

Minireview

Microbial diversity and biogeography in Arctic soils

Lucie A. Malard*  and David A. Pearce

Faculty of Health and Life Sciences, Northumbria University, Newcastle-upon-Tyne, NE1 8ST, UK.

Summary

Microorganisms dominate terrestrial environments in the polar regions and Arctic soils are known to harbour significant microbial diversity, far more diverse and numerous in the region than was once thought. Furthermore, the geographic distribution and structure of Arctic microbial communities remains elusive, despite their important roles in both biogeochemical cycling and in the generation and decomposition of climate active gases. Critically, Arctic soils are estimated to store over 1500 Pg of carbon and, thus, have the potential to generate positive feedback within the climate system. As the Arctic region is currently undergoing rapid change, the likelihood of faster release of greenhouse gases such as CO₂, CH₄ and N₂O is increasing. Understanding the microbial communities in the region, in terms of their diversity, abundance and functional activity, is key to producing accurate models of greenhouse gas release. This review brings together existing data to determine what we know about microbial diversity and biogeography in Arctic soils.

Introduction

The polar cryosphere represents approximately 14% of the Earth's surface (Morita, 1975; Boetius *et al.*, 2015). Yet, it has long been considered that life, where it existed, was dormant in these regions as, in order to survive, living organisms have to be well adapted or highly resistant to extreme cold, variable temperature and melt/thaw cycles, low nutrient and liquid water availability and seasonally variable UV radiation levels (Larose *et al.*, 2013; Boetius *et al.*, 2015). Today, however, it is well recognized that microorganisms can thrive in the Arctic region and are present in abundance in all northern polar environments; from tundra (Lee *et al.*, 2013) to taiga (Neufeld and Mohn, 2005), snow (Larose *et al.*, 2013), glaciers

(Anesio *et al.*, 2009), permafrost (Mackelprang *et al.*, 2011), air (Harding *et al.*, 2011; Cuthbertson *et al.*, 2017), marine (Ghiglione *et al.*, 2012) and freshwater (Crump *et al.*, 2012) ecosystems. The Arctic tundra covers about 8% of Earth's land surface (Nemergut *et al.*, 2005) and is characterized by a unique soil profile where the subsoil is perennially frozen, the permafrost which, in turn, covers up to 25% of Earth surface (Steven *et al.*, 2006; Lee *et al.*, 2013).

In the Arctic, microorganisms play major roles in biogeochemical cycling despite slow growth and low activity rates due to environmental conditions (Nemergut *et al.*, 2005). The active layer of the permafrost is estimated to store 500 Pg of carbon whilst the Arctic permafrost below is estimated to store over 1000 Pg of carbon, amounting to an overall terrestrial Arctic carbon pool of over 1500 Pg (Koven *et al.*, 2011; Mackelprang *et al.*, 2011). In summer, the active layer of the permafrost thaws, leading to a sharp increase in microbial activity and to increased nutrient cycling activity. Increased microbial activity may lead to increased release of climate active gases such as carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O) into the atmosphere (Fierer *et al.*, 2007; Mackelprang *et al.*, 2011), creating positive feedback on the climate system. Understanding the diversity, structure and stability of microbial communities and how they may be altered with environmental change is essential to understand potential changes in ecosystem function, especially in the context of Arctic warming.

Currently, the main difficulty in assessing Arctic microbial communities resides in the remoteness of the region, which greatly limits the number of studies and samples available. Here, we provide the first broad overview of Arctic microbial communities across the region.

Diversity and biogeography

Biogeography is the description of biodiversity patterns across space and time, and although biogeography has been intensively studied for higher organisms, the question of microbial biogeography has only recently received significant attention (Fierer and Jackson, 2006; Delgado-Baquerizo *et al.*, 2018). Indeed, for a long time, microbial ubiquity was assumed, influenced by the prevailing paradigm that 'everything is everywhere, but, the environment selects' by Baas-Becking in 1934, which has persisted

Received 10 November, 2017; accepted 17 July, 2018. *For correspondence. E-mail lucie.malard@northumbria.ac.uk.

© 2018 The Authors. Environmental Microbiology Reports published by Society for Applied Microbiology and John Wiley & Sons Ltd. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

over the years (De Wit and Bouvier, 2006). This adage suggested that all species of microorganism are everywhere and, thus, microbial biogeography does not strictly exist as it does for higher organisms (O'Malley, 2007). An increasing number of studies now focus on microbial biogeography worldwide (Tedersoo *et al.*, 2014; Delgado-Baquerizo *et al.*, 2018), but the Arctic region has received comparatively little attention.

Regional comparison

The current number of studies focusing on Arctic soil microbial diversity remains low, with a limited number of sites being investigated (Fig. 1). However, we can observe a steady increase in the number of microbial DNA sequences deposited in international nucleotide sequence databases (Fig. 2A), which reflects an increase in the number of studies of Arctic soil communities. Despite the increasing number of sequences available, clear disparities remain, with some Arctic regions recording a large number of sequences (Fig. 2B) whilst Russia, Greenland, Iceland and Sweden, for instance, still have low to no sequence data available. We can also observe a clear focus on bacterial communities and lack of information on Arctic archaeal, fungal, eukaryotic and viral communities.

The active layer of Arctic soils is directly exposed to the climatic conditions, which are characterized by strong winds, extremely low temperatures, low UV radiation in winter and intense UV radiation in summer with generally low rates of precipitations (Nemergut *et al.*, 2005). Despite these apparently extreme environmental conditions, studies have shown that Arctic tundra soils may harbour similar and even higher microbial diversity to other biomes (Neufeld and Mohn, 2005; Chu *et al.*, 2010; Lee *et al.*, 2013). Although polar microorganisms have lower activity rates due to climatic conditions, their role in nutrient cycling is nevertheless essential (Jakosky *et al.*, 2003).

To compare microbial communities across Arctic soils, we documented all available studies investigating microbial diversity in the active layer of pristine Arctic tundra soils, despite large methodological differences. We considered DNA-based studies, from clone libraries to amplicon sequencing and metagenomics (studies used listed in Table 1) and extracted taxonomic ranks and abundance data (Supporting Information). It should also be noted that various primers, PCR conditions and sequencing platforms were used.

Typically, Proteobacteria and, specifically, N-fixing Rhizobiales (Alphaproteobacteria), Burkholderiales (Betaproteobacteria), Xanthomonadales (Gammaproteobacteria) and Myxococcales (Deltaproteobacteria) dominated Arctic soil bacterial communities (Fig. 3A and B). The shift in communities seemed largely directed by the variations in abundance of Acidobacteria, Bacteroidetes and

Actinobacteria whilst other phyla remained relatively stable across the region. Acidobacteria were widely distributed across the Arctic region except in Svalbard and Siberia where they were present in much lower frequencies. The Acidobacteria and Solibacteres classes dominated the region despite high variability. Generally, Actinobacteria occurred at lower abundances in Greenland and Finland (3%–6%), whilst Bacteroidetes had much higher abundances than in Alaskan, Canadian and Svalbard soils (up to 26%). Verrucomicrobia, Planctomycetes, Firmicutes, Chloroflexi, Gemmatimonadetes, AD3 and Cyanobacteria were less abundant taxa, generally representing less than 15% of the population in total (Fig. 3A). These results would suggest that biogeographic variation does occur in Arctic soils.

At this stage, for most identified microorganisms, inferring function even from the order level remains extremely difficult, considering each phylum harbours a wide diversity of organisms with a large number of ecological functions. However, some critical functional activity could potentially be assessed. For instance, in Arctic soils, besides plants and their associated root bacteria, Cyanobacteria are largely responsible for CO₂ and N₂ uptake (Zakhia *et al.*, 2008) and as plants are unable to fix N₂, Arctic ecosystems are largely reliant on Cyanobacteria. Although they can be free living in tundra soil, mainly from the Oscillatoriales and Nostocales orders (Steven *et al.*, 2013), they are often identified in biofilms or soil crusts, likely due to the protection provided against environmental conditions (Zakhia *et al.*, 2008). In Arctic soil crusts, Synechococcales, Nostocales and Oscillatoriales have been consistently identified as dominant orders of Cyanobacteria (Steven *et al.*, 2013; Pushkareva *et al.*, 2015). Specialized N₂ fixation species form heterocysts, which are specialized cells with thicker cell walls to protect nitrogenase from O₂ inactivation (Kumar *et al.*, 2010). *Nostoc* sp. are found in abundance in Arctic soils across the region and are the main N₂ fixers identified, thus transforming N₂ into organic N, which can be used by plants and microorganisms (Dodds *et al.*, 1995). With the essential role of Cyanobacteria in carbon and nitrogen uptake, their biogeography can significantly impact the carbon and nitrogen cycle dynamics, yet to date, their distribution and diversity has not been thoroughly investigated in Arctic soils.

Another group of microorganisms with important roles in the nitrogen cycle are the Planctomycetes. They are generally more abundant in marine and freshwater environments but have been identified at varying abundances in terrestrial environments including in all Arctic soils (Fig. 3A). Planctomycetes participate in the anaerobic oxidation of ammonium (anammox), which leads to the production of N₂ (Humbert *et al.*, 2010). Whether they thrive in Arctic soils and are functionally active is yet to



Fig. 1. Distribution of soil bacterial diversity studies in the Arctic region to date.

