Chapter 5

The Role of Microbial Ecology in Glacier Retreat

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Additional information is available at the end of the chapter

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Abstract

Glaciers have been considered too hostile to harbor life for a long time. However, they are now recognized as unique biomes dominated by microbial communities which maintain active biochemical routes. Microbial communities inhabiting glaciers are diverse depending on the type of glacier and the area studied. Some glaciers have a marine margin and finish in a calving front, with partly or completely temperate tidewater tongues, this establishes important differences with respect to glaciers with a land margin. Depending on the glacier area studied, microorganisms are also characteristic as they establish a vertical food chain, from the surface photosynthesizers in upper illuminated layers to heterotrophs confined in the inner part. Glaciers are retreating in many areas of the world due to global warming. Microorganisms are their most abundant and unknown occupants. They play a main role, carrying out key processes in the development of soil and facilitating plant colonization when glaciers have ultimately retired. These microorganisms are perfectly adapted to their harsh environment and are very susceptible to environmental changes. This chapter summarizes the role of microbial ecology as indicator of the conservation status of glaciers.

Keywords: global warming, ecosystem, microorganism, extremophile, psychrophile

1. Introduction

Earth's cold environments have been considered uninhabited for a long time. Icy deserts seemed too hostile to harbor life (**Figure 1**). However, glaciers and ice sheets are unique biomes dominated by microbial communities which maintain active biochemical routes [1].

Glaciers are dominated by very specific environmental characteristics such as the low temperatures associated with precipitation in the form of snow, the exposure to the intense wind, and the extreme solar radiation. In summer, there are processes of melting and sublimation

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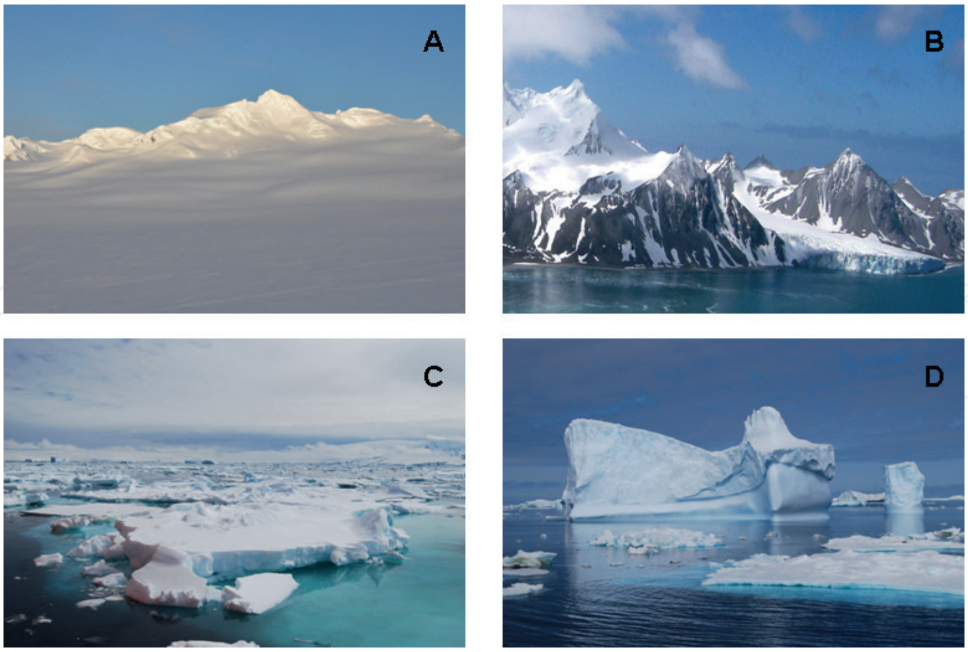

Figure 1. Ecosystems in cold environments. (A) Polar deserts, (B) Glaciers, (C) Icy seas and (D) Icebergs.

that are contrasted with the accumulation of ice in winter, producing an imperceptible but constant dynamism. This is the basis of the life of many of the organisms that inhabit them [2].

Microbial communities in glaciers are different depending on the type of glacier and the area studied. Thanks to DNA sequencing methods, a lot of information about their biodiversity and ecology has been acquired. Firstly, glaciers are of various kinds [3, 4] (**Figure 2**). Some of them have a marine margin and finish in a calving front (**Figure 2(C)**), this establishes important differences with respect to glaciers with a land margin (**Figures 2(A), (B)**). In glaciers ending on land, there is continuous permafrost at ice front (**Figure 2(A)**), while calving glaciers present partly or completely temperate tidewater tongues [4]. Secondly, the growth areas of the glacier (accumulation area) are oligotrophic media for microorganisms. They establish a vertical food chain, from surface photosynthesizers in the upper illuminated layers to protists and bacteria confined in the inner part [5]. These microorganisms are greatly influenced by the melting of surface layers. The diversity of microorganisms in the areas of regression of glaciers (ablation zone and glacial lake) can be lower than in the accumulation area [6], although they are usually more abundant. Predatory species are numerous in these areas, so microbial

Figure 2. Types of glaciers. (A) Gébroulaz glacier ending on land. (B) Literola glacier at Pyrenees, ending on a lake and river. (C) Marine glacier at Livingston Island, South Shetland Antarctica.

diversity decreases. At last, taking into account the horizontal stratification of glaciers, they can be divided into three ecosystems: supraglacial, englacial, and subglacial. Additionally, there has been an increasing interest in characterizing retreating ice fronts of deglaciated forefields with the aim of getting to know how both the richness and the abundance of microorganisms vary in a glacier due to climate change [6–8]. In forefields, mixed communities are observed, whose composition changes very quickly.

