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Subglacial and Proglacial Ecosystem Responses to Climate Change

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1. Introduction

Life beneath glaciers requires efficient adaptive strategies in order to thrive in these extreme habitats that are characterized by nutrient and energy limitation, low temperatures and reduced water availability. Together with the deep subsurface and the deep oceanic basins, subglacial (beneath glaciers) environments are among the last biosphere-exploration frontiers on Earth. At present we have only a vague idea about the types of organisms that live beneath ice sheets and glaciers as well as their characteristics (Willerslev *et al.*, 1999, 2007). As a consequence we do not know what will happen to them as climate amelioration causes glaciers worldwide to recede and disappear. What we observe today in almost all glacierised regions of the World is that previous subglacial environments change into proglacial (in front of glaciers) environments, where the environmental conditions are very different. In this chapter we will provide an overview of our current knowledge on the subglacial and proglacial ecosystems, and highlight potential consequences of climate change on these habitats.

The multidisciplinary study of subglacial and proglacial ecosystems, is only in its infancy and the literature is rapidly expanding. The reported results are not only relevant for our understanding of biological diversity and adaptability in general, but they also provide the foundation for hypotheses on how we imagine life survived during the periods where the Earth was totally ice-covered (the so-called Snowball Earth glaciations) and how life may survive on Earth in case of a global nuclear disaster (the so-called Nuclear Winter). In fact, the results may seed far-reaching theories on whether subglacial environments may host past or present extra-terrestrial (astrobiological) habitats on Mars, Jupiter's moon Europa, Saturn's moon Titan, and even on planets and moons beyond our solar system (Des Marais *et al.*, 2008). In addition, cold-adapted organisms may also provide a valuable source for enzymes that may have biotechnological applications (Reddy *et al.*, 2009).

A prerequisite for life as we know it is liquid water required for biochemical processes, electrochemical gradients and transfer of chemical substances. The occurrence of water in subglacial environments is largely dependent on the subglacial thermal regime. Beneath cold-based glaciers, i.e. glaciers where the sole is frozen to the substratum, liquid water is a limited resource and may be primarily restricted to a few subglacial channels. However, it

has been argued that liquid water is present at subfreezing temperatures in the micron-diameter vein network between ice crystals (Price, 2000) and as a nanometer-thick water film interface between ice and entrained mineral grains (Price, 2007). These two potential habitats may both contain ion-rich solutions that allow immobilized microbial life to extract energy from redox reactions (Price, 2007). Rohde and Price (2007) have proposed the existence of a third habitat within ice crystals, where metabolism is achieved by diffusion of small molecules through the ice crystal structure. It is likely that microorganisms in these habitats go into a state of 'survival metabolism' or 'dormancy', sufficient to repair DNA damage as it occurs but not sufficient to grow (Price, 2009). In addition, embedded viable endospores, i.e. bacterial spores, and bacterial endospore formers have been observed in ice cores (Christner *et al.*, 2003; Sheridan *et al.*, 2003; Miteva *et al.*, 2004; Miteva and Brenchley, 2005; Yung *et al.*, 2007). These endospores may return to a metabolic state when the conditions for water and nutrient access improve, but the long-term accumulation of damages DNA may not be repairable. Hence, it is likely that the most successful strategy for surviving in sub-zero environments on glaciation-interglaciation scales ($\sim 10^5$ years) is to enter a survival metabolism state rather than convert to endospores (Price, 2009). If subfreezing environments, containing endospores and metabolizing microbes, undergo environmental changes in the form of thawing and accessibility to essential substrates, the surviving microbes may experience rapid growth and found a new microbial consortium adapted to unfrozen subglacial conditions (Humlum *et al.*, 2005).

Beneath polythermal glaciers (i.e. glaciers where the peripheral areas are frozen to the substratum while the central part of the glacier bed is at the pressure-melting point of ice) and temperate glaciers (i.e. glaciers where the entire bed is unfrozen), water flow is routed along various pathways from large fast-flow channels to thin slow-flow water films or as groundwater flow within subglacial aquifers (e.g., Benn and Evans, 2010). Subglacial drainage systems are very dynamic, and spatial and temporal changes occur frequently. Microorganisms that live beneath these types of glaciers must therefore be able to adapt to environmental changes in order to survive. The most common causes of death for microorganisms besides desiccation due to freezing may be cold shock, exhaustion of nutrients, and α -particle radiation from decay of U and Th-containing minerals in subglacial rocks and sediments (Price, 2009).

The origins of subglacial and proglacial microbial communities are closely related to the history of glaciers and, thus, to regional and global climate changes (Figure 1A). When glaciers grow during a cold climatic period, they increase in volume and advance across their proglacial forelands towards a state where their mass balances are in equilibrium with the prevailing climate conditions (Figure 1B). Opposite, when the climate changes towards a warmer period glaciers recede and previous subglacial environments become proglacial environment (Figure 1C). In this context, it must be emphasized that not all glacier fluctuations are directly linked to short-term ($10^1 - 10^4$ years) climate change, although climate is the dominant control on long-term ($\sim 10^5$ years) scales (Yde and Paasche, 2010). Nevertheless, proglacial forelands may harbor sediment, soil, forest, lake, or marine ecosystems that, when overridden by glacier advance, provide founding microbial communities for subglacial ecosystems (Figure 1B). Additional microorganisms may be added by melt-out of microorganisms that have been buried in snow on the glacier surface and transported in ice to the glacier bed, or by subglacial deposition of microorganisms that have been entrained in meltwater on the glacier surface and transported to the glacier bed

via crevasses or glacier wells (moulins) (Hodson *et al.*, 2008). Since the end of the Little Ice Age, the global climate has ameliorated and glaciers around the world have receded or even disappeared (IPCC, 2007). As a consequence, large areas have been deglaciated and subglacial ecosystems are now exposed to proglacial conditions. If global warming accelerates or continues at the present rate for centuries, it is easy to imagine that many subglacial communities, which have survived in niches beneath glaciers during several interglaciation periods, may disappear.

