia)	FISH	Vertical distribution of methanotrophic bacteria was correlated with CH_4 concentrations
Negandhi *et al.* (2013)	*in situ*	Bylot Island, Nunavut (Canada)	Amplicon sequencing	Abundance of methanogens and CH_4 emissions increased in thawed ponds
Allan *et al.* (2014)	Anaerobic incubation	Various locations, Nunavut (Canada)	Amplicon sequencing	Methanogen diversity increased with CH_4 production rates upon permafrost thawing
Christiansen *et al.* (2015)	*in situ*, aerobic and anaerobic incubation	Flakkerhuk (Greenland)	Amplicon sequencing	Different methanotrophic groups affect CH_4 fluxes
Liebner *et al.* (2015)	*in situ*, anaerobic incubation	Bøttemyra (Norway)	Amplicon sequencing	Methanogenic gene abundance and CH_4 production rates increased upon permafrost thawing
McCalley *et al.* (2014)	*in situ*	Stordalen mire (Sweden)	Amplicon sequencing	Acetoclastic methanogenic gene abundance and CH_4 emission rates increased upon permafrost thawing
Müller *et al.* (2018)	Anaerobic incubation	Adventdalen, Svalbard (Norway)	Amplicon sequencing, metagenome	Vertical distribution of microbial communities was correlated with CO_2 fluxes
Taş *et al.* (2018)	*in situ*	Barrow, Alaska (USA)	Amplicon sequencing, metagenome	CO_2 and CH_4 fluxes and microbial functions were affected by landscape topography in polygonal tundra
Lipson *et al.* (2013)	*in situ*	Barrow, Alaska (USA)	Metagenome	Methanogenesis genes and methanogen genomes were related to CH_4 production rates
Mackelprang *et al.* (2011)	Anaerobic incubation	Hess Creek, Alaska (USA)	Metagenome	Shifts in Microbial, phylogenetic, and functional gene abundances, as well as pathways including CH_4 oxidation rates shifted upon permafrost thawing
Singleton *et al.* (2018)	*in situ*	Stordalen mire (Sweden)	Metagenome, metatranscriptome	Most active CH_4 oxidation occurred below the oxic-anoxic interface of thawed bog
Tveit *et al.* (2015)	Anaerobic incubation	Knudsenheia, Svalbard (Norway)	Metatranscriptome, metagenome, metabolic profiling	Temperature increase modified CH_4 production rates by modulating metabolic and trophic interactions of Arctic peat microbiota

Abbreviations: PLFA, phospholipid fatty acid; DGGE, denaturing gradient gel electrophoresis; FISH, fluorescence *in situ* hybridization.

(which emits CO_2 as a result) in permafrost soils was not correlated with changes in microbial diversity and community composition (Steven *et al.*, 2008). Furthermore, there was no apparent relationship between CH_4 production and the methanogenic or whole microbial community structure (Wagner *et al.*, 2005; Ganzert *et al.*, 2007). This is largely because many previous studies relied on DNA-based approaches, which can reveal microbial metabolic potential, but cannot identify active microbes at the time of sampling. In addition, quantifying microbial parameters that affect CO_2 emissions is especially challenging since lots of microbes produce CO_2 by respiration and it is tough to define who is involved.

The application of recent multi-omics approaches enabled researchers to closely associate GHG emissions with active microorganisms, by providing process-level information about the transcripts and proteins expressed by microbes. For example, CO_2 and CH_4 dynamics were linked to transcript-level changes in the soil microbiome, and the inferred association was interpreted together with metabolic profiles (Tveit *et al.*, 2015). The *in situ* dynamics and isotopic fractionation of emitted CH_4 were related to key microbial players at the species-resolved level using a genome-centric approach (McCalley *et al.*, 2014; Woodcroft *et al.*, 2018). With the help of these recent omics approaches, we can better understand

the relationship between active microbes and CO_2 and CH_4 emissions, however, the acquired information is still incomplete since the inference was largely made by correlation-based approaches, which need further evidence to prove genuine causal relationships. Targeted approaches, such as stable isotope probing (SIP), can be a way to directly link active microbes to CO_2 and CH_4 emissions. SIP usage is quite common in microbial ecological studies, but surprisingly, only a few studies have applied it to the Arctic tundra microbiome (Pinnell *et al.*, 2014; Tuorto *et al.*, 2014; Verastegui *et al.*, 2014). The combination of DNA-SIP and gas isotope measurements can simultaneously track the dynamics of both microbial communities and gas fluxes (Martinez-Cruz *et al.*, 2017), however, there are still challenges to be able to show clear and refined relationships between the two. Although the abundance changes in the isotope assimilated microbial population can be successfully tracked, CO_2 and CH_4 emissions sometimes cannot be explained solely by their activities and the associated changes in biogeochemistry, since isotope-assimilated microbes (active microbes) are usually engaged in a complex network of soil food webs, and their functional role is eventually determined by their interactions with neighboring populations. For example, quorum sensing, which is a cell density-dependent communication mechanism between microbes, was recently reported in an aerobic methane-oxidizing bacterium (Puri *et al.*, 2017). Furthermore, an increased microbe grazing activity by soil protists was shown to be one of the important regulating processes determining methane metabolism under anaerobic conditions (Tveit *et al.*, 2015).