This map shows the number of studies published in English and indexed in Scopus. Striated areas indicate most intensively studied sites in the Arctic region.

be determined. Thus, rates of anammox in terrestrial Arctic environments are currently unknown.

A critical functional role to be investigated is the production and release of nitrous oxide (N_2O) to the atmosphere. N_2O is 298 times more potent than CO_2 as a greenhouse gas and is released upon permafrost thaw (Palmer *et al.*, 2012). N_2O reacts with ozone (O_3), leading to the destruction of the ozone layer whilst forming nitrite (NO_2^-), which returns to Earth as nitrous acid (HNO_2) rain (Madigan *et al.*, 1997; Fierer *et al.*, 2007). N_2O is produced through aerobic nitrification and anaerobic denitrification (Marushchak *et al.*, 2011; Palmer *et al.*, 2012). *Paracoccus denitrificans* (Alphaproteobacteria), *Thiobacillus denitrificans* (Betaproteobacteria) and some *Pseudomonas* sp. (Gammaproteobacteria) (Baumgärtner *et al.*, 1996) are known to be denitrifiers but their presence in Arctic soils is still to be investigated fully, despite studies showing that denitrification occurs and N_2O is being released to the atmosphere (Fierer *et al.*, 2007; Palmer

et al., 2012). The Arctic region was not considered a large N_2O producer until studies showed a large increase in N_2O production and subsequent release in the atmosphere following freeze–thaw cycles and rewetting of Arctic soils (Elberling *et al.*, 2010). Surprisingly, these rates of N_2O release after rewetting, up to $34 \text{ mg N m}^{-2} \text{ day}^{-1}$, are equivalent to the release of N_2O by tropical forests, which are amongst the top N_2O producers (Elberling *et al.*, 2010; Palmer *et al.*, 2012). Studies suggest hotspots of N_2O production exist in the Arctic region, and further research is needed to provide estimations of N_2O release, especially in the context of climate change and permafrost thawing (Elberling *et al.*, 2010; Marushchak *et al.*, 2011).

Archaeal and fungal communities are essential parts of Arctic microbial communities; however, their abundance, diversity and distribution remain largely understudied in the region. Arctic archaeal communities appeared largely variable across the region, with the large abundance of

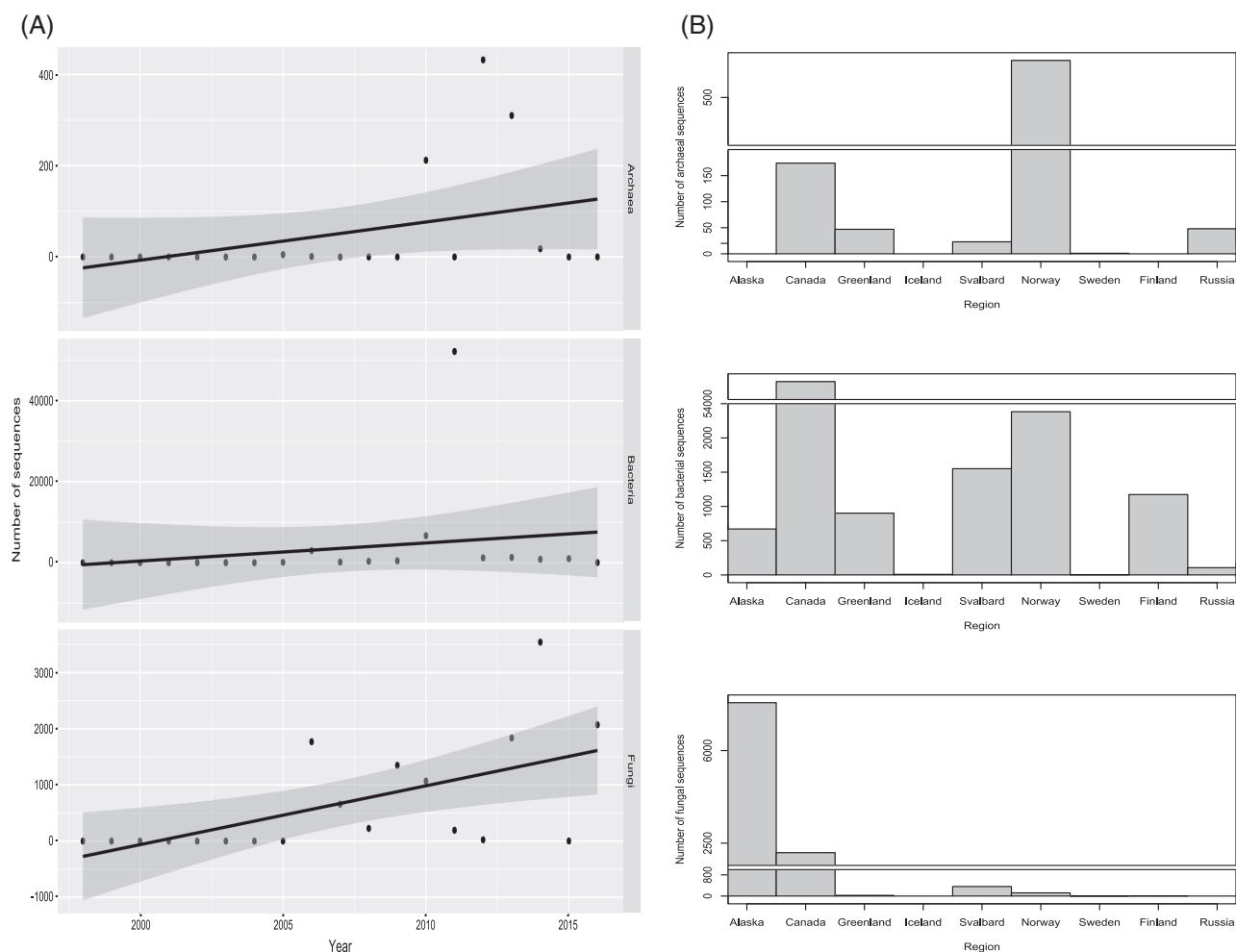


Fig. 2. Number of sequences available on NCBI per year and per country. A. The number of Archaeal, Bacterial and Fungal sequences released on NCBI per year, for Arctic soil samples. B. Bar chart of the number of Archaeal, Bacterial and Fungal sequences from Arctic soils available on NCBI by Region.

Methanomicrobia and Methanobacteria (Euryarchaeota) in Alaskan and Greenlandic soils whilst Thaumarchaeota, Crenarchaeota and Euryarchaeota abundance varied in other regions (Fig. 3C). Euryarchaeota are known methanogens and due to the adverse role of CH_4 as a climate gas, understanding the distribution of archaea across the landscape is important. The release of methane to the atmosphere is balanced by the action of methanotrophs, which use CH_4 as their carbon source. Methanotrophic species belong mainly to the Gammaproteobacteria (type I) and Alphaproteobacteria (type II), although some archaeal species such as members of the Methanosarcinales are known methanotrophs (Martineau *et al.*, 2014). Understanding this balance between methanogens and methanotrophs is important in the view of the significant change in these communities upon permafrost thaw (Coolen *et al.*, 2011; Mackelprang *et al.*, 2011). Arctic fungal communities appeared variable but were generally dominated by the Ascomycota and

Basidiomycota (Fig. 3D), which are the main terrestrial decomposers (Wallenstein *et al.*, 2007; Zhang *et al.*, 2016). Further studies in archaeal and fungal diversity will provide a better understanding of microbial assemblages and ecosystem structure.

Identifying clear patterns of microbial biogeography across the Arctic region using data from studies with different methodologies is difficult, especially considering the challenge of demonstrating absence. Each region appears to have similarities, such as comparable abundance of Alphaproteobacteria in Finland, Alaska and Svalbard soils whilst, in these same soils, variation of Acidobacteria can range from 4% to 20%. Whilst these differences are clear across different studies between regions and indicate potential biogeographic variation, only a Pan-Arctic study using a standardized method could be used to suggest biogeographical patterns and potentially relate them to environmental variables.

Table 1. Summary of studies used for analysis of microbial biogeography.

Studies	Location
Wallenstein and colleagues (2007), Campbell and colleagues (2010), Koyama and colleagues (2014), Kim and colleagues (2016), Wagner and colleagues (2017)	Alaska
Neufeld and Mohn (2005), Steven and colleagues (2008), Wilhelm and colleagues (2011), Frank-Fahle and colleagues (2014), Shi and colleagues (2015)	Canada
Ganzert and colleagues (2014) and Gittel and colleagues (2014b)	Greenland
Lee and colleagues (2013), Tveit and colleagues (2013), Schostag and colleagues (2015), Zhang and colleagues (2016)	Svalbard
Männistö and colleagues (2009) and Männistö and colleagues (2013)	Finland
Liebner and colleagues (2008) and Gittel and colleagues (2014a)	Siberia
Lipson and Schmidt (2004), Zinger and colleagues (2009), Shen and colleagues (2013), Zhang and colleagues (2014), Shen and colleagues (2015), Frey and colleagues (2016), He and colleagues (2016), and Siles and Margesin (2016)	Alpine
Smith and colleagues (2006), Yergeau and colleagues (2007), Niederberger and colleagues (2008), Chong and colleagues (2012), and Teo and Wong (2014)	Antarctica

Cryosphere comparison

In contrast to the Arctic, the alpine tundra undergoes greater seasonal shifts but despite this difference with Arctic environments, alpine soils experience similar seasonal environmental pressures such as high UV radiation and extreme cold temperature (reviewed by Nemergut *et al.*, 2005). These environmental conditions appeared to be reflected in the Alpine microbial assemblage (Fig. 4). Alpine soils harboured a higher abundance of Alphaproteobacteria, Betaproteobacteria, Acidobacteria_6, Planctomycetia and Spartobacteria, whilst Bacteroidia seemed absent from these communities, against 10% in Arctic soils (Fig. 4A and B). Archaeal communities appeared largely dominated by Thaumarchaeota (up to 90%) which contrasts with the balanced Arctic archaeal communities (Supporting Information Fig. S1A). Alpine and Arctic fungal communities, on the other hand, seemed relatively similar, both dominated by Ascomycota and Basidiomycota (Supporting Information Fig. S1B). However, archaeal and fungal communities are based on a very low number of studies and require further investigation.