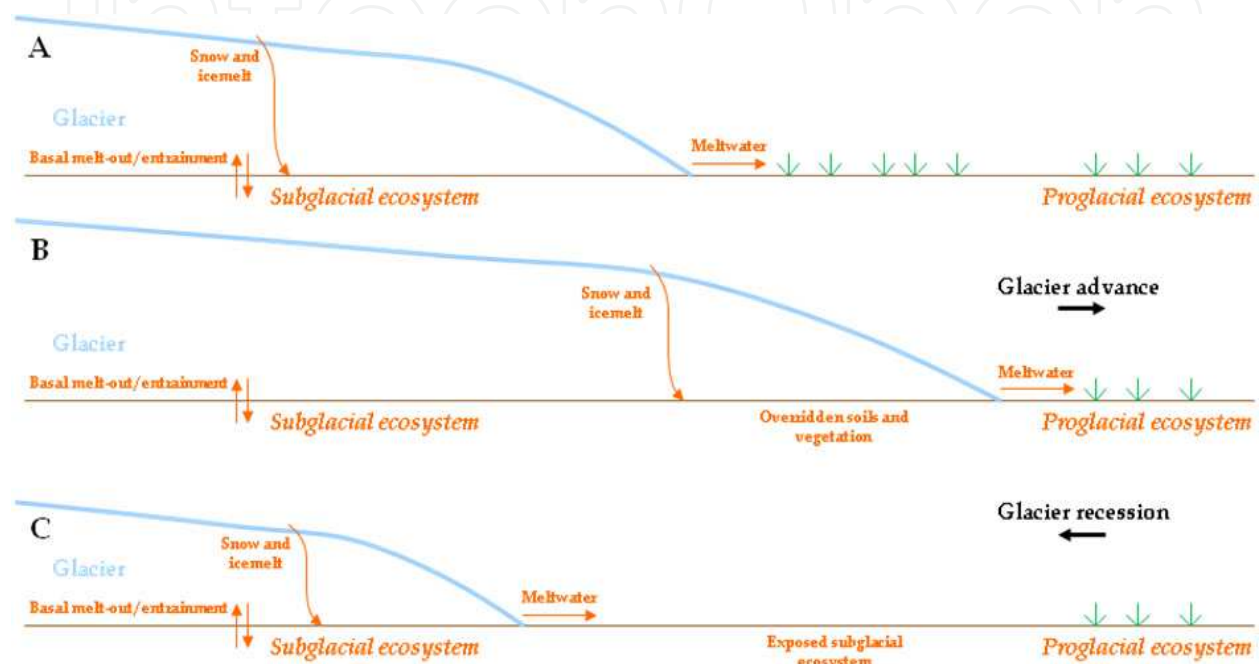


Fig. 1. Potential pathways for the flow of microorganisms in subglacial and adjacent ecosystems. (A) The subglacial ecosystem receives microorganisms from the glacier surface via snow- and icemelt and from basal melt-out, and exports microorganisms through outflow meltwater and basal entrainment; (B) during glacier advance, microorganisms in overridden soils and vegetation are incorporated into the subglacial ecosystem; whereas (C) during glacier recession, subglacial microorganisms become exposed to atmospheric conditions and the system changes into a proglacial ecosystem.

2. Microbial influence on greenhouse gas cycles

Microorganisms play a major role in the cycling of macronutrients, such as carbon and nitrogen, through a variety of aerobic and anaerobic processes. These processes include respiration, methane oxidation and production, nitrification and denitrification, sulfur oxidation and reduction, and are relevant in climatic terms since they directly affect greenhouse gas (GHG) budgets on a global scale. Therefore, focus on carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O) has increased considerably in recent years due to the warming potential of these gases and their importance for the present and future climate.

Much attention has been given to the anthropogenic sources of major GHGs and how human emissions affect their budgets, but the microbially-mediated pathways governing

CO₂, CH₄ and N₂O fluxes in various environments have also attracted increasing research efforts. At present, the physiology of many of the involved microorganisms and their responses to changing environmental conditions are not yet fully understood, especially when it comes to extreme habitats as it is the case for subglacial and proglacial ecosystems. Due to the harsh physical environmental conditions commonly found in subglacial and proglacial environments, biological enzymatic processes slow down due to the low temperatures and limited nutrient supply, forcing microorganisms to develop adaptive strategies that enable them to harvest available substrates. Therefore microorganisms found in these habitats are often characterized as oligotrophs, i.e. organisms that thrive in low nutrient level environments.

In subglacial and proglacial environments, GHGs are produced and assimilated by microorganisms in a number of ways (Figure 2). Generation of CO₂ occurs during autotrophic and heterotrophic respiration and microbial oxidation of organic carbon. Anoxic conditions may occur both in subglacial (Wadham *et al.*, 2008) and proglacial (Wadham *et al.*, 2007) environments, favoring fermentative formation of CH₄ from substrates such as hydrogen gas and CO₂ by methanogenic microorganisms (Boyd *et al.*, 2010, in press). However, uptake of CH₄ by methanotrophs also seems to be a common process on proglacial forefields (Bárcena *et al.*, 2011). Not much is known about generation and assimilation of N₂O in subglacial and proglacial environments. Studies of Midtre Lovénbreen, Svalbard, have provided indirect evidence of subglacial nitrification, denitrification and microbial assimilation of ammonia (Wynn *et al.*, 2006, 2007; Hodson *et al.*, 2010), indicating active microbial influence on nitrogen cycling.