2. Earth is a cold planet

From a biological perspective, Earth is a cold planet. Most of the Earth's surface is covered by oceans where temperatures are below 5°C [9], and 80% of the terrestrial biosphere is permanently frozen [10]. Some examples of these cold environments are upper atmosphere, benthic marine zones, polar deserts (**Figure 1(A)**), glaciers (**Figure 1(B)**), subglacial lakes, and icy seas (**Figure 1(C), (D)**) [11].

Snow and ice cover over 108 km^2 of the Earth's surface. Snow in winter can cover up to 12% of the Earth's surface [12], and approximately 10% of the planet's land surface is covered by glacial ice in the form of ice caps, ice sheets, or glaciers, accumulating 75% of the world's fresh water [13]. Mean temperatures observed in snow and ice environments can be highly variable at different depths, sites, or seasons. For example, surfaces exposed to wind are influenced by air temperature. Temperature can range from −50 to −70°C during the winter in the Arctic and Antarctic, respectively, to 0°C in summer [14].

3. Glaciers as biomes

Among cold environments, glaciers are considered biomes that should be recognized as such in their own right [1, 2]. A great diversity of microorganisms belonging to the three main domains (Bacteria, Eucarya and Archaea) has been discovered inhabiting these cold environments. Most of the microorganisms isolated from cold environments are psychotolerant (also called psychrotrophs) and psychrophiles. Psychotolerant organisms can grow at temperatures close to 0°C but have their optimum growth temperature at about 20°C. However, psychrophiles have their optimal growth temperature at 15°C or less [15].

Glaciers are inhabited by microorganisms which maintain active biochemical processes.

To grow efficiently at low temperatures, microorganisms have developed complex structural and functional strategies for their adaptation [16]. The study of these adaptation strategies aims to identify the limits of life at these temperatures. Adaptations include the production of psychrophilic enzymes that are functional at low temperatures with a high catalytic efficiency; the incorporation of unsaturated fatty acids in the cell membrane to improve its fluidity; the synthesis of certain proteins that allow synthesizing others at low temperatures [17]; and the production of compounds that allow the cell to protect itself from frostbite (e.g. sugars, extracellular polysaccharides, antifreeze proteins) [18, 19].

4. Microbial ecology in glaciers

Considering the horizontal stratification of glaciers, they can be divided into three parts: the supraglacial ecosystem, the subglacial system, and the englacial ecosystem [2, 5] (**Figure 3**). These three ecosystems differ in terms of their solar radiation, water content, nutrient abundance, and redox potential [2]. These factors greatly determine the biogeochemical cycles, the type of metabolism, and the diversity and abundance of microbial populations inhabiting glaciers.

4.1. The supraglacial ecosystem

The main habitats in the supraglacial ecosystem are the snowpack, cryoconite holes, supraglacial streams, and moraines. On the glacier surface, the absorption of solar radiation by dark organic matter causes snow and ice melting yielding liquid water that is necessary for microorganisms. Meltwater dissolves nutrients from adjacent debris and even directly from the atmosphere [20].

The sunlit and oxygenated supraglacial surface are populated by autotrophic microorganisms such as microalgae and diatoms; by chemolitotrophic bacteria, which feed on inorganic sand particles; and by heterotrophic bacteria and microeukaryotes.