Antarctica could be viewed as a proxy of Arctic communities as environmental pressures appear similar year-round. Antarctic soils harboured lowered abundances of all classes of Proteobacteria but higher proportions of Chloracidobacteria, Saprospirae (Bacteroidetes), Actinobacteria and Cyanobacteria (Fig. 4A and B). However, Antarctica is much more isolated than the Arctic region, with the closest land mass over 1000 km away and surrounded by the Southern Ocean's circumpolar current and the atmospheric circumpolar vortex. This is reflected in the literature by the differences between Alpine, Arctic and Antarctic microbial communities (Fig. 4). These studies indicated apparent differences in microbial diversity despite similar environmental selection pressures across the cryosphere.

Global comparison

Despite polar environmental conditions, the microbial biomass and diversity of tundra ecosystems appears equivalent

to the microbial biomass and diversity in temperate and tropical forests (Lauber *et al.*, 2009; Chu *et al.*, 2010). However, tundra microbial communities generally cluster away from other biomes in global diversity studies (Fierer *et al.*, 2012; Tedersoo *et al.*, 2014). Worldwide bacterial soil communities appear dominated by Proteobacteria, Actinobacteria, Acidobacteria and Planctomycetes (Delgado-Baquerizo *et al.*, 2018), whilst Proteobacteria and Acidobacteria dominate Arctic soil microbial communities. Crenarchaeota are most abundant in global archaeal communities (Auguet *et al.*, 2010), whilst 90% of Arctic archaeal communities can be dominated by Euryarchaeota (Fig. 3C). Finally Agaricomycetes (Basidiomycota) largely dominate fungal communities, especially in tropical and temperate soils (Tedersoo *et al.*, 2014), whilst Ascomycota appear to dominate by up to 80% in Arctic soils (Fig. 3D). These variations in microbial communities are likely driven by environmental conditions; however, other factors such as proximity to human activities or high plant and animal biomass are known to have strong impacts. Whilst global and Arctic soil communities do appear different, only large-scales studies, such as the Earth Microbiome project (Thompson *et al.*, 2017), can identify and highlight these differences.

Drivers of Arctic microbial communities

Environmental influence

pH. pH has been identified as the main factor driving bacterial diversity in many soil studies (Fierer and Jackson, 2006; Rousk *et al.*, 2010; Griffiths *et al.*, 2011; Chong *et al.*, 2012; Docherty *et al.*, 2015), including in Arctic soils (Chu *et al.*, 2010; Siciliano *et al.*, 2014). Some taxon abundances are closely correlated with soil pH, notably the Acidobacteria (Lauber *et al.*, 2009; Rousk *et al.*, 2010). However, not all Acidobacteria subdivisions behave the same way and whilst some subdivisions increase in abundance in low pH, such as SD1 and SD2, others increase in high pH, such as SD6 and SD16 (Lauber *et al.*, 2009;

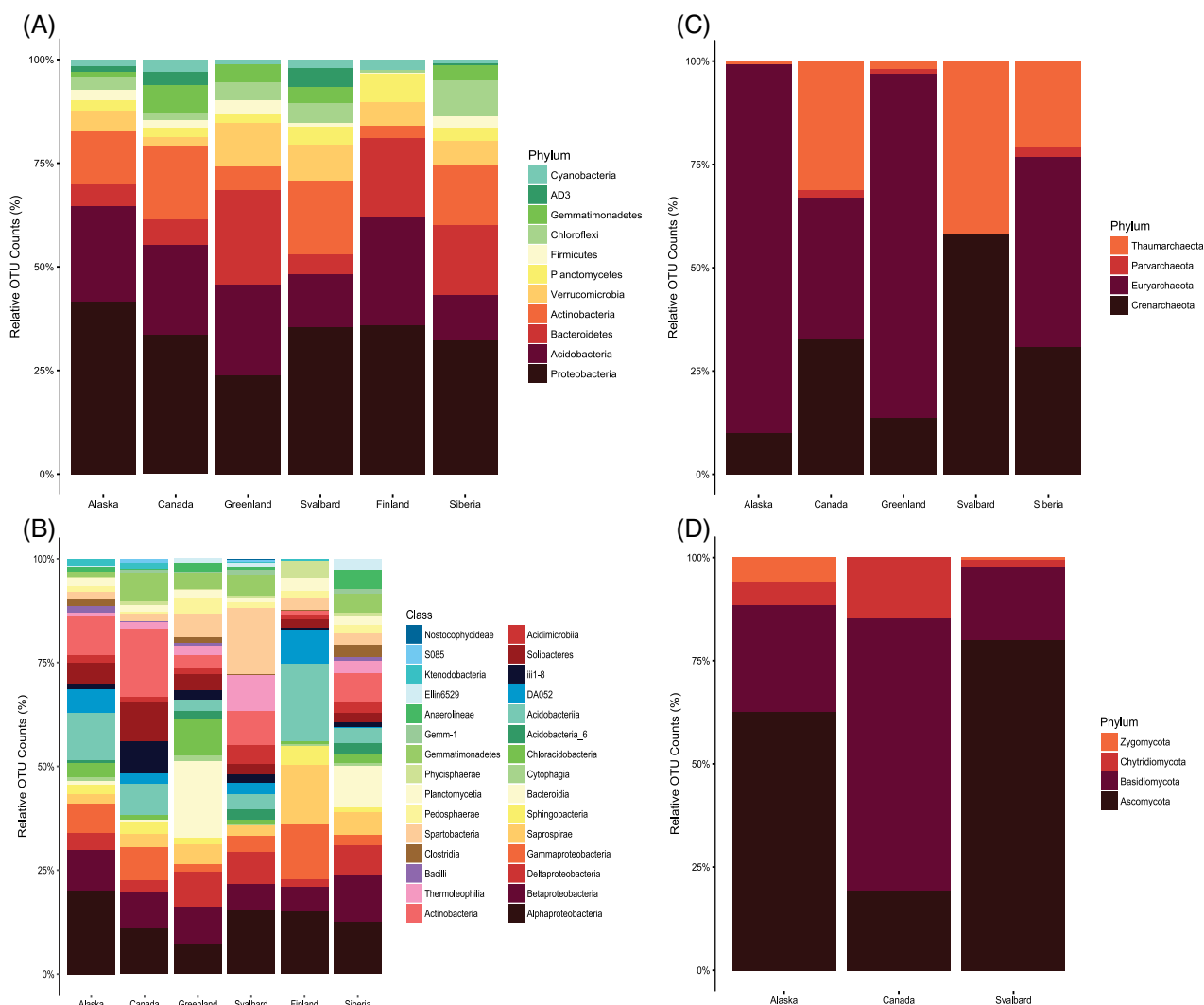


Fig. 3. Relative abundance of microorganisms in the Arctic region.

A. stacked bar chart of bacterial phyla abundance extracted from the literature and combined by country. Sweden, Iceland and mainland Norway are not represented as there were no known studies at the time of investigation.

B. stacked bar chart of bacterial classes.

C. Archaeal phyla identified in each region. Missing Arctic regions had no known studies at the time of analysis.

D. Fungal phyla identified in each region. Missing Arctic regions had no known studies at the time of analysis.

Rousk *et al.*, 2010; Griffiths *et al.*, 2011). Whether other taxa vary with soil pH is still largely undetermined. Lauber and colleagues (2009) showed that Actinobacteria and Bacteroidetes abundance decrease with lower pH in a wide variety of soils whilst Rousk and colleagues (2010) demonstrated they remained unaffected in arable soils. These results suggest that pH has a strong impact on bacterial communities but may be species specific and vary geographically. The study by Siciliano and colleagues (2014) suggests pH may also be a major driver of microbial diversity in northern polar regions. pH, in turn, can be impacted by many processes both microbial and nonmicrobial such as plant growth, microbial metabolism or weathering (Kwon *et al.*, 2015), nutrient

cycling such as nitrification, or acid rain and acid mine drainage (Baker and Banfield, 2003). Although studies correlate pH with microbial communities, the processes by which pH regulates these communities still remain unknown.