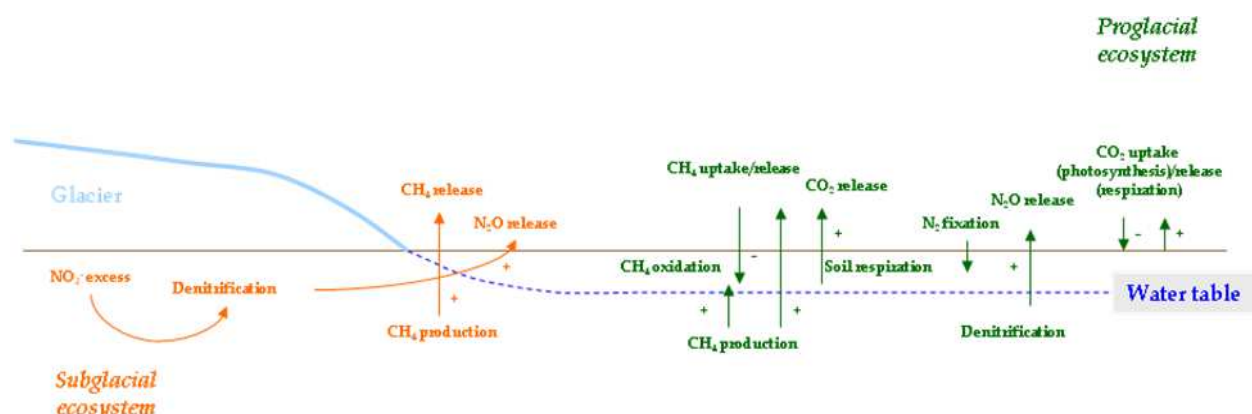


Fig. 2. Conceptual overview of potential processes to greenhouse gas fluxes in subglacial and proglacial ecosystems.

3. Subglacial ecosystems

The study on subglacial ecosystems has started within the last decade and is rapidly growing. At present, most investigations have focused on the basic characteristics, such as who is there (biodiversity) and how do they obtain energy and nutrients (metabolism). So far, non-photosynthetic *Bacteria* from a variety of phylogenetic groups have been described from subglacial environments (Christner *et al.*, 2008; Hodson *et al.*, 2008), and as psychrophilic *Archaea* (Finster, 2008) and viruses (Anesio *et al.*, 2007) are known to exist in other cold environments there are high expectations of their presence in subglacial microbial

communities. In addition, studies of glacial meltwater and basal ice have shown that basidiomycetous yeasts inhabit subglacial ecosystems (Buzzini *et al.*, 2005; Butinar *et al.*, 2007, 2009; de Garcia *et al.*, 2007; Turchetti *et al.*, 2008), and Kornobis *et al.* (2010) suggest that endemic groundwater arthropods on Iceland have survived in subglacial refugia during glaciations. Thus, the consortium of microorganisms beneath glaciers is not only restricted to prokaryotes but also includes eukaryotes. In the following, we will focus on the biodiversity and metabolic processes of *Bacteria* as this domain is likely to dominate in subglacial ecosystems, but first we will examine the physical conditions and ice-bed interface processes that define the subglacial environment.

3.1 Physical environmental conditions

The subglacial zone consists of three components: (1) basal ice, (2) subglacial meltwater, and (3) the substratum. Basal ice is defined as ice formed by processes occurring at the lower part of glaciers and ice sheets (for comprehensive reviews of basal ice, see Knight (1997) and Hubbard *et al.* (2009)). Basal ice is generally composed of a series of ice layers with distinctive characteristics (basal ice facies) formed by different processes at the ice-bed interface, which are able to incorporate significant amounts of debris into the basal ice. The most common processes are *regelation* where ice is formed by pressure-melting on the up-glacier side and refreezing on the lee side of minor bedrock obstacles; *ice infiltration* where low porewater pressure in unconsolidated sediments allows ice to pressure-melt and refreeze into subglacial debris; and *net adfreezing* where the freezing front migrates downwards into water-saturated subglacial debris as a consequence of heat deficit at the ice bed. All these processes result in incorporation of sediments, solutes and microorganisms into the basal ice. After formation, basal ice may undergo metamorphic processes within the ice layer, which cause recrystallisation of ice and redistribution of incorporated particles. Basal ice is also disturbed by deformation and thrusting due to ice-flow extension and compression stress-formation and stress-release.

The configuration of the subglacial hydrological system controls atmospheric oxygen concentrations and, hence, redox potentials (Eh) (Tranter *et al.*, 2005). The main channelized system rapidly routs snow and ice meltwater from the glacier surface through the glacier with a residence time of hours to a few days. Microorganisms inhabiting the channelized drainage system and its hyporheic zone (the channel marginal zone) are likely to have access to oxygen and other atmospheric gasses, and a steady supply of flushed nutrients and organic material from the surface during the ablation season. Allochthonous (derived from adjacent environments) microorganisms originating from supraglacial ecosystems, e.g. cryoconite hole habitats, are also exposed to potential in-wash into the subglacial hydrological system where they must compete with autochthonous (indigenous) microorganisms, providing an important coupling between the two ecosystems (Sharp *et al.*, 1999; Hodson *et al.*, 2008).