Conclusions and future directions

In recent decades, the Arctic has been rapidly warming at a higher rate than in the lower latitudes, which may lead to the permafrost thawing and ground ice melting. These changes, in turn, may dramatically reshape terrestrial landscapes and the distribution of surface water in the Arctic, both spatially and temporally. One of the major concerns in the warming Arctic is the increase in GHG emissions mediated by climate-driven changes, such as thaw-induced changes, in terrestrial ecosystems. This review described changes in the soil microbiome and CO_2 and CH_4 fluxes following permafrost thawing, and the subsequent modifications in soil hydrology. In wetter conditions, the abundances of *Bacteriodetes*, *Chloroflexi*, *Firmicutes*, methanogens, and methanotrophs have been found to increase, which may enhance anaerobic SOM degradation as well as CH_4 emissions. In drier conditions, however, the abundances of *Acidobacteria* and *Alphaproteobacteria* have been shown to increase, and those of methanogens and methanotrophs have been shown to decrease, which may accelerate aerobic SOM degradation and CO_2 emission, but reduce CH_4 emission, usually resulting in negative CH_4 fluxes, i.e., atmospheric CH_4 being taken up by soils (Fig. 3).

With the recent application of meta-omics technologies, previously unknown diversity and *in situ* activities of microbial communities in the Arctic tundra have begun to be uncovered. In addition, the key microbial players and metabolic processes in the active layer and thawing permafrost have been further elucidated using the combined measurements of geochemistry, metabolites, and CO_2 and CH_4 emissions. Even though some general patterns in the soil microbiome and CO_2 and CH_4 fluxes have been observed in response to permafrost thawing and the subsequent hydrological changes, the diverse and sometimes opposing patterns, depending on the tundra types and environmental variations, suggest a complexity that may further increase with a range of thaw-induced scenarios. Furthermore, insufficient genomic and proteomic information on the Arctic microbiome hinders the in-depth analyses of meta-omics data. Thus, a detailed understanding of microbial metabolic interactions calls for more laboratory-based physiological studies coupled with high-resolution metabolic profiling. Consideration of microbial interactions with other taxa, for example biotic interactions with other soil taxa such as soil protists, is also essential to understand and predict ecosystems' responses, such as GHG emissions, to changes in the climate. Moreover, it would be beneficial to obtain comprehensive information from various locations that represent diverse Arctic ecotypes, as well as on multiple scales from a fine scale, e.g., microbial community dynamics in soil aggregates or microhabitats, to an ecosystem scale. Considering that CO_2 and CH_4 fluxes are regulated to a large extent by microbial community dynamics together with other environment variables, future research should be carried out incorporating *in vitro* and *in situ* studies to gain a mechanistic understanding of microbial processes and the associated community changes, which will enable us to better understand GHG dynamics.

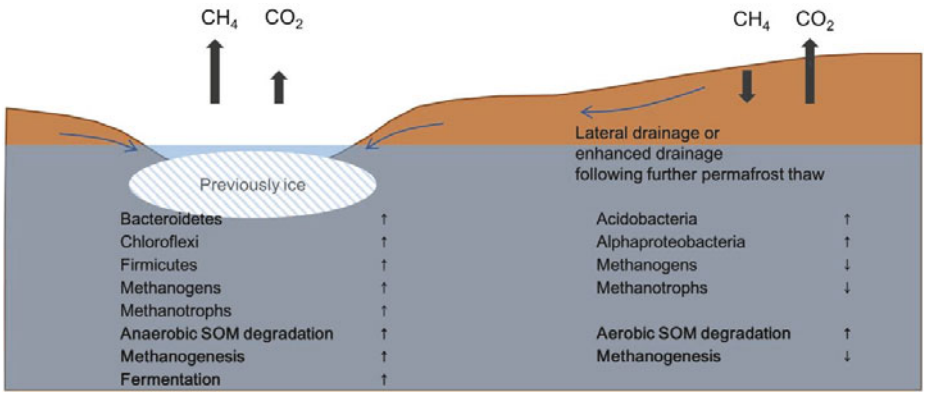

Fig. 3. A schematic showing changes in the soil microbiome and GHG fluxes in wetter versus drier conditions following a permafrost thaw.

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References

Abbott, B.W. and Jones, J.B. 2015. Permafrost collapse alters soil carbon stocks, respiration, CH_4, and N_2O in upland tundra. *Glob. Chang. Biol.* **21**, 4570–4587.

Allan, J., Ronholm, J., Mykytczuk, N.C.S., Greer, C.W., Onstott, T.C., and Whyte, L.G. 2014. Methanogen community composition and rates of methane consumption in Canadian High Arctic permafrost soils. *Environ. Microbiol. Rep.* **6**, 136–144.

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.

Bates, S.T., Berg-Lyons, D., Capraso, J.G., Walters, W.A., Knight, R., and Fierer, N. 2011. Examining the global distribution of dominant archaeal populations in soil. *ISME J.* **5**, 908–917.

Bellemain, E., Davey, M.L., Kauserud, H., Epp, L.S., Boessenkool, S., Coissac, E., Geml, J., Edwards, M., Willerslev, E., Gussarova, G., *et al.* 2013. Fungal palaeodiversity revealed using high-throughput metabarcoding of ancient DNA from arctic permafrost. *Environ. Microbiol.* **15**, 1176–1189.