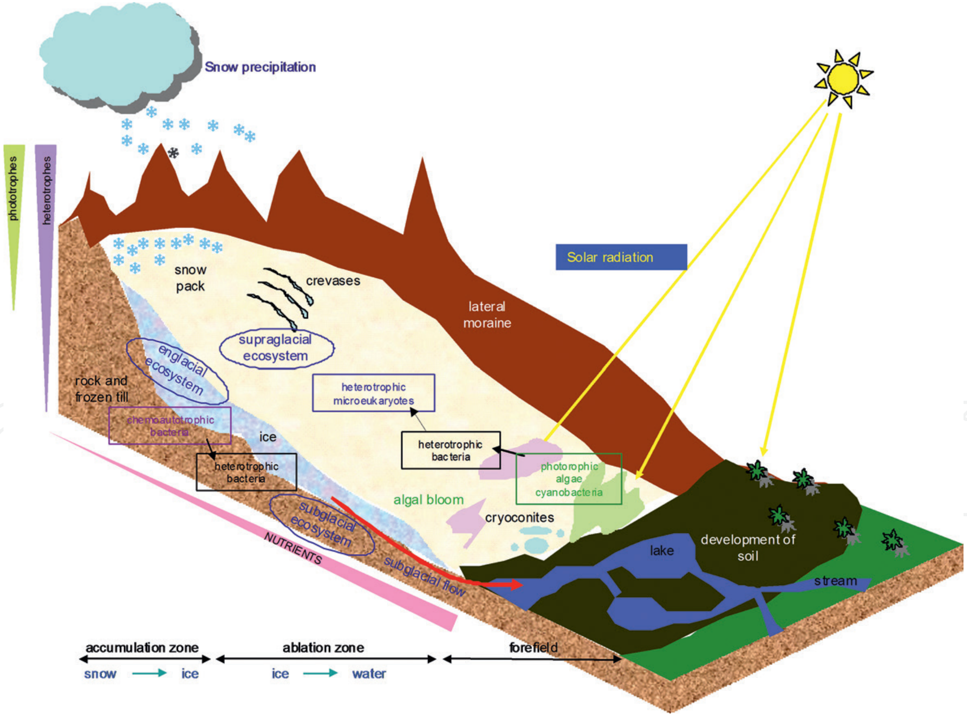

Figure 3. A schematic of different habitats of a glacier colonized by microorganisms. Supraglacial ecosystem is dominated by phototrophic algae and cyanobacteria that take advantage of sunlight and by heterotrophic bacteria and microeukaryotes that feed on organic particles from atmospheric deposition. Microorganisms in englacial ecosystem can be chemoautotrophs, but they can also be heterotrophic bacteria that feed of solubilized products. Subglacial ecosystem is dominated by microorganisms which obtain energy from inorganic compounds and occupy basal ice/till veins and subglacial lakes.

The lithotrophic microorganisms degrade the till and black carbon on the surface of the glaciers. So, the concentration of dissolved ions in water increases and its melting point decreases. This fact develops cryoconite holes, vertical cylindrical melt holes in a glacier surface, which have a thin layer of sediment at the bottom and are filled with water [21]. The materials comprising cryoconite can be divided into two main types: organic and inorganic [22]. Organic matter includes living and dead microorganisms and their products of decomposition, while inorganic matter in cryoconites is dominated by mineral fragments, mainly silicates [22]. Cryoconites are an important microbial habitat in supraglacial ecosystems [1]. Cryoconite holes may converge and origin small streams of liquid water that run downhill [21]. Food webs in cryoconite are dominated by photoautotrophs, mainly cyanobacteria, which provide substrate for heterotrophic communities from a wide range of bacteria. All major groups of heterotrophic bacteria and many fungal groups are represented in cryoconite holes [5]. In addition, microbial eukaryotes such as ciliates are crucial for nutrient recycling through the metabolism of primary producers [23]. Heterotrophic activities in supraglacial habitats are substantial but typically occur at lower rates than the rates of photosynthetic production, which leads to the accumulation of organic matter over time.

Microorganisms inhabiting glacial surface produce a wide diversity of pigmented molecules, which allow their adaptation to cold conditions and solar radiation. They use pigments to obtain energy [24], develop photosynthesis [25], stress resistance [26], and for ultraviolet light protection [27, 28]. For instance, green snow is caused by young, trophic stages of snow algae, whereby more mature and carotenoid-rich resting stages result in all shades of red snow [29]. Dominant species on snow fields belong to the unicellular Chlamydomonaceae. Additionally, some examples of cold-adapted bacteria that produce pigments are the bacterium *Sphingobacterium antarcticus*, which produces zeaxanthin, b-cryptoxanthin, and b-carotene [30]. Other examples include the polar bacteria *Octadecabacter arcticus* and *Octadecabacter antarcticus*, producers of xanthorhodopsin [31], and *Shewanella frigidimarina* which produces the red cytochrome c3 [32, 33]. Colored melanized fungi also live on glaciers, for instance, the oligotrophic genus *Cladosporium* [34]. These pigments absorb solar light and heat, melting snow on glacial surfaces. Microorganisms on glacial surfaces also bear high solar radiation, but in a way, this radiation is beneficial for them. In spring, light radiation melts the glacial surface and leads to the increase in wet areas and the dilution of solutes on snow and ice surfaces, which facilitates the growth of microbial mats [14].

4.2. The englacial ecosystem

The englacial ecosystem presents a minor impact upon nutrient dynamics [2]. Surface meltwaters flood the englacial sediments by means of drainage channels. In englacial ecosystems, live motile bacteria that can reach more than 3000 m of depth. These bacteria live at grain boundaries and other interstices. Mineral substrates such as clay particles [35] provide nutrients and a supply of water for microorganisms. Microorganisms can also live in narrow veins between ice crystals. When the water freezes, dissolved and particulate impurities (including microorganisms) are excluded from the ice matrix into interstitial aqueous channels at the ice-grain boundaries [11]. In turn, these microorganisms and impurities diminish the growth of ice crystals and even break them, facilitating the existence of liquid water. The liquid vein habitat provides water, energy, and nutrients. In contrast with this, the metabolism of microbes encased in solid ice must overcome the diffusion of nutrients in a solid media [36].

Microorganisms in englacial ecosystems can be chemoautotrophs, but they can also be heterotrophic bacteria that feed on solubilized products from pollen grains, invertebrates, and other microorganisms. At great depth, anaerobic respiration can take place [35, 37], and methanogens could be active [2].

4.3. The subglacial ecosystem

At glacial sediments and bedrock, debris contains minerals and sedimentary organic carbon that, combined with subglacial water, create microniches where microorganisms can live [5]. A strong coupling is likely to exist between the hydraulic conditions at the glacier bed and the bacterial processes that take place [20]. The subglacial system is dominated by aerobic/anaerobic bacteria and probably viruses in basal bedrock and subglacial lakes. It also contains diverse, metabolically active archaeal, bacterial and fungal species [38]; although eukaryotes have not been detected in all subglacial environments examined [5].