The hyporheic zone defines a transition between the channelized drainage system and the distributed drainage system, which is characterized by water-saturated, pressurized conditions in a tortuous slow-flowing network. Water flow and nutrient exchange between the channelized and distributed systems passes the hyporheic zone, making it a particular favorable habitat for subglacial ecosystems (Tranter *et al.*, 2005). In the distributed drainage system oxygen is released by geothermal or frictional melting of bubble-containing glacier ice and consumed by microbially mediated chemical weathering reactions (Tranter *et al.*, 2002). However, the distributed drainage system is almost isolated from atmospheric gasses and is generally considered to be anoxic (e.g., Sharp *et al.*, 1999).

The temperature at the ice bed is constantly close to zero degrees Celsius. There may be slightly higher temperatures in infiltrating water from tributary streams that enter glaciers along the lateral ice-margins, but beneath most parts of warm-based glaciers the temperature is at the pressure-melting point (0 – -2°C). It is impossible for light to penetrate the ice thickness all the way to the subglacial zone, prohibiting photosynthesis to take place.

3.2 Subglacial microbiology

Subglacial microbial communities have now been described from a number of glaciers worldwide. The main focus has been to present total cell count numbers and phylogenetic analyses of 16S ribosomal DNA sequences of isolates. A short overview is provided below and presented in Table 1.

3.2.1 Greenland

The bottom 13 m of basal ice from the deep Greenland ice core (GISP2) has attracted significant attention as this provides a rare opportunity to study subglacial ice sheet microbiology. Sheridan *et al.* (2003) found 6.1×10^7 and 9.1×10^7 cells ml⁻¹ in two duplicate samples, while Tung *et al.* (2006) counted about 10^{11} cells g⁻¹ of sediment. Isolated anaerobic and aerobic enrichment culture studies show a diverse community represented by several major phylogenetic groups: α -, β - and γ -*Proteobacteria*, *Thermus-Deinococcus*, *Bacteroides*, *Eubacterium*, *Clostridium*, *Fusobacterium* and *Actinobacteria* (Sheridan *et al.*, 2003; Miteva *et al.*, 2004; Miteva and Brenchley, 2005). The CH₄ concentration in basal ice at GRIP and GISP2 ice cores is much higher (6,000 and 12,000 ppm, respectively) than atmospheric concentrations (1.8 ppm) (Tison *et al.*, 1998; Price and Sowers, 2004), and Tung *et al.* (2005, 2006) have detected methanogens that are likely to be responsible for producing excess CH₄ concentrations. Similarly, Fe-reducers are inferred to be responsible for excess CO₂ concentrations (Souchez *et al.*, 1995) in the GRIP ice core (Tung *et al.*, 2005, 2006). At the Greenland Ice Sheet margin, Yde *et al.* (2010) found a total cell count 2.3×10^8 cells cm⁻³ in basal ice and sequenced a clone library dominated by α -, β - and δ -*Proteobacteria*, *Bacteroidetes* and *Firmicutes*, but also including *Actinobacteria*, *Acidobacteria*, *Gemmatimonadetes*, *Chloroflexi*, *Caldiserica*, and spore-formers. The presence of Fe-reducers in the form of *Rhodoferrax* and *Geobacter* sequences indicates a high potential for Fe reduction, but lithotrophic β -*Proteobacteria* Fe-oxidizers within the genera *Gallionella* and *Ferritrophicum* were also identified.

3.2.2 Iceland

Microbial communities have been described in two of the three subglacial volcanic lakes beneath the Vatnajökull Ice Cap. Gaidos *et al.* (2004) retrieved lake water and tephra sediments from the Grímsvötn caldera lake with cell counts of 2×10^4 cells ml⁻¹ and 4×10^7 cells g⁻¹, respectively. They primarily identified isolates affiliated with β -, γ - and ϵ -*Proteobacteria*. At western Skaftá lake, Gaidos *et al.* (2009) examined anoxic bottom lake water in detail and discovered a wide variety of bacterial phylotypes including α -, β -, γ -, δ - and ϵ -*Proteobacteria*, *Thermus-Deinococcus*, *Bacteroidetes*, *Clostridium*, *Bacillus*, *Actinobacteria*, *Caldilinea*, *Erysipelotrichi*, *Gemmatimonadetes*, *Verrucomicrobia* and *Chlamydiae*. In the anoxic bottom waters of this subglacial lake it seems that acetogenic bacteria thrive instead of methanogens. The cell counts were 4.7 - 5.7×10^5 cells ml⁻¹.

3.2.3 Svalbard

Subglacial sediments from below Werenskioldbreen and Torellbreen have been analyzed to characterize their microbial community structures (Kaštovská *et al.*, 2007). Viable cyanobacteria and microalgae were found in addition to bacterial cells. Bacterial cell counts showed 2.1×10^8 cells g^{-1} of sediment.

3.2.4 Alaska

The subglacial ecosystem beneath Bench Glacier has shown to include α -, β -, γ -, δ - and ϵ -*Proteobacteria*, *Bacteroidetes*, *Holophaga/Acidobacteria*, and *Spirochaeta* (Skidmore *et al.*, 2005). The clone library consisted almost exclusively of *Proteobacteria* (97% of clones) with β -*Proteobacteria* being the dominant group (68% of clones). Cell counts in snowmelt, ice-marginal and subglacial bulk meltwater and subglacial borehole water ranged between 6.6×10^4 and 3.7×10^5 cells ml^{-1} .

3.2.5 Canada

John Evans Glacier on Ellesmere Island, Nunavut, has the currently best-examined subglacial ecosystem. Skidmore *et al.* (2000) conducted aerobic and anaerobic incubations to show the presence of heterotrophs, NO_3 -reducers, SO_4 -reducers and methanogens. The microbial community comprised α -, β - and γ -*Proteobacteria*, *Bacteroidetes*, *Holophaga/Acidobacteria*, *Planctomycetales*, *Actinobacteria* and *Verrucomicrobia* (Skidmore *et al.*, 2005), although a later study using different gene primers and sequence techniques only found β -*Proteobacteria*, *Bacteroidetes* and *Actinobacteria* (Cheng and Foght, 2007). The subglacial community was different from supraglacial and proglacial communities and, thus, appeared to be adapted to subglacial conditions (autochthonous) rather than allochthonous (Bhatia *et al.*, 2006).