Biasi, C., Jokinen, S., Marushchak, M.E., Hämäläinen, K., Trubnikova, T., Oinonen, M., and Martikainen, P.J. 2014. Microbial respiration in Arctic upland and peat soils as a source of atmospheric carbon dioxide. *Ecosystems* **17**, 112–126.

Biasi, C., Rusalimova, O., Meyer, H., Kaiser, C., Wanek, W., Barsukov, P., Junger, H., and Richter, A. 2005. Temperature-dependent shift from labile to recalcitrant carbon sources of Arctic heterotrophs. *Rapid Commun. Mass Spectrom.* **19**, 1401–1408.

Billings, W.D., Peterson, K.M., Shaver, G.R., and Trent, A.W. 1977. Root growth, respiration, and carbon dioxide evolution in an Arctic tundra soil. *Arct. Alp. Res.* **9**, 129–137.

Blake, L.I., Tveit, A., Øvreås, L., Head, I.M., and Gray, N.D. 2015. Response of methanogens in Arctic sediments to temperature and methanogenic substrate availability. *PLoS One* **10**, e0129733.

Blazewicz, S.J., Petersen, D.G., Waldrop, M.P., and Firestone, M.K. 2012. Anaerobic oxidation of methane in tropical and boreal soils: ecological significance in terrestrial methane cycling. *J. Geophys. Res. Biogeosci.* **117**, G02033.

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**, fiy110.

Buckeridge, K.M., Cen, Y.P., Layzell, D.B., and Grogan, P. 2010a. Soil biogeochemistry during the early spring in low arctic mesic tundra and the impacts of deepened snow and enhanced nitrogen availability. *Biogeochemistry* **99**, 127–141.

Buckeridge, K.M., Zufelt, E., Chu, H., and Grogan, P. 2010b. Soil nitrogen cycling rates in low arctic shrub tundra are enhanced by litter feedbacks. *Plant Soil* **330**, 407–421.

Čapek, P., Diáková, K., Dickopp, J.E., Bárta, J., Wild, B., Schnecker, J., Alves, R.J.E., Aiglsdorfer, S., Guggenberger, G., Gentsch, N., *et al.* 2015. The effect of warming on the vulnerability of subducted organic carbon in arctic soils. *Soil Biol. Biochem.* **90**, 19–29.

Chen, L., Liu, L., Mao, C., Qin, S., Wang, J., Liu, F., Blagodatsky, S., Yang, G., Zhang, Q., Zhang, D., *et al.* 2018. Nitrogen availability regulates topsoil carbon dynamics after permafrost thaw by altering microbial metabolic efficiency. *Nat. Commun.* **9**, 3951.

Christiansen, J.R., Romero, A.J.B., Jørgensen, N.O.G., Glaring, M.A., Jørgensen, C.J., Berg, L.K., and Elberling, B. 2015. Methane fluxes and the functional groups of methanotrophs and methanogens in a young Arctic landscape on Disko Island, West Greenland. *Biogeochemistry* **122**, 15–33.

Chu, H., Fierer, N., Lauber, C.L., Caporaso, J., Knight, R., and Grogan, P. 2010. Soil bacterial diversity in the arctic is not fundamentally different from that found in other biomes. *Environ. Microbiol.* **12**, 2998–3006.

Chu, H., Neufeld, J.D., Walker, V.K., and Grogan, P. 2011. The influence of vegetation type on the dominant soil bacteria, archaea, and fungi in a low arctic tundra landscape. *Soil Sci. Soc. Am. J.* **75**, 1756–1765.

Conrad, R. 1999. Contribution of hydrogen to methane production and control of hydrogen concentrations in methanogenic soils and sediments. *FEMS Microbiol. Ecol.* **28**, 193–202.

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

Dedysh, S.N., Kulichevskaya, I.S., Serkebaeva, Y.M., Mityaeva, M.A., Sorokin, V.V., Suzina, N.E., Rijpstra, W.I.C., and Damsté, J.S.S. 2012. *Bryocella elongata* gen. nov., sp. nov., a member of subdivision 1 of the *Acidobacteria* isolated from a methanotrophic enrichment culture, and emended description of *Edaphobacter aggregans* Koch *et al.* 2008. *Int. J. Syst. Evol. Microbiol.* **62**, 654–664.

Deng, J., Gu, Y., Zhang, J., Xue, K., Qin, Y., Yuan, M., Yin, H., He, Z., Wu, L., and Schuur, E.A.G. 2015. Shifts of tundra bacterial and archaeal communities along a permafrost thaw gradient in Alaska. *Mol. Ecol.* **24**, 222–234.

Diáková, K., Čapek, P., Kohoutová, I., Mpamah, P.A., Bárta, J., Biasi, C., Martikainen, P.J., and Šantrůčková, H. 2016. Heterogeneity of carbon loss and its temperature sensitivity in East-European subarctic tundra soils. *FEMS Microbiol. Ecol.* **92**, fiw140.

Eckhardt, T., Knoblauch, C., Kutzbach, L., Simpson, G., Abakumov, E., and Pfeiffer, E.M. 2018. Partitioning CO_2 net ecosystem exchange fluxes on the microsite scale in the Lena River Delta, Siberia. *Biogeosci. Discuss.* DOI: https://doi.org/10.5194/bg-2018-311.

Ejarque, E. and Abakumov, E. 2016. Stability and biodegradability of organic matter from Arctic soils of Western Siberia: Insights from ^{13}C-NMR spectroscopy and elemental analysis. *Solid Earth* **7**, 153–165.