Vegetation cover. Vegetation cover is known to have a strong impact on microbial communities, and in the Arctic, studies have shown variations in microbial diversity and abundance linked to vegetation. Wallenstein and colleagues (2007) identified differences in bacterial diversity between shrub and tussock tundra soils. Acidobacteria represented up to 45% of the tussock tundra community, against less than 10% in shrub soils. This shift in

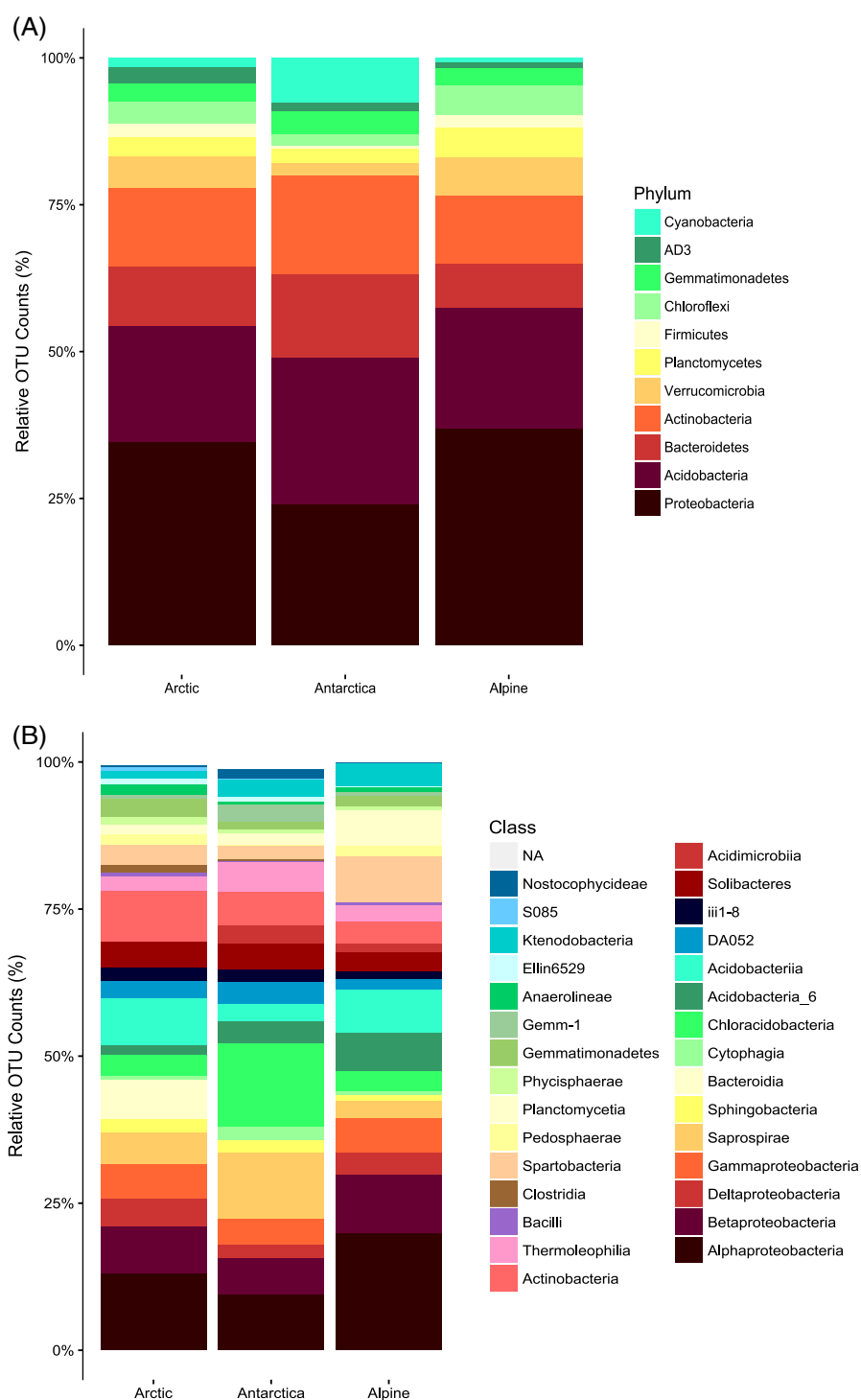


Fig. 4. Comparison of bacterial relative abundance in soil by environment.

A. Bar chart of bacterial phyla abundance extracted from the literature and combined by ecosystem.

B. Bar chart of bacterial class abundance extracted from the literature and combined by ecosystem.

Acidobacteria was balanced by the abundance of Proteobacteria, which increased with decreasing Acidobacteria. Chu and colleagues (2011) corroborated the hypothesis that vegetation has a strong impact on microbial

communities by showing communities from various vegetation types cluster independently of one another. In contrast, Shi and colleagues (2015) investigated the bulk soil of four typical tundra vegetation types and found only

slight shifts in the abundance phyla within prokaryotic communities whilst eukaryotic communities varied greatly with large shifts in both Basidiomycota and Chytridiomycota. These studies have demonstrated the impact of vegetation on microbial communities in the Arctic; however, the magnitude of impact appears to vary by location.

Rhizosphere. The rhizosphere is defined by the plant root system and its exudates (Berg and Smalla, 2009). As a result, microbial abundance and activity are enhanced (Berendsen *et al.*, 2012), whilst microbial diversity is generally lower with the dominance of few taxa (Philippot *et al.*, 2013). In the Arctic region, studies have shown that rhizosphere microbial diversity is higher than in nonrhizosphere bulk soils (Tam *et al.*, 2001; Kumar *et al.*, 2016). However, the number of Arctic studies differentiating bulk and rhizosphere microbial communities is low.

Other factors. pH and vegetation are the main known drivers of worldwide microbial communities, and Arctic microbial communities are no exception. However, other factors may be involved, as studies of worldwide soils have demonstrated the impact of salinity (Lozupone and Knight, 2007), moisture content (Dimitriu and Grayston, 2010) and C:N ratio (Docherty *et al.*, 2015) on microbial communities. Other factors may include temperature, ice formation/duration, light, altitude, soil age and texture, nutrient and elemental composition, water availability or pollution. Whilst all these factors are likely to have some impact of microbial assemblages, the magnitude and influence have not yet been established for Arctic soil communities.

Time

Time, on different scales, is known to impact higher organisms, but the impact on microbial communities is not well established, especially for the Arctic Region. Short-term variation has been demonstrated by seasonal fluctuations, especially in Alpine environments, where the snowmelt and growing season impact microbial communities (Lipson *et al.*, 2002; Zinger *et al.*, 2009) with an increase in biomass in summer (Lipson *et al.*, 2002; Lipson and Schmidt, 2004) corresponding to an increase of Verrucomicrobia and an overall decrease of Acidobacteria and Alphaproteobacteria (Lipson and Schmidt, 2004). A similar seasonal pattern has been observed in Arctic tundra, likely linked to the sudden availability of water and nutrient, promoting microbial growth (Buckeridge *et al.*, 2013). However, only year-long studies or monitoring studies could identify changes in microbial communities with time.

Space

Spatial patterns of biodiversity give insights into ecological mechanisms such as speciation, extinction, dispersal and species interactions (Martiny *et al.*, 2006). High habitat heterogeneity can lead to many niches harbouring different microbial communities, which is a major challenge in investigating microbial biodiversity and biogeography (Vos *et al.*, 2013). The scale of investigation is important as different scales may uncover alternative drivers of microbial community diversity. For instance, Martiny and colleagues (2011) identified sediment moisture as a strong driver of ammonia-oxidizing bacteria diversity on small and regional scales, but it was not significant on continental scales.

Understanding large-scale patterns is increasingly important to understand large-scale biogeochemical cycling and how it may be impacted as a result of climate change. One of the earliest large-scale biogeographical studies carried by Fierer and Jackson (2006) demonstrated that distinct types of forest and grassland ecosystems harboured similar microbial communities, regardless of geographic distances. Later on, Fierer and colleagues (2012) further supported these results by demonstrating that most environment types cluster together, except cold and hot deserts, which cluster independently of other ecosystems. These results suggest that microbial diversity of extreme ecosystems may be particularly different, whilst other nonextreme environments may harbour similar communities. Whilst this is still unclear, few studies have shown latitudinal and altitudinal gradients (Yergeau *et al.*, 2007; Wang *et al.*, 2015; Siles and Margesin, 2016) in both Alpine regions and Antarctica, as well as distinct geographic regions harbouring variable diversity in Antarctica (Chong *et al.*, 2015). Multiple studies have also shown the decrease in diversity with soil depth in Arctic soils (Liebner *et al.*, 2008; Frank-Fahle *et al.*, 2014), suggesting stratification of Arctic microbial communities in the active layer and the permafrost.

Although terrestrial microbial biogeography is still debated, clear biogeographic patterns have been identified in the oceans and the air (Womack *et al.*, 2010), two of the most connected environments. Studies have demonstrated that microorganisms exhibit biogeographical distribution, varying seasonally (Ghiglione *et al.*, 2012) and with temperature (Ngugi *et al.*, 2012), depth (Qian *et al.*, 2011) and salinity gradients (Herlemann *et al.*, 2011). Furthermore, Ghiglione and colleagues (2012) showed that marine microbial communities cluster apart from one another, suggesting that biomes with similar environmental pressure may still harbour different microbial communities. In terms of terrestrial biogeography, for the Arctic, this review suggests that the North American

Table 2. Summary of key ideas and findings.

