Microbial activity monitoring by the Integrated Arctic Earth Observing System (MamSIOS)

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Scientific background

Microorganisms, though already integral elements, are likely to play an increasingly important role in the Earth's climate system (Falkowski et al., 2008) and are known to affect polar biogeochemical cycles (Larose et al., 2013a). In particular, they play important roles in the generation and decomposition of climate active gases. However, current climate models do not take into account the response of microbial activity and their influence in biochemical cycles (Incorporating microbial processes into climate models, ASM report). To improve the predictive ability of climate models, it is important to understand the mechanisms by which microorganisms regulate terrestrial greenhouse gas flux and to determine whether changes in microbial processes will lead to net positive or negative feedbacks on greenhouse gas emissions (Singh et al., 2010). This contribution has been particularly overlooked for the polar regions (Figure 1), where the environment has traditionally been considered too harsh for significant microbial activity to occur. It has long been considered that any life, if present at all, was either dormant or functioning sub-optimally, as living organisms have to be well adapted or highly resistant to extreme cold and desiccation, low nutrient availability and seasonally variable UV radiation levels in order to survive (Harding et al., 2011; Cameron et al., 2012; Goordial et al., 2013; Larose et al., 2013a). However, it is now clear that microbial presence is ubiquitous across the polar regions, and recent research into the polar aerobiome points toward a potentially dynamic polar microbial community and with it, the possibility of significant microbial activity within the snowpack (Redeker et al., 2017), even in the most remote locations (Pearce et al., 2009). Research into the aerobiome has also demonstrated that microorganisms in aerial fallout may remain both viable and active (Sattler et al., 2001; Harding et al., 2011). Furthermore, the presence of microbes in remote, low nutrient, low water, very cold environments such as polar glacial surfaces is now well established for a number of key sites (Hodson et al., 2008; Larose et al., 2010).
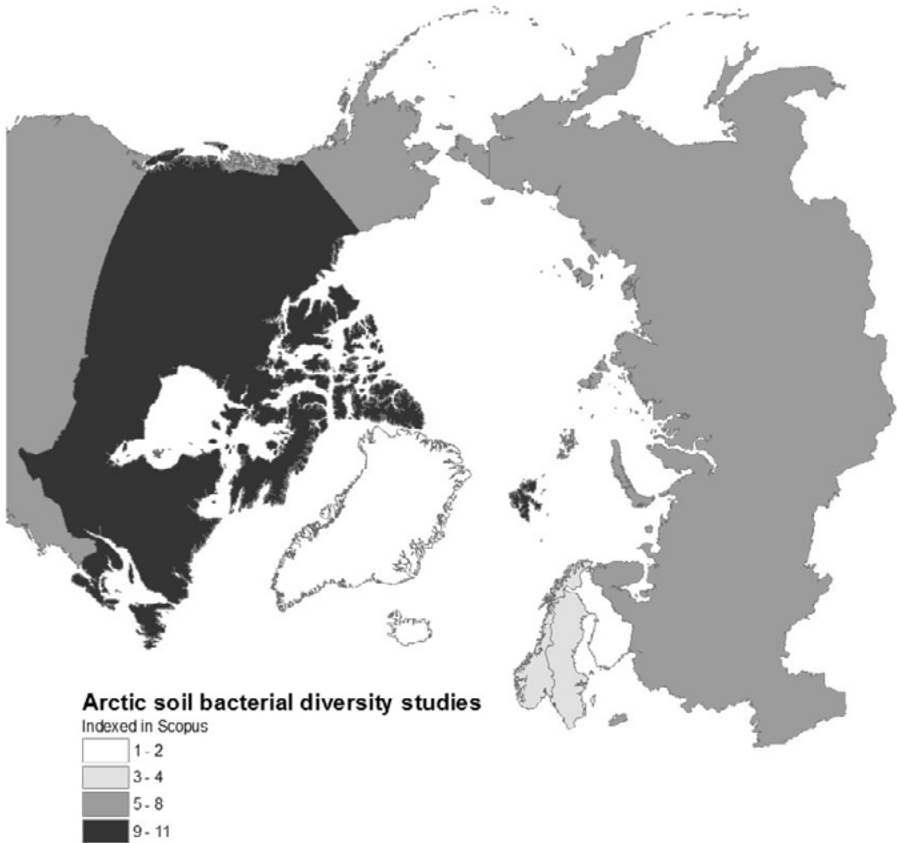
Arctic soil bacterial diversity studies
Indexed in Scopus
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Figure 1: Soil bacterial diversity studies across the Arctic region as evidenced by publications in the literature cited in SCOPUS (2017). Adapted from Malard and Pearce (2018).

Polar terrestrial environments, including snow and ice, are dominated by microorganisms. Arctic soils are known to harbour significant microbial abundance and diversity, with huge potential to alter the global climate system. For example, Arctic soils alone are known to store over 1500 Pg of carbon (Koven et al., 2011) and, as the Arctic region continues to undergo drastic changes linked to human activities, the likelihood of release of greenhouse gases such as CO_2, CH_4 and N2O will continue to increase. Environments so far thought to be microbiologically inactive, such as ice caps and the polar firn, have increasingly been demonstrated to influence greenhouse gas cycling. These then present a huge potential for positive feedback effects on climate, highlighting the pressing need to understand and monitor changes in the abundance, diversity and particularly ecological function of microbial communities in the polar regions in order to produce more accurate greenhouse gas release models.

The polar cryosphere represents approximately 14% of the Earth's surface (Morita, 1975; Larose et al., 2010; Boetius et al., 2015; Lutz et al., 2016). In this region, microorganisms can thrive and are present in abundance. This includes the tundra (Lee et al., 2013), taiga (Neufeld and Mohn, 2005), snow (Larose et al., 2013a), glaciers (Anesio et al., 2009), permafrost (Mackelprang et al., 2011) as well as marine (Ghiglione et al., 2012), freshwater (Crump et al., 2012) and aerial (Cuthbertson et al., 2017) ecosystems.

Microbial metabolic activity can potentially influence climate and biogeochemical processes through:
1. Physical albedo (through ice nucleation activity and cloud formation)
2. Biological albedo (through significant pigmentation associated with snow algal blooms)
3. Methane cycling – production (methanogenesis)
4. Methane cycling - degradation (methane oxidation)
5. Carbon fixation (autotrophy and bacteriorhodopsins)
6. Carbon sequestration dynamics (in deep sea sediments)
7. Nitrogen cycling (in particular N_2O production)
8. Sulphur cycling (dimethyl sulphide production in soil)
9. Permafrost thaw (and the microbial response)
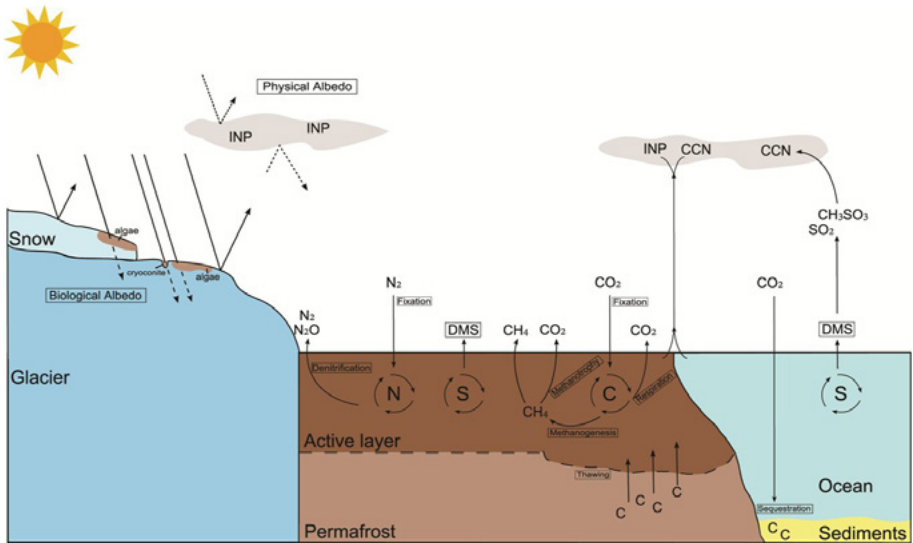10. Recent discoveries (such as methyl halide degradation)

Figure 2: Diagram of microbial metabolic activities influencing climate and biogeochemical processes. Cloud condensation nuclei (CCN) and ice nucleating particles (INP) can come from all environments, including glacial ice, sea ice and snow. Sulphate aerosols such as Sulphur dioxide (SO_2) and methanosulphate (CH_3SO_3) react with cloud condensation nuclei (CCN).

Physical albedo (Ice nucleation)

Bacteria and other primary biological aerosol particles are now known to enhance cloud formation through acting as cloud condensation nuclei (CCN) or through the expression of ice nucleation proteins in their cell membranes, hence acting as ice nucleating particles (INP). Clouds play an important role in the global climate system (IPCC, 2013). Depending on their optical properties either their reflection of shortwave solar radiation dominates - hence exerting a cooling effect - or reflection of terrestrial longwave radiation dominates – resulting in a warming effect. The net radiative effect of a cloud is a function of its altitude, size, thickness, and the number of liquid droplets and ice crystals (Shupe and Intrieri, 2004). Furthermore, the brightness (albedo) of the underlying ground is decisive. This is particularly important in the Arctic, where snow and sea ice feature a very high albedo and clouds hence act as a 'blanket' increasing the temperature at the surface (Stramler et al., 2011). This effect is most critical in the transition from winter to spring time, when the Arctic becomes more cloudy and the net cloud radiative effect results in warming, moving the sea ice and snow closer to the melting temperature (Stramler et al., 2011).

With the recognition of the importance of cloud radiative effects on the Arctic cryosphere, it becomes apparent that improving the representation of cloud properties in climate models is essential. To date, however, a number of studies have shown that radiation biases through the misrepresentation of clouds in climate models are alarmingly high in the Arctic (Tjernstrom et al., 2008; English et al., 2014; English et al., 2015), in the range 10 – 25 W m$_{-2}$. For reference, an imbalance of +10 W m$_{-2}$ is roughly equivalent to the annual loss of 1000kg of ice per m$_2$. One of the uncertainties associated with cloud properties in the Arctic is the presence of CCN and INP that determine the liquid and ice water content of the clouds and hence their optical properties.

The sources of aerosols for cloud formation in the Arctic are limited. Excluding situations in which long-range transport is present, for which it is known that the additional particles form clouds and modify their properties (Stohl et al., 2007; Maahn et al., 2017), microbial particles originating from the sea surface micro layer are thought to play an important role. The sea surface micro layer (SML) (Leck and Bigg, 2005) can contain aggregates of whole microorganisms, such as bacteria, viruses or phytoplankton, or their fragments, together with micro-gels or transparent exopolymer particles (Leck and Bigg, 2005; Hawkins et al., 2010; Russell et al., 2010; Orellana et al., 2011; Quinn et al., 2015; Schwier et al., 2015; Wilson et al., 2015). Several studies have stressed the importance of SML biological material as marine CCN and INP (Leck and Bigg, 2005; Bigg and Leck, 2008; Alpert et al., 2011a; Alpert et al., 2011b; Knopf et al., 2011; Karl et al., 2013; Heintzenberg et al., 2015; Wilson et al., 2015). However, other studies showed that marine micro-gels and bacteria have a low hygroscopicity (Després et al., 2012; Dawson et al., 2016). In fact, microbial exudates in seawater were found to decrease the CCN activity of sea spray particles (Wex et al., 2010).

Perhaps more important is the role of microorganisms to the Arctic INP population because of the presence of ice nucleating proteins on their cell surfaces. These ice nucleation proteins serve to encourage the crystallization of ice outside the cell and thereby protect the cell itself from ice damage. The expression of such proteins leads to the condensation of liquid water and freezing and hence enhances cloud production (Amato et al., 2005; Amato et al., 2006; Burrows et al., 2009; Bowers et al., 2011; Joly et al., 2013; Amato et al., 2015; Moffett et al., 2015; Moffett, 2015; Mortazavi et al., 2015; Šantl-Temkiv et al., 2015; Wilson et al., 2015; Hara et al., 2016; Lu et al., 2016; Smets et al., 2016). To date the quantity and origin of airborne INP over the remote oceans in general remains elusive (Bigg, 1973; Fall and Schnell, 1985; Rosinski et al., 1986; Junge and Swanson, 2008; Burrows et al., 2013; Wilson et al., 2015), even though research in the 1970s already showed that laboratory cultured phytoplankton can produce large amounts of INP (Schnell, 1975). The scarcity of data is particularly true for the Arctic where only very recently the role of marine organisms has been elucidated and particles < 0.2 μm, likely ultra-microbacteria, viruses or extracellular material from phytoplankton or bacteria exudates, were identified as candidates for INP (Irish et al., 2017). For a long time, no marine organism had been unambiguously identified

as effective INP (Fall and Schnell, 1985; Junge and Swanson, 2008). Recently, Knopf et al. (2011) and Alpert et al. (2011a) were able to show that the marine diatom *Thalassiosira pseudonana* initiates ice formation under circumstances relevant to the marine mixed-phase and ice cloud regimes. Conversely, others attributed marine INP to the species' exudates, heat-sensitive organic material < 0.2 μm (Wilson et al., 2015). While there are indications that marine INP are associated with decaying phytoplankton blooms (Wang et al., 2015; McCluskey et al., 2017), the origin of INP remains completely unclear over ice covered regions like the central Arctic Ocean.