As there is no sunlight, chemoautotrophic or chemolithotrophic bacteria obtain energy from inorganic compounds. The inorganic processes associated with chemoautotrophs and chemolithotrophs may make these bacteria one of the most important sources of weathering and erosion of rocks on Earth [39].

5. Glacier retreat

Glaciers are highly sensitive indicators of past and present climate change. Their current area and volume are a response to changes in both temperature and precipitation [13], as glaciers respond to slight but prolonged changes in climate. The study of glacier fluctuations is relevant to provide an understanding of climate change over temporal scales [13].

Most glaciers are currently retreating. According to the National Snow and Ice Data Center (NSIDC), the total glacier loss per year since 1994 is approximate 400 billion tons [40–46]. The retreat of glaciers is particularly concerning, since it represents hazards for human communities living near them such as outburst floods, landslides, debris flows, and debris avalanches. Additionally, glaciers contribute substantially to water resources, which can be substantially reduced in many areas of the world [47].

6. Microorganisms in retreat glaciers

Global warming is having a great impact on glaciers, because of the change in air temperature and precipitation [48, 49]. Glacier retreat directly affects various atmospheric, climatic, and ecological phenomena. In retreat glaciers, the thickness of ice and snow decreases, and fossil ice emerges, forefield surface increases (**Figure 4**), new soil develops; and they are colonized by new prokaryotic and eukaryotic microbial species.

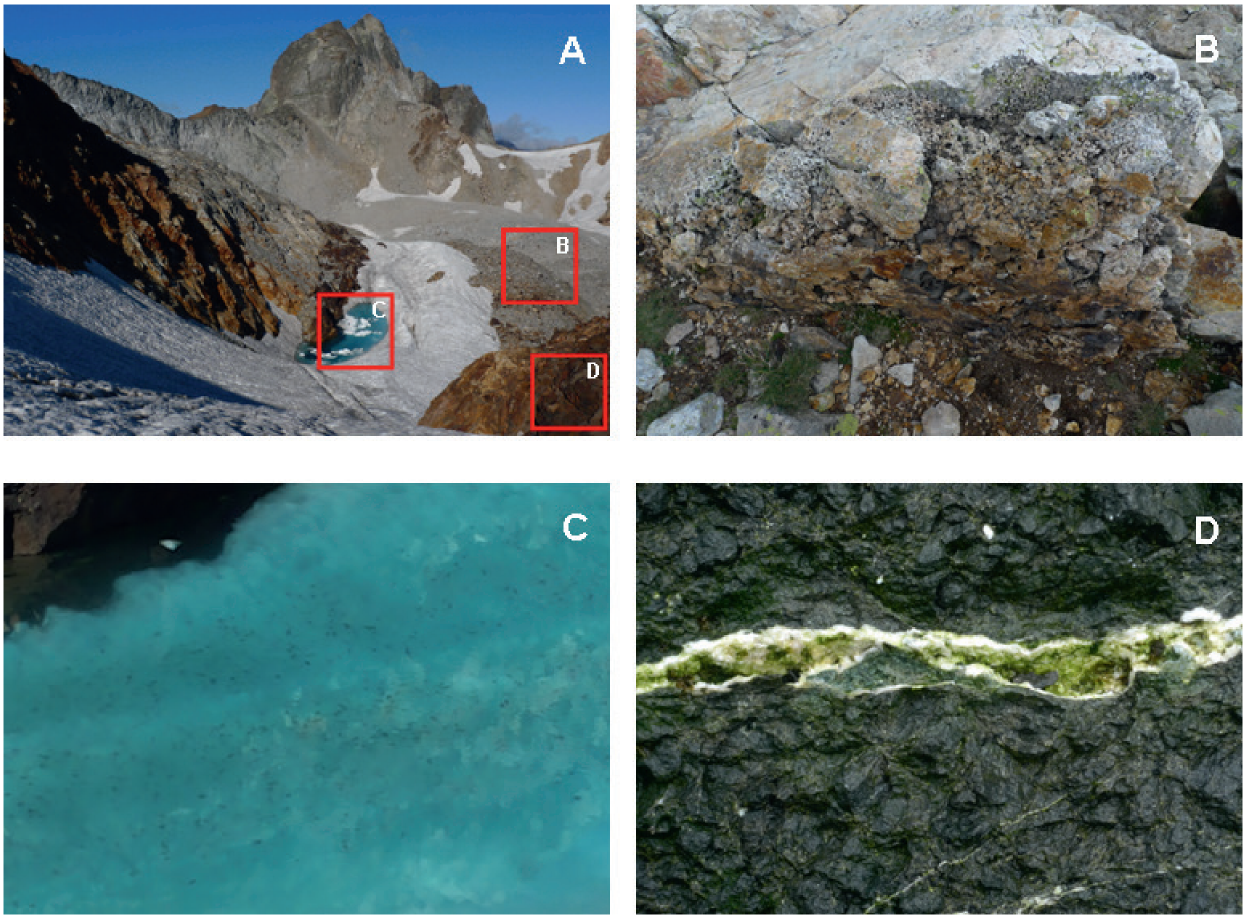

Figure 4. Retreat glacier. (A) In retreat glaciers, the thickness of ice and snow decreases, and it is colonized by new species. (B) Rock with lichens. (C) Microorganisms in the newly formed lake. (D) A rock showing the layer of endolithic phototrophic green algae.