#	Key idea	Importance and implications
1	1500 Pg of carbon are stored in Arctic soils	Large potential for C release in the atmosphere leading to negative feedback on the climatic system
2	Arctic soils harbour very high microbial diversity, potentially even higher than other regions of the world	Identification of high diversity and high biomass in Arctic soils has changed the perspective on cold environments
3	Biogeographic variation might occur in the Arctic	Further research is needed to identify clear biogeographical patterns and hotspots of diversity
4	N ₂ O release seems much higher than previously estimated	N ₂ O is 300 times more potent than CO ₂ . Bulk release could have major climatic impacts but rates of N ₂ O release by Arctic environments are not taken into account in climate models
5	Antarctica, despite being a pole with similar environmental pressures, cannot be used as a model to understand microbial diversity of Arctic soils	Both poles need to be seen as different entities as they are hard to compare due to large difference in dominating ecosystems and the amount of anthropogenic pressures
6	pH and vegetation appear as the main factors structuring Arctic microbial communities	Similar as for global soils where pH is consistently identified as a key factor
7	Time and space are also likely important factors	Long-term, year-round and large-scale studies of microbial communities are needed to identify biogeographical patterns and seasonal variations
8	The bioprospecting potential is high in the region, due to much unexplored ecosystems and the nature of climatic conditions and related adaptations	Effective bioprospecting efforts could reveal high metabolic activity with commercial, industrial and even medical interests, notably against antimicrobial resistance and diseases
9	Even with current technology, it is still difficult to identify species accurately and many biases remain	Coarse identification obscure potential biogeographical patterns. Lack of identification should not lead to the conclusion that organisms are absent from an environment
10	Many studies stop at the phylum level and compare locations at this taxonomical level	Similar phyla distribution across regions does not give much information. Although organisms may be in the same phylum, they may have distinct roles and functions
11	As technology improves, studies adapt and, thus, different methods of identification are used through time	The variations and biases involved lead to great difficulties in accurate comparison between ecosystems across space and time

Arctic might differ from the European Arctic whilst Greenland and Siberia appear to harbour similar microbial communities (Fig. 3A).

Importance of understanding Arctic microbial biogeography

Understanding microbial assemblages and biogeographical variation can have important implications not only for our understanding of ecosystem functioning but also for human interests such as bioprospecting for industrial, commercial and medical purposes.

Hotspots of biodiversity can be defined by strong gradients in local selection pressures and high heterogeneity. The Arctic region presents such characteristics, and thus, hotspots of diversity could potentially occur. For larger organisms, hotspots of biodiversity can be found worldwide, from the Amazon forest to the coral triangle in the Pacific, and Madagascar with 90% of endemic species. Despite the essential role of microorganisms in ecosystem function, only few studies have identified such microbial diversity hotspots worldwide. Identified areas include Hawaii (Donachie *et al.*, 2004), Chile (Dorador *et al.*, 2013) and even Antarctica (Ji *et al.*, 2016). Many studies in the Arctic region report high diversity, similar to levels observed in worldwide soils (Torsvik *et al.*, 1996; Neufeld and Mohn, 2005; Lee

et al., 2013), yet, no geographical region has been characterized as significantly harbouring higher diversity. Arctic soil diversity may increase due to inoculation from other environments such as snow cover or meltwater (Larose *et al.*, 2010) or even through aerial dispersal (Pearce *et al.*, 2016). Areas of convergence could be hotspots of diversity but may support many allochthonous organisms with little functional significance for the environment (Neufeld and Mohn, 2005). Identifying such hotspots of biodiversity may indicate areas with high bioprospecting potential.

Commercial and industrial bioprospecting

Current research activity is skewed towards groups of organisms presenting high potential for economic exploitation. In this light, identifying hotspots of microbial diversity will indicate areas with high bioprospecting potential for industrial, commercial or medical purposes. This is certainly one area of activity, which is ongoing and which, in the future, will help to develop further knowledge of microbial diversity in this area. Extremophiles are especially relevant for bioprospecting as they exhibit commercially exploitable traits. True psychrophiles, although rare, are the most common type of extremophile in the Arctic region. *Cryptococcus* species are psychrophilic yeasts identified in Arctic habitats, notably soils and glaciers (D'Amico *et al.*, 2006; Buzzini *et al.*, 2012), but

many other species are still being identified, such as members of the *Psychrobacter* (Bakermans *et al.*, 2006). Extremophiles are often polyextremophilic or highly tolerant to multiple stress factors such as low pH or high salinity. A few *Psychrobacter* species are both psychrophilic and halotolerant (Bakermans *et al.*, 2006) whilst *Nesterenkonia* sp. AN1, isolated from Antarctic soils, is psychrotolerant but haloalkaliphilic (Aliyu *et al.*, 2016). When the environment becomes unfavourable, some organisms are capable of producing endospores to ensure survival (Madigan *et al.*, 1997). Species from the Bacillaceae family such as *Virgibacillus arcticus*, isolated from the Canadian high Arctic permafrost are known to form endospores (Niederberger *et al.*, 2009). Yukimura and colleagues (2009) identified strains in Greenland genetically identical to previously identified species from the Gobi Desert, suggesting the role of endospores not only for survival but also for long distance dispersal. Despite polar environmental conditions, most microorganisms living in Arctic soils are not extremophilic. Psychrotrophs dominate cold environments, and although most of these organisms can survive at low to subzero temperatures, they grow optimally at higher temperatures (Morita, 1975; Huston *et al.*, 2000). *Pseudomonas* sp. stains B17 and B18 grow between 0 and 30 °C with optimum growth at 25 °C. However, they are metabolically active at 5 °C and can degrade both, alkanes and naphthalene, from petroleum hydrocarbon (Whyte *et al.*, 1997). Some cold-adapted organisms are able to produce antifreeze proteins, which, in the food industry, are widely used to prevent microbial contamination, enhance cryopreservation of cell tissues and preserve texture and flavour of frozen foods (Robinson, 2001; Leary, 2008). These proteins have been identified in microorganisms such as fungi (reviewed by Robinson, 2001) and in few bacterial species, mainly Gammaproteobacteria isolated from Antarctic lakes (Gilbert *et al.*, 2004). Some microorganisms also produce cold-active or psychrophilic enzymes, which are more active and stable at low temperatures than mesophilic enzymes and thus, could be used for low temperature industrial processes (Feller and Gerday, 2003).

Medical bioprospecting

In the coming decades, bioprospecting for medical purposes will potentially become a priority due to the increased abundance of antibiotic resistance and multi drug resistant strains. Diversity hotspots will be prime targets as microorganisms live in close proximity and compete for resources and thus, develop ways to compete with each other. Soils, especially close to human activity, are reservoirs and incubators for antibiotic resistance (Walsh, 2013), but recent studies suggest

pristine environments, such as Arctic soils, may also act as reservoirs for resistance and thus, reservoirs for antimicrobial compounds (Mindlin *et al.*, 2008; Segawa *et al.*, 2013). Fungi are a promising source of new metabolites as they have been identified in many extreme environments and have developed specialized ways to survive and thrive in harsh conditions (reviewed by Gostinčar *et al.*, 2010). For instance, some fungal species associated with Antarctic sponges have been shown to have antimicrobial and antitumoral activities (Henríquez *et al.*, 2014). Actinomycetes are one of the major sources of antibiotics worldwide and Arctic Actinomycetes have strong potential for bioprospecting (Bredholdt *et al.*, 2007; Liao *et al.*, 2016). For example, the *Streptomyces* sp. ART5 strain, isolated from Eastern Siberia sediments, shows inhibitory activity against *Candida albicans* (Moon *et al.*, 2014). A significant finding is that of Augustine and colleagues (2012) who identified three species of Arctic Actinomycetes, two *Streptomyces* species and one *Nocardiopsis* species, isolated from sediments in Svalbard, with the potential to inhibit *Vibrio cholerae* biofilms.

Challenges

The number of Arctic studies specifically on microbial diversity is sparse (Fig. 1), and older studies lack taxonomic depth due to sequencing limitations at the time. Even now, most studies report identification only to the phylum level as the depth of sequencing does not always allow the accurate identification of microorganisms at other levels of classification making functional assessment challenging. For instance, classification at the class level could inform that *Bacillus* and *Clostridium*, both known cellulose degraders (Killham and Prosser, 2015), are present and potentially active. At the genus level, information on the potential for ammonia-oxidation could be obtained if the *Nitrosomonas* genus is identified. Either a change in taxonomic classification towards more ecologically meaningful categories (Fierer *et al.*, 2007) or improved sequencing tools (Sangal *et al.*, 2016) are required if we aim to understand the role of microorganisms in the environment from diversity data. Otherwise, whole genome sequencing should be prioritized. Furthermore, microorganisms, which are not detected, are not necessarily absent from the investigated environment. It should also be noted that Arctic sites are restricted by logistical access and most sampled sites are coastal sites (Fig. 1), which may receive oceanic influences. The magnitude of oceanic influence on these sites has not been investigated but should be considered. Technological improvements combined with a larger variety of sampling sites and deeper taxonomic classification would lead to a

better understanding of biogeography and likely uncover new patterns of distribution worldwide.