From the above, it is evident that the sources and activity of Arctic INPs are not well understood. However, to estimate the radiative properties of Arctic clouds in the future, to enhance e.g. sea ice predictions, understanding the mix of liquid and ice water content in clouds is important. It is known that liquid-only clouds have a three times stronger longwave radiative effect (warming) than ice-only clouds in the Arctic (Shupe and Intrieri, 2004). As the Arctic becomes rapidly warmer, the cloud water phase might shift toward more liquid clouds, resulting in positive feedback. However, if Arctic microorganisms were efficient INP and become more abundant in a warmer Arctic, e.g. through more exposed open ocean, they could induce a negative feedback. Some biological particles are known to be very efficient ice nuclei, and they can nucleate ice at temperatures as high as – 4°C (Després et al., 2012).

To understand what the source of INP in the Arctic are today, and how they will change and influence Arctic clouds in the future, dedicated studies need to be initiated. We suggest installing e.g. filter samplers at observatories and remote locations around Svalbard that represent marine and terrestrial aerosol sources. With these filters, ice nucleation studies can be conducted in parallel with microscopy and microbiological investigations that attempt to close the link between the presence of biological particles and INP concentrations.

Biological albedo: snow algae

Microbes can darken the surfaces of snow and ice, thus reducing its reflectance or albedo, and increasing the rate of ablation during the summer (Kohshima et al., 1994). The process is best understood in the context of the direct effects, which relate to the production of pigments in response to either high levels of irradiance or nutrient limitation (Cook et al., 2017b). Pigment change to an existing surface population, the exposure of a previously buried community and the proliferation of cells as a result of biological growth all result in darker snow surfaces, and thus enhance the melt for a given solar irradiance value. Heavily pigmented snows have been described in some of the earliest scientific literature from the polar regions (Horner, 2017). Ongoing research in Svalbard and elsewhere has sought

a deeper understanding of the biosynthesis of pigments, in conjunction with work on cell physiology (Müller et al., 1998; Remias et al., 2005) and, more recently, molecular techniques (Lutz et al., 2015). Until recently, biotechnology, rather than an interest in bioalbedo *per se*, has been the principal driver of such research (Leya et al., 2009).

The indirect effects of microorganisms upon albedo, linked to the feedbacks associated with snow grain metamorphosis and increased water content adjacent to the cells, have been largely overlooked. This means our understanding of so-called "bioalbedo" is incomplete. The most promising way forward, resulting in a predictive understanding of how microorganisms influence the rate of snow ablation through both direct and indirect processes, involves the application of radiative transfer theory, rather than empirical techniques. However, establishing empirical relationships between cell biomass and snow albedo are still valid for monitoring purposes (Stibal et al., 2017). The fully physically-based approach offered by radiative transfer theory has resulted in a first generation of models that predict the spectral albedo of snow under different physical and biological conditions, the latter incorporating snow algal cell counts and pigment concentrations (Cook et al., 2017a). More recent work has refined the underlying physical basis of the modelling and has also developed a workflow for the successful measurement of snow algae and other parameters during fieldwork and sample processing (Cook et al., 2017b).

The links between cell biomass, albedo, and melting have led to great interest in the climate change feedbacks associated with snowpacks becoming wetter for longer periods during the summer, and therefore potentially darker on account of there being more opportunity for pigmented bloom development (Ganey et al., 2017). The direct link between pigment production and surface melt rate has been heavily exploited via the community response to funding calls. However, the spatial variability in snow biomass across large parts of the Arctic is poorly resolved and, hence, our understanding of the true impact of bioalbedo. Current work suggests that the direct influence of pigmented snow algae upon albedo is clear in some relatively large sub-Arctic 'snowfields' (Painter et al., 2001; Takeuchi et al., 2006; Ganey et al., 2017). These sites are fascinating, but there is a risk that the data they generate will be used to over-generalise the global influence of biological albedo forcing. Establishing the regional distribution of snow biomass is, therefore, a clear research priority, and Svalbard can offer much in this context with respect to the development, ground truthing and application of relevant techniques for addressing this problem. Furthermore, there also needs to be a better emphasis upon the vertical distribution of biomass, because solar radiation penetrates snow packs to enable sub-surface photosynthesis and biomass change (Hodson et al., 2017). The contribution made by the absorption of such light to snow grain metamorphosis and melt is almost completely unexplored.

Biological albedo: ice algae

The exposure of bare glacier ice following the retreat of seasonal snow is the largest event in the seasonal albedo evolution of glacier surfaces. This is because the ablation area of glaciers accumulates dust and other debris over long periods, resulting in a heterogeneous veneer of debris aggregates called "cryoconite" (Cook et al., 2016). Microorganisms play a cardinal role in the persistence and impact of cryoconite because they induce aggregation through bioflocculation (Langford et al., 2010; Takeuchi et al., 2010), often using debris particles as a surface for attachment and growth. The attachment processes are often facilitated by the production of extra-cellular exudates and aggregate growth can last for several ablation seasons (Takeuchi et al., 2001; Hodson et al., 2010). Measurements of the reflectance of dry cryoconite from a range of locations (including Svalbard) typically show values of < 20% across the entire visible to near-infra-red spectrum in cases where the granules contain an appreciable amount of organic matter (Takeuchi, 2002). When wetted by meltwater, the albedo of cryoconite granules can be as low as 5%, an order of magnitude lower than bare glacier ice with no such impurities, and almost 20 times lower than fresh snow (Bøggild et al., 2010). However, the thermodynamics of enhanced melting beneath cryoconite are such that the aggregates melt into the ice to become shaded, thus reducing their impact until they are melted out by non-solar-derived energy (turbulent heat fluxes). Therefore quantifying the impact of cryoconite upon ablation is not a simple calculation, as it depends upon the ratio of turbulent to radiative heat (Tedstone et al., 2017). Furthermore, the stronger the melt, the greater the probability that cryoconite and other dark impurities will be washed off the glacier (Takeuchi et al., 2003). However, one thing is clear, microorganisms are essential to the persistence and therefore the duration of biological albedo forcing on the ice surface. Svalbard research has been critical to the development of this realization and has been the location of many pioneering process studies (Cook et al., 2010) and monitoring applications (Hodson et al., 2007; Irvine-Fynn et al., 2011) relevant to bioalbedo. For example, airborne UAV mapping was pioneered in Svalbard (Hodson et al., 2007) some ten years before it was undertaken in Greenland (Ryan et al., 2018), where interest in ice surface albedo has received considerable recent coverage. Here, cryoconite is a strong contributor to the lowest albedo surfaces found in the so-called "Dark Zone" (Wientjes and Oerlemans, 2010; Tedstone et al., 2017). Future research in Svalbard can add a much-needed addition to that on Greenland, especially if the emphasis is given to its ice caps, which offer an idealized, whole system perspective on the life cycle of dust and other albedo-reducing impurities at a very manageable spatial scale.

In recent years, there has been increasing attention to the influence of heavily pigmented micro-algae growing on the ice surface and often between the melt pools formed by the denser, mineral-rich cryoconite (Yallop et al., 2012; Stibal et al., 2017; Williamson et al., 2018). Unlike cryoconite, algae such as *Mesotaenium berggrenii* do not melt into the ice and can develop strong purpurogallin pigmentation due to almost constant, direct illumination

(Remias et al., 2012). These algae, along with cryoconite, contribute strongly to albedo reduction in the important "Dark Zone" of the Greenland Ice Sheet, but research is required to understand their importance elsewhere. They are certainly present in Svalbard, but often not in high densities. Furthermore, the overlapping spectral reflectance characteristics of purpurogallins, dust, black carbon and other biological pigments such as chlorophyll, mean that unravelling their separate albedo influence will take some time and is beyond simple empirical techniques.

Future research in Svalbard and other areas subject to intense mass loss by surface melting will, therefore, have to address this problem. In so doing, particular attention needs to be given to the extremely complex nature of the upper metre or so of melting glacier ice: the so-called "weathering crust". Work in Svalbard and other regions has demonstrated that significant, additional complexity is associated with the transient water storage and ice crystal metamorphosis in the weathering crust (Cook et al., 2012; Irvine-Fynn et al., 2012; Rassner et al., 2016; Stevens et al., 2018). This storage provides prolonged opportunities for biological processes, but its rapidly changing reflectance properties will make accurate predictions of bare ice albedo and surface biomass distribution a major challenge for some years.

Methanogenesis (Methane cycling – production)

The active layer of permafrost is estimated to store 500 Pg of carbon while the permafrost in its entirety may store over 1000 Pg, giving an overall terrestrial Arctic carbon pool of over 1500 Pg (Koven et al., 2011; Mackelprang et al., 2011). In summer, the active layer affects soils thawing, leading to a sharp increase in microbial activity and thus, to increased nutrient cycling activity (Mackelprang et al., 2011). Although CO_2 will be released to the atmosphere upon permafrost thaw through increased microbial respiration, the release of methane in substantial amounts is more worrying to climate scientists, as it is a greenhouse gas over twenty times more potent than CO_2 (Wagner et al., 2005; Madigan et al., 2010; Coolen et al., 2011; Mackelprang et al., 2011). Methane is produced through anaerobic microbial respiration, exclusively by methanogenic Euryarchaeota (Mackelprang et al., 2011).

Research on methane biogeochemistry in Svalbard is dominated by the attention given to sea floor emissions (Sahling et al., 2014; Mau et al., 2017). This reflects the fact that very significant emissions of both biogenic and thermogenic methane occur along the continental shelf. Emissions also appear to have occurred in Svalbard fjords in response to deglaciation, resulting in multiple fjord floor features known as pockmarks (Crémière et al., 2016; Portnov et al., 2016). Recent research shows that the contemporary release of methane makes very little impact upon the methane content of the atmosphere on account of effective removal

processes that include an active methanotrophic community in the sea (Gentz et al., 2014; Myhre et al., 2016) and sediments (Hong et al., 2016). However, it is not known whether methanotrophy and other removal processes accounted for as much of the emissions during ice sheet retreat and the formation of the pockmarks.

Research on the terrestrial methane cycle associated with Arctic soils, wetlands and lakes is well documented on account of the globally important organic carbon resource in permafrost and its sensitivity to climate change and permafrost thaw (Schuur et al., 2015). In Svalbard, research has therefore focused upon methanogenesis and methane oxidation in these habitats, albeit with less intensity than other Arctic regions such as Alaska and Siberia. One reason for this is the fact that yedoma-type sedimentary habitats, known for their very high organic carbon and methanogenesis potential, are not well represented in Svalbard, and especially near the international research station at Ny Ålesund. However, there have been meaningful emission studies in valley wetlands (Pirk et al., 2016; Pirk et al., 2017), glacier forefields (Adachi et al., 2006) and bird colonies (Zhu et al., 2012), as well as detailed studies of methanotrophy in Svalbard soils (Graef et al., 2011; Müller et al., 2018). These include molecular studies of both the methanogenic and methanotrophic communities (Wartiainen et al., 2003; Høj et al., 2005; Graef et al., 2011; Tveit et al., 2013; Tveit et al., 2014) and their response to climate change (Høj et al., 2006; Tveit et al., 2015). However, research on the source of atmospheric methane in the atmospheric boundary layer from Ny Ålesund has assigned little importance to local emissions, indicating instead that biomass burning, Siberian wetlands, and anthropogenic gas flares are the dominant sources (Fisher et al., 2011). The inference, therefore, is that rates of local methanogenesis are either low, or methane oxidation, including methanotrophy, is sufficient to minimize its influence on the local atmospheric boundary layer.

However, one significant issue that has been overlooked is that there are significant methane reserves beneath the permafrost with the capacity to by-pass methane oxidation in the active layer or water column. These include sub-permafrost ground water springs, which contain high dissolved gas concentrations up to the solubility limit for methane in water (ca. 41 mg L^{-1} at 0 °C) (Hodson et al, in review). The source of the sub-permafrost methane is a mixture of both thermogenic and biogenic methane. Strong relationships between the stable isotopic composition of the water and gas in the fluids escaping via springs point to an active methanogenic community of microorganisms beneath the permafrost that has yet to be characterized (Hodson et al, in review).

Methane oxidation (Methane cycling – degradation)

Methanotrophs are a highly specialized group of Gram-negative bacteria widespread in various environments that use CH_4 as the sole energy and carbon source (Hanson and Hanson, 1996). This functional group of bacteria therefore play an important role in modulating CH_4 fluxes, as they are the only known biotic terrestrial sink of CH_4 (Dedysh et al., 1998; Bárcena et al., 2011; Knief, 2015; Chiri et al., 2017). The common view has been that aerobic methanotrophs can only utilize C1 compounds, and are unable to grow on organic compounds with carbon-carbon bonds.

However, recent data have shown that *Methylocella* species can use compounds such as acetate as an energy source, this then suppressing their CH_4 oxidation (Dedysh et al., 2005; Theisen et al., 2005; Degelmann et al., 2010). Therefore, facultative methanotrophs that can use multicarbon compounds may also be found in various environments in addition to the obligate methanotrophs (Dedysh et al., 2005).

