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Malard, Lucie; Pearce, David A

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## 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 CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O 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 (CO<sub>2</sub>), methane (CH<sub>4</sub>) and nitrous oxide (N<sub>2</sub>O) 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.

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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 CO<sub>2</sub> and N<sub>2</sub> uptake (Zakhia *et al.*, 2008) and as plants are unable to fix N<sub>2</sub>, 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 N<sub>2</sub> fixation species form heterocysts, which are specialized cells with thicker cell walls to protect nitrogenase from O<sub>2</sub> inactivation (Kumar *et al.*, 2010). *Nostoc* sp. are found in abundance in Arctic soils across the region and are the main N<sub>2</sub> fixers identified, thus transforming N<sub>2</sub> 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 (annamox), which leads to the production of N<sub>2</sub> (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.

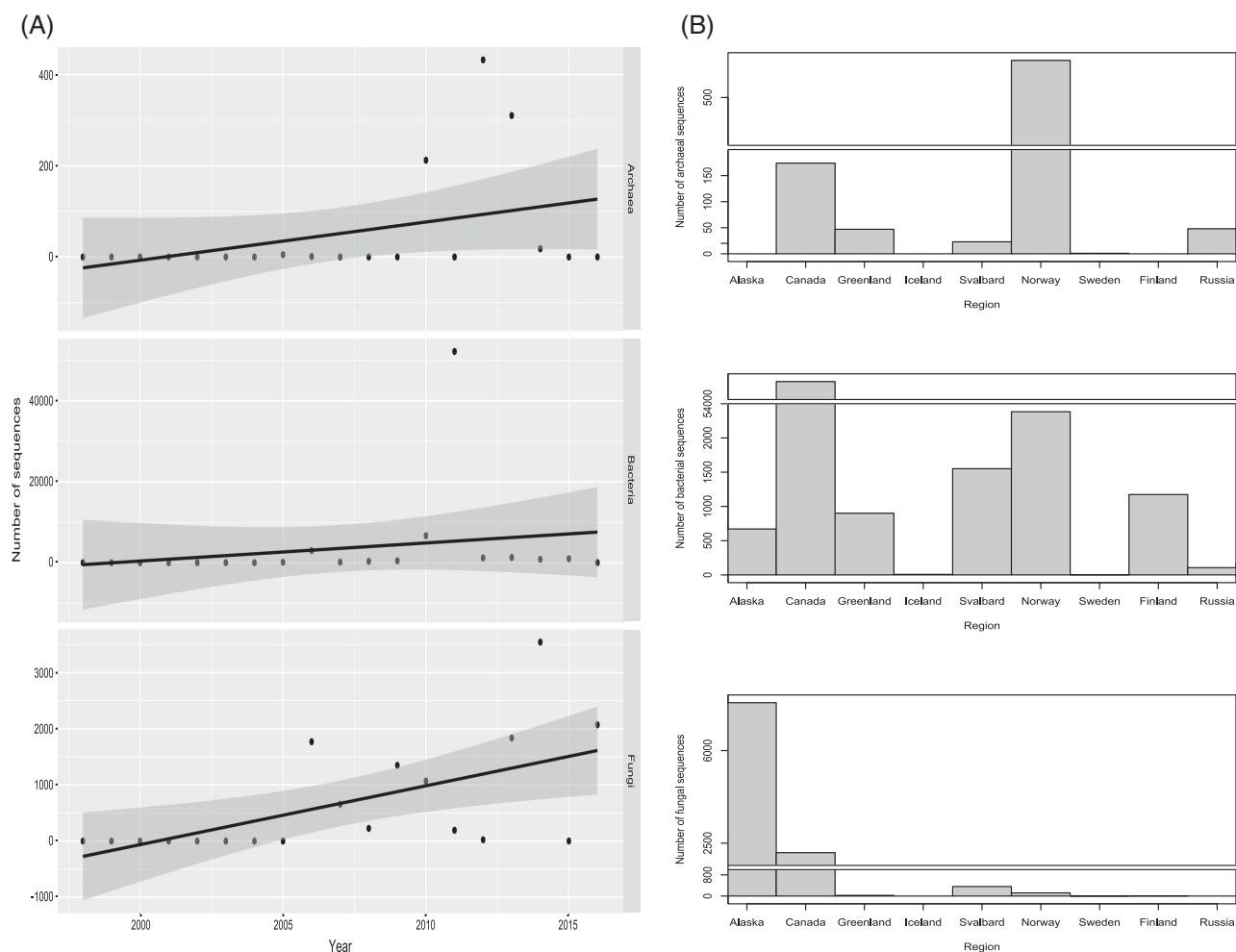
This map shows the number of studies published in English and indexed in Scopus. Striated areas indicate most intensively studied sites in the Arctic region.