Concluding remarks

The emerging patterns of microbial biodiversity identified in this review give a clear indication that microbial communities might exhibit biogeographical patterns in the Arctic region. As they are the result of studies using different methodologies, only a large pan-Arctic study could provide a deeper understanding of these patterns and the drivers associated with them. As the Arctic region is currently undergoing rapid change and the International Panel on Climate Change (IPCC) is predicting an increase in temperature of 2–5°C by the end of the 21st century (IPCC, 2014), increased research efforts are necessary to understand the potential consequences of such change on microbial communities and their functional potential. Indeed, increase in temperature will lead to faster and deeper thawing of the permafrost and thus, to higher microbial activity and likely increased release of greenhouse gases. With Arctic warming, will Arctic microbial communities experience high rates of extinctions, will they adapt to new environmental conditions or will their range change towards their preferred environmental conditions at the same rate of climatic modification and how will this impact ecosystems? Understanding the current diversity of Arctic microbial communities and biogeographical patterns is the basis to answer these questions and to improve the understanding of ecosystem function, which will allow the production of more accurate climate models through a deeper understanding of microbial interactions and the potential perturbation of their roles in nutrient cycling. It will also provide a baseline to monitor changes in these communities in the future. Research on microbial diversity in Arctic soils is still ongoing, and key information mentioned in this review is summarized in Table 2.

Acknowledgement

This project has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement no 675546.

References

Aliyu, H., De Maayer, P., and Cowan, D. (2016) The genome of the Antarctic polyextremophile *Nesterenkonia* sp. AN1 reveals adaptive strategies for survival under multiple stress conditions. *FEMS Microbiol Ecol* **92**: fiw032.

Anesio, A.M., Hodson, A.J., Fritz, A., Psenner, R., and Sattler, B. (2009) High microbial activity on glaciers: importance to the global carbon cycle. *Glob Chang Biol* **15**: 955–960.

Auguet, J.-C., Barberan, A., and Casamayor, E.O. (2010) Global ecological patterns in uncultured Archaea. *ISME J* **4**: 182–190.

Augustine, N., Kerkar, S., and Thomas, S. (2012) Arctic actinomycetes as potential inhibitors of *Vibrio cholerae* biofilm. *Curr Microbiol* **64**: 338–342.

Baker, B.J., and Banfield, J.F. (2003) Microbial communities in acid mine drainage. *FEMS Microbiol Ecol* **44**: 139–152.

Bakermans, C., Ayala-del-Río, H.L., Ponder, M.A., Vishnivetskaya, T., Gilichinsky, D., Thomashow, M.F., and Tiedje, J.M. (2006) *Psychrobacter cryohalolentis* sp. nov. and *Psychrobacter arcticus* sp. nov., isolated from Siberian permafrost. *Int J Syst Evol Microbiol* **56**: 1285–1291.

Baumgärtner, M., Koschorreck, M., and Conrad, R. (1996) Oxidative consumption of nitric oxide by heterotrophic bacteria in soil. *FEMS Microbiol Ecol* **19**: 165–170.

Berendsen, R.L., Pieterse, C.M., and Bakker, P.A. (2012) The rhizosphere microbiome and plant health. *Trends Plant Sci* **17**: 478–486.

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.

Boetius, A., Anesio, A.M., Deming, J.W., Mikucki, J.A., and Rapp, J.Z. (2015) Microbial ecology of the cryosphere: sea ice and glacial habitats. *Nat Rev Microbiol* **13**: 677–690.

Bredholdt, H., Galatenko, O.A., Engelhardt, K., Fjærvik, E., Terekhova, L.P., and Zotchev, S.B. (2007) Rare actinomycete bacteria from the shallow water sediments of the Trondheim fjord, Norway: isolation, diversity and biological activity. *Environ Microbiol* **9**: 2756–2764.

Buckeridge, K.M., Banerjee, S., Siciliano, S.D., and Grogan, P. (2013) The seasonal pattern of soil microbial community structure in mesic low arctic tundra. *Soil Biol Biochem* **65**: 338–347.

Buzzini, P., Branda, E., Goretti, M., and Turchetti, B. (2012) Psychrophilic yeasts from worldwide glacial habitats: diversity, adaptation strategies and biotechnological potential. *FEMS Microbiol Ecol* **82**: 217–241.

Campbell, B.J., Polson, S.W., Hanson, T.E., Mack, M.C., and Schuur, E.A. (2010) The effect of nutrient deposition on bacterial communities in Arctic tundra soil. *Environ Microbiol* **12**: 1842–1854.

Chong, C., Pearce, D., Convey, P., Yew, W., and Tan, I. (2012) Patterns in the distribution of soil bacterial 16S rRNA gene sequences from different regions of Antarctica. *Geoderma* **181**: 45–55.

Chong, C.-W., Pearce, D.A., and Convey, P. (2015) Emerging spatial patterns in Antarctic prokaryotes. *Front Microbiol* **6**: 1058.

Chu, H., Fierer, N., Lauber, C.L., Caporaso, J.G., 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.

Coolen, M.J., van de Giessen, J., Zhu, E.Y., and Wuchter, C. (2011) Bioavailability of soil organic matter and microbial

- community dynamics upon permafrost thaw. *Environ Microbiol* **13**: 2299–2314.
- Crump, B.C., Amaral-Zettler, L.A., and Kling, G.W. (2012) Microbial diversity in arctic freshwaters is structured by inoculation of microbes from soils. *ISME J* **6**: 1629–1639.
- Cuthbertson, L., Amores-Arrocha, H., Malard, L.A., Els, N., Sattler, B., and Pearce, D.A. (2017) Characterisation of Arctic bacterial communities in the air above Svalbard. *Biology* **6**: 29.
- D'Amico, S., Collins, T., Marx, J.C., Feller, G., and Gerday, C. (2006) Psychrophilic microorganisms: challenges for life. *EMBO Rep* **7**: 385–389.
- De Wit, R., and Bouvier, T. (2006) 'Everything is everywhere, but, the environment selects'; what did Baas Becking and Beijerinck really say? *Environ Microbiol* **8**: 755–758.
- Delgado-Baquerizo, M., Oliverio, A.M., Brewer, T.E., Benavent-González, A., Eldridge, D.J., Bardgett, R.D., et al. (2018) A global atlas of the dominant bacteria found in soil. *Science* **359**: 320–325.
- Dimitriu, P.A., and Grayston, S.J. (2010) Relationship between soil properties and patterns of bacterial β -diversity across reclaimed and natural boreal forest soils. *Microb Ecol* **59**: 563–573.
- Docherty, K.M., Borton, H.M., Espinosa, N., Gebhardt, M., Gil-Loaiza, J., Gutknecht, J.L., et al. (2015) Key edaphic properties largely explain temporal and geographic variation in soil microbial communities across four biomes. *PLoS One* **10**: e0135352.
- Dodds, W.K., Gudder, D.A., and Mollenhauer, D. (1995) The ecology of Nostoc. *J Phycol* **31**: 2–18.
- Donachie, S., Hou, S., Lee, K., Riley, C., Pikina, A., Belisle, C., et al. (2004) The Hawaiian archipelago: a microbial diversity hotspot. *Microb Ecol* **48**: 509–520.
- Dorador, C., Vila, I., Witzel, K.-P., and Imhoff, J.F. (2013) Bacterial and archaeal diversity in high altitude wetlands of the Chilean Altiplano. *Fundamental and Applied Limnology/Archiv für Hydrobiologie* **182**: 135–159.
- Elberling, B., Christiansen, H.H., and Hansen, B.U. (2010) High nitrous oxide production from thawing permafrost. *Nat Geosci* **3**: 332–335.
- Feller, G., and Gerday, C. (2003) Psychrophilic enzymes: hot topics in cold adaptation. *Nat Rev Microbiol* **1**: 200–208.
- Fierer, N., and Jackson, R.B. (2006) The diversity and biogeography of soil bacterial communities. *Proc Natl Acad Sci U S A* **103**: 626–631.
- Fierer, N., Bradford, M.A., and Jackson, R.B. (2007) Toward an ecological classification of soil bacteria. *Ecology* **88**: 1354–1364.
- Fierer, N., Leff, J.W., Adams, B.J., Nielsen, U.N., Bates, S. T., Lauber, C.L., et al. (2012) Cross-biome metagenomic analyses of soil microbial communities and their functional attributes. *Proc Natl Acad Sci U S A* **109**: 21390–21395.
- Frank-Fahle, B.A., Yergeau, É., Greer, C.W., Lantuit, H., and Wagner, D. (2014) Microbial functional potential and community composition in permafrost-affected soils of the NW Canadian Arctic. *PLoS One* **9**: e84761.
- Frey, B., Rime, T., Phillips, M., Stierli, B., Hajdas, I., Widmer, F., and Hartmann, M. (2016) Microbial diversity in European alpine permafrost and active layers. *FEMS Microbiol Ecol* **92**: fiw018.
- Ganzert, L., Bajerski, F., and Wagner, D. (2014) Bacterial community composition and diversity of five different permafrost-affected soils of Northeast Greenland. *FEMS Microbiol Ecol* **89**: 426–441.
- Ghiglione, J.-F., Galand, P.E., Pommier, T., Pedrós-Alió, C., Maas, E.W., Bakker, K., et al. (2012) Pole-to-pole biogeography of surface and deep marine bacterial communities. *Proc Natl Acad Sci U S A* **109**: 17633–17638.
- Gilbert, J.A., Hill, P.J., Dodd, C.E., and Laybourn-Parry, J. (2004) Demonstration of antifreeze protein activity in Antarctic lake bacteria. *Microbiology* **150**: 171–180.
- Gittel, A., Bárta, J., Kohoutová, I., Mikutta, R., Owens, S., Gilbert, J., et al. (2014a) Distinct microbial communities associated with buried soils in the Siberian tundra. *ISME J* **8**: 841–853.
- Gittel, A., Bárta, J., Kohoutová, I., Schneckner, J., Wild, B., Šapek, P., et al. (2014b) Site- and horizon-specific patterns of microbial community structure and enzyme activities in permafrost-affected soils of Greenland. *Front Microbiol* **5**: 541.
- Gostinčar, C., Grube, M., De Hoog, S., Zalar, P., and Gunde-Cimerman, N. (2010) Extremotolerance in fungi: evolution on the edge. *FEMS Microbiol Ecol* **71**: 2–11.
- 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.
- Harding, T., Jungblut, A.D., Lovejoy, C., and Vincent, W.F. (2011) Microbes in high Arctic snow and implications for the cold biosphere. *Appl Environ Microbiol* **77**: 3234–3243.
- He, D., Xiang, X., He, J.-S., Wang, C., Cao, G., Adams, J., and Chu, H. (2016) Composition of the soil fungal community is more sensitive to phosphorus than nitrogen addition in the alpine meadow on the Qinghai-Tibetan Plateau. *Biol Fertil Soils* **52**: 1059–1072.
- Henríquez, M., Vergara, K., Norambuena, J., Beiza, A., Maza, F., Ubilla, P., et al. (2014) Diversity of cultivable fungi associated with Antarctic marine sponges and screening for their antimicrobial, antitumoral and antioxidant potential. *World J Microbiol Biotechnol* **30**: 65–76.
- Herlemann, D.P., Labrenz, M., Jürgens, K., Bertilsson, S., Wanek, J.J., and Andersson, A.F. (2011) Transitions in bacterial communities along the 2000 km salinity gradient of the Baltic Sea. *ISME J* **5**: 1571–1579.
- Humbert, S., Tarnawski, S., Fromin, N., Mallet, M.-P., Aragno, M., and Zopfi, J. (2010) Molecular detection of anammox bacteria in terrestrial ecosystems: distribution and diversity. *ISME J* **4**: 450–454.
- Huston, A.L., Krieger-Brockett, B.B., and Deming, J.W. (2000) Remarkably low temperature optima for extracellular enzyme activity from Arctic bacteria and sea ice. *Environ Microbiol* **2**: 383–388.
- IPCC. (2014) In *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Core writing team, Pachauri, R.K., and Meyer, L.A. (eds). IPCC: Geneva, Switzerland, p. 151.
- Jakosky, B.M., Nealson, K.H., Bakermans, C., Ley, R.E., and Mellon, M.T. (2003) Subfreezing activity of microorganisms and the potential habitability of Mars' polar regions. *Astrobiology* **3**: 343–350.