Carbon fixation (autotrophy and more recently bacteriorhodopsins)

The biological carbon cycle is driven by the interactions between photosynthesis, respiration, and decomposition (Horwath, 2015). The balance between these processes determines whether ecosystems are sources or sinks of carbon. In soils, cyanobacteria are largely responsible for CO_2 uptake, in addition to plants. Although they can be free living in tundra soil, mainly Oscillatoriales and Nostocales orders (Steven et al., 2013) are often identified in biofilms or soil crusts, where they are likely protected against environmental conditions (Zakhia et al., 2008). In soil crusts, Synechoccales, Nostocales, and Oscillatoriales have been consistently identified as the dominating orders of cyanobacteria (Yoshitake et al., 2010; Steven et al., 2013; Pushkareva et al., 2015). Studies of glacial forefields have also shown that cyanobacteria are early colonizers of soils, and generally, Synechoccales and Nostocales are the dominant orders (Kaštovská et al., 2005; Yoshitake et al., 2010).

Generally, Arctic cyanobacteria are psychrotrophic with specific adaptations to survive cold temperature, desiccation and UV radiation (Dodds et al., 1995). Increased polyunsaturated fatty acids in the membrane provide increased fluidity, complex DNA repair mechanisms allow UV damaged DNA to be repaired (Zakhia et al., 2008), while the production of akinetes facilitates survival when environmental conditions are not favourable (Olsson-Francis et al., 2009). Fixed carbon is then available for other microorganisms through the food web or through decomposition of organic matter.

Decomposition of organic matter can be a large source of CO_2 release to the atmosphere. Fungi are the main decomposers of organic matter in terrestrial ecosystems (Ludley and Robinson, 2008). Arctic studies have demonstrated that fungal communities are dominated by Ascomycota and Basidiomycota (Wallenstein et al., 2007; McGuire et al., 2013) and that communities are influenced by soil horizon, soil properties, depth, and vegetation (Wallenstein et al., 2007; McGuire et al., 2013). Other large sources of CO_2 release to the atmosphere include microbial aerobic respiration by heterotrophic organisms. The balance between photosynthesis, decomposition, and respiration will determine the amounts of CO_2 and CH_4 released to the atmosphere and consequently, their impact on Earth's climate.

Autotrophic CO_2 fixation is arguably one of the most important biosynthetic processes globally, if not the most important, being responsible for the net fixation of 7×10^{16} g carbon annually (Berg, 2011). This process is especially critical in oligotrophic environments, such as those found in Arctic terrestrial ecosystems, and can constitute the main carbon source for microbial communities inhabiting them. The photosynthetic path of carbon (reductive pentose phosphate - Calvin-Benson Cycle) was first discovered in the 1940s and fully characterized in the 1950s and since then, five more pathways have been elucidated. In order of discovery, these pathways are: the CB cycle, the reductive citric acid cycle (Evans et al., 1966), the reductive Acetyl-CoA pathway (Fuchs and Stupperich, 1980), the hydroxyproprionate bi-cycle (3-hydroxyproprionate cycle) (Holo, 1989; Herter et al., 2002), the 3-hydroxyproprionate/4-hydroxybutyrate cycle (Berg et al., 2007) and finally the dicarboxylate/4-hydroxybutyrate cycle (Huber et al., 2008). The enzymes, oxygen requirements and organisms involved in each pathway are summarized in Table I. The variety and the distribution of these pathways in the environment is a reflection of both the ecological niches available and the diversity of organisms that have evolved to carry out this process (Thauer, 2007; Berg, 2011).

Table I: Summary of carbon fixation pathways (summarized from Thauer (2007) and Berg (2011))

Pathway	Environmental conditions	Organisms
Calvin-Benson Cycle	*Aerobic, anaerobic*	*Plants, algae, Cyanobacteria, Proteobacteria (anaerobes and aerobes, alpha, beta, gamma)*
Reductive citric acid cycle	*Anaerobic, microaerobic*	*Green sulfur bacteria, Proteobacteria (delta, epsilon), Nitrospirae, Thermoproteus (anaerobic Crenarchaeota), Aquifex/hydrogenobacter*
Reductive Acetyl-CoA pathway	*Strictly anaerobic*	*Methanogenic archaea, acetogenic bacteria, anaerobic ammonia-oxidizing planctomycetes*
3-hydroxyproprionate cycle	*Neutrophilic, alkaliohilic*	*Green nonsulfur bacteria Chloroflexus*
3-hydroxyproprionate/4-hydroxybutyrate cycle	*Aerobic, microaerobic*	*Microaerophilic Crenarchaeota (Metallosphaera, Sulfolobus, Acidianus, Nitrosopumulis, Crenarchaeum)*
dicarboxylate/4-hydroxybutyrate cycle	*Anaerobic*	*Crenarachaeota, Thermoproteales, Desulforococcales*

Aquatic environments - Carbon fixation has been identified and characterized in several aquatic- terrestrial ecosystems such as cryoconite (Stibal and Tranter, 2007), perennial cold springs (Perreault et al., 2008) and Arctic lakes (Markager et al., 1999). Microbial communities in cryoconite holes both respire and photosynthesize at rates comparable to microbial ecosystems in much warmer nutrient-rich environments (Hodson et al., 2007; Anesio et al., 2009; Anesio et al., 2010; Hodson et al., 2010; Telling et al., 2011). In cryoconite holes, laboratory experiments suggested that cyanobacterial photosynthesis (75–93%) was the main process responsible for inorganic carbon fixation, while heterotrophic uptake (6–15%) only accounted for a minor part. The major sources of primary production in Arctic lakes are phytoplankton, aquatic plants, benthic macroalgae, photosynthetic microbes, and chemosynthetic bacteria, but their photosynthetic yields have been shown to be three- to six-fold lower than for polar marine environments, which is likely due to nutrient limitation (Markager et al., 1999). Primary production by chemoautotrophs was shown to be an important process in perennial cold springs, and they represented up to 40% of the total microbial community (Perreault et al., 2008).

Snow - Snow algae are a group of freshwater algae representing several genera that are capable of thriving on semi-permanent to permanent snow and ice fields in polar and alpine regions (Kol and Flint, 1968). In a recent survey of 21 glaciers across the Arctic, Lutz et al. (2016), showed that snow algae were cosmopolitan, and that their biodiversity was low. In wet, carbon and nutrient rich green snow, *Microglena* spp. dominate, while dry, nutrient poor red snow is colonized by *Chloromonas* spp. In dry, cold snow packs, algae are rarely observed, however, autotrophic bacteria can be abundant (Harding et al., 2011; Larose et al., 2013a).

Soils - Carbon fixation is a critical process in Arctic soils, especially in recently deglaciated forefields. Prior to plant colonization, microorganisms use both autochthonously produced and allochtohonously delivered nutrients for growth (Bradley et al., 2014). Based on a combined field, laboratory and modelling approach, Bradley et al. (2016) showed that initial microbial communities were dominated by bacteria outwashed from the glacial environment, while older soils were characterized by autotrophic and heterotrophic bacteria. In older, established tundra soils, carbon fixation is also an important process. The presence of a permafrost layer, in addition to high soil moisture and low organic carbon concentrations, limits air diffusion in Arctic soils (Bockheim and Tarnocai, 1998), likely favoring carbon fixation. Based on recent work by Šantrůčková et al. (2018), dark CO_2 fixation appears to be a ubiquitous process in Arctic tundra soils, which becomes increasingly important with soil depth. This process, involving carboxylase enzymes, was shown to account for up to 16% of net respiration in permafrost soils and could be attributed to a broad range of heterotrophic microorganisms (Šantrůčková et al., 2018). However, dark inorganic carbon fixation was not linked to biomass production (Alonso-Sáez et al., 2010), suggesting that it may only enable microorganisms to maintain metabolic activity and not growth (Šantrůčková et al., 2018).

There is consequently an urgent need to understand the balance between fixation and decomposition of organic compounds through the microbial community, and in particular, its seasonal variability and long-term change.

Carbon sequestration (in deep sea sediment)

As the ice and snow retreat, soil formation leads to the creation of a standing carbon pool. Whilst this is dynamic, the average biomass of carbon remains locked in the solid phase. Fixation of atmospheric CO_2 by marine phytoplankton is an important mechanism by which CO_2 is drawn out of the atmosphere and sequestered in marine sediment (particularly deep-sea sediment). The efficacy of the process largely rests on the ability of the microbial community in the surface waters to break it down again and release it back into the atmosphere.

The deep ocean represents the largest active carbon sink on Earth (~38,000 Pg), with sediments also forming a globally significant reservoir (~6000 Pg) (Houghton, 2007). Ocean fertilisation with increased primary production and carbon fluxes into the deep ocean has been suggested as a potential way of removing or offsetting increased levels of atmospheric carbon dioxide. However, evidence suggests that in regions of high surface water productivity, most of the total primary production is consumed within the water column, where it either supports elevated biomass (Steinberg et al., 2008) or results in higher rates of microbial activity (Zubkov et al., 2007). Accordingly, carbon export from the surface layer and, in particular, the ability of the ocean and its sediments to sequester carbon for many years remains poorly understood.

In shallow seas, evidence for a clear link between bacterioplankton diversity and surface water productivity has been widely reported and both benthic and mesocosm studies have demonstrated that temporal changes in sediment bacterial abundance and distribution can be linked to surface-derived labile organic matter. Conversely, in the deep-sea, bacteria do not show significant differences in biomass and abundance with changes in depth, regardless of the continual decrease of food supply with increasing distance from the sea surface and from land. However, some studies have suggested a rapid increase in deep sea sediment bacterial activity in response to particulate organic matter input from the euphotic zone (Lochte, 1992; Witte et al., 2003; Moodley et al., 2005). Resource availability (derived from primary production) as well as microbial biomass may also be a key determinant of benthic biodiversity in marine systems. It has, therefore, been suggested that deep-sea processes are likely to differ from those occurring in shallow waters and the processes that define species composition in deep-sea sediments are largely unknown (Moodley et al., 2005).

High similarity between surface sediment bacterial communities from different productivity regimes reflects the stability of the deep-sea environment. Changes that occur in the water column and sediment contact water before reaching the sediment, however, suggest that additional carbon might be remineralized in the water column before it reaches the sea bed. This is mediated by combinations of changes in microbial community structure; microbial activity in the water column (Zubkov et al., 2007) and some two-fold higher respiration rates in the sediment. It is therefore possible that additional CO_2 fixation in marine surface waters

will not lead to increased carbon sequestration in deep-sea sediment.

The difference between sediment and water column bacterial communities beneath areas of contrasting productivity indicates that most of the POM produced at the ocean surface is remineralized before reaching the sea bed. This suggests that enhancing atmospheric CO_2 sequestration through ocean fertilisation may not result in increased sediment accumulation.

Nitrogen cycling (in particular N_2O production)

Nitrogen is a key growth limiting nutrient in soil and can take many forms through various complex processes, driven by microorganisms. Nitrogen is often the limiting nutrient for plant growth, and thus, limits primary production (Chapin et al., 1991). Dinitrogen (N_2) is the most abundant form of nitrogen, yet, plants are unable to use it and only a small proportion of prokaryotes are able to fix N_2. Cyanobacteria, in addition to their role in CO_2 uptake, are the main N_2 fixers and thus, the main source of nitrogen in Arctic environments (Chapin et al., 1991). Specialized N_2 fixing species form heterocysts, which are specialized cells with thicker cell walls to protect nitrogenase from O_2 inactivation (Kumar et al., 2010). *Nostoc* sp. are found in abundance in Arctic soils (Dodds et al., 1995; Steven et al., 2013; Pushkareva et al., 2015), transforming N_2 into organic N, which can then be used by plants and other microorganisms. As most microorganisms cannot fix N_2, they use available organic nitrogen to produce ammonia/ammonium (NH3/NH_4^+) through ammonification. NH_3/NH_4^+ can then be oxidized through nitrification to form nitrite (NO_2^-) or nitrate (NO_3^-).

Some Betaproteobacteria, notably in the genera *Nitrosomonas* and *Nitrosospira*, are well known ammonia-oxidizing bacteria (AOB) (Fierer et al., 2007; Palmer et al., 2012) while Thaumarchaeota are ammonia-oxidizing archaea (AOA) (Alves et al., 2013). Studies have shown that, although AOB are often identified, AOA usually have a greater abundance (Leininger et al., 2006; Alves et al., 2013). Anaerobic oxidation of NH_3/NH_4^+ through anammox is carried out by Planctomycetes and leads to the production of N_2 (Humbert et al., 2010; Robertson and Groffman, 2015). Planctomycetes inhabit marine and freshwater environments but have also been identified in low abundances in terrestrial environments (Humbert et al., 2010), including in Arctic soils (Wagner et al., 2009; Hultman et al., 2015).