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  $\text{CH}_4$  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  $\text{CH}_4$  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

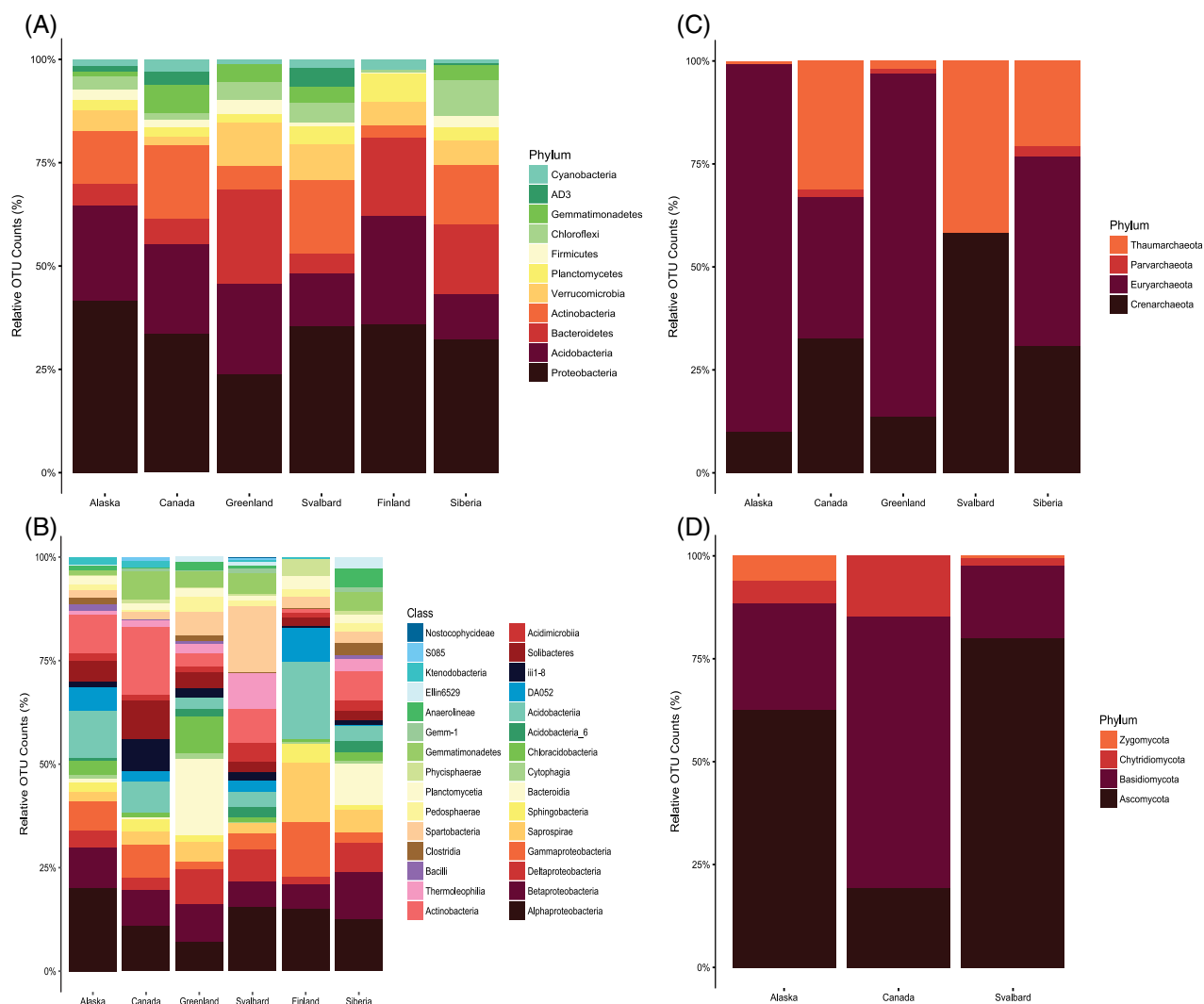
Despite polar environmental conditions, the microbial biomass and diversity of tundra ecosystems appears equivalent

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.