- Ji, M., van Dorst, J., Bissett, A., Brown, M.V., Palmer, A. S., Snape, I., *et al.* (2016) Microbial diversity at Mitchell Peninsula, Eastern Antarctica: a potential biodiversity "hotspot". *Polar Biology* **39**: 237–249.
- Killham, K., and Prosser, J.I. (2015) The bacteria and archaea. In *Soil Microbiology, Ecology, and Biochemistry*. Paul, E.A. (ed). Cambridge, MA: Academic Press.
- Kim, H.M., Lee, M.J., Jung, J.Y., Hwang, C.Y., Kim, M., Ro, H.-M., *et al.* (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.
- Koven, C.D., Ringeval, B., Friedlingstein, P., Ciais, P., Cadule, P., Khvorostyanov, D., *et al.* (2011) Permafrost carbon-climate feedbacks accelerate global warming. *Proc Natl Acad Sci U S A* **108**: 14769–14774.
- Koyama, A., Wallenstein, M.D., Simpson, R.T., and Moore, J.C. (2014) Soil bacterial community composition altered by increased nutrient availability in Arctic tundra soils. *Front Microbiol* **5**: 516.
- Kumar, K., Mella-Herrera, R.A., and Golden, J.W. (2010) Cyanobacterial heterocysts. *Cold Spring Harb Perspect Biol* **2**: a000315.
- Kumar, M., Männistö, M.K., van Elsas, J.D., and Nissinen, R. M. (2016) Plants impact structure and function of bacterial communities in Arctic soils. *Plant Soil* **399**: 319–332.
- Kwon, H.Y., Jung, J.Y., Kim, O.-S., Laffly, D., Lim, H.S., and Lee, Y.K. (2015) Soil development and bacterial community shifts along the chronosequence of the Midtre Lovénbreen glacier foreland in Svalbard. *J Ecol Environ* **38**: 461–476.
- Larose, C., Berger, S., Ferrari, C., Navarro, E., Dommergue, A., Schneider, D., and Vogel, T.M. (2010) Microbial sequences retrieved from environmental samples from seasonal Arctic snow and meltwater from Svalbard, Norway. *Extremophiles* **14**: 205–212.
- Larose, C., Dommergue, A., and Vogel, T.M. (2013) The dynamic arctic snow pack: an unexplored environment for microbial diversity and activity. *Biology* **2**: 317–330.
- 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.
- Leary, D. (2008) *Bioprospecting in the Arctic*. United Nations University Institute of Advanced Studies (UNI-IAS), Yokohama, Japan.
- Lee, S.-H., Jang, I., Chae, N., Choi, T., and Kang, H. (2013) Organic layer serves as a hotspot of microbial activity and abundance in Arctic tundra soils. *Microb Ecol* **65**: 405–414.
- Liao, L., Chen, R., Jiang, M., Tian, X., Liu, H., Yu, Y., *et al.* (2016) Bioprospecting potential of halogenases from Arctic marine actinomycetes. *BMC Microbiol* **16**: 1.
- Liebner, S., Harder, J., and Wagner, D. (2008) Bacterial diversity and community structure in polygonal tundra soils from Samoylov Island, Lena Delta, Siberia. *Int Microbiol* **11**: 195–202.
- Lipson, D.A., and Schmidt, S.K. (2004) Seasonal changes in an alpine soil bacterial community in the Colorado Rocky Mountains. *Appl Environ Microbiol* **70**: 2867–2879.
- Lipson, D., Schadt, C., and Schmidt, S. (2002) Changes in soil microbial community structure and function in an alpine dry meadow following spring snow melt. *Microb Ecol* **43**: 307–314.
- Lozupone, C.A., and Knight, R. (2007) Global patterns in bacterial diversity. *Proc Natl Acad Sci U S A* **104**: 11436–11440.
- Mackelprang, R., Waldrop, M.P., DeAngelis, K.M., David, M. M., Chavarria, K.L., Blazewicz, S.J., *et al.* (2011) Metagenomic analysis of a permafrost microbial community reveals a rapid response to thaw. *Nature* **480**: 368–371.
- Madigan, M.T., Martinko, J.M., and Parker, J. (1997) *Brock Biology of Microorganisms*. Upper Saddle River, NJ: Prentice Hall.
- Männistö, M.K., Tirola, M., and Häggblom, M.M. (2009) Effect of freeze-thaw cycles on bacterial communities of Arctic tundra soil. *Microb Ecol* **58**: 621–631.
- Männistö, M.K., Kurhela, E., Tirola, M., and Häggblom, M.M. (2013) Acidobacteria dominate the active bacterial communities of Arctic tundra with widely divergent winter-time snow accumulation and soil temperatures. *FEMS Microbiol Ecol* **84**: 47–59.
- Martineau, C., Pan, Y., Bodrossy, L., Yergeau, E., Whyte, L. G., and Greer, C.W. (2014) Atmospheric methane oxidizers are present and active in Canadian high Arctic soils. *FEMS Microbiol Ecol* **89**: 257–269.
- Martiny, J.B.H., Bohannan, B.J., Brown, J.H., Colwell, R.K., Fuhrman, J.A., Green, J.L., *et al.* (2006) Microbial biogeography: putting microorganisms on the map. *Nat Rev Microbiol* **4**: 102–112.
- Martiny, J.B., Eisen, J.A., Penn, K., Allison, S.D., and Horner-Devine, M.C. (2011) Drivers of bacterial β -diversity depend on spatial scale. *Proc Natl Acad Sci U S A* **108**: 7850–7854.
- Marushchak, M., Pitkämäki, A., Koponen, H., Biasi, C., Seppälä, M., and Martikainen, P. (2011) Hot spots for nitrous oxide emissions found in different types of permafrost peatlands. *Glob Chang Biol* **17**: 2601–2614.
- Mindlin, S., Soina, V., Petrova, M., and Gorlenko, Z.M. (2008) Isolation of antibiotic resistance bacterial strains from Eastern Siberia permafrost sediments. *Russ J Genet* **44**: 27–34.
- Moon, K., Ahn, C.-H., Shin, Y., Won, T.H., Ko, K., Lee, S.K., *et al.* (2014) New benzoxazine secondary metabolites from an Arctic actinomycete. *Mar Drugs* **12**: 2526–2538.
- Morita, R.Y. (1975) Psychrophilic bacteria. *Bacteriol Rev* **39**: 144.
- 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.
- Ngugi, D.K., Antunes, A., Brune, A., and Stingl, U. (2012) Biogeography of pelagic bacterioplankton across an antagonistic temperature–salinity gradient in the Red Sea. *Mol Ecol* **21**: 388–405.
- Niederberger, T.D., McDonald, I.R., Hacker, A.L., Soo, R.M., Barrett, J.E., Wall, D.H., and Cary, S.C. (2008) Microbial

