Microbial ecology of the cryosphere: sea ice and glacial habitats

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Abstract | The Earth's cryosphere comprises those regions that are cold enough for water to turn into ice. Recent findings show that the icy realms of polar oceans, glaciers and ice sheets are inhabited by microorganisms of all three domains of life, and that temperatures below 0 °C are an integral force in the diversification of microbial life. Cold-adapted microorganisms maintain key ecological functions in icy habitats: where sunlight penetrates the ice, photoautotrophy is the basis for complex food webs, whereas in dark subglacial habitats, chemoautotrophy reigns. This Review summarizes current knowledge of the microbial ecology of frozen waters, including the diversity of niches, the composition of microbial communities at these sites and their biogeochemical activities.

Psychrophilic
Organisms that thrive at low temperatures. From the Greek words psychrōs (ψυχρός) meaning cold, and phīlos (φίλος) meaning loving.

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In the Earth's history, the size of the cryosphere has varied greatly between the two extreme phases that are known as 'Snowball' and 'Greenhouse', with the spatial and temporal variations in climate having a profound influence on the diversity and distribution of life on Earth[1]. Today, the cryosphere covers about one-fifth of the surface of the Earth, with substantial seasonal variations and a long-term trend of losses in its area and volume due to climate warming[2].

In its solid form as ice and snow, water is not available for cellular processes; however, most icy habitats represent porous matrices and contain some liquid. Furthermore, temperatures below 0 °C slow down cellular reaction rates by altering the functionality of the molecular building blocks (BOX 1). The freezing process itself represents another threat for the survival of life, as growing ice crystals can pierce cells and disrupt their membranes. It is well documented that the temperature ranges of microbial habitats have a pivotal role in the selection and adaptation of the resident microorganisms, and hence in microbial diversification[3]. Microorganisms that can grow in ice are cold-adapted or psychrophilic (BOX 1). They possess lipids and enzymes that retain sufficient physical flexibility below the freezing point to support cellular membrane homeostasis and biochemical catalysis[4]. Other important means of adaptation include the production of anti-freeze proteins and carbohydrate-based extracellular polymeric substances (EPS), which serve as cryo- and osmo-protectants[5,6]. EPS also influence the physical properties of the ice matrix[5], promote cell aggregation[7,8] and enable biofilm formation in and under the ice[9–11]. In this regard, all cryospheric microorganisms seem to share similar adaptations for living in ice (BOX 1).

In this Review, we summarize our current knowledge of the key biogeochemical processes, the community composition and metagenome-predicted functions of the microbial communities of sea ice, supraglacial and subglacial habitats. We focus on bacteria, as they numerically dominate such habitats (for an overview of viruses in the cryosphere, see BOX 2), and on the functional and phylogenetic diversity in the cryosphere. We also briefly cover eukaryotic microorganisms in the habitats where they have key roles in primary productivity. The microbial ecology of permafrost — frozen soils — has been reviewed recently[12] and so is not covered here.

Distribution of microorganisms

The Earth's cryosphere currently comprises an impressive volume of >33 million km (REF. 3) of frozen water. This includes the terrestrial ice sheets of Antarctica and Greenland, mountain glaciers and polar marine ice shelves, and sea ice in Antarctica and in the Arctic Ocean. Most of the biomass of the cryosphere[13], including the deep aquifer, deep-sea and subseafloor realms, is made up of members of the bacterial and archaeal domains. FIGURE 1 shows the different cryosphere realms discussed in this Review, including glacial and sea ice.

Snow, whether falling on sea ice, glaciers or land, deposits a small number of cells, as low as ~10^2 cells per millilitre (calculated from melted samples; TABLE 1) because it is composed largely of air (an uninhabited

Box 1 | **Habitability of ice**

Ice is habitable when some fraction of it remains unfrozen; that is, when physicochemical processes sustain water in its liquid form at temperatures that are below the freezing point, even at −20 °C — a temperature known to allow bacterial activity[33] — and below. Microbial colonization of ice is typically initiated passively via physical processes, such as the concentration of cells during freezing of source waters or the deposition of cells in snow. Those microorganisms that thrive in these habitats are commonly referred to as psychrophiles (for the history and debate relating to the terminology for cold-adapted microorganisms, see REFS 4,129).

Microorganisms that are active within the ice matrix have unique adaptations to the cold (reviewed in REFS 4,124,129), including alterations in membrane lipid compositions that protect against rigidity, providing a flexible interface with the environment for the continued uptake of nutrients and the release of by-products. They also include altered amino acid sequences of proteins and enzymes, both intracellular and extracellular, which provide more flexible tertiary structures for proper functioning in the cold. Cold-shock proteins are constitutively produced by some cold-adapted bacteria and facilitate the correct folding of proteins that are not inherently adapted to low temperatures.

Ice inhabitants must also cope with higher solute concentrations in the liquid networks of their niches, whether those networks represent a significant volume of the ice (as in sea ice) or a very small fraction of it (as in glacial ice). The use of compatible solutes to maintain cell turgor and enzymatic functions seems to be a common cellular strategy to survive these conditions[124]. Another approach involves the expression of specific compounds on the cell surface or their release outside of the cell. For example, some ice-dwelling microalgae and bacteria produce ice-binding or anti-freeze proteins that block the formation of additional ice crystals, which could damage cellular membranes[124,130,131]. The release of complex exopolymeric substances (EPS) is thought to contribute to microbial success in the cold as they function as anti-freeze agents and buffer against high salt concentrations[124,132–134]. Ice-active proteins may also be embedded in the EPS coatings of some microorganisms, thereby increasing their affinity for ice[5,119,135]. Surface-expressed proteins that mimic ice structures turn bacteria into ice-nucleating particles, which contributes to the formation of snow[136].

space) until seasonal melting begins. Desiccation and other extreme tropospheric conditions (such as low temperature, high irradiation including ultraviolet, photoreactive chemistry, low nutrients and instability) also influence the habitability of snow. This has led to the notion that snow does not support a functional ecosystem but rather a collection of organisms that may have survived transport from the troposphere but are not actively growing or metabolizing. However, recent work challenges this concept for deposited snow, with evidence of seasonal changes in the microbial communities that seem to be driven by corresponding changes in the environment[14–17]. For example, metagenomic analyses of functional genes involved in oxidative stress suggest that the variation in light conditions between the surface layer and base layer of the snow are particularly important for shaping both the composition and functionality of the resident microbial community[17].