3.2.6 The European Alps

Basal ice and sediment at Glacier de Tsanfleuron and subglacial meltwater at Haut Glacier d'Arolla, Switzerland, were analyzed for microbiological activity by Sharp *et al.* (1999). Total cell counts ranged between 9.3×10^5 and 5.9×10^7 cells ml^{-1} at Glacier de Tsanfleuron and 5.3×10^4 and 1.8×10^6 cells ml^{-1} at Haut Glacier d'Arolla. Incubation experiments with basal ice from Glacier de Tsanfleuron revealed a considerable production of SO_4^{2-} , leading Sharp *et al.* (1999) to infer that microbial-mediated sulfide oxidation enhances the oxidation rate in subglacial environments.

3.2.7 New Zealand

Unfrozen subglacial sediments and basal ice were collected at Fox Glacier and Franz Josef Glacier by Foght *et al.* (2004). The total cell counts in the sediment samples were 2.3 and 7.4×10^6 cells g^{-1} sediment at Fox Glacier and Franz Josef Glacier, respectively. Phylogenetic analyses detected α - and β -*Proteobacteria* and *Actinobacteria* at Fox Glacier, and α - and β -*Proteobacteria*, *Thermus-Deinococcus*, *Bacteroidetes*, *Actinobacteria* and *Firmicutes* at Franz Josef Glacier.

3.2.8 Antarctica

In Antarctica there have been microbiological investigations in different subglacial environments at the West and East Antarctic Ice Sheets and in basal ice at a local glacier. At

the West Antarctic Ice sheet, unfrozen subglacial sediment from beneath Kamb Ice Stream (formerly Ice Stream C) had a cell abundance of $2\text{--}4 \times 10^5$ cells g^{-1} wet sediment (corrected for 15 months storage growth from cell counts of $1.5\text{--}2.7 \times 10^7$ cells g^{-1}) and a clone library represented by α - and β -*Proteobacteria* and *Actinobacteria* (Lanoil *et al.*, 2009).

At Taylor Glacier, an outlet glacier from the East Antarctic Ice Sheet, the saline Fe-rich anoxic subglacial discharge called Blood Falls has been investigated for microbial composition. Cell counts ranged between 0.3×10^4 and 7.6×10^5 cells ml^{-1} (Mikuchi *et al.*, 2004, 2009; Mikuchi and Priscu, 2007). The clone library consists of α -, β -, γ -, and δ -*Proteobacteria*, *Bacteroidetes* and *Chloroflexi* (Mikuchi and Priscu, 2007). At Victoria Upper Glacier, a local glacier in the McMurdo Dry Valleys, Klassen (2009) counted 2.7×10^3 cells ml^{-1} in the lowest part of the basal ice and identified α - and β -*Proteobacteria*, *Thermus-Deinococcus*, *Bacteroidetes*, *Arthrobacter*, *Flavobacterium*, *Frigoribacterium*, *Janthinobacterium*, *Kocuria* and *Microbacterium*. Detailed studies of heterotrophic, aerobic *Hymenobacter*-like strains (belonging to *Bacteroidetes*) have revealed non-vertical evolution, i.e. not by diversification by descent, within this genus (Klassen and Foght, 2011).

The potential for lacustrine ecosystems in subglacial lakes beneath the East Antarctic Ice Sheet has received much attention (e.g. Price, 2000; Siegert *et al.*, 2001, 2003). At the largest of the subglacial lakes, Lake Vostok, an ice core has been drilled into the accretion ice (refrozen lake water) facies above the lake. This ice contained $2\text{--}3 \times 10^2$ cells ml^{-1} (Karl *et al.*, 1999) and a low biodiversity comprising α - and β -*Proteobacteria* and *Actinobacteria*, which likely derived from lake water (Priscu *et al.*, 1998). At present, there has not been any sampling of Antarctic subglacial lakes in order to avoid contamination of these pristine ecosystems.

	α - <i>Proteobacteria</i>	β - <i>Proteobacteria</i>	γ - <i>Proteobacteria</i>	δ - <i>Proteobacteria</i>	ϵ - <i>Proteobacteria</i>	<i>Thermus-Deinococcus</i>	<i>Bacteroidetes</i>	<i>Firmicutes</i>	<i>Actinobacteria</i>	Others
GIS interior	✓	✓	✓			✓	✓	✓	✓	✓
GIS margin	✓	✓		✓			✓	✓	✓	✓
GL, Iceland		✓	✓		✓					
SL, Iceland	✓	✓	✓	✓	✓	✓	✓		✓	✓
BG, Alaska	✓	✓	✓	✓	✓		✓			✓
JEG, Canada	✓	✓		✓			✓		✓	✓
FG, New Zealand	✓	✓							✓	
FJG, New Zealand	✓	✓				✓	✓	✓	✓	
KIS, WAIS	✓	✓							✓	
VUG, Antarctica	✓	✓				✓	✓			✓
TG, EAIS	✓	✓	✓	✓			✓			✓
LV, EAIS	✓	✓							✓	

Table 1. Identified *Bacteria* phyla in subglacial environments; Greenland Ice Sheet (GIS), Grímsvötn caldera lake (GL), Skaftá subglacial lake (SL), Bench Glacier (BG), John Evans Glacier (JEG), Fox Glacier (FG), Franz Josef Glacier (FJG), Kamb Ice Stream (KIS) belonging to the West Antarctic Ice Sheet, Victoria Upper Glacier (VUG), Taylor Glacier (TG) and Lake Vostok accretion ice (LV) belonging to the East Antarctic Ice Sheet. See references in the text.