Fey, A. and Conrad, R. 2000. Effect of temperature on carbon and electron flow and on the archaeal community in methanogenic rice field soil. *Appl. Environ. Microbiol.* **66**, 4790–4797.

Fierer, N. and Jackson, R.B. 2006. The diversity and biogeography of soil bacterial communities. *Proc. Natl. Acad. Sci. USA* **103**, 626–631.

Finger, R.A., Turetsky, M.R., Kielland, K., Ruess, R.W., Mack, M.C., and Euskirchen, E.S. 2016. Effects of permafrost thaw on nitrogen availability and plant-soil interactions in a boreal Alaskan lowland. *J. Ecol.* **104**, 1542–1554.

Ganzert, L., Jurgens, G., Münster, U., and Wagner, D. 2007. Methanogenic communities in permafrost-affected soils of the Laptev Sea coast, Siberian Arctic, characterized by 16S rRNA gene fingerprints. *FEMS Microbiol. Ecol.* **59**, 476–488.

Gittel, A., Bárta, J., Kohoutová, I., Mikutta, R., Owens, S., Gilbert, J., Schnecker, J., Wild, B., Hannisdal, B., Maerz, J., *et al.* 2014a. Distinct microbial communities associated with buried soils in the Siberian tundra. *ISME J.* **8**, 841–853.

Gittel, A., Bárta, J., Kohoutova, I., Schnecker, J., Wild, B., Čapek, P., Kaiser, C., Torsvik, V.L., Richter, A., and Schleper, C. 2014b. Site- and horizon-specific patterns of microbial community structure and enzyme activities in permafrost-affected soils of Greenland. *Front. Microbiol.* **5**, 541.

Glissman, K., Chin, K.J., Casper, P., and Conrad, R. 2004. Methanogenic pathway and archaeal community structure in the sediment of eutrophic Lake Dagow: effect of temperature. *Microb. Ecol.* **48**, 389–399.

Griffiths, R.I., Thomson, B.C., James, P., Bell, T., Bailey, M., and Whiteley, A.S. 2011. The bacterial biogeography of British soils. *Environ. Microbiol.* **13**, 1642–1654.

Haroon, M.F., Hu, S., Shi, Y., Imelfort, M., Keller, J., Hugenholtz, P., Yuan, Z., and Tyson, G.W. 2013. Anaerobic oxidation of methane coupled to nitrate reduction in a novel archaeal lineage. *Nature* **500**, 567–570.

Heal, O.W. 1999. Looking north: Current issues in Arctic soil ecology. *Appl. Soil Ecol.* **11**, 107–109.

Hicks Pries, C.E., Schuur, E.A.G., and Crummer, K.G. 2013. Thawing permafrost increases old soil and autotrophic respiration in tundra: Partitioning ecosystem respiration using $\delta^{13}C$ and $\Delta^{14}C$. *Glob. Chang. Biol.* **19**, 649–661.

Hodkinson, I.D. and Wookey, P. 1999. Functional ecology of soil organisms in tundra ecosystems: Towards the future. *Appl. Soil Ecol.* **11**, 111–126.

Høj, L., Olsen, R.A., and Torsvik, V.L. 2005. Archaeal communities in High Arctic wetlands at Spitsbergen, Norway (78°N) as characterized by 16S rRNA gene fingerprinting. *FEMS Microbiol. Ecol.* **53**, 89–101.

Høj, L., Olsen, R.A., and Torsvik, V.L. 2008. Effects of temperature on the diversity and community structure of known methanogenic groups and other archaea in high Arctic peat. *ISME J.* **2**, 37.

Høj, L., Rusten, M., Haugen, L.E., Olsen, R.A., and Torsvik, V.L. 2006. Effects of water regime on archaeal community composition in Arctic soils. *Environ. Microbiol.* **8**, 984–996.

Huang, J., Zhang, X., Zhang, Q., Lin, Y., Hao, M., Luo, Y., Zhao, Z., Yao, Y., Chen, X., Wang, L., *et al.* 2017. Recently amplified arctic warming has contributed to a continual global warming trend. *Nat. Clim. Chang.* **7**, 875–879.

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. *Biogeosci.* **11**, 6573–6593.

Hultman, J., Waldrop, M.P., Mackelprang, R., David, M.M., McFarland, J., Blazewicz, S.J., Harden, J., Turetsky, M.R., McGuire, A.D., Shah, M.B., *et al.* 2015. Multi-omics of permafrost, active layer and thermokarst bog soil microbiomes. *Nature* **521**, 208–212.

Jansson, J.K. and Taş, N. 2014. The microbial ecology of permafrost. *Nat. Rev. Microbiol.* **12**, 414–425.

Johnston, E.R., Rodriguez, R.L.M., Luo, C., Yuan, M.M., Wu, L., He, Z., Schuur, E.A.G., Luo, Y., Tiedje, J.M., Zhou, J., *et al.* 2016. Metagenomics reveals pervasive bacterial populations and reduced community diversity across the Alaska tundra ecosystem. *Front. Microbiol.* **7**, 579.

Jorgenson, M.T., Shur, Y.L., and Pullman, E.R. 2006. Abrupt increase in permafrost degradation in Arctic Alaska. *Geophys. Res. Lett.* **33**, L02503.