Glacial ice includes mountain glaciers, ice caps, ice sheets and shelf ice, which together cover >10% of land (FIG. 1). However, at an average thickness of 2 km, they constitute more than 70% of all freshwater on Earth. This thick ice matrix forms slowly over hundreds to thousands of years, as newly precipitated snow compacts the underlying snow layer into firn, which later forms solid ice. Although glacial ice is formed from snow, the microbial community composition and biomass of snow differs substantially from that of the ice surface[15,18]. The surfaces of glaciers provide a range of microbial habitats (termed here supraglacial habitats, comprising the top metre of ice), which seasonal studies[18] show to be colonized by microorganisms from the air (through atmospheric deposition; FIG. 2a) that later develop into distinctive communities within the ice (FIG. 2a). Clean surface ice hosts approximately 10^4 cells per ml, whereas at sites where cells, dust and other mineral particles accumulate, albedo decreases and the ice melts to form cryoconite holes, which are hotspots for life in glacial ice, containing up to 10^8 microbial cells per ml (REFS 19–21; TABLE 1). By areal coverage, cryoconite holes comprise 1–20% of glacier ablation zones worldwide, but the abundance of dispersed cryoconite material at the ice surface is much higher[22].

Beneath the sunlit zone (at a few metres depth) lies the bulk of the glacial ice mass (englacial zone), which has very low cell numbers (10^1–10^3 cells per ml; TABLE 1). This environment pushes life to its limits owing to the low availability of liquid water and space within the ice matrix (pore space), and the lack of energy sources[23]. However, some bacteria survive over geological timescales deep within the ice matrix[24] (for example, in the Greenland ice core) and may thus reflect depositional conditions that occurred in the past[25]. The bottom of glaciers (the basal zone of the subglacial system) was once considered to be devoid of biological activity[26], until the discovery of substantial amounts of viable cells in debris-rich basal material[27,28]. Compared with the bulk of the glacial ice mass, higher cell numbers (10^3–10^5 cells per ml; TABLE 1) are found in the basal zone of subglacial systems, where water remains liquid through a variety of mechanisms. In some Arctic and temperate glaciers, surface meltwater descends through deep cracks in the glacier and accumulates at the glacier base[21,29]. Liquid water also forms at the base of glaciers and ice sheets as a result of melting caused by the pressure of the overlying ice or from geothermal heat[30]. Viable microorganisms have been detected in all subglacial environments sampled, with cell numbers ranging from 10^1 to 10^5 cells per ml (TABLE 1). Lower cell abundances tend to be associated with subglacial lake waters and higher abundances with accretion ice and basal sediments[31,32].

Sea ice covers a larger area of the Earth than glaciers, approaching 10% of the ocean's surface (FIG. 1). But with an average thickness of only 2–3 metres, the global volume of sea ice is much lower than that of the glacial environment (TABLE 1). Despite this difference, sea ice is more dynamic biologically and is generally richer in microorganisms, containing more bacteria (and microalgae) than glacial ice[33,34] (TABLE 1). Sea ice grows rapidly when ice crystals form at the freezing point of seawater (below −1.9 °C). The freezing process concentrates seawater salts and microbial cells within a porous ice matrix. Bacterial densities are higher in this network of subzero liquid brine channels and pockets than in the water column (and higher than when scaled to melted ice volume), sometimes exceeding 10^7 cells per ml of brine[35]. The interconnected pores enable the vertical and horizontal movement of brine and microorganisms between different habitats within the ice. Active movement towards the underlying ocean has been documented

Extracellular polymeric substances
(EPS). High-molecular-weight, carbohydrate-rich exudates that are released by microorganisms in response to a shift in environmental conditions, including temperature, salinity and nutrient availability. EPS are composed primarily of polysaccharides but can also include proteins, DNA or lipopolysaccharides.

Aquifer
A body of permeable rock that can contain or transmit groundwater.

Albedo
A measure of how much solar energy a surface reflects, whereby light-coloured surfaces such as sea ice reflect more solar energy than dark surfaces such as open water. Dust particles and pigmentation by algal growth on the surface of ice lower albedo by decreasing ice reflectivity.

Box 2 | **Viruses in ice**

Viruses that infect microorganisms (phages) are expected to be particularly important in cryospheric habitats[137] because the inhospitality of these habitats tends to support only simple food webs, which are susceptible to gene transfer or microbial death by phages. Viral pressure in habitats at the surface of glaciers and in sea ice has been shown to be particularly strong[3,66]. Evidence that phage infection rates may exceed those in temperate oceans and freshwaters has been obtained in studies of the surface of cryoconite holes[138,139] and of the interior brine networks of sea ice[35,140,141]. The host specificity of viruses from glaciers and sea ice, compared with other types of habitats, is under debate[3]. An *in situ* experiment, where viruses from cryoconite holes were transplanted to a bacterial community from a nearby lake, resulted in successful infection, suggesting that viruses from glaciers can infect bacteria across different cold freshwater ecosystems[138]. Comparable experiments are not available for marine ice, but comparative analyses of the genomes of the marine Colwelliaphage 9A, which can infect *Colwellia psychrerythraea* strain 34H at the lowest temperature recorded for infectivity (−12 °C), and its host did not uncover typical evidence for tight host–phage coupling; for example, no phage-specific defences in the host or auxiliary metabolic genes in the phage were detected[113]. This dearth of evidence, combined with its ability to infect a different host and to infect across a range of environmental conditions[35], suggests that Colwelliaphage 9A and possibly other cold-active marine phages may have a broad host range[113].

Studies of viral diversity in cold environments are rare: the first viral metagenome of an ice-covered Antarctic lake revealed a greater richness of viral families, including single-stranded and double-stranded phages and eukaryotic viruses, than observed in other aquatic viral metagenomes[142]. More recently, an analyses of circular viral genome scaffolds, assembled from cryoconite material from Svalbard in the Norwegian archipelago and from Greenland, revealed several new groups of viruses that possess unusual life strategies, including a satellite phage-plasmid group and a phage that encodes a clustered regularly interspaced short palindromic repeat (CRISPR)–Cas adaptive bacterial immune system[143]. Studies of phages in subglacial habitats are unavailable to our knowledge. The extent to which horizontal gene transfer, particularly when mediated by viruses, has contributed to the genomic adaptations of psychrophiles to their icy habitats[116] is an area of active research, with studies showing gene transfers between bacterial orders[115] and even domains[130], and high levels of exchange between genera[144].