The consequences of climate change are different according to the type of glacier. Depending on the location of the glaciers, these can be classified as terrestrial and marine (**Figure 2**). From the terrestrial glaciers, new lakes and rivers are shaped by runoff waters. On the contrary, some glaciers have a marine margin and terminate in a calving front. In glaciers ending on land, there is continuous permafrost at ice front, while calving glaciers present partly or completely temperate tidewater tongues [4].

One of the effects of climate change on glaciers is that the glacial ice melts and disappears, and microbial communities inhabiting them are being seriously affected [50]. Global warming is changing the basal temperature of the ice, going from cold to polythermal, which causes the growth of new microorganisms that are not psychrophiles but mesophiles thus leading to changes in the diversity and composition of microbial populations [51, 52].

The microorganisms that inhabit glaciers can also contribute to the production of heat as a consequence of their metabolic activity [53]. The amount of heat produced in cryoconite holes of glacial surface has been quantified and reaches 10% of the heat that melts the cryoconite walls during the summer [54]. Although these works have been much questioned [22], a recent work by Hollesen et al. [55] has shown that bioheat can accelerate ice melting on glacier surfaces.

Microorganisms play a main role in glaciers, mainly carrying out key processes in the development of soil, biogeochemical cycling and facilitating plant colonization when glaciers have ultimately retired.

6.1. Development of soil

Global climate change has accelerated glacial retreat. When the glacier ice melts and disappears, recently deglaciated soils establish a new ecosystem at the glacier forefield. Microorganisms are the initial colonizers of these recently exposed soils [7]. Thanks to their metabolic activity, new molecules are obtained that act as nutrients [7]. The microbial community of the newly formed soil is composed of heterotrophic microorganisms, autotrophic microorganisms, and nitrogen-fixing diazotrophs. Allochthonous material is derived from the glacier surface [21, 56], precipitation and aerial deposition [57] and biological sources such as mammal and bird droppings [58]. Additionally, adjacent ecosystems such as marine and subglacial environments are likely to contribute to the nutrient dynamics [58–60].

Downstream of the glacier, torrents are formed from the runoff water. These watercourses carry mineral salts and organic matter that allow the growth of new microorganisms. Biofilms grow on the banks of the streams, containing new microbial communities that although may remain psychrophilic, begin to have majority of psycrotrophic or mesophilic microorganisms.

Endolithic phototrophs, especially green algae and cyanobacteria, grow inside rocks, inhabiting porous rocks near the glacier surface [24]. Rocks are heated by the sun, and water from snow melt can be absorbed, supplying moisture needed for the growth of microorganisms. In addition to being free-living phototrophs, green algae and cyanobacteria coexist with fungi in endolithic lichen communities. Metabolism and growth of these internal rock communities slowly weathers the rock, allowing gaps to develop where water can enter, freeze, and thaw, and eventually crack the rock, producing new habitats for microbial colonization. The decomposing rock also forms a crude soil that can support the development of plant and animal communities in environments where conditions (temperature, moisture, and so on) allow [24].

The ice from the glaciers draws till, forming moraines around and inside the glacier. But it also draws organic matter from bird droppings and from dead plants and animals. In the development of soil, microorganisms break down this organic matter and produce carbon dioxide, water, and heat. Bacteria are responsible for a very little amount of the heat generation in ice, using a broad range of enzymes to chemically break down a variety of organic materials. Many bacteria are motile and can move into the ice channels of permafrost. When conditions become unfavorable, some bacteria survive by forming endospores, which are highly resistant to the cold and the lack of water and food sources. Microbial eukaryotes such as fungi are important because they break down debris, enabling bacteria to continue the decomposition process. They spread and grow by producing many cells and filaments. They can attack organic residues that are too dry or low in nitrogen for bacterial decomposition. Molds are strict aerobes that grow both as unseen filaments and as black, gray, or white fuzzy colonies on the surface. Most fungi are saprophytes; they live on dead material and obtain energy by breaking down organic matter. At last, protists obtain their food from organic matter in the same way as bacteria do but also act as secondary consumers ingesting bacteria and fungi.

6.2. Plant colonization

Retreating glacier fronts expose large expanses of deglaciated forefield, which become colonized by microbes and plants. The space that had been occupied by a glacier which only contained psychrophilic microorganisms is occupied primarily by mesophilic microorganisms inside and on the ice. When this ice disappears and soil begins to develop, rocks and tilt emerge in the moraines; this soil is colonized by lichens on rocks, by algae in streams and by higher plants and animals on the forefield. Most green algae inhabit freshwater, while others are found in moist soil [24]. Other green algae live as symbionts in lichens growing on rocks. In the newly formed soil, mainly consisting of permafrost, the growth of small plants begins. Their roots fragment the ground, forming small channels through which the water that carries ions in solution runs. In this way, the permafrost is fragmented, and it freezes less and less.