As only a limited number of studies have identified Planctomycetes in Arctic soils, whether they thrive there and are functionally active has not yet been investigated. Thus, rates of anaerobic ammonia oxidation in terrestrial Arctic environments are unknown. Some organisms can, in turn, take in NO_3^- and through denitrification, transform it to NO_2^- or even gaseous forms such as nitric oxide (NO), nitrous oxide (N_2O) or back to stable N_2. Nitrous oxide,

a greenhouse gas, is 298 times more potent than CO_2 (IPCC, 2007; Palmer et al., 2012) and is also released upon permafrost thaw. When released in the atmosphere, N_2O reacts with ozone (O_3) in the stratosphere, damaging the ozone layer while forming nitrite (NO_2^-) which returns to the surface as nitric acid (HNO_2) in rain (Madigan et al., 1997; Fierer et al., 2007; Marushchak et al., 2011; Palmer et al., 2012). N_2O is produced through aerobic nitrification and anaerobic denitrification (Fierer et al., 2007; Elberling et al., 2010; Marushchak et al., 2011; Palmer et al., 2012). *Paracoccus denitrificans*, *Thiobacillus denitrificans* and some *Pseudomonas* sp. (Baumgärtner et al., 1996) are known denitrifiers but their presence in Arctic soils is still to be investigated, although many studies have shown denitrification occurs and N_2O is released to the atmosphere (Fierer et al., 2007; Elberling et al., 2010; Palmer et al., 2012). N_2O production seems to be strongly influenced by O_2 availability as well as moisture content in soils (Fierer et al., 2007; Elberling et al., 2010; Marushchak et al., 2011). The Arctic region was not considered a large N_2O producer until studies showed the potential release rate of N_2O into the atmosphere. In fact, studies have shown a large increase in N_2O production and subsequent release in the atmosphere following freeze-thaw cycles and rewetting of soils (Elberling et al., 2010). These rates of N_2O release are equivalent to the release of N_2O by tropical forests, which are among the top N_2O producers (Elberling et al., 2010; Palmer et al., 2012). Studies suggest that hotspots of N_2O production and release exist and further research should be conducted to provide estimations of N_2O release in the context of climate change and permafrost thawing (Elberling et al., 2010; Marushchak et al., 2011). The Arctic region should now be considered a potentially large source of N_2O emission and further studies are required to estimate the amounts released associated with climate change and Arctic warming.

There are currently four ongoing projects on N_2O emissions in Svalbard (RiS). All projects involve air sampling to measure N_2O levels in the atmosphere. However, no research is investigating sources and sinks of N_2O and the processes by which it is produced and released to the atmosphere. Investigating the nitrogen cycle in Svalbard soils through measurements of ammonium (NH_4^+), nitrite (NO_2^-) and nitrate (NO_3^-) combined with the investigation of microbial communities through 16S rRNA sequencing and shotgun metagenomics would provide information on the processes involved in N_2O production and emissions. It would also allow the identification of emission hotspots in Svalbard, as with cryoturbated peat soils identified in the Russian Arctic (Palmer et al., 2012).

Sulphur cycling (more recently the description of dimethyl sulphide production in soil)

Bacteria produce dimethyl-sulphide (DMS), traditionally considered to be an oceanic process. It is becoming increasingly apparent, however, that they can also generate DMS in terrestrial environments such as the soil (Levasseur, 2013; Carrión et al., 2015). This implies that existing estimates of DMS production from marine sources could be an underestimate for the polar regions as a whole. Sulphur is released through weathering and can then be mineralized, oxidized, reduced or incorporated into organic compounds (Kertesz and Frossard, 2015). *Thiobacillus* and *Acidithiobacillus* are the main genera of bacteria using S or S-compounds as their primary source of energy. Many heterotrophic bacteria are able to oxidize S-compounds, including members of *Bacillus*, *Micrococcus*, *and Pseudomonas* (Kertesz and Frossard, 2015). The sulphur cycle has been particularly studied in the atmosphere in association with marine environments (Levasseur et al., 1994; Levasseur, 2013). The largest concentration of DMS is found in surface seawater, and is the product of the degradation of dimethylsulfoniopropionate (DMSP) by phytoplankton (Dacey and Wakeham, 1986; Lomans et al., 1997; Bopp et al., 2003; Cameron-Smith et al., 2011). When DMS is released to the atmosphere, it can be oxidized into sulphur dioxide (SO_2), sulphate (SO_4^{2-}) and methanosulphate (CH_3SO_3) (Madigan et al., 1997; Ayers and Gillett, 2000; Bopp et al., 2003). Sulphate aerosols react with cloud condensation nuclei (CCN) and thus, participate in cloud formation over the oceans (Ayers and Gillett, 2000; Cameron-Smith et al., 2011). Conversely, when DMS is released in anoxic environments, it can be fixed to yield dimethyl sulphoxide (DMSO) or it can be used for methanogenesis, yielding CH_4 and hydrogen sulphide (H_2S) which in turn, if not oxidized, play an essential role in climate alteration (Lomans et al., 1997; Madigan et al., 1997; Lomans et al., 1999).

There are two ongoing projects investigating DMS concentration in the atmosphere around Svalbard (RiS) but none investigating production rates and emissions of DMS from terrestrial sources. Measurements of the different states of sulphur in soils such as reduced S (sulphotanes), oxidized S (sulphate esters) and intermediate redox states (sulfones, sulfoxides), would provide a better understanding of the sulphur cycle in soils. These should be complemented by 16S rRNA and metagenomic studies to investigate the microbial communities actively involved in sulphur cycling. Measuring DMS concentration in the air over different regions of the Svalbard tundra would inform on the potential of soils for DMS production and emission.

DMS emissions have been extensively studied in the marine environment but the production of DMS by terrestrial systems has yet to be investigated. It is estimated that 80% of DMS emissions come from oceanic sources while the remaining 20% combine anthropogenic sources, potential terrestrial emissions and plant emissions (Schäfer et al., 2009).

Permafrost thaw (and the microbial response)

Polar environments represent some of the most extreme environments on Earth, and until recently the assumption of a biological inactivity was considered as well within reason. For example, Arctic average winter daytime temperatures range from -34° to 0° C, and available water, nutrients and sunlight are limited throughout the year (Przybylak et al., 2003). However, as the climate warms and the active layer of the permafrost starts to increase in depth, so this trapped carbon is increasingly being released leading to a positive feedback loop.

The Arctic includes some of the most rapidly warming regions on the planet. Arctic soils are thus currently the focus of intense research initiatives due to their recognized vulnerability to climate change, in particular with respect to the unknown consequences of warming on the enormous carbon reserves that are sequestered in permafrost. Permafrost is defined as material frozen for two consecutive years. Climate fluctuations in the Arctic are expected to have a major impact on soil microbial community composition and activity, and it is assumed that this will consequently affect nutrient turnover in Arctic soil environments. Measurements and monitoring of permafrost on Svalbard started seriously in 2000, although the surface few centimetre of soil where the large majority of microbial activity is, is not typically monitored in detail in permafrost studies (Convey et al., 2018), and since then the temperature has gradually increased. The year 2016 was measured as exceptionally hot, and in recent years, the rate of temperature increase has been very strong throughout the Svalbard region.

Permafrost in Svalbard is up to 450 m thick in the mountains surrounding Adventdalen (Liestøl, 1977) and thins towards the shore in the valley bottom (Humlum et al., 2003). Mean annual ground temperatures in Adventdalen vary from -3.5 to -6.9 °C (Christiansen et al., 2010; Cable et al., 2018). In Adventdalen, the active layer reaches down to about 1 m depth (Christiansen et al., 2010). Samples from the active surface layer are expected to have a higher microbial biomass and complexity compared to the deeper layers, including permafrost. In studies from permafrost cores collected in Adventdalen in 2012, a lower microbial diversity was found in permafrost compared to the active layer (Müller et al., 2018) and this is in agreement with studies reported from the Canadian Arctic (Mackelprang et al., 2011). In the samples from Adventdalen a distinct shift in community composition along the depth profile was seen, with a high biomass and diversity in the upper 60 cm representing the active layer. A distinct shift in community composition with a dominance of the phylum Bacterioidetes was reported indicating a transition zone. A further shift in composition occurred in the permafrost layer, where a microbial community strongly dominated by one single Actinobacteria family (Intrasporangiaceae) was seen. The contrasting abundances of these two taxa caused a community difference of about 60%, within just 3 cm from the transition zone and into the permafrost layer (Müller et al., 2018). Samples from the three distinct layers were used for incubation experiments at 4 (±1) °C to measure the potential

for microbial activity response upon thawing using gas flux analysis (CO2, CH4, and N2O) to identify potential connections between the microbial community structure and greenhouse gas fluxes. Independent of soil layer and community structure, respiration rates were higher under aerobic than anaerobic conditions, with up to four times more CO2 produced. These results are in agreement with a permafrost study from Greenland (Elberling et al., 2013) and a comparative study investigating aerobic and anaerobic permafrost incubations from different locations in Alaska and Siberia (Lee et al., 2012).

Current studies focus on understanding the role of microbial communities in cycling of carbon and regulation of greenhouse gas fluxes. Although microbes are recognized as key players in these processes, their contribution is poorly incorporated into existing climate models. This deficiency is largely due to the difficulty in the study of largely uncultivated and unknown permafrost microbes. We need to improve our understanding of the underlying mechanisms that control microbial diversity in low temperature environments and the possible impact on these of climate variability in the Arctic. In order to properly understand how carbon processing is controlled by microorganisms in the Arctic and how these processes are impacted by climate change a combination of state-of-the-art sequencing and omics technologies to reveal the identities and functions of the key players in Arctic ecosystems is needed.

In transiently cold environments, methanogen communities have been shown to rapidly respond to moderate short-term increases in temperature, but not necessarily to the seasonal release of previously frozen organic carbon from thawing permafrost soils. As temperatures increase such inputs of carbon will likely have a greater influence on methane production and methanogen community structure. Understanding the action and limitations of anaerobic microorganisms within cold environments may also provide important information, which can be used in defining biogeographical differences in microbially-mediated processes, which ultimately control the methane flux to the atmosphere (Blake et al., 2015).

Recent discoveries (e.g. methyl halide degradation)

As frozen environments have increasingly become recognized as true habitats, their exploration has revealed high levels of microbial diversity and complexity using a combination of both culture-dependent and culture-independent techniques. In 2006 a novel methane-oxidizing bacterium, *Methylobacter tundripaludum* sp. nov., was isolated from Arctic wetland soil on Svalbard. Tveit et al. (2013) then reported a population of CH_4-oxidising bacteria closely related to *M. tundripaludum* to be the dominating active group of methanotrophs. Based on this in-depth characterisation of the microbes and their genes, they concluded that Arctic peat soils will in time become CO_2 sources owing to increased active layer

depth and prolonged growing season. However, the extent of future CH_4 emissions will critically depend on the response of the methanotrophic bacteria. Microbial diversity has been studied in various habitats such as soil (Zhou et al., 1997; Chu et al., 2010; Edwards et al., 2011; van Dorst et al., 2014), ice (Junge et al., 2002; Brinkmeyer et al., 2003; Yu et al., 2006; Bottos et al., 2008; Collins et al., 2010), permafrost soil (Hansen et al., 2007; Steven et al., 2007; Wilhelm et al., 2011), sediments (Lysnes et al., 2004; Li et al., 2006a; Li et al., 2006b; Perreault et al., 2007; Forschner et al., 2009; Li et al., 2009; Bienhold et al., 2012; Zhang et al., 2014), snow (Larose et al., 2013b) and cryoconite (Edwards et al., 2011; Chrismas et al., 2016). Several organisms have also been cultivated, including a strain that is active at -15°C (Mykytczuk et al., 2013), thus challenging our perception of the limits of life. The desire to better understand the functioning of microorganisms in the cryosphere has led to discoveries of adaptations to conditions at both the molecular and cellular level, such as the synthesis of antifreeze proteins and cold-active enzymes (Feller and Gerday, 2003; Singh et al., 2014) that help them sustain metabolic activities of the cell at non-permissible temperatures.

High industrial/biotechnological interest has also been displayed in enzymes obtained from organisms living in extreme ecosystems because the harsh environments in which they live can provide analogous challenges to life to those found in certain industrial processes (Santiago et al., 2016). Psychrophilic enzymes have been shown to be advantageous over mesophilic/thermophilic enzymes, because of their high catalytic efficiency at low and moderate temperatures, leading to shorter process times and lower energy costs. These features have garnered interest from a variety of industries, such as molecular biology, medical research, industrial food or feed technologies, detergents and cosmetics (Kuddus, 2015). Some cold-adapted bacteria are already being used in waste water treatment (Margesin and Feller, 2010). These microorganisms and their genes could be invaluable also in the development of low temperature technologies for temperate climates, for example, low temperature anaerobic digestion, which could help pave the way to the low carbon economies we will need in the future. As sequencing technologies become more accessible, the potential for new discoveries is growing. Future research directions include the search for new antibiotic molecule discovery but also using polar microorganisms for bioremediation of contaminated sites (Kuddus, 2015).

Elsewhere, methyl halides are known to be produced and degraded by photochemical processes in the snow. It has recently emerged, however, that methyl halides can also be degraded through the action of microorganisms in the polar snowpack (Redeker et al., 2017).