Cryoconite holes
Small holes (submetre scale) in the ablation zone on glacial ice surfaces. They form as a result of the deposition of cryoconite (a mixture of dark-coloured inorganic and organic particles, including microorganisms), which absorbs solar radiation and causes the ice to melt.

Ablation zones
Areas of a glacier or ice sheet where ice loss (caused by melting, sublimation, evaporation or ice calving) exceeds ice gain (due to snow accumulation).

Accretion ice
Ice that forms when liquid water freezes to the base of a glacier or ice sheet. An example is lake water from Lake Vostok, which has frozen to the base of the ice sheet, forming a layer of accretion ice.

for eukaryotes[36–38], and bacterial motility within sea ice seems likely[33,39] but has not been shown experimentally. Where ice algae accumulate they support exceptionally high bacterial numbers, up to 10^8 cells per mg of aggregated algal material or algal mats, which are found on the underside of sea ice[9,11] (FIG. 2b). Although bacteria inhabit the full extent of sea ice, they are more abundant on the bottom of the ice and on its surface because of the higher amounts of brine, nutrients and primary productivity at these interfaces with seawater, snow or the atmosphere (FIG. 2b). The surface environment of new sea ice also supports high cell abundances in ice structures called frost flowers[40,41]. These crystallize from moisture at the surface of new sea ice that has frozen rapidly owing to a steep temperature gradient between the atmosphere and the ocean, as occurs in winter (FIG. 2b). The brines within the underlying sea ice matrix, and the microorganisms they contain, wick upwards into the frost flowers, the saltiest of which contain cells in excess of 10^6 per ml (REF. 40). Lower bacterial abundances (of 10^4 cells per ml) occur in summer melt ponds, an oligotrophic environment where only freshwater bacteria survive[42].

Over the past decade, microbiological studies have thus revealed that viable microorganisms are found in all cryosphere habitats on Earth (FIG. 2). The range of cell counts reported from these frozen realms (TABLE 1) reveals that cell numbers can reach those of unfrozen habitats, especially in the presence of sufficient liquid phase and sunlight or other readily available energy sources. Given this body of evidence showing that microorganisms inhabit even the coldest and most remote forms of ice on our planet, ice can no longer be considered a hostile environment that is devoid of life.

Microbial communities of sea ice

In sea ice, temperatures vary seasonally, from lows of less than −30 °C in surface ice, which is exposed to the colder atmosphere in the winter[43], to highs above 0 °C when the ice begins to melt in the summer. Corresponding salinities of the brine entrapped in the ice matrix range from 24%[43], which exceeds saturation for some sea salts[33], to near freshwater (0.05%) values in meltwaters. Despite such extremes, sea ice sustains microbial activity throughout the year. During winter, brines maintain the habitable liquid phase in the cold surface ice[33,44,45], and the underlying ocean continuously warms the basal ice. During spring and summer, when sunlight facilitates photosynthetic production, phototrophs thrive in the extensive brine pores and channels of the warming ice[34], forming the basis of an ice-associated food web that comprises heterotrophic bacteria, protists (such as ciliates, flagellates and foraminifera) and small sympagic meiofauna (such as nematodes, copepods, rotifers and polychaetes)[46]. Most of this biomass is contributed by sea ice diatoms, such as the bipolar species *Fragilariopsis cylindrus* and *Nitzschia frigida*, and the Arctic species *Melosira arctica*[34] (FIG. 2b).

The sea ice habitat is net-autotrophic during the sunlit seasons[34,47], and its productivity feeds the communities in and below the ice through the release of dissolved and colloidal organic compounds[48]. In late summer, as a consequence of the ice melting, sea ice algae sink to the seafloor, thereby feeding deep ocean life[49]. Depending on snow cover, light and nutrient supplies, sea ice productivity can range from a few to several hundred milligrams of carbon per m^2 per day[11,50,51]. The tight spatial association between algae and bacteria in the pores and channels of the ice (FIG. 2b), the higher concentration of relatively labile dissolved organic matter and the lower grazing pressure in ice all result in the accumulation of dense populations of large bacterial cells (a few micrometres in diameter) compared with the smaller-sized bacteria in the underlying water column[52,53]. Compared with the biomass and diversity of eukaryotic phototrophs, photosynthetic bacteria are rare in sea ice for unknown reasons, but cyanobacteria[54] and purple sulfur bacteria[55] have been detected. Archaea are also a minor component of sea ice communities[56–58], with sequences from Thaumarchaeota dominating over those from Euryarchaeota. Archaea that live in sea ice have yet to be cultured.

The bacterial communities of Arctic and Antarctic sea ice are dominated by heterotrophic members of the classes Flavobacteriia and Gammaproteobacteria, with lower contributions from Alphaproteobacteria, Verrucomicrobia and Bacilli (FIG. 3). The most abundant genera of the two dominant classes are *Polaribacter*,

Basal sediments
The loose debris that is produced by glacial erosion of the underlying material at the ice–bedrock interface of a glacier or ice sheet.

Brine
Salt-rich liquid trapped in channels and pockets within the ice matrix. In very cold sea ice, some sea salts approach saturating levels and precipitate.

Algal mats
A dense accumulation of phototrophic eukaryotic microorganisms, which grow, for example, on the underside of sea ice.

Foraminifera
A group of single-celled eukaryotes with a characteristic calcium carbonate shell and either a planktonic or benthic lifestyle. The remains of their calcareous fossils in seafloor sediments have important roles in paleoclimatology and paleooceanography.

Sympagic meiofauna
Small animals of < 1 mm in size that inhabit sea ice.

Diatoms
Unicellular algae, with silicate walls, that constitute the major fraction of phytoplankton in most coastal and polar oceans; they are also the dominant primary producers in sea ice.

Grazing pressure
Stress on a population of organisms due to grazing or consumption by other, typically larger organisms.

Proteorhodopsin
A photoactive protein that functions as a light-driven proton pump and is used by some marine microorganisms to generate additional energy.

Polyunsaturated fatty acids
(PUFAs). Lipids that contain carbon backbones with two or more carbon–carbon double bonds. They are unsaturated with respect to the number of hydrogen atoms per carbon atom.