- community composition in soils of Northern Victoria Land, Antarctica. *Environ Microbiol* **10**: 1713–1724.
- Niederberger, T.D., Steven, B., Charvet, S., Barbier, B., and Whyte, L.G. (2009) *Virgibacillus arcticus* sp. nov., a moderately halophilic, endospore-forming bacterium from permafrost in the Canadian high Arctic. *Int J Syst Evol Microbiol* **59**: 2219–2225.
- O'Malley, M.A. (2007) The nineteenth century roots of 'everything is everywhere'. *Nat Rev Microbiol* **5**: 647–651.
- Palmer, K., Biasi, C., and Horn, M.A. (2012) Contrasting denitrifier communities relate to contrasting N₂O emission patterns from acidic peat soils in arctic tundra. *ISME J* **6**: 1058–1077.
- Pearce, D.A., Alekhina, I.A., Terauds, A., Wilmotte, A., Quesada, A., Edwards, A., et al. (2016) Aerobiology over Antarctica – a new initiative for atmospheric ecology. *Front Microbiol* **7**: 16.
- Philippot, L., Raaijmakers, J.M., Lemanceau, P., and Van Der Putten, W.H. (2013) Going back to the roots: the microbial ecology of the rhizosphere. *Nat Rev Microbiol* **11**: 789–799.
- Pushkareva, E., Pessi, I.S., Wilmotte, A., and Elster, J. (2015) Cyanobacterial community composition in Arctic soil crusts at different stages of development. *FEMS Microbiol Ecol* **91**: fiv143.
- Qian, P.-Y., Wang, Y., Lee, O.O., Lau, S.C., Yang, J., Lafi, F.F., et al. (2011) Vertical stratification of microbial communities in the Red Sea revealed by 16S rDNA pyrosequencing. *ISME J* **5**: 507–518.
- Robinson, C.H. (2001) Cold adaptation in Arctic and Antarctic fungi. *New Phytol* **151**: 341–353.
- Rousk, J., Bååth, E., Brookes, P.C., Lauber, C.L., Lozupone, C., Caporaso, J.G., et al. (2010) Soil bacterial and fungal communities across a pH gradient in an arable soil. *ISME J* **4**: 1340–1351.
- Sangal, V., Goodfellow, M., Jones, A.L., Schwalbe, E.C., Blom, J., Hoskisson, P.A., and Sutcliffe, I.C. (2016) Next-generation systematics: an innovative approach to resolve the structure of complex prokaryotic taxa. *Sci Rep* **6**: 38392.
- Schostag, M., Stibal, M., Jacobsen, C.S., Bælum, J., Taş, N., Elberling, B., et al. (2015) Distinct summer and winter bacterial communities in the active layer of Svalbard permafrost revealed by DNA- and RNA-based analyses. *Front Microbiol* **6**: 399.
- Segawa, T., Takeuchi, N., Rivera, A., Yamada, A., Yoshimura, Y., Barcaza, G., et al. (2013) Distribution of antibiotic resistance genes in glacier environments. *Environ Microbiol Rep* **5**: 127–134.
- Shen, C., Xiong, J., Zhang, H., Feng, Y., Lin, X., Li, X., et al. (2013) Soil pH drives the spatial distribution of bacterial communities along elevation on Changbai Mountain. *Soil Biol Biochem* **57**: 204–211.
- Shen, C., Ni, Y., Liang, W., Wang, J., and Chu, H. (2015) Distinct soil bacterial communities along a small-scale elevational gradient in alpine tundra. *Front Microbiol* **6**: 582.
- 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.
- Siciliano, S.D., Palmer, A.S., Winsley, T., Lamb, E., Bissett, A., Brown, M.V., et al. (2014) Soil fertility is associated with fungal and bacterial richness, whereas pH is associated with community composition in polar soil microbial communities. *Soil Biol Biochem* **78**: 10–20.
- Siles, J.A., and Margesin, R. (2016) Abundance and diversity of bacterial, archaeal, and fungal communities along an altitudinal gradient in alpine forest soils: what are the driving factors? *Microb Ecol* **72**: 207–220.
- Smith, J.J., Tow, L.A., Stafford, W., Cary, C., and Cowan, D. A. (2006) Bacterial diversity in three different Antarctic cold desert mineral soils. *Microb Ecol* **51**: 413–421.
- Steven, B., Leveille, R., Pollard, W.H., and Whyte, L.G. (2006) Microbial ecology and biodiversity in permafrost. *Extremophiles* **10**: 259–267.
- 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.
- Steven, B., Lionard, M., Kuske, C.R., and Vincent, W.F. (2013) High bacterial diversity of biological soil crusts in water tracks over permafrost in the high arctic polar desert. *PLoS One* **8**: e71489.
- Tam, L., Derry, A., Kevan, P., and Trevors, J. (2001) Functional diversity and community structure of microorganisms in rhizosphere and non-rhizosphere Canadian arctic soils. *Biodivers Conserv* **10**: 1933–1947.
- Tedersoo, L., Bahram, M., Pölme, S., Kõljalg, U., Yorou, N. S., Wijesundera, R., et al. (2014) Global diversity and geography of soil fungi. *Science* **346**: 1256688.
- Teo, J.K.C., and Wong, C.M.V.L. (2014) Analyses of soil bacterial diversity of the Schirmacher Oasis, Antarctica. *Polar Biol* **37**: 631–640.
- Thompson, L.R., Sanders, J.G., McDonald, D., Amir, A., Ladau, J., Locey, K.J., et al. (2017) A communal catalogue reveals Earth's multiscale microbial diversity. *Nature* **551**: 457–463.
- Torsvik, V., Sørheim, R., and Goksøyr, J. (1996) Total bacterial diversity in soil and sediment communities – a review. *J Ind Microbiol* **17**: 170–178.
- Tveit, A., Schwacke, R., Svenning, M.M., and Ulrich, T. (2013) Organic carbon transformations in high-Arctic peat soils: key functions and microorganisms. *ISME J* **7**: 299–311.
- Vos, M., Wolf, A.B., Jennings, S.J., and Kowalchuk, G.A. (2013) Micro-scale determinants of bacterial diversity in soil. *FEMS Microbiol Rev* **37**: 936–954.
- Wagner, R., Zona, D., Oechel, W., and Lipson, D. (2017) Microbial community structure and soil pH correspond to methane production in Arctic Alaska soils. *Environ Microbiol* **19**: 3398–3410.
- 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.
- Walsh, F. (2013) Investigating antibiotic resistance in non-clinical environments. *Front Microbiol* **4**: 19.
- Wang, J.-T., Cao, P., Hu, H.-W., Li, J., Han, L.-L., Zhang, L.-M., et al. (2015) Altitudinal distribution patterns of soil bacterial and archaeal communities along Mt. Shigyla on the Tibetan Plateau. *Microb Ecol* **69**: 135–145.

- Whyte, L.G., Bourbonniere, L., and Greer, C.W. (1997) Biodegradation of petroleum hydrocarbons by psychrotrophic *Pseudomonas* strains possessing both alkane (alk) and naphthalene (nah) catabolic pathways. *Appl Environ Microbiol* **63**: 3719–3723.
- Wilhelm, R.C., Niederberger, T.D., Greer, C., and Whyte, L. G. (2011) Microbial diversity of active layer and permafrost in an acidic wetland from the Canadian high Arctic. *Can J Microbiol* **57**: 303–315.
- Womack, A.M., Bohannon, B.J., and Green, J.L. (2010) Biodiversity and biogeography of the atmosphere. *Philos Trans R Soc B: Biol Sci* **365**: 3645–3653.
- Yergeau, E., Newsham, K.K., Pearce, D.A., and Kowalchuk, G. A. (2007) Patterns of bacterial diversity across a range of Antarctic terrestrial habitats. *Environ Microbiol* **9**: 2670–2682.
- Yukimura, K., Nakai, R., Kohshima, S., Uetake, J., Kanda, H., and Naganuma, T. (2009) Spore-forming halophilic bacteria isolated from Arctic terrains: implications for long-range transportation of microorganisms. *Polar Sci* **3**: 163–169.
- Zakhia, F., Jungblut, A.-D., Taton, A., Vincent, W.F., and Wilmotte, A. (2008) Cyanobacteria in cold ecosystems. In *Psychrophiles: From Biodiversity to Biotechnology*. Margesin, R., Schinner, F., Marx, J.C., and Gerday, C. (eds). Dordrecht: Springer, pp. 121–135.
- Zhang, W., Wu, X., Liu, G., Dong, Z., Zhang, G., Chen, T., and Dyson, P.J. (2014) Tag-encoded pyrosequencing analysis of bacterial diversity within different alpine grassland ecosystems of the Qinghai-Tibet Plateau, China. *Environ Earth Sci* **72**: 779–786.
- Zhang, T., Wang, N.-F., Liu, H.-Y., Zhang, Y.-Q., and Yu, L.-Y. (2016) Soil pH is a key determinant of soil fungal community composition in the Ny-Ålesund region, Svalbard (high Arctic). *Front Microbiol* **7**: 227.
- Zinger, L., Shahnava, B., Baptist, F., Geremia, R.A., and Choler, P. (2009) Microbial diversity in alpine tundra soils correlates with snow cover dynamics. *ISME J* **3**: 850–859.

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1: Supplementary Table

Fig. S1 Supplementary Fig. S1