Kim, H.M., Chae, N., Jung, J.Y., and Lee, Y.K. 2013. Isolation of facultatively anaerobic soil bacteria from Ny-Ålesund, Svalbard. *Polar Biol.* **36**, 787–796.

Kim, M., Jung, J.Y., Laffly, D., Kwon, H.Y., and Lee, Y.K. 2017. Shifts in bacterial community structure during succession in a glacier foreland of the High Arctic. *FEMS Microbiol. Ecol.* **93**, fiw213.

Kim, H.M., Lee, M.J., Jung, J.Y., Hwang, C.Y., Kim, M., Ro, H.M., Chun, J., and Lee, Y.K. 2016. Vertical distribution of bacterial community is associated with the degree of soil organic matter decomposition in the active layer of moist acidic tundra. *J. Microbiol.* **54**, 713–723.

Kirtman, B., Power, S.B., Adedoyin, J.A., Boer, G.J., Bojariu, R., Camilloni, F.J., Doblas-Reyes, A.M., Kimoto, M., Meehl, G.A., Prather, M., *et al.* 2013. Near-term climate change: Projections and predictability, pp. 953–1028. *In* Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., and Midgley, P.M. (eds.), Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge and New York, USA.

Krivushin, K.V., Shcherbakova, V.A., Petrovskaya, L.E., and Rivkina, E.M. 2010. *Methanobacterium veterum* sp. nov., from ancient Siberian permafrost. *Int. J. Syst. Evol. Microbiol.* **60**, 455–459.

Kutzbach, L., Wagner, D., and Pfeiffer, E.M. 2004. Effect of microrilief and vegetation on methane emission from wet polygonal tundra, Lena Delta, Northern Siberia. *Biogeochemistry* **69**, 341–362.

Kwon, M.J., Beulig, F., Ilie, I., Wildner, M., Küsel, K., Merbold, L., Mahecha, M.D., Zimov, N., Zimov, S.A., Heimann, M., *et al.* 2017. Plants, microorganisms and soil temperatures contribute to a decrease in methane fluxes on a drained Arctic floodplain. *Glob. Chang. Biol.* **23**, 2396–2412.

Kwon, M.J., Heimann, M., Kolle, O., Luus, K.A., Schuur, E.A.G., Zimov, N., Zimov, S.A., and Goeckede, M. 2016. Long-term drainage reduces CO_2 uptake and increases CO_2 emission on a Siberian floodplain due to shifts in vegetation community and soil thermal characteristics. *Biogeosci.* **13**, 4219–4235.

Larsen, K.S., Grogan, P., Jonasson, S., and Michelsen, A. 2007. Respiration and microbial dynamics in two subarctic ecosystems during winter and spring thaw: effects of increased snow depth. *Arct. Antarct. Alp. Res.* **39**, 268–276.

Lau, M.C., Stackhouse, B., Layton, A.C., Chauhan, A., Vishnivetskaya, T., Chourey, K., Ronholm, J., Mykytczuk, N., Bennett, P., and Lamarche-Gagnon, G. 2015. An active atmospheric methane sink in high Arctic mineral cryosols. *ISME J.* **9**, 1880–1891.

Lauber, C.L., Hamady, M., Knight, R., and Fierer, N. 2009. Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. *Appl. Environ. Microbiol.* **75**, 5111–5120.

Lee, H., Schuur, E.G., Vogel, J.G., Lavoie, M., Bhadra, D., and Staudhammer, C.L. 2011. A spatially explicit analysis to extrapolate carbon fluxes in upland tundra where permafrost is thawing. *Glob. Chang. Biol.* **17**, 1379–1393.

Liebner, S., Ganzert, L., Kiss, A., Yang, S., Wagner, D., and Svenning, M.M. 2015. Shifts in methanogenic community composition and methane fluxes along the degradation of discontinuous permafrost. *Front. Microbiol.* **6**, 356.

Liebner, S. and Wagner, D. 2007. Abundance, distribution and potential activity of methane oxidizing bacteria in permafrost soils from the Lena Delta, Siberia. *Environ. Microbiol.* **9**, 107–117.

Liljedahl, A.K., Boike, J., Daanen, R.P., Fedorov, A.N., Frost, G.V., Grosse, G., Hinzman, L.D., Iijma, Y., Jorgenson, J.C., Matveyeva, N., *et al.* 2016. Pan-Arctic ice-wedge degradation in warming permafrost and its influence on tundra hydrology. *Nat. Geosci.* **9**, 312–318.

Lipson, D.A., Haggerty, J.M., Srinivas, A., Raab, T.K., Sathe, S., and Dinsdale, E.A. 2013. Metagenomic insights into anaerobic metabolism along an Arctic peat soil profile. *PLoS One* **8**, e64659.

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.* **11**, 2305–2318.

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.

Martinez-Cruz, K., Leewis, M.C., Herriott, I.C., Sepulveda-Jauregui, A., Anthony, K.W., Thalasso, F., and Leigh, M.B. 2017. Anaerobic oxidation of methane by aerobic methanotrophs in sub-Arctic lake sediments. *Sci. Total Environ.* **607**, 23–31.

McCalley, C.K., Woodcroft, B.J., Hodgkins, S.B., Wehr, R.A., Kim, E.H., Mondav, R., Crill, P.M., Chanton, J.P., Rich, V.I., Tyson, G.W., *et al.* 2014. Methane dynamics regulated by microbial community response to permafrost thaw. *Nature* **514**, 478–481.