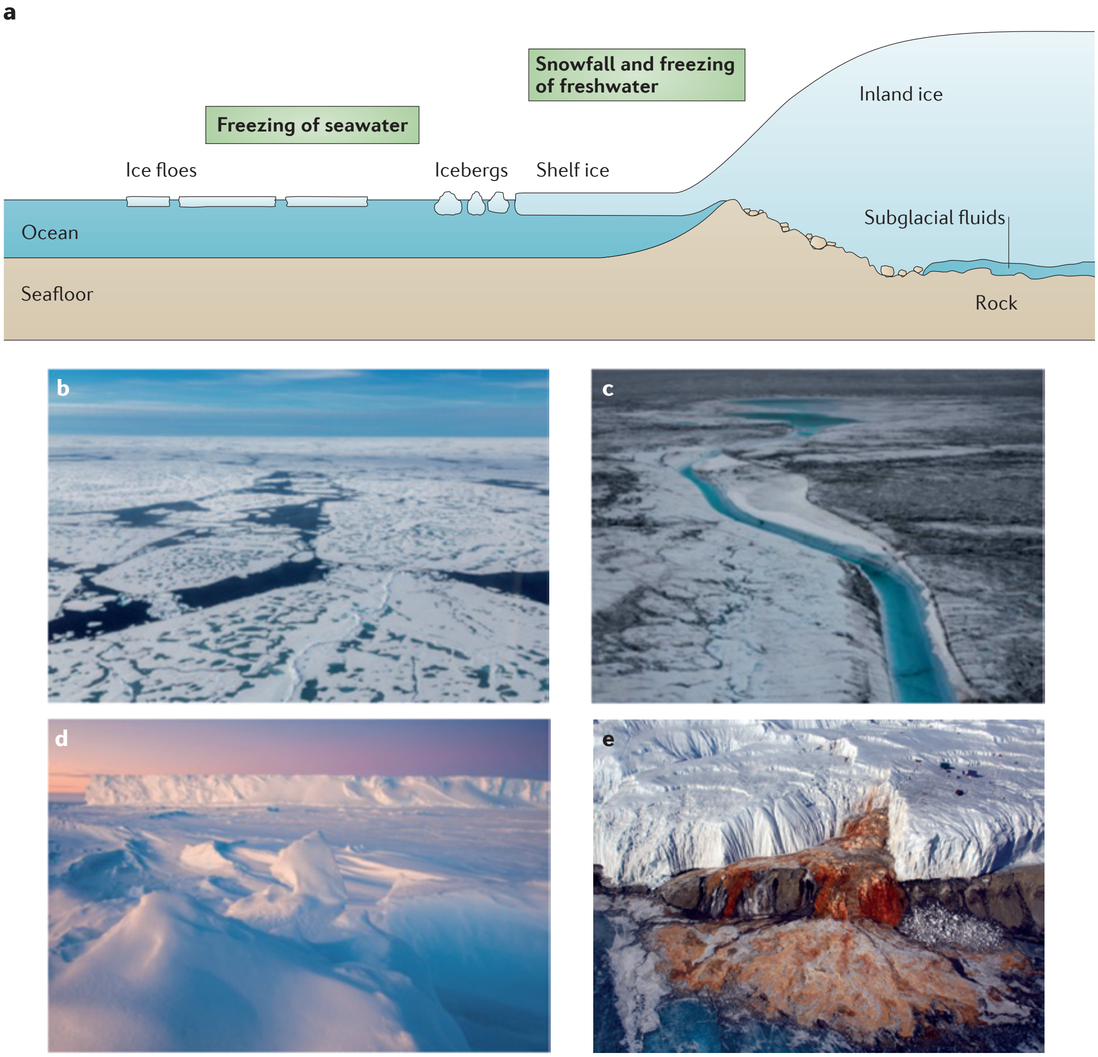


Figure 1 | **The cryosphere's frozen water realms.** **a** | A schematic of different ice habitats inhabited by microorganisms. Freezing of seawater forms sea ice that takes the form of ice floes. Snowfall and freezing of fresh water form inland ice, in the form of terrestrial ice sheets, glaciers and ice shelves, from which icebergs are released into the sea. **b** | Arctic sea ice with melt ponds near the North Pole in 2012. **c** | The surface of the Greenland ice sheet, with a flowing river of meltwater. **d** | An iceberg surrounded by sea ice in Atka Bay, Antarctica, in 2012. **e** | Blood Falls, a subglacial outflow from the Taylor Glacier, Antarctica. The red colouration of the ice is caused by high amounts of iron from the subglacial bedrock that is released into the subglacial liquid. Image in part **b** is courtesy of S. Hendricks, ARK27-3, Alfred Wegener Institute, Bremerhaven, Germany. Image in part **c** is courtesy of C. Bellas, School of Geographical Sciences, University of Bristol, UK. Image in part **d** is courtesy of S. Christmann, Alfred Wegener Institute, Bremerhaven, Germany. Image in part **e** is courtesy of P. Rejcek, National Science Foundation, USA.

Psychrobacter, *Psychroflexus* and *Flavobacterium* in the case of Flavobacteriia, and *Glaciecola* and *Colwellia* in the case of Gammaproteobacteria[58–61]. Members of the flavobacterial and gammaproteobacterial classes are thought to dominate owing to their abilities to exploit the high concentrations of EPS and dissolved organic matter (DOM) produced by sea ice algae[52,62], although some bacteria may supplement their energy needs by using light-driven proteorhodopsin, which was recently discovered in sea ice[54]. Members of the genus *Colwellia* are particularly efficient polymer degraders and contain specific polyunsaturated fatty acids (PUFAs), such as omega-3 docosahexaenoic acid, that may be nutritionally relevant in the sea ice food web[63,64]. Other sea ice genera, such as *Octadecabacter* and *Polaromonas*, include species (such as *Polaromonas vacuolata*) that possess gas vacuoles; these structures are presumably an adaptation to the environment as they keep cells afloat in surface waters between periods of ice melting and refreezing. Many sea ice bacterial genera occur at both poles, but at the species level only *Polaribacter irgensii*[56,65] and *Colwellia psychrerythraea*[64,66] are known to inhabit both poles, and so the extent of polar diversification is unclear[63].