In glacier forelands, soil microorganisms are essential for plant growth as they play a key role in the nutrient cycling. In this phase, nitrogen, phosphorus, and other nutrients accumulate and facilitate succeeding plant growth [61]. Nitrogen-fixing plants are common in the primary succession of newly deglaciated soils [62]. Such plant-driven changes to soil nitrogen cycling have significant effects on the establishment of subsequent plant communities [63]. Rhizosphere microbial communities are fundamental for soil cycling, and they are mainly dominated by Proteobacteria, Bacteroidetes, Acidobacteria, Actinobacteria [64], and Firmicutes [65].

6.3. Biogeochemical cycling

Given their coverage at a global scale, snow and ice could have a major and underestimated role in global biogeochemical cycling [14]. It is essential to know how climate change is shaping the distribution and diversity of microbial communities, since microorganisms are very important components in several biogeochemical processes [66] and in food webs [67].

Nutrient matter in retreat glaciers is variable. The carbon content in forefields is very little. It comes from three distinct sources: autochthonous primary production by autotrophic microorganisms; the deposition of allochthonous material; and ancient organic pools derived from under the glacier [7]. Carbon dioxide is removed from the atmosphere primarily by photosynthesis of snow algae and cyanobacteria, and marine microorganisms in marine glaciers; and it is returned to the atmosphere by chemoorganotrophic microorganisms. Glaciers also provide organic matter to downstream ecosystems [7].

Other important nutrients in forefield soils such as nitrogen in the forms of nitrate, nitrite, and ammonia are microbially fixed from atmospheric nitrogen by cyanobacteria and some other bacteria. There are also external sources such as snowmelt, aerial deposition, and the breakdown of complex organic material or sedimentary bedrocks [7]. Bioavailable phosphorus and iron are usually abundant in the topsoil or bedrock of glaciated regions from weathering of the mineral surface [5].

6.4. Acidification or alkalinization of runoff waters

Another important effect of glacier retreat is the modification in the chemical composition of the runoff water of the glaciers. When a part of the terrain that had been covered by the glacier is open to the elements, rocks appear on the surface, whose minerals dissolve and change the physical and chemical characteristics of the runoff water. Occasionally, the waters become even toxic because of the presence of heavy metals [68]. Sometimes the formation of alkaline lakes can be observed, due to the mineral salts entrained by the water of runoff in the ground that had been occupied by a glacier, like the Amarga Lagoon in Chile (**Figure 5(A)**). These lagoons can be inhabited by cyanobacteria which grow forming laminar colonies whose calcareous skeletons fossilize generating sedimentary rocks named stromatolites (**Figure 5(B)**). They are formed when cells build up a carbonate skeleton, integrating particles present in the lake water.

Otherwise, when certain minerals such as pirite are exposed to air and water, a slow chemical reaction with molecular oxygen occurs. While this abiotic reaction can lead to the development of acidic conditions, the degree to which acid mineral drainage becomes an overwhelming burden on the environment results from the oxidative dissolution, a reaction catalyzed by microorganisms [69]. This process affects differently to the terrestrial and marine glaciers. In land glaciers, the runoff waters become more acidic, which affects the rivers and lakes that receive their waters. This can affect the flora and fauna, the crops and the human populations that live downstream. When this fact affects the marine glaciers, the composition of marine tidewater tongues changes their chemical composition: water salinity decreases, and at the same time, water becomes more acidic. Acidification of sea water impacts ocean species to varying degrees. A more acidic environment has a dramatic effect on some calcifying species, including oysters, clams, sea urchins, corals, and calcareous plankton [70].

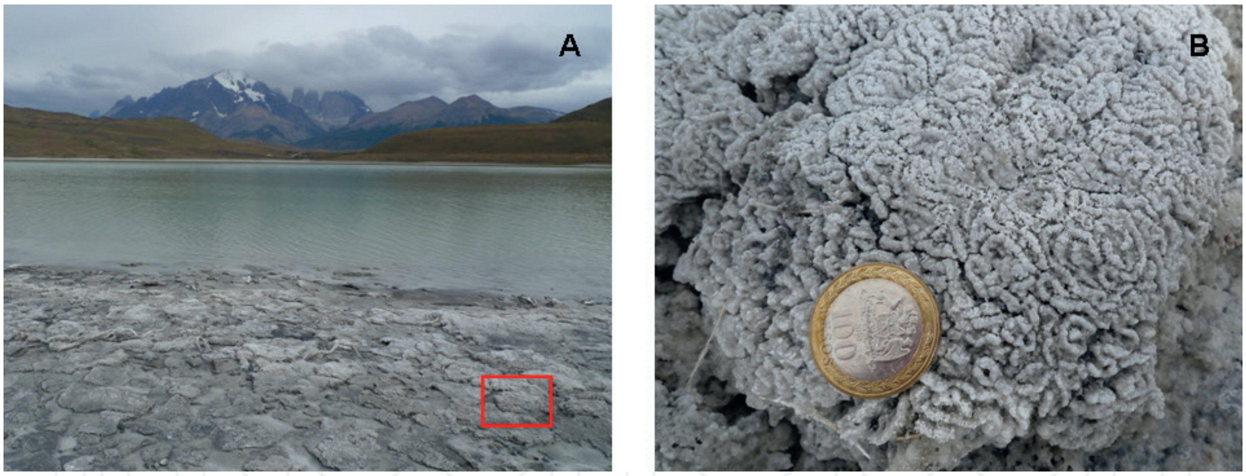

Figure 5. Alkalinization of runoff waters. (A) Formation of an alkaline lake (pH 9.1) due to the mineral salts entrained by the water of runoff in the ground that had been occupied by a glacier. The inset shows the location of **Figure 5(B)**. (B) Calcareous skeleton of a stromatolite of Amarga Lagoon at Chile.