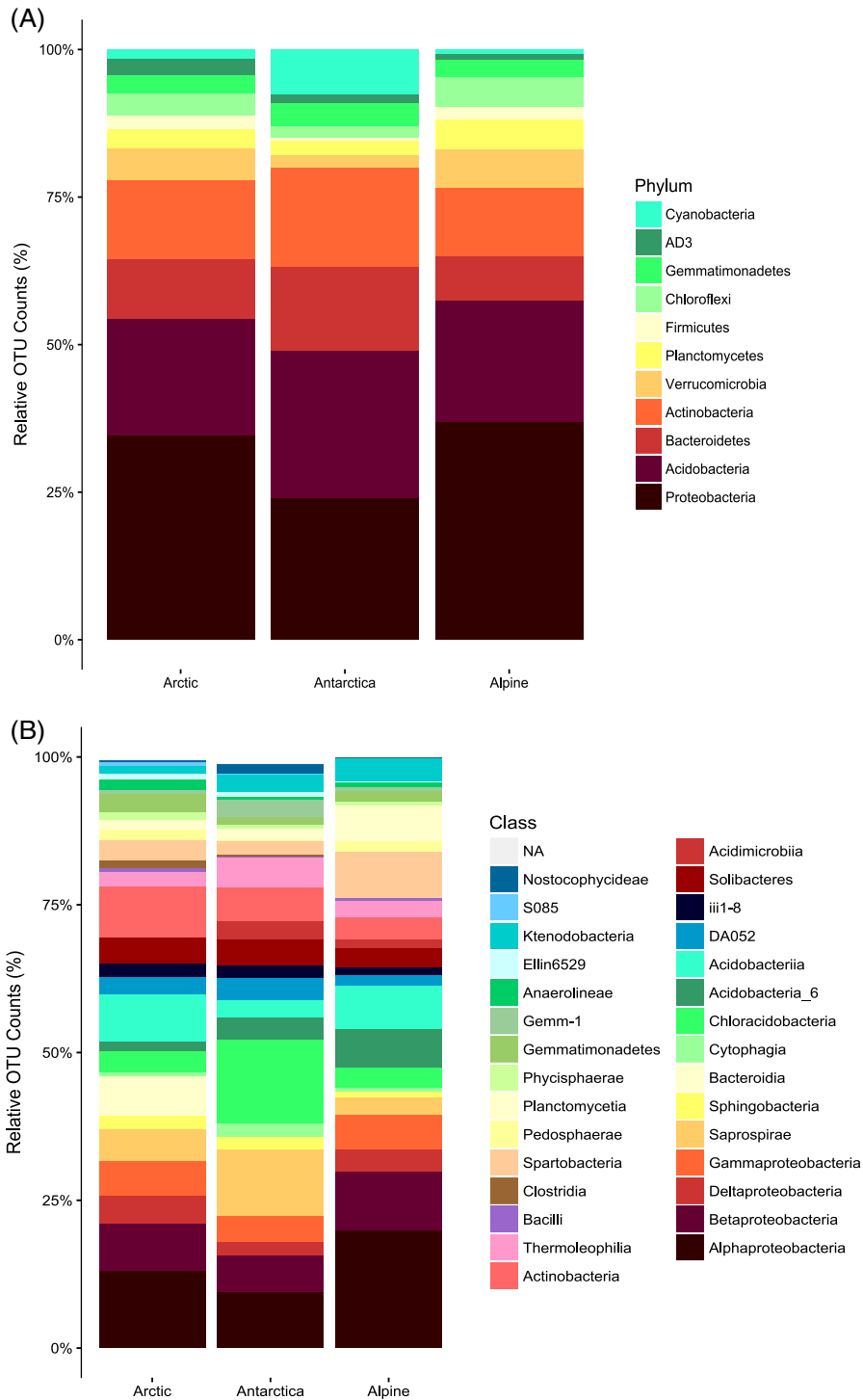
C. Archaeal phyla identified in each region. Missing Arctic regions had no known studies at the time of analysis.

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 <sub>2</sub> O release seems much higher than previously estimated  | N <sub>2</sub> O is 300 times more potent than CO <sub>2</sub> . Bulk release could have major climatic impacts but rates of N <sub>2</sub> 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.

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### 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