> *Whilst it is clear that photochemical activity in the atmosphere is primarily responsible for climate processes, it is now becoming clear that microorganisms may have a significant role to play and our understanding of the extent of this role may be limited only by research activity in this area to date.*

Future directions

Priorities and opportunities (for development under SIOS):

1. Conduct a comprehensive census of both microbial biodiversity and functional diversity on Svalbard

Much of the work concerning microbial communities on Svalbard to date is focused at key sites or around specific functional questions. In order to fully understand the role and activity of microbial communities, it is necessary to conduct a full and broad-ranging bio-geographical microbial biodiversity survey, taking into account the full range of microbial life, from viruses to prokaryotes (eubacteria including cyanobacteria, Archaea) and eukaryotes (fungi and protozoa to pico-eukaryotes).

Recommendation: A comprehensive microbial biodiversity study across Svalbard

2. Look at the distribution of this diversity in terms of habitat type

Svalbard contains a wide range of habitats for microbial growth, from the rock itself (endolith and sublithic communities), diverse soil types (Malard and Pearce, 2018), freshwaters (including meltwater, streams, rivers and lakes but also the ice and snow itself), brackish and transitional waters to the marine ecosystem itself, and into the air. It also contains a wide range of 'hotspots' for specific diversity, such as hydrothermal systems, within and in association with animals and plants and acid mine drainage systems (to name but a few). A full habitat survey with respect to microbial communities would allow Svalbard to form a case study for the wider integration of microbial influences on climate active gas cycling across the globe.

Recommendation: A comprehensive habitat classification study across Svalbard

3. Determine the stability of the communities in which this biodiversity exists

Microbial communities are not static and are subject to strong and cyclical selection pressures in a relatively extreme environment. Coupled with this, microorganisms are raining down onto the surface from the atmosphere in precipitation and via air movements. For

this reason, measuring activity at one point in time may not be representative of the community as a whole. We need to understand how these communities change over time (and in response to which environmental signals) to put their activity into context.

Recommendation: A time series study at a series of key 'indicator' sites to establish stability

4. Link this biodiversity & active gene composition to climate active gas flux (as measured currently)

There are current studies ongoing that are measuring the flux of climate active gases. These fluxes need to be matched to microbial activity at the location through functional gene enumeration, functional gene expression studies and stable isotope probing to start to unpick how much of the observed gas flux is influenced by microbial activity.

Recommendation: Link current and future flux measurements to concurrent microbial activity

5. Use this raw data to construct preliminary models in order to open the debate with the climate change community more widely about the relative significance and potential of microbially-mediated processes to generate a paradigm shift in our understanding of climate processes.

In order to determine the effect on the climate system, the impact of microbial activity toward climate active gases needs to be incorporated into global climate models. The best approach to enable this to happen would be to develop a case study that would demonstrate unequivocally that the impact is significant at the regional scale. Svalbard is ideally suited for this initial study given its research infrastructure, current monitoring capability, and field logistics.

Recommendation: Develop a small-scale model including microbial activity for Svalbard

Capacity building - Much of this work could potentially be conducted at current research stations on Svalbard. To enable this to happen the further development of microbiology facilities and infrastructure (such as class II microbiological safety cabinets, autoclaves, clean rooms, and molecular biology facilities) is an essential and pressing need.

Acknowledgements

References

Adachi, M., Ohtsuka, T., Nakatsubo, T., and Koizumi, H. (2006) The methane flux along topographical gradients on a glacier foreland in the High Arctic, Ny-Alesund, Svalbard.

Alonso-Sáez, L., Galand, P.E., Casamayor, E.O., Pedros-Alio, C., and Bertilsson, S. (2010) High bicarbonate assimilation in the dark by Arctic bacteria. *The ISME journal* **4**: 1581.

Alpert, P.A., Aller, J.Y., and Knopf, D.A. (2011a) Ice nucleation from aqueous NaCl droplets with and without marine diatoms. *Atmos Chem Phys* **11**: 5539-5555.

Alpert, P.A., Aller, J.Y., and Knopf, D.A. (2011b) Initiation of the ice phase by marine biogenic surfaces in supersaturated gas and supercooled aqueous phases. *Physical Chemistry Chemical Physics* **13**: 19882-19894.

Alves, R.J.E., Wanek, W., Zappe, A., Richter, A., Svenning, M.M., Schleper, C., and Urich, T. (2013) Nitrification rates in Arctic soils are associated with functionally distinct populations of ammonia-oxidizing archaea. *The ISME journal* **7**: 1620-1631.

Amato, P., Ménager, M., Sancelme, M., Laj, P., Mailhot, G., and Delort, A.-M. (2005) Microbial population in cloud water at the Puy de Dôme: implications for the chemistry of clouds. *Atmospheric Environment* **39**: 4143-4153.

Amato, P., Parazols, M., Sancelme, M., Laj, P., Mailhot, G., and Delort, A.-M. (2006) icroorganisms isolated from the water phase of tropospheric clouds at the Puy de Dôme: major groups and growth abilities at low temperatures. *FEMS microbiology ecology* **59**: 242-254.

Amato, P., Joly, M., Schaupp, C., Attard, E., Möhler, O., Morris, C. et al. (2015) Survival and ice nucleation activity of bacteria as aerosols in a cloud simulation chamber. *Atmospheric Chemistry and Physics* **15**: 6455-6465.

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. *Global Change Biology* **15**: 955-960.

Anesio, A.M., Sattler, B., Foreman, C., Telling, J., Hodson, A., Tranter, M., and Psenner, R. (2010) Carbon fluxes through bacterial communities on glacier surfaces. *Annals of Glaciology* **51**: 32-40.

Ayers, G., and Gillett, R. (2000) DMS and its oxidation products in the remote marine atmosphere: implications for climate and atmospheric chemistry. *Journal of Sea Research* **43**: 275-286.

Bárcena, T.G., Finster, K.W., and Yde, J.C. (2011) Spatial patterns of soil development, methane oxidation, and methanotrophic diversity along a receding glacier forefield, Southeast Greenland. *Arctic, Antarctic, and Alpine Research* **43**: 178-188.

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

Berg, I.A. (2011) Ecological aspects of the distribution of different autotrophic CO2 fixation pathways. *Applied and environmental microbiology* **77**: 1925-1936.

Berg, I.A., Kockelkorn, D., Buckel, W., and Fuchs, G. (2007) A 3-hydroxypropionate/4-hydroxybutyrate autotrophic carbon dioxide assimilation pathway in Archaea. *Science* **318**: 1782-1786.

Bienhold, C., Boetius, A., and Ramette, A. (2012) The energy–diversity relationship of complex bacterial communities in Arctic deep-sea sediments. *The ISME journal* **6**: 724.

Bigg, E.K. (1973) Ice Nucleus Concentrations in Remote Areas. *Journal of the Atmospheric Sciences* **30**: 1153-1157.

Bigg, E.K., and Leck, C. (2008) The composition of fragments of bubbles bursting at the ocean surface. *Journal of Geophysical Research: Atmospheres* **113**.

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

Bockheim, J.G., and Tarnocai, C. (1998) Recognition of cryoturbation for classifying permafrost-affected soils. *Geoderma* **81**: 281-293.

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. *Nature reviews Microbiology*.

Bøggild, C.E., Brandt, R.E., Brown, K.J., and Warren, S.G. (2010) The ablation zone in northeast Greenland: ice types, albedos and impurities. *Journal of Glaciology* **56**: 101-113.

Bopp, L., Aumont, O., Belviso, S., and Monfray, P. (2003) Potential impact of climate change on marine dimethyl sulfide emissions. *Tellus B* **55**: 11-22.

Bottos, E.M., Vincent, W.F., Greer, C.W., and Whyte, L.G. (2008) Prokaryotic diversity of arctic ice shelf microbial mats. *Environmental microbiology* **10**: 950-966.

Bowers, R.M., McLetchie, S., Knight, R., and Fierer, N. (2011) Spatial variability in airborne bacterial communities across land-use types and their relationship to the bacterial communities of potential source environments. *The ISME journal* **5**: 601.

Bradley, J.A., Singarayer, J.S., and Anesio, A.M. (2014) Microbial community dynamics in the forefield of glaciers. *Proc R Soc B* **281**: 20140882.

Bradley, J.A., Arndt, S., Sabacká, M., Benning, L.G., Barker, G.L., Blacker, J.J. et al. (2016) Microbial dynamics in a High Arctic glacier forefield: a combined field, laboratory, and modelling approach. *Biogeosciences* **13**: 5677.

Brinkmeyer, R., Knittel, K., Jürgens, J., Weyland, H., Amann, R., and Helmke, E. (2003) Diversity and structure of bacterial communities in Arctic versus Antarctic pack ice. *Applied and Environmental Microbiology* **69**: 6610-6619.

Burrows, S.M., Elbert, W., Lawrence, M., and Pöschl, U. (2009) Bacteria in the global atmosphere–Part 1: Review and synthesis of literature data for different ecosystems. *Atmospheric Chemistry and Physics* **9**: 9263-9280.

Burrows, S.M., Hoose, C., Pöschl, U., and Lawrence, M.G. (2013) Ice nuclei in marine air: biogenic particles or dust? *Atmos Chem Phys* **13**: 245-267.

Cable, S., Elberling, B., and Kroon, A. (2018) Holocene permafrost history and cryostratigraphy in the High-Arctic Adventdalen Valley, central Svalbard. *Boreas* **47**: 423-442.

Cameron-Smith, P., Elliott, S., Maltrud, M., Erickson, D., and Wingenter, O. (2011) Changes in dimethyl sulfide oceanic distribution due to climate change. *Geophysical Research Letters* **38**.

Cameron, K.A., Hodson, A.J., and Osborn, A.M. (2012) Structure and diversity of bacterial, eukaryotic and archaeal communities in glacial cryoconite holes from the Arctic and the Antarctic. *FEMS microbiology ecology* **82**: 254-267.

Carrión, O., Curson, A., Kumaresan, D., Fu, Y., Lang, A., Mercadé, E., and Todd, J. (2015) A novel pathway producing dimethylsulphide in bacteria is widespread in soil environments. *Nature communications* **6**: 6579.

Chapin, D.M., Bliss, L., and Bledsoe, L. (1991) Environmental regulation of nitrogen fixation in a high arctic lowland ecosystem. *Canadian Journal of Botany* **69**: 2744-2755.

Chiri, E., Nauer, P.A., Rainer, E.-M., Zeyer, J., and Schroth, M.H. (2017) High Temporal and Spatial Variability of Atmospheric-Methane Oxidation in Alpine Glacier Forefield Soils. *Applied and environmental microbiology* **83**: e01139-01117.

Chrismas, N.A., Barker, G., Anesio, A.M., and Sánchez-Baracaldo, P. (2016) Genomic mechanisms for cold tolerance and production of exopolysaccharides in the Arctic cyanobacterium *Phormidesmis priestleyi* BC1401. *BMC genomics* **17**: 533.

Christiansen, H.H., Etzelmüller, B., Isaksen, K., Juliussen, H., Farbrot, H., Humlum, O. et al. (2010) The thermal state of permafrost in the nordic area during the international polar year 2007–2009. *Permafrost and Periglacial Processes* **21**: 156-181.

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. *Environmental Microbiology* **12**: 2998-3006.

Collins, R.E., Rocap, G., and Deming, J.W. (2010) Persistence of bacterial and archaeal communities in sea ice through an Arctic winter. *Environmental microbiology* **12**: 1828-1841.

Convey, P., Coulson, S., Worland, M., and Sjöblom, A. (2018) The importance of understanding annual and shorter-term temperature patterns and variation in the surface levels of polar soils for terrestrial biota. *Polar Biology*: 1-19.

Cook, J., Edwards, A., Takeuchi, N., and Irvine-Fynn, T. (2016) Cryoconite: the dark biological secret of the cryosphere. *Progress in Physical Geography* **40**: 66-111.

Cook, J., Hodson, A.J., Taggart, A., Mernild, S.H., and Tranter, M. (2017a) A predictive model for the spectral "bioalbedo" of snow. *Journal of Geophysical Research: Earth Surface* **122**: 434-454.

Cook, J., Hodson, A., Telling, J., Anesio, A., Irvine-Fynn, T., and Bellas, C. (2010) The mass–area relationship within cryoconite holes and its implications for primary production. *Annals of Glaciology* **51**: 106-110.

Cook, J., Hodson, A., Anesio, A., Hanna, E., Yallop, M., Stibal, M. et al. (2012) An improved estimate of microbially mediated carbon fluxes from the Greenland ice sheet. *Journal of Glaciology* **58**: 1098-1108.

Cook, J.M., Hodson, A.J., Gardner, A.S., Flanner, M., Tedstone, A.J., Williamson, C. et al. (2017b) Quantifying bioalbedo: A new physically-based model and critique of empirical methods for characterizing biological influence on ice and snow albedo. *The Cryosphere Discussions*: 1-29.

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. *Environmental microbiology* **13**: 2299-2314.

Crémière, A., Lepland, A., Chand, S., Sahy, D., Condon, D.J., Noble, S.R. et al. (2016) Timescales of methane seepage on the Norwegian margin following collapse of the Scandinavian Ice Sheet. *Nature communications* **7**: 11509.

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. *The ISME journal* **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.

Dacey, J.W., and Wakeham, S.G. (1986) Oceanic dimethylsulfide: production during zooplankton grazing on phytoplankton. *Science* **233**: 1314-1316.