There are differences between sea ice and seawater communities at the class level: flavobacterial and gammaproteobacterial sequences typically dominate surveys of sea ice, and alphaproteobacterial sequences

Table 1 | **Cell numbers in cryosphere habitats**[*]

Habitat	Average area[‡] (10^6 km^2)	Average volume[§] (10^3 km^3)	Cell density (number of cells per ml)	Total cell numbers	Refs
Seasonal snow	47	2	10^2–10^5	10^{20}–10^{23}	33
Sea ice	25	50	10^4–10^7	10^{23}–10^{26}	33
Supraglacial habitats	17	0.02[‖]	10^4–10^8	10^{23}–10^{27}	22,93
Englacial habitats	As above	33,000	10^1–10^3	10^{23}–10^{25}	22,93
Subglacial basal zone	As above	0.02[‖]	10^3–10^5	10^{22}–10^{24}	22,93
Subglacial lake waters	>0.05[¶]	16[¶]	10^2–10^5	10^{21}–10^{24}	91
Permafrost	23	300	10^5–10^8	10^{25}–10^{28}	12
Sum of cryosphere habitats	112	~33,400	10^1–10^8	10^{25}–10^{28}	

[*] The cell counts are based on fluorescent staining of nucleic acids and typically include micrometre-sized bacteria and archaea. Numbers were obtained by filtering the cells in melted ice and have been scaled to the original volume of ice. [‡] Areas from National and Snow Ice Data Center (accessed in February, 2015). [§] Volumes from National Snow and Ice Data Center (NSIDC) and United States Geological Survey (USGS; accessed in February, 2015). [‖] Based on an estimated average depth of 1 metre. [¶] Data from REF. 156.

dominate surveys of seawater (FIG. 3). Although seasonal deviations occur[56], this general trend is consistent with the higher DOM concentrations in sea ice pores (than in seawater), which selects for bacteria that can exploit these conditions and counter-selects organisms that are better adapted to low-nutrient conditions (such as Alphaproteobacteria and archaea). At the species level, sea ice microorganisms show little overlap with planktonic bacteria and archaea in the underlying water column[59,56,61,67,68], with the exceptions of *P. irgensii* and *C. psychrerythraea*. This minimal overlap is perhaps surprising, given that the cover of sea ice shrinks every summer in the Arctic and Antarctic by >50% and 80%, respectively, such that microorganisms released from the ice during the melt season must seek a temporary refuge in the surrounding environment (the seawater presumably) before refreezing in autumn. Seed communities could also be derived from sediments or even the atmosphere, as aerosols from seawater and sea ice are known to occur[58]. In addition, sea ice undergoes strong seasonal changes in temperature and radiation between the winter and summer; thus, the microbial community must be tolerant to such variations[44]. The observed differences in community composition between ice that has existed for only 1 year (first-year sea ice) compared with ice that has existed for multiple years (multi-year sea ice) (FIG. 3) are attributable to the fact that multi-year ice is older and therefore has passed through partial melting–refreezing cycles, which expose its microbial inhabitants to stronger selective pressures than those in first-year sea ice[58,69]. Recent experiments that have examined sea ice formation indicate an important role for freezing in the selection of sea ice communities[41,70]. The thawing process also alters sea ice communities; for example, closed melt ponds that form on top of the sea ice select for Betaproteobacteria owing to the reduced salinity of this niche[42,61]. These findings suggest strong environmental selection in which those organisms that can adapt to the extreme temperature and salinity variations in sea ice[44], and to the energy and carbon sources present at these sites, become predominant[71].

Microbial communities of frost flowers

Frost flowers, which grow on the top of newly formed sea ice, have been the focus of much research into, for example, their role in mercury depletion at high latitudes[72] (FIG. 2b). Recent studies have shown that the microbial communities of frost flowers are distinct from those in the underlying sea ice[73,74] and seawater[41].

Although the few natural fields of frost flowers that have been examined show high inter-site variability in terms of microbial composition, the data confirm that specific microorganisms are selected during frost flower formation: in one case, selection for members of the order Rhizobiales was evident[73]; in another, for oligotrophic and even autotrophic bacteria[41] (members of the SAR11 clade of the order Pelagibacterales and members of the genus *Nitrospina*). Like their counterparts in the sea ice matrix, frost flower bacteria are surrounded by EPS, which presumably function as cryoprotectants, as they do in sea ice. However, in frost flowers these polymers are also subject to photolysis and atmospheric exchange[40]. As fields of frost flowers on new sea ice age and become covered by snow (typically within a week), the delicate crystals collapse, forming a brine-wetted snow layer in which many bacteria seem to thrive. In one study, 85% of the population were classified as alive by 'live/dead' staining[75]. However, the microbial community composition of such saline snow layers is still largely unknown; a single study that included two samples reinforces the expectation that these communities are primarily of marine origin[41].