7. Microorganisms as indicators of the conservation status of glaciers

In the last few decades, recently deglaciated areas present in different glacial zones in the world, are available for colonization and primary succession, especially initiated by pioneer microorganisms [71] followed by plants [72] and animals [73].

In retreat glaciers, the microbial populations of the glaciers are very different from those found in the surrounding soils. Some reports [61] have demonstrated that both bacterial and fungal community structures show significant differences between deglaciated sites and successional sites that had been ice-free over more than 100 years [74]. These changes have a strong influence on the processes of colonization and succession in the areas where glacier ice has melted [72]. Firstly, microbial communities change as psychrophilic microorganisms are replaced by mesophilic microorganisms. Then, plants and animals colonize these newly formed environments. Additionally, characteristic bacterial species can be found in each glacier zone and not found in the others. So, there are "type species" that can subsist thanks to their special metabolism and molecular mechanisms of adaptation. An example is shown in **Figure 6**, in which the population of microorganisms in three habitats: glacier snow [51, 75, 76], glacier front [6], and forefield [6, 62, 71] are compared. Although the compared glaciers are located in very different places around the world, it can be observed that the distribution of the main groups of microorganisms is different for each of the three habitats.

7.1. Glacier snow

Several reports have been published [77] about the little microbial abundance observed on glacier snow. For example, in Alpine snow packs, bacterial abundances range between 10^3 and10^5 cells/ml [78, 79], and in Svalbard archipelago, snow bacterial abundances are about 2×10^4 cells/ml [75, 80]. In cell counts performed on Antarctic snow, it was observed that the microbial abundance was even lower ($<10^3$ cells/ml).

Regarding microbial diversity in glacier snow (**Figure 6(A)**), the effect of snow melt on bacterial community structure and diversity of surface environments of a Svalbard glacier has been

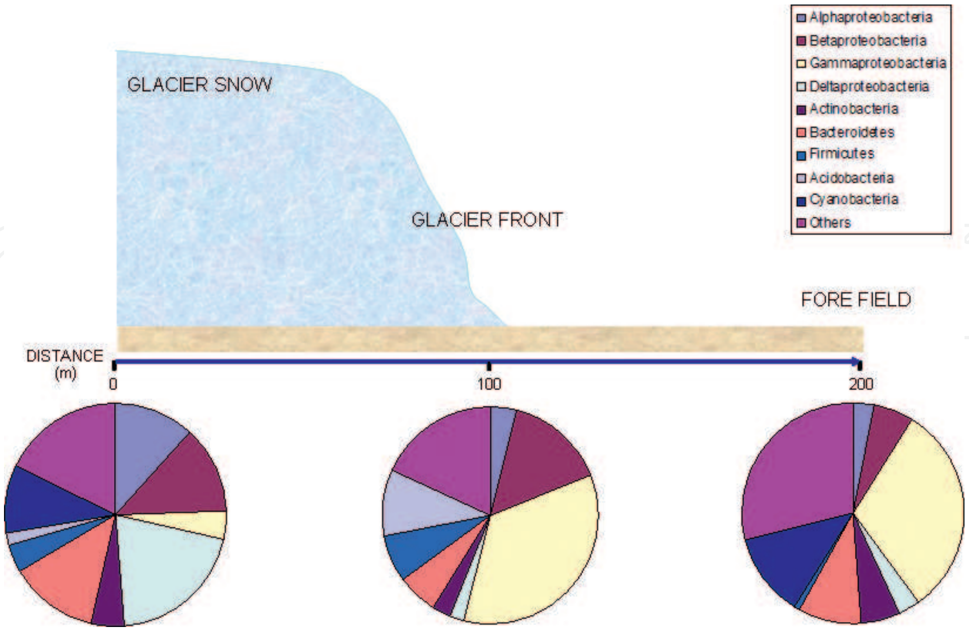

Figure 6. Bacterial community structure along a glacier front based on 16S rRNA gene sequences. Pie charts represent relative abundances of bacterial classes for three glacier environments: glacier snow, glacier front and forefield. The data come from Refs. [51, 76, 77] for glacier snow, from Ref. [6] for glacier front and from Refs. [6, 62, 74] for forefield.

examined using analyses of 16S rRNA genes [51]. In these studies, it was observed that the bacterial community structure depends on the type of snow deposition. However, the most interesting fact, from the point of view of monitoring the state of conservation of the glacier is that slush (the product of decomposition of snow when it melts) contains lineages of bacteria completely different from those of freshly fallen snow, which implies a change in the composition of the community structure that is post-depositional.

Other studies carried out in Greenland demonstrated that the phylogenetic composition of the microbial communities was different within the snow layers [75]. Proteobacteria, Bacteroidetes, and Cyanobacteria dominated in the middle and top snow layers, although Actinobacteria and Firmicutes were also abundant. In the deepest snow layer, large percentages of Firmicutes and Fusobacteria were found [75]. Large numbers of eukaryotic chloroplasts belonging to Streptophyta and Chlorophyta were also observed, demonstrating that microeukaryotes were also present in snow. Cyanobacteria and algae were almost exclusively found in the top and middle layers of the snow pack which are probably feeding the heterotrophic members of the microbial communities.