3.2.9 Microbial diversity

From this summary it seems clear that lithotrophic β -*Proteobacteria* dominates the microbial diversity in many subglacial ecosystems, and α -*Proteobacteria*, *Bacteroidetes* and *Actinobacteria* are relatively common (Table 1). It can also be concluded that subglacial ecosystems may host a wide variety of microbes, including aerobic and microaerophilic heterotrophs; obligate and facultative aerobes and anaerobes; Fe-reducers; denitrifiers; sulfate-reducers and sulfur-oxidizers; homoacetogens; methanogens; strict psychrophiles and psychrotolerants; and spore-formers and non-spore-formers. However, it is noteworthy that while some phyla and genera are abundant in some subglacial environments, they may be rare or absent in others (Skidmore *et al.*, 2005). Also, the total cell counts indicate that subglacial sediments contain a higher number of microbial cells than debris-poor basal ice. The reasons for this may be due to a higher area of debris surfaces where microbes can metabolize, a higher nutrient transport in liquid water flow and the presence of an initial preglacial microbial population that has become glacier-covered.

3.3 Subglacial biogeochemical processes

Throughout the last decade it has become clear that microorganisms have a strong impact on mineral weathering rates and biogeochemical cycling in subglacial environments (Sharp *et al.*, 1999). Microbial mediation may increase the rate of redox reactions such as sulfide oxidation. Where the hydrological drainage system is distributed and the water residence time is long, atmospheric CO₂ and O₂ in meltwater may become exhausted (Tranter *et al.*, 2005). Hence, anoxia is likely to occur in many subglacial environments, and microbially-produced CO₂ may be a significant driver for subglacial carbonation reactions (Wadham *et al.*, 2010).

3.3.1 Organic matter

Organic matter (OM) is a potential metabolic substrate for heterotrophic microorganisms. OM is incorporated into the subglacial substratum when glaciers advance across their proglacial forelands (Barker *et al.*, 2009). The amount of subglacial OM is heterogeneously distributed and relict soils (e.g. Humlum *et al.*, 2005) and vegetation (e.g. Knudsen *et al.*, 2008) may be preserved *in situ* beneath glaciers. For instance, during the formation of Pleistocene continental ice sheets such as the Laurentide Ice Sheet and the Scandinavian Ice Sheet, boreal forests, tundra and organic-rich lake sediments were overridden and their organic content became available for subglacial oxidation reactions (Wadham *et al.*, 2008). The organic carbon (OC) content can be used as a proxy for the amount of OM. In basal ice at the margin of the Greenland Ice Sheet, Yde *et al.* (2010) found that OC comprised 0.15 – 0.21% by mass of the total debris content. This is in accordance with previous findings of 0.27% OC by mass in suspended sediment emanating from Kuannersuit Glacier on Disko Island, West Greenland (Yde *et al.*, 2005), and indicates that OC is potentially available for heterotrophic metabolism after centuries of glacier cover (Yde *et al.*, 2010). Even after about 100,000 years of glacier cover, OC of 0.002% has been detected beneath the Greenland Ice Sheet (Tung *et al.*, 2006). This subglacial reservoir of organic carbon may be metabolized by methanogens, producing subglacial methane that may be releasing to the atmospheric (Wadham *et al.*, 2008). We will discuss this in more detail later, but the overall impression is that organic matter, and particularly organic carbon, may be a valuable nutrient resource for subglacial microorganisms, influence biogeochemical weathering rates and be subglacially converted to greenhouse gasses.

3.3.2 Biogeochemical weathering

Interpretations of the chemical composition of subglacial meltwater often reveal circumstantial evidences of microbially-mediated chemical weathering reactions (Tranter *et al.*, 2002; Hodson *et al.*, 2004, 2005; Skidmore *et al.*, 2005, 2010; Wynn *et al.*, 2006, 2007; Wadham *et al.*, 2010). The exact effect of microbial activity on the total solute flux from glaciers have not yet been quantified because it requires very detailed knowledge on biodiversity and metabolic rates, biotic and abiotic geochemical weathering rates, subglacial thermodynamic processes, hydrology, and the temporal and spatial fluctuations of these variables over the sampling period. However, as more and more information becomes available we are approaching a state where realistic conceptual models may simulate solute fluxes from glacierized catchments based on scenarios with entirely abiotic and assumed biotic geochemical reactions.

3.4 Subglacial ecosystem responses to climate change

Subglacial ecosystems may be sensitive to climate-driven environmental changes such as (1) changes in the basal thermal regime; (2) changes in the hydrological regime; or (3) changes in glacier extent. In the High Arctic, small glaciers may become thinner as a consequence of negative net mass balances during a warming climate. This may change their basal thermal regimes from polythermal or temperate to cold-based because the isolation effects of a thinner glacier cover are unable to keep the basal temperature at the pressure melting point. This will terminate the distributed drainage regime and thereby reduce the accessibility of water-transported nutrient supply to the subglacial communities. Changes in liquid and solid precipitation, the magnitude and frequency of precipitation events, and contribution from ice melt may also affect the hydrological regime and supply of nutrients to subglacial habitats. Unfortunately, we know little about how subglacial ecosystems will respond to these changes due to the inaccessibility of the glacier bed. It is, however, easier to study how atmospherically-exposed subglacial communities change following glacier recession. This will be discussed in the following section.