Dawson, K.W., Petters, M.D., Meskhidze, N., Petters, S.S., and Kreidenweis, S.M. (2016) Hygroscopic growth and cloud droplet activation of xanthan gum as a proxy for marine hydrogels. *Journal of Geophysical Research: Atmospheres* **121**: 11,803-811,818.

Dedysh, S.N., Knief, C., and Dunfield, P.F. (2005) Methylocella species are facultatively methanotrophic. *Journal of bacteriology* **187**: 4665-4670.

Dedysh, S.N., Panikov, N.S., Liesack, W., Großkopf, R., Zhou, J., and Tiedje, J.M. (1998) Isolation of acidophilic methane-oxidizing bacteria from northern peat wetlands. *Science* **282**: 281-284.

Degelmann, D.M., Borken, W., Drake, H.L., and Kolb, S. (2010) Different atmospheric methane-oxidizing communities in European beech and Norway spruce soils. *Applied and environmental microbiology* **76**: 3228-3235.

Després, V., Huffman, J.A., Burrows, S.M., Hoose, C., Safatov, A., Buryak, G. et al. (2012) Primary biological aerosol particles in the atmosphere: a review. *Tellus B: Chemical and Physical Meteorology* **64**: 15598.

Dodds, W.K., Gudder, D.A., and Mollenhauer, D. (1995) The ecology of Nostoc. *Journal of Phycology* **31**: 2-18.

Edwards, A., Anesio, A.M., Rassner, S.M., Sattler, B., Hubbard, B., Perkins, W.T. et al. (2011) Possible interactions between bacterial diversity, microbial activity and supraglacial hydrology of cryoconite holes in Svalbard. *The ISME journal* **5**: 150.

Elberling, B., Christiansen, H.H., and Hansen, B.U. (2010) High nitrous oxide production from thawing permafrost. *Nature Geoscience* **3**: 332-335.

Elberling, B., Michelsen, A., Schädel, C., Schuur, E.A., Christiansen, H.H., Berg, L. et al. (2013) Long-term CO 2 production following permafrost thaw. *Nature Climate Change* **3**: 890.

English, J.M., Gettelman, A., and Henderson, G.R. (2015) Arctic Radiative Fluxes: Present-Day Biases and Future Projections in CMIP5 Models. *Journal of Climate* **28**: 6019-6038.

English, J.M., Kay, J.E., Gettelman, A., Liu, X., Wang, Y., Zhang, Y., and Chepfer, H. (2014) Contributions of Clouds, Surface Albedos, and Mixed-Phase Ice Nucleation Schemes to Arctic Radiation Biases in CAM5. *Journal of Climate* **27**: 5174-5197.

Evans, M., Buchanan, B.B., and Arnon, D.I. (1966) A new ferredoxin-dependent carbon reduction cycle in a photosynthetic bacterium. *Proceedings of the National Academy of Sciences* **55**: 928-934.

Falkowski, P.G., Fenchel, T., and Delong, E.F. (2008) The microbial engines that drive Earth's biogeochemical cycles. *science* **320**: 1034-1039.

Fall, R., and Schnell, R.C. (1985) Association of an ice-nucleating pseudomonad with cultures of the marine dinoflagellate, *Heterocapsa niei*. *Journal of Marine Research* **43**: 257-265.

Feller, G., and Gerday, C. (2003) Psychrophilic enzymes: hot topics in cold adaptation. *Nature reviews Microbiology* **1**: 200.

Fierer, N., Bradford, M.A., and Jackson, R.B. (2007) Toward an ecological classification of soil bacteria. *Ecology* **88**: 1354-1364.

Fisher, R.E., Sriskantharajah, S., Lowry, D., Lanoisellé, M., Fowler, C., James, R. et al. (2011) Arctic methane sources: Isotopic evidence for atmospheric inputs. *Geophysical Research Letters* **38**.

Forschner, S.R., Sheffer, R., Rowley, D.C., and Smith, D.C. (2009) Microbial diversity in Cenozoic sediments recovered from the Lomonosov Ridge in the Central Arctic Basin. *Environmental microbiology* **11**: 630-639.

Fuchs, G., and Stupperich, E. (1980) Acetyl CoA, a central intermediate of autotrophic CO2 fixation in *Methanobacterium thermoautotrophicum*. *Archives of microbiology* **127**: 267-272.

Ganey, G.Q., Loso, M.G., Burgess, A.B., and Dial, R.J. (2017) The role of microbes in snowmelt and radiative forcing on an Alaskan icefield. *Nature Geoscience* **10**: 754.

Gentz, T., Damm, E., von Deimling, J.S., Mau, S., McGinnis, D.F., and Schlüter, M. (2014) A water column study of methane around gas flares located at the West Spitsbergen continental margin. *Continental Shelf Research* **72**: 107-118.

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. *Proceedings of the National Academy of Sciences* **109**: 17633-17638.

Goordial, J., Lamarche-Gagnon, G., Lay, C.-Y., and Whyte, L. (2013) Left out in the cold: life in cryoenvironments. In *Polyextremophiles*: Springer, pp. 335-363.

Graef, C., Hestnes, A.G., Svenning, M.M., and Frenzel, P. (2011) The active methanotrophic community in a wetland from the High Arctic. *Environmental microbiology reports* **3**: 466-472.

Hansen, A.A., Herbert, R.A., Mikkelsen, K., Jensen, L.L., Kristoffersen, T., Tiedje, J.M. et al. (2007) Viability, diversity and composition of the bacterial community in a high Arctic permafrost soil from Spitsbergen, Northern Norway. *Environmental microbiology* **9**: 2870-2884.

Hanson, R.S., and Hanson, T.E. (1996) Methanotrophic bacteria. *Microbiological reviews* **60**: 439-471.

Hara, K., Maki, T., Kobayashi, F., Kakikawa, M., Wada, M., and Matsuki, A. (2016) Variations of ice nuclei concentration induced by rain and snowfall within a local forested site in Japan. *Atmospheric Environment* **127**: 1-5.

Harding, T., Jungblut, A.D., Lovejoy, C., and Vincent, W.F. (2011) Microbes in High Arctic snow and implications for the cold biosphere. *Applied and Environmental Microbiology* **77**: 3234-3243.

Hawkins, L.N., Russell, L.M., and (2010) Polysaccharides, Proteins, and Phytoplankton Fragments: Four Chemically Distinct Types of Marine Primary Organic Aerosol Classified by Single Particle Spectromicroscopy. *Advances in Meteorology*: 612132-612146.

Heintzenberg, J., Leck, C., and Tunved, P. (2015) Potential source regions and processes of aerosol in the summer Arctic. *Atmos Chem Phys* **15**: 6487-6502.

Herter, S., Fuchs, G., Bacher, A., and Eisenreich, W. (2002) A Bicyclic Autotrophic CO_2 Fixation Pathway in *Chloroflexus aurantiacus*. *Journal of Biological Chemistry* **277**: 20277-20283.

Hodson, A., Cameron, K., Bøggild, C., Irvine-Fynn, T., Langford, H., Pearce, D., and Banwart, S. (2010) The structure, biological activity and biogeochemistry of cryoconite aggregates upon an Arctic valley glacier: Longyearbreen, Svalbard. *Journal of Glaciology* **56**: 349-362.

Hodson, A., Anesio, A.M., Tranter, M., Fountain, A., Osborn, M., Priscu, J. et al. (2008) Glacial ecosystems. *Ecological monographs* **78**: 41-67.

Hodson, A., Nowak, A., Cook, J., Sabacka, M., Wharfe, E., Pearce, D. et al. (2017) Microbes influence the biogeochemical and optical properties of maritime Antarctic snow. *Journal of Geophysical Research: Biogeosciences*.

Hodson, A., Anesio, A.M., Ng, F., Watson, R., Quirk, J., Irvine-Fynn, T. et al. (2007) A glacier respires: quantifying the distribution and respiration CO2 flux of cryoconite across an entire Arctic supraglacial ecosystem. *Journal of Geophysical Research: Biogeosciences* **112**.

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

Høj, L., Rusten, M., Haugen, L.E., Olsen, R.A., and Torsvik, V.L. (2006) Effects of water regime on archaeal community composition in Arctic soils. *Environmental Microbiology* **8**: 984-996.

Holo, H. (1989) *Chloroflexus aurantiacus* secretes 3-hydroxypropionate, a possible intermediate in the assimilation of CO2 and acetate. *Archives of microbiology* **151**: 252-256.

Hong, W.L., Sauer, S., Panieri, G., Ambrose, W.G., James, R.H., Plaza-Faverola, A., and Schneider, A. (2016) Removal of methane through hydrological, microbial, and geochemical processes in the shallow sediments of pockmarks along eastern Vestnesa Ridge (Svalbard). *Limnology and Oceanography* **61**.

Horner, R. (2017) History of ice algal investigations. In *Sea ice biota*: CRC Press, pp. 1-19.

Horwath, W. (2015) Carbon cycling: the dynamics and formation of organic matter. In *Soil microbiology, ecology and biochemistry*. Paul, E.A. (ed): Academic press.

Houghton, R. (2007) Balancing the global carbon budget. *Annu Rev Earth Planet Sci* **35**: 313-347.

Huber, H., Gallenberger, M., Jahn, U., Eylert, E., Berg, I.A., Kockelkorn, D. et al. (2008) A dicarboxylate/4-hydroxybutyrate autotrophic carbon assimilation cycle in the hyperthermophilic Archaeum *Ignicoccus hospitalis*. *Proceedings of the National Academy of Sciences* **105**: 7851-7856.

Hultman, J., Waldrop, M.P., Mackelprang, R., David, M.M., McFarland, J., Blazewicz, S.J. et al. (2015) Multi-omics of permafrost, active layer and thermokarst bog soil microbiomes. *Nature* **521**: 208.

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. *The ISME Journal* **4**: 450.

Humlum, O., Instanes, A., and Sollid, J.L. (2003) Permafrost in Svalbard: a review of research history, climatic background and engineering challenges. *Polar research* **22**: 191-215.

IPCC (2007) The Physical Science Basis. In: IPCC.

IPCC (2013) Climate Change 2013: The Physical Science Basis. Working Group I Contribution to the IPCC 5th Assessment Report - Changes to the Underlying Scientific/Technical Assessment. . In. (available at http://www.ipcc.ch/report/ar5/wg1).

Irish, V.E., Elizondo, P., Chen, J., Chou, C., Charette, J., Lizotte, M. et al. (2017) Ice-nucleating particles in Canadian Arctic sea-surface microlayer and bulk seawater. *Atmos Chem Phys* **17**: 10583-10595.

Irvine-Fynn, T.D., Bridge, J.W., and Hodson, A.J. (2011) In situ quantification of supraglacial cryoconite morphodynamics using time-lapse imaging: an example from Svalbard. *Journal of Glaciology* **57**: 651-657.

Irvine-Fynn, T., Edwards, A., Newton, S., Langford, H., Rassner, S., Telling, J. et al. (2012) Microbial cell budgets of an Arctic glacier surface quantified using flow cytometry. *Environmental microbiology* **14**: 2998-3012.

Joly, M., Attard, E., Sancelme, M., Deguillaume, L., Guilbaud, C., Morris, C.E. et al. (2013) Ice nucleation activity of bacteria isolated from cloud water. *Atmospheric environment* **70**: 392-400.

Junge, K., and Swanson, B.D. (2008) High-resolution ice nucleation spectra of sea-ice bacteria: implications for cloud formation and life in frozen environments. *Biogeosciences* **5**: 865-873.

Junge, K., Imhoff, F., Staley, T., and Deming, W. (2002) Phylogenetic diversity of numerically important Arctic sea-ice bacteria cultured at subzero temperature. *Microbial Ecology* **43**: 315-328.

Karl, M., Leck, C., Coz, E., and Heintzenberg, J. (2013) Marine nanogels as a source of atmospheric nanoparticles in the high Arctic. *Geophysical Research Letters* **40**: 3738-3743.

Kaštovská, K., Elster, J., Stibal, M., and Šantrůčková, H. (2005) Microbial assemblages in soil microbial succession after glacial retreat in Svalbard (High Arctic). *Microbial Ecology* **50**: 396.

Kertesz, M.A., and Frossard, E. (2015) Biological cycling of inorganic nutrients and metals in soils and their role in soil biogeochemistry. In *Soil Microbiology, Ecology, and Biochemistry*. Paul, E.A. (ed): Academic Press.

Knief, C. (2015) Diversity and habitat preferences of cultivated and uncultivated aerobic methanotrophic bacteria evaluated based on pmoA as molecular marker. *Frontiers in microbiology* **6**: 1346.

Knopf, D.A., Alpert, P.A., Wang, B., and Aller, J.Y. (2011) Stimulation of ice nucleation by marine diatoms. *Nature Geosci* **4**: 88-90.

Kohshima, S., Yoshimura, Y., Seko, K., and Ohata, T. (1994) Albedo reduction by biotic impurities on a perennial snow patch in the Japan alps. *IAHS Publications-Series of Proceedings and Reports-Intern Assoc Hydrological Sciences* **223**: 323-330.

Kol, E., and Flint, E.A. (1968) Algae in green ice from the Balleny Islands, Antarctica. *New Zealand Journal of Botany* **6**: 249-261.