McGuire, A.D., Melillo, J.M., Kicklighter, D.W., Pan, Y., Xiao, X., Helfrich, J., Moore, B., Vorosmarty, C.J., and Schloss, A.L. 1997. Equilibrium responses of global net primary production and carbon storage to doubled atmospheric carbon dioxide: Sensitivity to changes in vegetation nitrogen concentration. *Global Biogeochem. Cycles* **11**, 173–189.

Mondav, R., McCalley, C.K., Hodgkins, S.B., Frolking, S., Saleska, S.R., Rich, V.I., Chanton, J.P., and Crill, P.M. 2017. Microbial network, phylogenetic diversity and community membership in the active layer across a permafrost thaw gradient. *Environ. Microbiol.* **19**, 3201–3218.

Mondav, R., Woodcroft, B.J., Kim, E.H., McCalley, C.K., Hodgkins, S.B., Crill, P.M., Chanton, J., Hurst, G.B., VerBerkmoes, N.C., and Saleska, S.R. 2014. Discovery of a novel methanogen prevalent in thawing permafrost. *Nat. Commun.* **5**, 3212.

Monteux, S., Weedon, J.T., Blume-Werry, G., Gavazov, K., Jassey, V.E.J., Johansson, M., Keuper, F., Olid, C., and Dorrepaal, E. 2018. Long-term *in situ* permafrost thaw effects on bacterial communities and potential aerobic respiration. *ISME J.* **12**, 2129–2141.

Moosavi, S.C. and Crill, P.M. 1998. CH_4 oxidation by tundra wetlands as measured by a selective inhibitor technique. *J. Geophys. Res. Atmos.* **103**, 29093–29106.

Müller, O., Bang-Andreasen, T., White, R.A. 3rd, Elberling, B., Taş, N., Kneafsey, T., Jansson, J.K., and Øvreås, L. 2018. Disentangling the complexity of permafrost soil by using high resolution profiling of microbial community composition, key functions and respiration rates. *Environ. Microbiol.* **20**, 4328–4342.

Mykytczuk, N.C.S., Foote, S.J., Omelon, C.R., Southam, G., Greer, C.W., and Whyte, L.G. 2013. Bacterial growth at -15°C; molecular insights from the permafrost bacterium *Planococcus halocryophilus* Or1. *ISME J.* **7**, 1211–1226.

Negandhi, K., Laurion, I., Whiticar, M.J., Galand, P.E., Xu, X., and Lovejoy, C. 2013. Small thaw ponds: an unaccounted source of methane in the Canadian High Arctic. *PLoS One* **8**, e78204.

Nemergut, D.R., Costello, E.K., Meyer, A.F., Pescador, M.Y., Weintraub, M.N., and Schmidt, S.K. 2005. Structure and function of alpine and Arctic soil microbial communities. *Res. Microbiol.* **156**, 775–784.

Neufeld, J.D. and Mohn, W.W. 2005. Unexpectedly high bacterial diversity in Arctic tundra relative to boreal forest soils, revealed by serial analysis of ribosomal sequence tags. *Appl. Environ. Microbiol.* **71**, 5710–5718.

Nobrega, S. and Grogan, P. 2008. Landscape and ecosystem-level controls on net carbon dioxide exchange along a natural moisture gradient in Canadian low Arctic tundra. *Ecosystems* **11**, 377–396.

Ping, C.L. 2013. Gelisols: Part I. Cryogenesis and state factors of formation. *Soil Horiz.* **54**, 1–5.

Pinnell, L.J., Dunford, E., Ronan, P., Hausner, M., and Neufeld, J.D. 2014. Recovering glycoside hydrolase genes from active tundra cellulolytic bacteria. *Can. J. Microbiol.* **60**, 469–476.

Pizano, C., Baron, A.F., Schuur, E.A.G., Crummer, K.G., and Mack, M.C. 2014. Effects of thermo-erosional disturbance on surface soil carbon and nitrogen dynamics in upland arctic tundra. *Environ. Res. Lett.* **9**, 075006.

Popp, T.J., Chanton, J.P., Whiting, G.J., and Grant, N. 2000. Evaluation of methane oxidation in therhizosphere of a *Carex* dominated fen in northcentral Alberta, Canada. *Biogeochemistry* **51**, 259–281.

Puri, A.W., Schaefer, A.L., Fu, Y., Beck, D.A., Greenberg, E.P., and Lidstrom, M.E. 2017. Quorum sensing in a methane-oxidizing bacterium. *J. Bacteriol.* **199**, e00773-16.

Reay, D., Smith, P., and Van Amstel, A. 2010., Methane sources and the global methane budget, pp. 1–13. *In* Methane and climate change. Earthscan.

Rime, T., Hartmann, M., Brunner, I., Widmer, F., Zeyer, J., and Frey, B. 2015. Vertical distribution of the soil microbiota along a successional gradient in a glacier forefield. *Mol. Ecol.* **24**, 1091–1108.

Rochette, P. and Hutchinson, G.L. 2005. Measurement of soil respiration *in situ*: chamber techniques, pp. 247–286. *In* Micrometeorology in agricultural systems. American Society of Agronomy, Madison, USA.