4. Proglacial ecosystems

Proglacial landscapes consist of a variety of landforms such as glaciofluvial outwash plains, moraine systems, till and dead-ice deposits, bedrock exposures, proglacial lakes and rivers. These landforms host different forms of life that either origin from the subglacial communities or later settlement of pioneering species. Hence, the proglacial landscape allows us to study how the microbial consortium changes from being dominated by subglacial structures to gradually adapt to proglacial environmental conditions. It also allows us to examine how colonizers and soil development processes affect biogeochemical processes and GHG fluxes over time.

The transition from subglacial to proglacial ecosystem is closely linked to climate warming via the dynamic response of glaciers. When the ecosystem has become proglacial its adaption rate is primarily controlled by the time since exposure (e.g. Bárcena *et al.*, 2010). Similar non-glacial processes are well known in the proglacial area after the withdrawal of glaciers and are generally in geological literature referred to as paraglacial processes (Church and Ryder, 1972). An interesting challenge is to assess and quantify the climatic feedback due to net microbiologically-driven changes in CO₂, CH₄ and N₂O fluxes. To date, we have limited knowledge on how proglacial ecosystems respond to climate change, but

research on proglacial ecosystems is rapidly growing and we start to get an impression of microbial diversity and biogeochemical processes from a number of proglacial sites worldwide.

In the following, we focus on proglacial ecosystems, where bacterial diversity and biogeochemical processes have been examined along deglaciation gradients. However, it must be emphasized that changes in proglacial microbial communities cannot be isolated from effects of pioneering plants (Tscherko *et al.*, 2003; Miniaci *et al.*, 2007) and soil invertebrates (Doblas-Miranda *et al.*, 2008), but at present there is little knowledge on the coupling between invasive eukaryotes and microbial processes (Bernasconi *et al.*, 2008).

4.1 Glacier forefields

The term *glacier forefields* generally refers to newly-formed landscapes in front of glaciers that recently have been exposed after glacier retreat (Matthews, 1992). Glacier forefields often provide excellent opportunities to study temporal and spatial variations along a chronological deglaciation transect, referred to as a chronosequence. The glacial recession history since the termination of the Little Ice Age can be reconstructed from old maps and expedition accounts, aerial photos and satellite imagery. This allows a quantitative assessment of the ecological variations of primary successional communities between sampling sites along transects as a consequence of time since deglaciation, without needing long-term observations from the same sites.

4.1.1 Microbial community structures

It is now generally believed that the initial stage after deglaciation is dominated by a development in heterotrophic communities, which decompose allochthonous organic carbon deposits previously overridden by glacier advance (Tscherko *et al.*, 2003; Bardgett *et al.*, 2007). This is followed by increased fixation of carbon by autotrophs that build-up an organic carbon pool, which sustains the heterotrophic community when the ancient organic carbon pool is exhausted (Bardgett *et al.*, 2007). The low availability of carbon and nitrogen is likely to be limiting factors in the early deglaciation stage (Yoshitake *et al.*, 2007), but as the proglacial ecosystem ages the nitrogen pool increases, probably due to fixation of nitrogen by a growing community of nitrogen-fixing bacteria such as *Cyanobacteria* (Nemergut *et al.*, 2007). Also, a molecular study by Kandeler *et al.* (2006) has shown changes in gene composition and abundance of the denitrifying community along a chronosequence. This could indicate a coupling between nitrogen fixers and denitrifiers, however this needs to be confirmed by further studies.

Little is known about the sulfur cycle in glacier forefields. Schmalenberger and Noll (2010) found a surprisingly high diversity of desulfonating *Bacteria* in young proglacial ecosystems at Damma Gletscher, Switzerland, indicating that atmospheric deposition or glacier-derived particles may inoculate glacier forefields. Also, the community structure of desulfonating genetic phylotypes varied along the chronosequence, suggesting that the desulfonating communities change with age based on their affiliation with plant host rhizospheres (Schmalenberger and Noll, 2010).

The potential role of glacier forefields as either CH₄ sinks or sources is very interesting in context to proglacial ecosystem responses to climate change. A study by Bárcena *et al.* (2010) has shown CH₄ production in young deglaciated sediments, in accordance with the methanogenesis observed in subglacial ecosystems (Wadham *et al.*, 2008). However, the microbial community changes from net methanogenic to net methanotrophic as a function

of time since deglaciation (Bárcena *et al.*, 2010). The highest CH₄ consumption rate of 0.76 μg_{CH₄} h⁻¹ m⁻² was measured at the top of the Little Ice Age moraine (Bárcena *et al.*, 2010), where incubation experiments at 10°C and 22°C showed atmospheric CH₄ rates of 1.2 and 2.1 nmol CH₄ day⁻¹ g⁻¹ sediment, respectively (Bárcena *et al.*, 2011). Similar to the denitrifying and desulfonating community studies, the high-affinity methanotrophic diversity also changes along the chronosequence, showing the highest diversity at the oldest sites.

Total cell counts in proglacial ecosystems have been conducted at a number of sites. At Damma Gletscher chronosequence the total cell count increased from 8.2 × 10⁷ to 1.5 × 10⁹ cells g⁻¹ sediment (youngest to oldest), whereas at near Rotfirn Gletscher, Switzerland, the total cell count increased from 1.1 × 10⁸ to 1.9 × 10⁹ cells g⁻¹ sediment (Sigler and Zeyer, 2002). The magnitude of about 1 × 10⁸ cells g⁻¹ sediment is confirmed by total cell counts from six Swiss glacier forefields, including Damma Gletscher (Lazzaro *et al.*, 2009). At five glacier forefields near Ny-Ålesund, Svalbard, the mean total cell count was 6.5 × 10⁷ cells g⁻¹ (Kaštovská *et al.*, 2005), and at Pindari Glacier in the Himalayas it ranged between 2.2 and 8.7 × 10⁸ cells g⁻¹ sediment (Shivaji *et al.*, 2011). Based on these studies, the magnitude range of proglacial communities is within 10⁷-10⁹ cells g⁻¹ sediment.