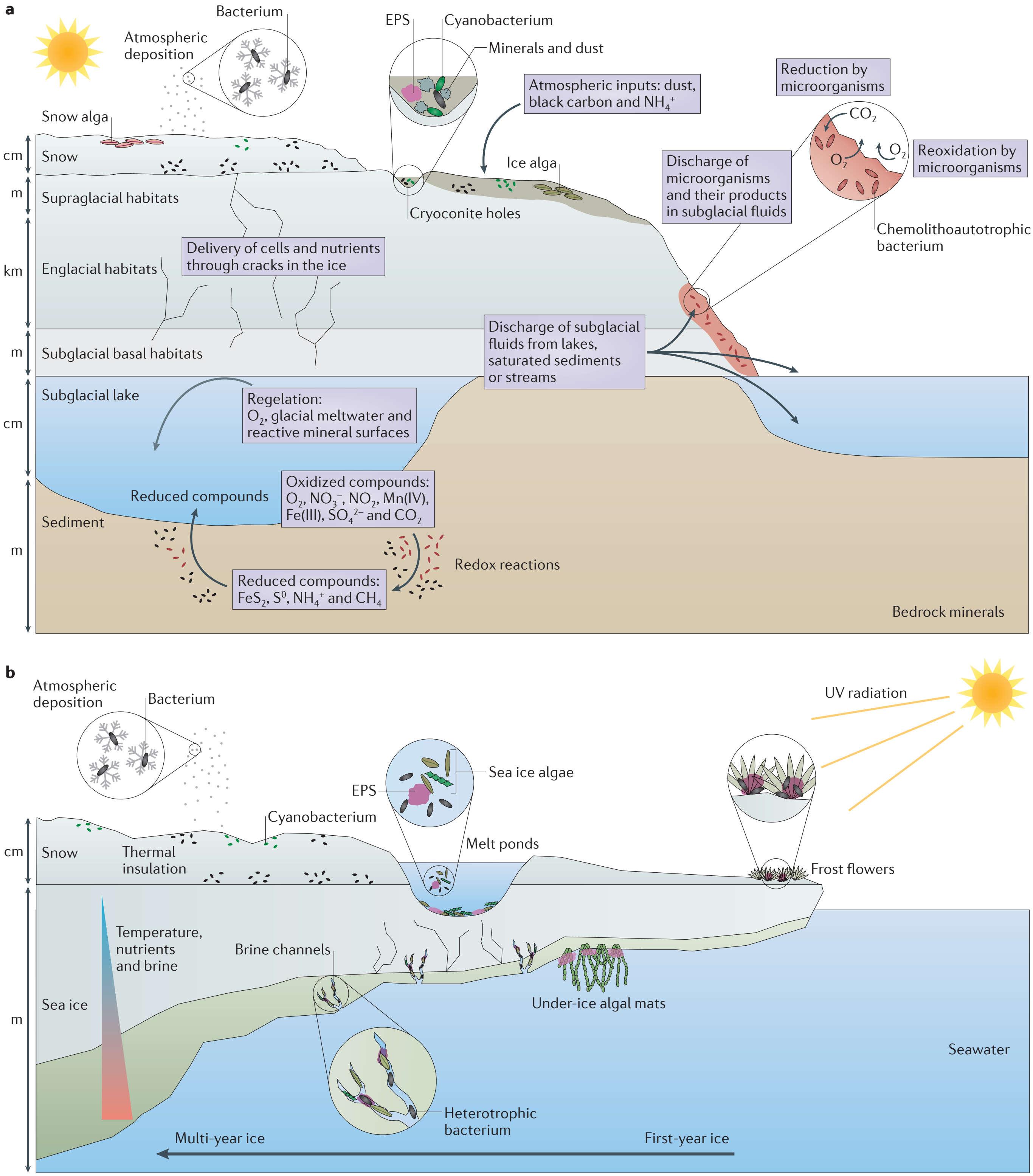
Microbial communities of supraglacial habitats

Activity measurements show that supraglacial communities during the melt season are photosynthetically active (1–10 mg of carbon per m^2 per day), with production rates often exceeding respiration rates[7,76,77]. The resulting accumulation of cells leads to a colouration of the snow and ice on glaciers (FIG. 1), from clean white snow to different shades of green and red snow[78,79]. The reddish colour in snow originates from blooms of algae that belong to the Chlamydomonaceae family[80]. More recently, algae belonging to the Zygnematophyceae have

Seed communities
The source of organisms to a transient ecosystem.

been detected that occupy vast areas of ice surfaces when the snow cover is lost during the summer[78,81]. Both types of algae produce strong secondary pigmentation during summer[77], which is suggested to be a mechanism to adapt to the harsh conditions of snow and ice surfaces, while reducing the ice albedo.

Cryoconite holes are microbial hotspots in supraglacial habitats, where carbon and nutrients from the wind-based deposition of mineral particles promote the growth of photosynthetic and heterotrophic microorganisms[79] (FIG. 2a). Quantifying the deposition and flux of microorganisms, nutrients and minerals at glacial



Glacial runoff
The meltwater draining from glaciers and ice sheets that may come from both surface (supraglacial) and subsurface (subglacial) melt.

Glacier forefields
The terrain most recently exposed by a retreating glacier. This region lies between the current terminus or leading edge of a glacier and the accumulation of glacial debris that marks the previous (greater) extent of the glacier.

Bedrock
The deeper layer of consolidated rock that underlies loose materials, such as soil, gravel and sediment.

Chemolithoautotrophs
Organisms that gain their energy through the oxidation of reduced inorganic compounds and use CO_2 as the sole carbon source for growth. The term is often used synonymously with chemoautotrophy and chemosynthesis.

surfaces via atmospheric transport is challenging. A recent study indicated that a substantial proportion of the particles deposited on the ice is retained from season to season, which contributes to the wastage of glaciers[8]. The main primary producers in cryoconite holes are cyanobacteria[21], whereas the ice surface is dominated mainly by eukaryotic algae. These groups of microorganisms photosynthesize despite the stressful conditions associated with glacial surfaces, including periodical freeze–thaw cycles, reduced water levels and exposure to ultraviolet radiation.

Most investigations of glacial cyanobacteria have focused on the filamentous mat-forming genera *Oscillatoria, Leptolyngbya, Phormidium* and *Nostoc*. These cyanobacteria are important players in cryoconite holes because they produce substantial amounts of organic material, including EPS, which hold minerals and other particles together, effectively increasing the lifetime of cryoconite holes on the ice surface[82]. Less focus has been placed on unicellular cyanobacteria in cryoconite ecosystems[32], but 16S rRNA gene analyses of the global distribution of cyanobacteria from a variety of cold terrestrial and freshwater habitats indicate that they are considerably diverse. Several glacial species, such as *Phormidium priestleyi*, *Leptolyngbya antarctica* and *Leptolyngbya frigida*, are present in both poles, indicating a shared evolutionary history for the colonization of cold habitats[83].