Rowland, J.C., Jones, C.E., Altmann, G., Bryan, R., Crosby, B.T., Hinzman, L.D., Kane, D.L., Lawrence, D.M., Mancino, A., Marsh, P., *et al.* 2010. Arctic landscapes in transition: Responses to thawing permafrost. *EOS* **91**, 229–230.

Schädel, C., Bader, M.K.F., Schuur, E.A.G., Biasi, C., Bracho, R., Čapek, P., De Baets, S., Diáková, K., Ernakovich, J., Estop-Aragones, C., *et al.* 2016. Potential carbon emissions dominated by carbon dioxide from thawed permafrost soils. *Nat. Clim. Chang.* **6**, 950–953.

Schuur, E.A.G., Bockheim, J., Canadell, J.G., Euskirchen, E., Field, C.B., Goryachkin, S.V., Hagemann, S., Kuhry, P., Lafleur, P.M., Lee, H., *et al.* 2008. Vulnerability of permafrost carbon to climate change: Implications for the global carbon cycle. *Bioscience* **58**, 701–714.

Schuur, E.A.G. and Mack, M.C. 2018. Ecological response to permafrost thaw and consequences for local and global ecosystem services. *Annu. Rev. Ecol. Evol. Syst.* **49**, 279–301.

Schuur, E.A., McGuire, A.D., Schadel, 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, A.D. and Sullivan, P.F. 2014. Identifying the sources and uncertainties of ecosystem respiration in Arctic tussock tundra. *Biogeochemistry* **121**, 489–503.

Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J., Thieler, K.K., Downs, M.R., Laundre, J.A., and Rastetter, E.B. 2006. Carbon turnover in Alaskan tundra soils: effects of organic matter quality, temperature, moisture and fertilizer. *J. Ecol.* **94**, 740–753.

Shcherbakova, V., Yoshimura, Y., Ryzhmanova, Y., Taguchi, Y., Segawa, T., Oshurkova, V., and Rivkina, E. 2016. Archaeal communities of Arctic methane-containing permafrost. *FEMS Microbiol. Ecol.* **92**, fiw135.

Shi, Y., Xiang, X., Shen, C., Chu, H., Neufeld, J.D., Walker, V.K., and Grogan, P. 2015. Vegetation-associated impacts on arctic tundra bacterial and microeukaryotic communities. *Appl. Environ. Microbiol.* **81**, 492–501.

Singh, B.K., Bardgett, R.D., Smith, P., and Reay, D.S. 2010. Microorganisms and climate change: Terrestrial feedbacks and mitigation options. *Nat. Rev. Microbiol.* **8**, 779.

Singleton, C.M., McCalley, C.K., Woodcroft, B.J., Boyd, J.A., Evans, P.N., Hodgkins, S.B., Chanton, J.P., Frolking, S., Crill, P.M., Saleska, S.R., *et al.* 2018. Methanotrophy across a natural permafrost thaw environment. *ISME J.* **12**, 2544–2558.

Smith, L.C., Sheng, Y., MacDonald, G.M., and Hinzman, L.D. 2005. Disappearing Arctic lakes. *Science* **308**, 1429.

Stackhouse, B.T., Vishnivetskaya, T.A., Layton, A., Chauhan, A., Pfiffner, S., Mykytczuk, N.C., Sanders, R., Whyte, L.G., Hedin, L., Saad, N., *et al.* 2015. Effects of simulated spring thaw of per-

mafrost from mineral cryosol on CO_2 emissions and atmospheric CH_4 uptake. *J. Geophys. Res. Biogeosci.* **120**, 1764–1784.

Steven, B., Pollard, W.H., Greer, C.W., and Whyte, L.G. 2008. Microbial diversity and activity through a permafrost/ground ice core profile from the Canadian high Arctic. *Environ. Microbiol.* **10**, 3388–3403.

Strauss, J., Schirrmeister, L., Mangelsdorf, K., Eichhorn, L., Wetterich, S., and Herzschuh, U. 2015. Organic-matter quality of deep permafrost carbon - a study from Arctic Siberia. *Biogeosciences* **12**, 2227–2245.

Suvanto, S., Le Roux, P.C., and Luoto, M. 2014. Arctic-alpine vegetation biomass is driven by fine-scale abiotic heterogeneity. *Geogr. Ann. Ser. A Phys. Geogr.* **96**, 549–560.

Taş, N., Prestat, E., McFarland, J.W., Wickland, K.P., Knight, R., Berhe, A.A., Jorgenson, T., Waldrop, M.P., and Jansson, J.K. 2014. Impact of fire on active layer and permafrost microbial communities and metagenomes in an upland Alaskan boreal forest. *ISME J.* **8**, 1904–1919.

Taş, N., Prestat, E., Wang, S., Wu, Y., Ulrich, C., Kneafsey, T., Tringe, S.G., Torn, M.S., Hubbard, S.S., and Jansson, J.K. 2018. Landscape topography structures the soil microbiome in arctic polygonal tundra. *Nat. Commun.* **9**, 777.

Timling, I., Walker, D.A., Nusbaum, C., Lennon, N.J., and Taylor, D.L. 2014. Rich and cold: diversity, distribution and drivers of fungal communities in patterned-ground ecosystems of the North American Arctic. *Mol. Ecol.* **23**, 3258–3272.

Treat, C.C., Wollheim, W.M., Varner, R.K., Grandy, A.S., Talbot, J., and Frolking, S. 2014. Temperature and peat type control CO_2 and CH_4 production in Alaskan permafrost peats. *Glob. Chang. Biol.* **20**, 2674–2686.