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

Kuddus, M. (2015) Cold-active microbial enzymes. *Biochem Physiol* **4**: e132.

Kumar, K., Mella-Herrera, R.A., and Golden, J.W. (2010) Cyanobacterial heterocysts. *Cold Spring Harbor Perspectives in Biology* **2**: a000315.

Langford, H., Hodson, A., Banwart, S., and Bøggild, C. (2010) The microstructure and biogeochemistry of Arctic cryoconite granules. *Annals of Glaciology* **51**: 87-94.

Larose, C., Dommergue, A., and Vogel, T.M. (2013a) The dynamic arctic snow pack: an unexplored environment for microbial diversity and activity. *Biology* **2**: 317-330.

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., Prestat, E., Cecillon, S., Berger, S., Malandain, C., Lyon, D. et al. (2013b) Interactions between snow chemistry, mercury inputs and microbial population dynamics in an arctic snowpack. *PloS one* **8**: e79972.

Leck, C., and Bigg, E.K. (2005) Biogenic particles in the surface microlayer and overlaying atmosphere in the central Arctic Ocean during summer. *Tellus Series B-Chemical and Physical Meteorology* **57**: 305-316.

Lee, H., Schuur, E.A., Inglett, K.S., Lavoie, M., and Chanton, J.P. (2012) The rate of permafrost carbon release under aerobic and anaerobic conditions and its potential effects on climate. *Global Change Biology* **18**: 515-527.

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. *Microbial ecology* **65**: 405-414.

Leininger, S., Urich, T., Schloter, M., Schwark, L., Qi, J., Nicol, G. et al. (2006) Archaea predominate among ammonia-oxidizing prokaryotes in soils. *Nature* **442**: 806.

Levasseur, M. (2013) Impact of Arctic meltdown on the microbial cycling of sulphur. *Nature Geoscience* **6**: 691.

Levasseur, M., Gosselin, M., and Michaud, S. (1994) A new source of dimethylsulfide (DMS) for the arctic atmosphere: ice diatoms. *Marine Biology* **121**: 381-387.

Leya, T., Rahn, A., Lütz, C., and Remias, D. (2009) Response of arctic snow and permafrost algae to high light and nitrogen stress by changes in pigment composition and applied aspects for biotechnology. *FEMS microbiology ecology* **67**: 432-443.

Li, H., Yu, Y., Zeng, Y., Chen, B., and Ren, D. (2006a) Phylogenetic analysis of bacterial diversity in Pacific Arctic sediments. *Acta microbiologica Sinica* **46**: 177-183.

Li, H., Yu, Y., Luo, W., Zeng, Y., and Chen, B. (2009) Bacterial diversity in surface sediments from the Pacific Arctic Ocean. *Extremophiles* **13**: 233-246.

Li, S., Xiao, X., Yin, X., and Wang, F. (2006b) Bacterial community along a historic lake sediment core of Ardley Island, west Antarctica. *Extremophiles* **10**: 461-467.

Liestøl, O. (1977) Pingos, springs and permafrost in Spitsbergen. *Norsk Polarinstitutt Årbok* **1975**: 7-29.

Lochte, K. (1992) Bacterial standing stock and consumption of organic carbon in the benthic boundary layer of the abyssal North Atlantic. In *Deep-sea food chains and the global carbon cycle*: Springer, pp. 1-10.

Lomans, B.P., den Camp, H.J.O., Pol, A., and Vogels, G.D. (1999) Anaerobic versus aerobic degradation of dimethyl sulfide and methanethiol in anoxic freshwater sediments. *Applied and environmental microbiology* **65**: 438-443.

Lomans, B.P., Smolders, A., Intven, L.M., Pol, A., Op, D., and Van Der Drift, C. (1997) Formation of dimethyl sulfide and methanethiol in anoxic freshwater sediments. *Applied and Environmental Microbiology* **63**: 4741-4747.

Lu, Z., Du, P., Du, R., Liang, Z., Qin, S., Li, Z., and Wang, Y. (2016) The diversity and role of bacterial ice nuclei in rainwater from mountain sites in China. *Aerosol Air Qual Res* **16**: 640-652.

Ludley, K.E., and Robinson, C.H. (2008) 'Decomposer'basidiomycota in Arctic and Antarctic ecosystems. *Soil Biology and Biochemistry* **40**: 11-29.

Lutz, S., Anesio, A.M., Field, K., and Benning, L.G. (2015) Integrated 'omics', targeted metabolite and single-cell analyses of Arctic snow algae functionality and adaptability. *Frontiers in microbiology* **6**: 1323.

Lutz, S., Anesio, A.M., Raiswell, R., Edwards, A., Newton, R.J., Gill, F., and Benning, L.G. (2016) The biogeography of red snow microbiomes and their role in melting arctic glaciers. *Nature Communications* **7**.

Lysnes, K., Thorseth, I.H., Steinsbu, B.O., Øvreås, L., Torsvik, T., and Pedersen, R.B. (2004) Microbial community diversity in seafloor basalt from the Arctic spreading ridges. *FEMS Microbiology Ecology* **50**: 213-230.

Maahn, M., de Boer, G., Creamean, J.M., Feingold, G., McFarquhar, G.M., Wu, W., and Mei, F. (2017) The observed influence of local anthropogenic pollution on northern Alaskan cloud properties. *Atmos Chem Phys Discuss* **2017**: 1-23.

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*: prentice hall Upper Saddle River, NJ.

Madigan, M.T., Clark, D.P., Stahl, D., and Martinko, J.M. (2010) *Brock Biology of Microorganisms 13th edition*: Benjamin Cummings.

Malard, L.A., and Pearce, D.A. (2018) Microbial diversity and biogeography in Arctic soils. *Environmental microbiology reports*.

Margesin, R., and Feller, G. (2010) Biotechnological applications of psychrophiles. *Environmental technology* **31**: 835-844.

Markager, S., Vincent, W.F., and Tang, E.P. (1999) Carbon fixation by phytoplankton in high Arctic lakes: implications of low temperature for photosynthesis. *Limnology and Oceanography* **44**: 597-607.

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. *Global Change Biology* **17**: 2601-2614.

Mau, S., Römer, M., Torres, M.E., Bussmann, I., Pape, T., Damm, E. et al. (2017) Widespread methane seepage along the continental margin off Svalbard-from Bjørnøya to Kongsfjorden. *Scientific reports* **7**: 42997.

McCluskey, C.S., Hill, T.C.J., Malfatti, F., Sultana, C.M., Lee, C., Santander, M.V. et al. (2017) A Dynamic Link between Ice Nucleating Particles Released in Nascent Sea Spray Aerosol and Oceanic Biological Activity during Two Mesocosm Experiments. *Journal of the Atmospheric Sciences* **74**: 151-166.

McGuire, K.L., Allison, S.D., Fierer, N., and Treseder, K.K. (2013) Ectomycorrhizal-dominated boreal and tropical forests have distinct fungal communities, but analogous spatial patterns across soil horizons. *PLoS One* **8**: e68278.

Moffett, B., Getti, G., Henderson-Begg, S., and Hill, T. (2015) Ubiquity of ice nucleation in lichen—Possible atmospheric implications. *Lindbergia* **38**: 39-43.

Moffett, B.F. (2015) Ice nucleation in mosses and liverworts. *Lindbergia* **38**: 14-16.

Moodley, L., Middelburg, J., Soetaert, K., Boschker, H., Herman, P., and Heip, C. (2005) Similar rapid response to phytodetritus deposition in shallow and deep-sea sediments. *Journal of Marine Research* **63**: 457-469.

Morita, R.Y. (1975) Psychrophilic bacteria. *Bacteriological reviews* **39**: 144.

Mortazavi, R., Attiya, S., and Ariya, P. (2015) Arctic microbial and next-generation sequencing approach for bacteria in snow and frost flowers: selected identification, abundance and freezing nucleation. *Atmospheric Chemistry and Physics* **15**: 6183-6204.

Müller, O., Bang-Andreasen, T., White III, R.A., Elberling, B., Taş, N., Kneafsey, T. et al. (2018) Disentangling the complexity of permafrost soil by using high resolution profiling of microbial community composition, key functions and respiration rates. *Environmental microbiology*.

Müller, T., Bleiss, W., Martin, C.-D., Rogaschewski, S., and Fuhr, G. (1998) Snow algae from northwest Svalbard: their identification, distribution, pigment and nutrient content. *Polar Biology* **20**: 14-32.

Myhre, C.L., Ferré, B., Platt, S.M., Silyakova, A., Hermansen, O., Allen, G. et al. (2016) Extensive release of methane from Arctic seabed west of Svalbard during summer 2014 does not influence the atmosphere. *Geophysical Research Letters* **43**: 4624-4631.

Mykytczuk, N.C., Foote, S.J., Omelon, C.R., Southam, G., Greer, C.W., and Whyte, L.G. (2013) Bacterial growth at− 15 C; molecular insights from the permafrost bacterium *Planococcus halocryophilus Or1*. *The ISME journal* **7**: 1211.

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. *Applied and Environmental Microbiology* **71**: 5710-5718.

Olsson-Francis, K., de La Torre, R., Towner, M.C., and Cockell, C.S. (2009) Survival of akinetes (resting-state cells of cyanobacteria) in Low Earth Orbit and simulated extraterrestrial conditions. *Origins of Life and Evolution of Biospheres* **39**: 565.

Orellana, M.V., Matrai, P.A., Leck, C., Rauschenberg, C.D., Lee, A.M., and Coz, E. (2011) Marine microgels as a source of cloud condensation nuclei in the high Arctic. *Proceedings of the National Academy of Sciences of the United States of America* **108**: 13612-13617.

Painter, T.H., Duval, B., Thomas, W.H., Mendez, M., Heintzelman, S., and Dozier, J. (2001) Detection and quantification of snow algae with an airborne imaging spectrometer. *Applied and Environmental Microbiology* **67**: 5267-5272.

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. *The ISME journal* **6**: 1058-1077.

Pearce, D.A., Bridge, P.D., Hughes, K.A., Sattler, B., Psenner, R., and Russell, N.J. (2009) Microorganisms in the atmosphere over Antarctica. *FEMS Microbiology Ecology* **69**: 143-157.

Perreault, N.N., Andersen, D.T., Pollard, W.H., Greer, C.W., and Whyte, L.G. (2007) Characterization of the prokaryotic diversity in cold saline perennial springs of the Canadian high Arctic. *Applied and environmental microbiology* **73**: 1532-1543.

Perreault, N.N., Greer, C.W., Andersen, D.T., Tille, S., Lacrampe-Couloume, G., Lollar, B.S., and Whyte, L.G. (2008) Heterotrophic and autotrophic microbial populations in cold perennial springs of the high arctic. *Applied and environmental microbiology* **74**: 6898-6907.

Pirk, N., Mastepanov, M., Parmentier, F.-J.W., Lund, M., Crill, P., and Christensen, T.R. (2016) Calculations of automatic chamber flux measurements of methane and carbon dioxide using short time series of concentrations. *Biogeosciences* **13**: 903.

Pirk, N., Mastepanov, M., López-Blanco, E., Christensen, L.H., Christiansen, H.H., Hansen, B.U. et al. (2017) Toward a statistical description of methane emissions from arctic wetlands. *Ambio* **46**: 70-80.

Portnov, A., Vadakkepuliyambatta, S., Mienert, J., and Hubbard, A. (2016) Ice-sheet-driven methane storage and release in the Arctic. *Nature communications* **7**: 10314.

Przybylak, R., Sadourny, R., and Mysak, L.A. (2003) *The climate of the Arctic*: Springer.

Pushkareva, E., Pessi, I.S., Wilmotte, A., and Elster, J. (2015) Cyanobacterial community composition in Arctic soil crusts at different stages of development. *FEMS microbiology ecology* **91**.

Quinn, P.K., Collins, D.B., Grassian, V.H., Prather, K.A., and Bates, T.S. (2015) Chemistry and Related Properties of Freshly Emitted Sea Spray Aerosol. *Chemical Reviews* **115**: 4383-4399.

Rassner, S.M., Anesio, A.M., Girdwood, S.E., Hell, K., Gokul, J.K., Whitworth, D.E., and Edwards, A. (2016) Can the bacterial community of a high Arctic glacier surface escape viral control? *Frontiers in microbiology* **7**: 956.

Redeker, K.R., Chong, J.P.J., Aguion, A., Hodson, A., and Pearce, D. (2017) Microbial metabolism directly affects trace gases in (sub) polar snowpacks. *Journal of The Royal Society Interface* **14**: 20170729.

Remias, D., Lütz-Meindl, U., and Lütz, C. (2005) Photosynthesis, pigments and ultrastructure of the alpine snow alga *Chlamydomonas nivalis*. *European Journal of Phycology* **40**: 259-268.

Remias, D., Schwaiger, S., Aigner, S., Leya, T., Stuppner, H., and Lütz, C. (2012) Characterization of an UV-and VIS-absorbing, purpurogallin-derived secondary pigment new to algae and highly abundant in M*esotaenium berggrenii* (Z ygnematophyceae, Chlorophyta), an extremophyte living on glaciers. *FEMS microbiology ecology* **79**: 638-648.