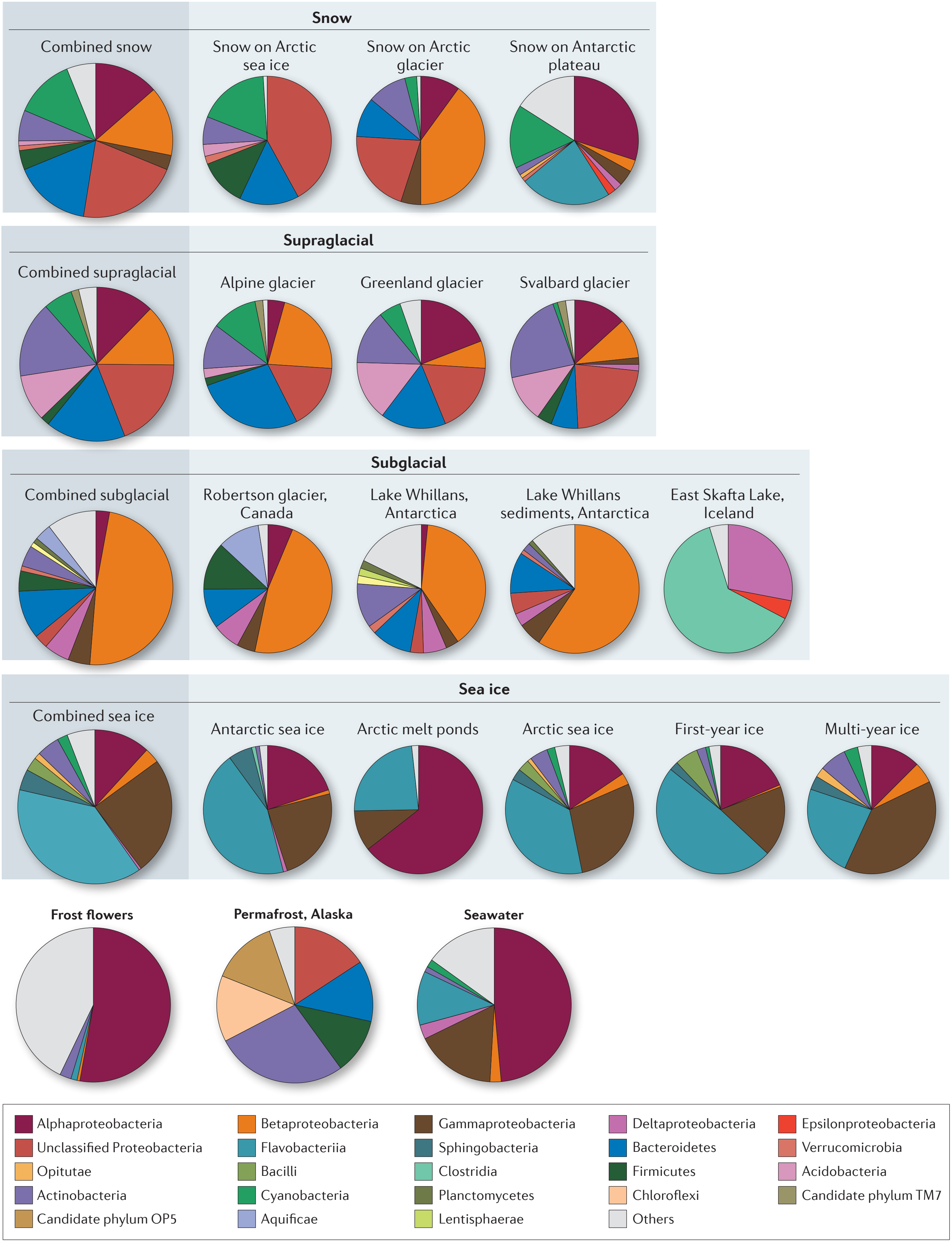
Heterotrophic activities in supraglacial habitats are also substantial but typically occur at lower rates than the rates of photosynthetic production, which leads to the accumulation of organic matter over time[6,7]. All major groups of heterotrophic bacteria and many fungal groups are represented in cryoconite holes[84]. In general, these communities are dominated by the phyla Proteobacteria and Actinobacteria; other important members are those from the phyla Bacteriodetes, Acidobacteria, Chloroflexi and Planctomycetes (FIG. 3). Supraglacial communities show regional differences at low taxonomic resolution, especially between polar and alpine glaciers, with the contribution of Betaproteobacteria and Bacteroidetes dominating alpine glaciers (FIG. 3). Bacterial isolates from cryoconite holes include members of the genera *Pseudomonas*, *Polarimonas*, *Micrococcus*, *Cryobacterium* and *Flavobacterium*, some of which express highly active cold-active hydrolases[85]. Other recent studies have shown that although glaciers and ice sheets retain considerable amounts of particulate organic matter, they also export dissolved organic carbon with a strong microbial signature via glacial runoff[86–88]. A substantial amount of the carbon fixed in supraglacial environments becomes available to downstream ecosystems, such as glacial forefields, coastal waters and subglacial habitats (FIG. 2a). Thus, glaciated systems are not isolated systems but show hydrological connections to other systems such as tundra, lakes and the ocean.

◀ Figure 2 | **Biogeochemical processes in frozen water ecosystems. a** | Supraglacial and subglacial microbial processes. Diverse microbial communities inhabit glacial habitats and use different strategies to fulfil their energy requirements. Snow and supraglacial ice are dominated by photosynthetic microorganisms, including cyanobacteria, ice algae and snow algae, the accumulation of which can colour the ice and snow surfaces brown or red, depending on the type of organism. Photosynthetic cyanobacteria and algae are responsible for the accumulation of greenish brown organic matter and, together with heterotrophic groups such as members of the Proteobacteria, Bacteroidetes and Actinobacteria, thrive in cryoconite holes at the ice surface, where the deposition of carbon and nutrients creates favourable growth conditions. Microorganisms can colonize the supraglacial habitats through atmospheric deposition and through the underlying ice, among other mechanisms. Chemolithoautotrophic communities, primarily composed of Proteobacteria, dominate the subglacial habitats, which include the basal ice, subglacial water and saturated sediment. One example of subglacial outflow is found in the Blood Falls in Antarctica, where the microbial community includes iron-metabolizing bacteria that liberate soluble Fe(II), which oxidizes at the surface to result in a red colouring. In the sediment, these microorganisms use the minerals and carbon substrates in the bedrock to generate energy through redox reactions. Heterotrophic groups are also present. **b** | Snow and sea ice microbial processes. Microorganisms, in particular heterotrophic bacteria, inhabit all dimensions of snow and sea ice, including thin first-year ice, thick multi-year ice, melt ponds and ice structures called frost flowers, despite exposure to high levels of potentially damaging radiation at the ice surface. Cyanobacteria, delivered by atmospheric deposition, have occasionally been detected: for example, in snow and surface melt ponds. Sea ice algae have been found in large aggregates at the bottom of melt ponds. These algae, especially diatoms, also inhabit brine channels and bottom ice, where they are bathed with seawater nutrients. Once algae such as the filamentous diatom *Melosira arctica* accumulate at the bottom and underside of the ice, a green or brownish colouration of the ice can be observed. The porous ice matrix and the frost flowers are filled with extracellular polymeric substances (EPS), and these are also relevant in the attachment of under-ice algal mats. High cell numbers at the interfaces between sea ice and seawater, snow or atmosphere have been attributed to higher primary productivity (for example, in under-ice mats of diatom algae) and higher concentrations of brine or nutrients (for example, brine channels and frost flowers).