Tripathi, B.M., Kim, M., Kim, Y., Byun, E., Yang, J.W., Ahn, J., and Lee, Y.K. 2018. Variations in bacterial and archaeal communities along depth profiles of Alaskan soil cores. *Sci. Rep.* **8**, 504.

Tripathi, B.M., Kim, M., Lai-Hoe, A., Shukor, N.A.A., Rahim, R.A., Go, R., and Adams, J.M. 2013. pH dominates variation in tropical soil archaeal diversity and community structure. *FEMS Microbiol. Ecol.* **86**, 303–311.

Tuorto, S.J., Darias, P., McGuinness, L.R., Panikov, N., Zhang, T., Häggblom, M.M., and Kerkhof, L.J. 2014. Bacterial genome replication at subzero temperatures in permafrost. *ISME J.* **8**, 139.

Tveit, A., Schwacke, R., Svenning, M.M., and Urich, T. 2013. Organic carbon transformations in high-Arctic peat soils: key functions and microorganisms. *ISME J.* **7**, 299–311.

Tveit, A.T., Urich, T., Frenzel, P., and Svenning, M.M. 2015. Metabolic and trophic interactions modulate methane production by Arctic peat microbiota in response to warming. *Proc. Nat. Acad. Sci. USA* **112**, E2507–E2516.

Vaughn, L.J.S., Conrad, M.E., Bill, M., and Torn, M.S. 2016. Isotopic insights into methane production, oxidation, and emissions in Arctic polygon tundra. *Glob. Chang. Biol.* **22**, 3487–3502.

Verastegui, Y., Cheng, J., Engel, K., Kolczynski, D., Mortimer, S., Lavigne, J., Montalibet, J., Romantsov, T., Hall, M., McConkey, B.J., *et al.* 2014. Multisubstrate isotope labeling and metagenomic analysis of active soil bacterial communities. *MBio* **5**, e01157-14.

Vishnivetskaya, T., Kathariou, S., McGrath, J., Gilichinsky, D., and Tiedje, J.M. 2000. Low-temperature recovery strategies for the isolation of bacteria from ancient permafrost sediments. *Extremophiles* **4**, 165–173.

Wagner, D., Lipski, A., Embacher, A., and Gattinger, A. 2005. Methane fluxes in permafrost habitats of the Lena Delta: effects of microbila community structure and organci matter quality. *Environ. Microbiol.* **7**, 1582–1592.

Walker, D.A., Everett, K.R., Webber, P.J., and Brown, J. 1980. Geobotanical atlas of the prudhoe bay region, Alaska. US Army Corps of Engineers.

Wallenstein, M.D., McMahon, S., and Schimel, J. 2007. Bacterial and fungal community structure in Arctic tundra tussock and shrub soils. *FEMS Microbiol. Ecol.* **59**, 428–435.

Walvoord, M.A. and Kurylyk, B.L. 2016. Hydrologic impacts of thawing permafrost–A review. *Vadose Zone J.* **15**, vzj2016.01.0010.

Wang, H., Shirong, L., Xiao, Z., Qinggong, M., Xiangzhen, L., Yeming, Y., Jingxin, W., Mianhai, Z., Wei, Z., Xiankai, L., *et al.* 2018. Nitrogen addition reduces soil bacterial richness, while phosphorus addition alters community composition in an old-growth N-rich tropical forest in southern China. *Soil Biol. Biochem.* **127**, 22–30.

Woodcroft, B.J., Singleton, C.M., Boyd, J.A., Evans, P.N., Emerson, J.B., Zayed, A.A., Hoelzle, R.D., Lamberton, T.O., McCalley, C.K., and Hodgkins, S.B. 2018. Genome-centric view of carbon processing in thawing permafrost. *Nature* **560**, 49.

Wrona, F.J., Johansson, M., Culp, J.M., Jenkins, A., Mård, J., Myers-Smith, I.H., Prowse, T.D., Vincent, W.F., and Wookey, P.A. 2016. Transitions in Arctic ecosystems: Ecological implications of a changing hydrological regime. *J. Geophys. Res. Biogeosci.* **121**, 650–674.

Ye, R., Jin, Q., Bohannan, B., Keller, J.K., McAllister, S.A., and Bridgham, S.D. 2012. pH controls over anaerobic carbon mineralization, the efficiency of methane production, and methanogenic pathways in peatlands across an ombrotrophic–minerotrophic gradient. *Soil Biol. Biochem.* **54**, 36–47.

Yergeau, E., Hogues, H., Whyte, L.G., and Greer, C.W. 2010. The functional potential of high Arctic permafrost revealed by metagenomic sequencing, qPCR and microarray analyses. *ISME J.* **4**, 1206–1214.

Yoshikawa, K. and Hinzman, L.D. 2003. Shrinking thermokarst ponds and groundwater dynamics in discontinuous permafrost near council, Alaska. *Permafrost Periglac.* **14**, 151–160.

Zak, D.R. and Kling, G.W. 2006. Microbial community composition and function across an Arctic tundra landscape. *Ecology* **87**, 1659–1670.

Zhang, C., Stapleton, R.D., Zhou, J., Palumbo, A.V., and Phelps, T.J. 1999. Iron reduction by psychrotrophic enrichment cultures. *FEMS Microbiol. Ecol.* **30**, 367–371.