Robertson, G.P., and Groffman, P.M. (2015) Nitrogen Transformation. In *Soil microbiology, ecology and biochemistry*. Paul, E.A. (ed): Academic Press.

Rosinski, J., Haagenson, P.L., Nagamoto, C.T., and Parungo, F. (1986) Ice-forming nuclei of maritime origin. *Journal of Aerosol Science* **17**: 23-46.

Russell, L.M., Hawkins, L.N., Frossard, A.A., Quinn, P.K., and Bates, T.S. (2010) Carbohydrate-like composition of submicron atmospheric particles and their production from ocean bubble bursting. *Proceedings of the National Academy of Sciences of the United States of America* **107**: 6652-6657.

Ryan, J.C., Hubbard, A., Stibal, M., Irvine-Fynn, T.D., Cook, J., Smith, L.C. et al. (2018) Dark zone of the Greenland Ice Sheet controlled by distributed biologically-active impurities. *Nature communications* **9**: 1065.

Sahling, H., Römer, M., Pape, T., Bergès, B., dos Santos Fereirra, C., Boelmann, J. et al. (2014) Gas emissions at the continental margin west of Svalbard: mapping, sampling, and quantification. *Biogeosciences* **11**: 6029.

Santiago, M., Ramírez-Sarmiento, C.A., Zamora, R.A., and Parra, L.P. (2016) Discovery, molecular mechanisms, and industrial applications of cold-active enzymes. *Frontiers in microbiology* **7**: 1408.

Šantl-Temkiv, T., Sahyoun, M., Finster, K., Hartmann, S., Augustin-Bauditz, S., Stratmann, F. et al. (2015) Characterization of airborne ice-nucleation-active bacteria and bacterial fragments. *Atmospheric Environment* **109**: 105-117.

Šantrůčková, H., Kotas, P., Bárta, J., Urich, T., Čapek, P., Palmtag, J. et al. (2018) Significance of dark CO 2 fixation in arctic soils. *Soil Biology and Biochemistry* **119**: 11-21.

Sattler, B., Puxbaum, H., and Psenner, R. (2001) Bacterial growth in supercooled cloud droplets. *Geophysical Research Letters* **28**: 239-242.

Schäfer, H., Myronova, N., and Boden, R. (2009) Microbial degradation of dimethylsulphide and related C1-sulphur compounds: organisms and pathways controlling fluxes of sulphur in the biosphere. *Journal of experimental botany* **61**: 315-334.

Schnell, R.C. (1975) Ice nuclei produced by laboratory cultured marine phytoplankton. *Geophysical Research Letters* **2**: 500-502.

Schuur, E., McGuire, A.D., Schädel, C., Grosse, G., Harden, J., Hayes, D. et al. (2015) Climate change and the permafrost carbon feedback. *Nature* **520**: 171-179.

Schwier, A.N., Rose, C., Asmi, E., Ebling, A.M., Landing, W.M., Marro, S. et al. (2015) Primary marine aerosol emissions from the Mediterranean Sea during pre-bloom and oligotrophic conditions: correlations to seawater chlorophyll-a from a mesocosm study. *Atmos Chem Phys* **15**: 7961-7976.

Shupe, M.D., and Intrieri, J.M. (2004) Cloud Radiative Forcing of the Arctic Surface: The Influence of Cloud Properties, Surface Albedo, and Solar Zenith Angle. *Journal of Climate* **17**: 616-628.

Singh, B.K., Bardgett, R.D., Smith, P., and Reay, D.S. (2010) Microorganisms and climate change: terrestrial feedbacks and mitigation options. *Nature Reviews Microbiology* **8**: 779.

Singh, P., Hanada, Y., Singh, S.M., and Tsuda, S. (2014) Antifreeze protein activity in Arctic cryoconite bacteria. *FEMS microbiology letters* **351**: 14-22.

Smets, W., Moretti, S., Denys, S., and Lebeer, S. (2016) Airborne bacteria in the atmosphere: presence, purpose, and potential. *Atmospheric Environment* **139**: 214-221.

Steinberg, D.K., Van Mooy, B.A., Buesseler, K.O., Boyd, P.W., Kobari, T., and Karl, D.M. (2008) Bacterial vs. zooplankton control of sinking particle flux in the ocean's twilight zone. *Limnology and Oceanography* **53**: 1327-1338.

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.

Steven, B., Briggs, G., McKay, C.P., Pollard, W.H., Greer, C.W., and Whyte, L.G. (2007) Characterization of the microbial diversity in a permafrost sample from the Canadian high Arctic using culture-dependent and culture-independent methods. *FEMS Microbiology Ecology* **59**: 513-523.

Stevens, I.T., Irvine-Fynn, T.D., Porter, P.R., Cook, J.M., Edwards, A., Smart, M. et al. (2018) Near-surface hydraulic conductivity of northern hemisphere glaciers. *Hydrological Processes* **32**: 850-865.

Stibal, M., and Tranter, M. (2007) Laboratory investigation of inorganic carbon uptake by cryoconite debris from Werenskioldbreen, Svalbard. *Journal of Geophysical Research: Biogeosciences* **112**.

Stibal, M., Box, J.E., Cameron, K.A., Langen, P.L., Yallop, M.L., Mottram, R.H. et al. (2017) Algae drive enhanced darkening of bare ice on the Greenland ice sheet. *Geophysical Research Letters* **44**.

Stohl, A., Berg, T., Burkhart, J.F., Fjaeraa, A.M., Forster, C., Herber, A. et al. (2007) Arctic smoke - record high air pollution levels in the European Arctic due to agricultural fires in Eastern Europe in spring 2006. *Atmospheric Chemistry and Physics* **7**: 511-534.

Stramler, K., Del Genio, A.D., and Rossow, W.B. (2011) Synoptically Driven Arctic Winter States. *Journal of Climate* **24**: 1747-1762.

Takeuchi, N. (2002) Optical characteristics of cryoconite (surface dust) on glaciers: the relationship between light absorbency and the property of organic matter contained in the cryoconite. *Annals of Glaciology* **34**: 409-414.

Takeuchi, N., Kohshima, S., and Seko, K. (2001) Structure, formation, and darkening process of albedo-reducing material (cryoconite) on a Himalayan glacier: a granular algal mat growing on the glacier. *Arctic, Antarctic, and Alpine Research*: 115-122.

Takeuchi, N., Kohshima, S., and Segawa, T. (2003) Effect of cryoconite and snow algal communities on surface albedo on maritime glaciers in south Alaska. *Bulletin of glaciological research* **20**: 21-27.

Takeuchi, N., Nishiyama, H., and Li, Z. (2010) Structure and formation process of cryoconite granules on Ürümqi glacier No. 1, Tien Shan, China. *Annals of Glaciology* **51**: 9-14.

Takeuchi, N., Dial, R., Kohshima, S., Segawa, T., and Uetake, J. (2006) Spatial distribution and abundance of red snow algae on the Harding Icefield, Alaska derived from a satellite image. *Geophysical research letters* **33**.

Tedstone, A.J., Bamber, J.L., Cook, J.M., Williamson, C.J., Fettweis, X., Hodson, A.J., and Tranter, M. (2017) Dark ice dynamics of the south-west Greenland Ice Sheet. *The Cryosphere* **11**: 2491.

Telling, J., Anesio, A.M., Tranter, M., Irvine-Fynn, T., Hodson, A., Butler, C., and Wadham, J. (2011) Nitrogen fixation on Arctic glaciers, Svalbard. *Journal of Geophysical Research: Biogeosciences* **116**.

Thauer, R.K. (2007) A Fifth Pathway of Carbon Fixation. *Science* **318**: 1732-1733.

Theisen, A.R., Ali, M.H., Radajewski, S., Dumont, M.G., Dunfield, P.F., McDonald, I.R. et al. (2005) Regulation of methane oxidation in the facultative methanotroph *Methylocella silvestris* BL2. *Molecular microbiology* **58**: 682-692.

Tjernstrom, M., Sedlar, J., and Shupe, M. (2008) How well do regional climate models reproduce radiation and clouds in the Arctic? An evaluation of ARCMIP simulations. *J App Met Clim* **47**: 2405-2422.

Tveit, A., Urich, T., and Svenning, M.M. (2014) Metatranscriptomic analysis of arctic peat soil microbiota. *Applied and environmental microbiology*: AEM. 01030-01014.

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

Tveit, A.T., Urich, T., Frenzel, P., and Svenning, M.M. (2015) Metabolic and trophic interactions modulate methane production by Arctic peat microbiota in response to warming. *Proceedings of the National Academy of Sciences* **112**: E2507-E2516.

van Dorst, J., Bissett, A., Palmer, A.S., Brown, M., Snape, I., Stark, J.S. et al. (2014) Community fingerprinting in a sequencing world. *FEMS microbiology ecology* **89**: 316-330.

Wagner, D., Kobabe, S., and Liebner, S. (2009) Bacterial community structure and carbon turnover in permafrost-affected soils of the Lena Delta, northeastern Siberia. *Canadian journal of microbiology* **55**: 73-83.

Wagner, D., Lipski, A., Embacher, A., and Gattinger, A. (2005) Methane fluxes in permafrost habitats of the Lena Delta: effects of microbial community structure and organic matter quality. *Environmental Microbiology* **7**: 1582-1592.

Wallenstein, M.D., McMahon, S., and Schimel, J. (2007) Bacterial and fungal community structure in Arctic tundra tussock and shrub soils. *FEMS microbiology ecology* **59**: 428-435.

Wang, X., Sultana, C.M., Trueblood, J., Hill, T.C.J., Malfatti, F., Lee, C. et al. (2015) Microbial Control of Sea Spray Aerosol Composition: A Tale of Two Blooms. *ACS Central Science* **1**: 124-131.

Wartiainen, I., Hestnes, A.G., and Svenning, M.M. (2003) Methanotrophic diversity in high arctic wetlands on the islands of Svalbard (Norway)-denaturing gradient gel electrophoresis analysis of soil DNA and enrichment cultures. *Canadian journal of microbiology* **49**: 602-612.

Wex, H., Fuentes, E., Tsagkogeorgas, G., Voigtländer, J., Clauss, T., Kiselev, A. et al. (2010) The Influence of Algal Exudate on the Hygroscopicity of Sea Spray Particles. *Advances in Meteorology* **2010**: 11.

Wientjes, I., and Oerlemans, J. (2010) An explanation for the dark region in the western melt zone of the Greenland ice sheet. *The Cryosphere* **4**: 261-268.

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. *Canadian Journal of Microbiology* **57**: 303-315.

Williamson, C., Anesio, A., Cook, J., Tedstone, A., Poniecka, E., Holland, A. et al. (2018) Ice algal bloom development on the surface of the Greenland Ice Sheet. *FEMS microbiology ecology* **94**: fiy025.

Wilson, T.W., Ladino, L.A., Alpert, P.A., Breckels, M.N., Brooks, I.M., Browse, J. et al. (2015) A marine biogenic source of atmospheric ice-nucleating particles. *Nature* **525**: 234-238.

Witte, U., Wenzhöfer, F., Sommer, S., Boetius, A., Heinz, P., Aberle, N. et al. (2003) In situ experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor. *Nature* **424**: 763.

Yallop, M.L., Anesio, A.M., Perkins, R.G., Cook, J., Telling, J., Fagan, D. et al. (2012) Photophysiology and albedo-changing potential of the ice algal community on the surface of the Greenland ice sheet. *The ISME journal* **6**: 2302.

Yoshitake, S., Uchida, M., Koizumi, H., Kanda, H., and Nakatsubo, T. (2010) Production of biological soil crusts in the early stage of primary succession on a High Arctic glacier foreland. *New Phytologist* **186**: 451-460.

Yu, Y., Li, H., Chen, B., Zeng, Y., and He, J. (2006) Phylogenetic diversity and cold-adaptive hydrolytic enzymes of culturable psychrophilic bacteria associated with sea ice from high latitude ocean, Artic. *Acta microbiologica Sinica* **46**: 184-190.

Zakhia, F., Jungblut, A.-D., Taton, A., Vincent, W.F., and Wilmotte, A. (2008) Cyanobacteria in cold ecosystems. *Psychrophiles: from biodiversity to biotechnology*: 121-135.

Zhang, G., Cao, T., Ying, J., Yang, Y., and Ma, L. (2014) Diversity and novelty of actinobacteria in Arctic marine sediments. *Antonie Van Leeuwenhoek* **105**: 743-754.

Zhou, J., Davey, M.E., Figueras, J.B., Rivkina, E., Gilichinsky, D., and Tiedje, J.M. (1997) Phylogenetic diversity of a bacterial community determined from Siberian tundra soil DNA. *Microbiology* **143**: 3913-3919.

Zhu, R., Chen, Q., Ding, W., and Xu, H. (2012) Impact of seabird activity on nitrous oxide and methane fluxes from High Arctic tundra in Svalbard, Norway. *Journal of Geophysical Research: Biogeosciences* **117**.

Zubkov, M.V., Tarran, G.A., Mary, I., and Fuchs, B.M. (2007) Differential microbial uptake of dissolved amino acids and amino sugars in surface waters of the Atlantic Ocean. *Journal of Plankton Research* **30**: 211-220.