Some reports have demonstrated that the composition of snow microbial communities depends on the proximity to the sea [76]. In glacier snow, typical species of marine environments such as the Alphaproteobacteria have been found in samples from Antarctica, although Bacteroidetes and Cyanobacteria are also present [76].

7.2. Glacier front

Microbial communities in glacier fronts have been especially studied in the Antarctic Peninsula which is among the regions with the fastest warming rates, and where regional climate change has been linked to an increase in the mean rate of glacier retreat [6].

Archaeal and bacterial 16S rRNA gene sequences obtained from soil samples collected in the Wanda Glacier forefield showed that the diversity and richness were surprisingly high, and that communities were dominated by Proteobacteria, Bacteroidetes, and Euryarchaeota, with many archaeal and bacterial phylotypes yet unclassified (**Figure 6(B)**). Some of the phylotypes found were also related to marine microorganisms, indicating the importance of the marine environment as a source of colonizers for these recently deglaciated environments [6].

Concerning microbial abundance, some examples have been published. In Greenland glacier fronts, between 6 and 30 × 10^7 cells/ml, it has been reported [77].

7.3. Fore field

It has been published that microbial abundance in an Antarctic glacier (Ecology Glacier) forefield is increased along several sampling points from the glacier front to the farther outskirts of the glacier [71]. The same effect has been observed in the Peruvian Andes glaciers, where abundances of Cyanobacteria and Diatoms increased over the time of succession [62].

Regarding diversity, new soils from recently deglaciated soils are colonized by a diverse community of microorganisms during the first years following glacial retreat. Taxonomically microorganisms from Ecology Glacier forefield [71] belonged to the alpha, beta, and gamma subdivisions of the Proteobacteria and to the Cytophaga-Flavobacterium-Bacteroides (CFB) group (**Figure 6(C)**). Filamentous fungi were relatively abundant and represented mainly by oligotrophs.

In the recently deglaciated areas of the Peruvian Andes [62], it has been observed that a significant increase in cyanobacterial diversity corresponded with increases in soil stability, heterotrophic microbial biomass, soil enzyme activity, and the presence of photosynthetic and photoprotective pigments.

In glaciers, increasing temperature leads to a rapid retreat of ice, which increases water production [45, 72]. In glacier forefields, the runoff water of the glaciers can origin rivers and lakes [81]. For example, in the High-Arctic, it has been reported that Bacteroidetes, Actinobacteria, and Verrucomicrobia were the most abundant phyla in freshwater, while relatively few Proteobacteria and Cyanobacteria were present. Possibly, light intensity controlled the distribution of the Cyanobacteria and algae which in turn fed the heterotrophic bacteria [75].

Photosynthetic and nitrogen-fixing microorganisms play an important role in acquiring nutrients and facilitating ecological succession in soils during the first years of succession, many years before the establishment of mosses, lichens, or vascular plants [62]. Afterward, species of green soil algae are important pioneers in the colonization process of the areas recently denuded of ice [72].

At last, soil macrofauna and mesofauna colonize the fore fields. The successional chronosequence of an Alpine glacier was studied at several stages from 4 to 150 years of age since deglaciation [73]. Within the first 50 years, macrofauna biomass and mesofauna abundance increased rapidly, and successional age was the major determinant of community composition [73]. Some studies about soil mesofauna in high alpine ecosystems of the Central Alps demonstrated the shifts in species richness and density of arthropod such as oribatid mites [82]. In newly formed soils, some arthropods populate new soils, which in turn, promote the growth of fungi and bacteria and contribute to the formation of the new soil microstructure [82]. Nevertheless, these new fungi and bacteria are different from those that used to live in glaciers, as the novel species of plants and animals, contain associated microorganisms; for example, new microorganisms contained in animal droppings or symbiotic rhizosphere microbial communities associated to plants [65].

Microbial ecology can be a tool for monitoring the biological change that happens in retreat glaciers. Ecological researches conducted along deglaciated chronosequences in some glaciers have been carried out in order to understand the development of ecosystems. In these studies, distance from a receding glacier is used as a proxy for soil age, with older soils being further from the glacier front [62].

8. Conclusion

In summary, glaciers are retreating in many areas of the world due to global warming, and many of them will be severely affected or will disappear in a few years. Glaciers are unique biomes dominated by microbial communities which maintain active biochemical routes. Their metabolic activity plays an important role in glaciers, mainly carrying out key processes in the development of soil, changing biogeochemical cycling, altering the composition of runoff waters and facilitating plant and animal colonization when glaciers have ultimately retired. These processes impact the planet not only locally but also globally. Microorganisms are perfectly adapted to their harsh environment and are very susceptible to environmental changes. Colonization and primary succession of a recently deglaciated area implies that the abundance of microorganisms increases along deglaciated areas. Yet, at the same time, the diversity of microbial populations changes. In many cases, the number of different species may be lower than it is in the glacier. Thus, abundance and distribution of microorganisms can be considered indicative of the conservation status of glaciers, because alterations in their abundance and distribution depend on glacier conditions. Microbial ecology can be a tool for monitoring the biological change that happens in retreat glaciers.

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