4.1.2 Soil development

Several studies on glacier forefield ecology have mainly focused on processes involving the establishment and development of soils after a glacier's recession (Cooper, 1923; Field, 1947; Crocker and Mayor, 1955; Evans, 1999; Hodkinson *et al.*, 2003; Egli *et al.*, 2006; He and Tang, 2007; Breen and Lévesque, 2008; Moreau *et al.*, 2008; Schmidt *et al.*, 2008; Strauss *et al.*, 2009), mostly based on approaches regarding plant colonization patterns and changes in soil properties along a chronosequence.

During the last decade, interest in microbial processes taking place in proglacial areas has increased due to the essential role of microbiology in nutrient cycling (Sigler *et al.*, 2002; Bekku *et al.*, 2004; Kaštovská *et al.*, 2005; Kandeler *et al.*, 2006; Bardgett *et al.*, 2007; Hämmerli *et al.*, 2007; Lazzaro *et al.*, 2009; Schütte *et al.*, 2010). The study of soil development is critical in glacier forefield ecology research. Pedological information may elucidate important aspects of a chronosequence such as age of glacial and glaciofluvial deposits and define successional patterns that determine the maturity of different zones in a forefield. In the early stage after deglaciation, soils are merely disorganized accumulations of moraine debris whose significant properties show no regular variation with depth. With the deposition of the stranded glacial till in a stable position, climate and vegetation begin to modify the soils, and to impart them other characteristics (Crocker and Mayor, 1955). Nevertheless, it is essential to address the role of microorganisms in soils from early after deglaciation, since inputs of nutrients and organic matter during ecosystem development are assumed to be dominated by microbial carbon and nitrogen fixation (Schmidt, 2008).

Soil formation on glacier forelands has both autogenic (endogenous) and allogenic (exogenous) components. The autogenic component refers to biotic driven variations; while allogenic refers to changes driven by external environmental factors. Soils in these types of environments are characteristic for being developed on relatively coarse-textured till material (e.g. Bárcena *et al.*, 2011) and the imprint from parent material is highly significant, especially in early stages after glacial recession.

4.1.3 Proglacial ecosystem responses to climate change

Proglacial ecosystems are likely to be affected by climate-driven environmental changes in sediment temperature and moisture. The transition from subglacial to proglacial ecosystem

is of particular interest since it may involve significant changes in net GHG sinks and sources. The study by Bárcena *et al.* (2010) indicates a rapid change from a subglacial methanogenic community to a methanotrophic community in newly-exposed deglaciated areas. This change is unlikely to have any effect on global climate as the CH₄ consumption rates are low compared to other CH₄ fluxes, but it has a significant ecological impact on these cold ecosystems. Future studies should also include investigations of CO₂, CH₄ and N₂O flux rates along chronosequences.

5. Conclusion

Both subglacial and proglacial ecosystems are likely to be affected by climate-forcing environmental changes. In subglacial environments microorganisms are sensitive to changes in the basal thermal regime, in the hydrological regime, and in glacier extent. The transition from subglacial to proglacial ecosystem due to glacier recession is of particular interest because studies indicate a climatic feedback response in the form of rapid changes from subglacial methanogenic communities to methanotrophic communities in deglaciated areas. In proglacial environments the rate of soil development is linked to climate change, and proglacial chronosequence studies have shown to provide essential assessments of how microbial communities change as a function of time since deglaciated.

At present we know very little about these harsh glacial ecosystems. Therefore, initial research efforts have attempted to provide qualitative and quantitative data on microbial biodiversity and abundance, microbial-mediated geochemical weathering processes, and primary succession rates. A review of current literature on subglacial biodiversity shows that lithotrophic β -*Proteobacteria* dominates the microbial diversity in many subglacial ecosystems, and α -*Proteobacteria*, *Bacteroidetes* and *Actinobacteria* are relatively common. However, it is clear that subglacial ecosystems host a wide variety of microbes, including aerobic and microaerophilic heterotrophs; obligate and facultative aerobes and anaerobes; Fe-reducers; denitrifiers; sulfate-reducers and sulfur-oxidizers; homoacetogens; methanogens; strict psychrophiles and psychrotolerants; and spore-formers and non-spore-formers.

This research topic is under rapid development, and future research will give more detailed information on the linkages between biodiversity, environmental conditions and biogeochemical processes. Especially, more research on ecological changes during transition from subglacial to proglacial ecosystems is needed in order to understand how the climatic feedback mechanisms of these ecosystems. So far, focus has been on CH₄ fluxes, but future studies should also include investigations of CO₂ and N₂O flux rates.

6. References

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This book offers an interdisciplinary view of the biophysical issues related to climate change. Climate change is a phenomenon by which the long-term averages of weather events (i.e. temperature, precipitation, wind speed, etc.) that define the climate of a region are not constant but change over time. There have been a series of past periods of climatic change, registered in historical or paleoecological records. In the first section of this book, a series of state-of-the-art research projects explore the biophysical causes for climate change and the techniques currently being used and developed for its detection in several regions of the world. The second section of the book explores the effects that have been reported already on the flora and fauna in different ecosystems around the globe. Among them, the ecosystems and landscapes in arctic and alpine regions are expected to be among the most affected by the change in climate, as they will suffer the more intense changes. The final section of this book explores in detail those issues.

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