Microbial communities of subglacial habitats

As glaciers move, they grind up the bedrock and sediments they pass over, creating finer material known as basal debris, which has an increased reactive surface area (FIG. 2a). This debris contains minerals and sedimentary organic carbon that, combined with subglacial water, create hotspots for microbial life. Over time, as water migrates under the ice sheets, aqueous features may form below the ice, including ‘wetlands’ and saturated sediments, streams and lakes[89]. Few subglacial environments have been sampled given the challenges associated with access to these environments (BOX 3); those that have been sampled contain diverse, metabolically active archaeal, bacterial and, in some cases, fungal species[90]. Eukaryotes have not been detected in all subglacial environments examined. Despite the challenges, a research team recently succeeded in sampling water and sediments from subglacial Lake Whillans in Antarctica[91], where they discovered a diverse community of bacteria and archaea.

Biogeochemical measurements, molecular surveys and enrichment assays have shown that all major metabolic lifestyles, with the exception of photosynthesis (owing to the lack of sunlight), are likely to occur in subglacial systems[92,93]. Chlorophyll and gene sequences that belong to photosynthetic organisms have been retrieved from some glacier beds where supraglacial water penetrates to the base[6,90,94]; however, these organisms, or their cellular remains, were probably transported from the surface, which in temperate glaciers can be over distances of tens of metres. Instead of photosynthesis, the dark fixation of inorganic carbon by chemolithoautotrophs


Snow
Combined snow
Snow on Arctic sea ice
Snow on Arctic glacier
Snow on Antarctic plateau
Supraglacial
Combined supraglacial
Alpine glacier
Greenland glacier
Svalbard glacier
Subglacial
Combined subglacial
Robertson glacier, Canada
Lake Whillans, Antarctica
Lake Whillans sediments, Antarctica
East Skafta Lake, Iceland
Sea ice
Combined sea ice
Antarctic sea ice
Arctic melt ponds
Arctic sea ice
First-year ice
Multi-year ice
Frost flowers
Permafrost, Alaska
Seawater
Alphaproteobacteria
Betaproteobacteria
Gammaproteobacteria
Deltaproteobacteria
Epsilonproteobacteria
Unclassified Proteobacteria
Flavobacteriia
Sphingobacteria
Bacteroidetes
Verrucomicrobia
Opitutae
Bacilli
Clostridia
Firmicutes
Acidobacteria
Actinobacteria
Cyanobacteria
Planctomycetes
Chloroflexi
Candidate phylum TM7
Candidate phylum OP5
Aquificae
Lentisphaerae
Others

◀ Figure 3 | **Bacterial composition of the cryosphere.** Bacterial community structure of different cryospheric habitats based on 16S rRNA gene surveys. Pie charts represent relative sequence abundances of different bacterial taxa for each cryosphere habitat; depending on the resolution of the study, these taxa represent bacterial classes (Alphaproteobacteria, Bacilli, Betaproteobacteria, Clostridia, Gammaproteobacteria, Deltaproteobacteria, Epsilonproteobacteria, Flavobacteria, Opitutae and Sphingobacteria) or phyla (Acidobacteria, Actinobacteria, Aquificae, Bacteroidetes, Chloroflexi, Cyanobacteria, Firmicutes, Lentisphaerae, Planctomycetes, Verrucomicrobia and unclassified Proteobacteria), as well as the candidate phyla OP5 and TM7. The pie charts are based on targeted next-generation sequencing surveys of 16S rRNA genes, with the exception of those representing frost flowers and permafrost, which are based on 16S rRNA data extracted from metagenomic surveys. The data sources for each cryospheric habitat were: REF. 14 for snow on Arctic sea ice; REF. 149 for snow on an Arctic glacier; REF. 150 for snow on the Antarctic plateau; REF. 151 for supraglacial habitats (including alpine, Greenland glacier and Svalbard glacier habitats); REF. 152 for Antarctic sea ice; REF. 61 for sea ice Arctic melt ponds; REFS 58,61,69,153 for Arctic sea ice; REFS 61,153 for first-year ice; REFS 58,69 for multi-year ice; REF. 94 for the subglacial habitat in the Robertson Glacier, Canada; REF. 91 for water and sediment from Lake Whillans, Antarctica; REF. 107 for the East Skafta lake, Iceland; REF. 73 for frost flowers; REF. 154 for permafrost in Alaska; and REFS 58,61,155 for seawater.

Heterotrophs
Organisms that use organic compounds as their carbon source and obtain energy through the oxidation of these compounds.

Redox chemistry
Pairs of reactions in which one compound becomes oxidized and releases electrons, and the other compound becomes reduced and accepts the released electrons.

Remotely operated vehicles
(ROVs). Tethered unmanned underwater robots often used for deep-water research or industrial purposes.

Methanogenesis
The biological production of methane (CH_4) in an anaerobic process mediated exclusively by methanogenic archaea.

Phylotypes
Different taxonomic groups of microorganisms that can be determined by comparative analyses of their 16S rRNA gene sequences.

Calvin cycle
A series of biochemical reactions used by many photosynthetic organisms to convert CO_2 into organic compounds.

Isotopic signature
The ratio of isotopes of a particular element in a molecule of interest, as measured by isotope ratio mass spectrometry.

forms the base of subglacial food webs, which is driven by chemical energy from the basal and subglacial environment (FIG. 2a). This activity (as measured by radiolabelled bicarbonate incorporation) reaches several micrograms of carbon per m^2 per day in subglacial Lake Whillans[91], which is comparable to the rates measured for other subglacial ecosystems, including Blood Falls in Antarctica[95] and Grímsvötn in Iceland[96]. Heterotrophs are also present and can derive organic carbon for biosynthesis from labile exudates of chemolithoautotrophic primary producers or can use ancient organic matter in sediments, which may have been deposited in preglacial times[97].

Bedrock composition influences microbial communities by providing mineral and carbon substrates that link redox chemistry with microbial metabolism[98]. Meltwater derived from basal ice contributes oxygen to the subglacial environment and therefore exerts control on the redox state[99]. As this supply of subglacial oxygen is consumed by aerobic heterotrophs and chemolithoautotrophs, alternative electron acceptors for microbial respiration become important. Nitrate reduction has been measured in sediments sampled near the terminus of Robertson Glacier[100], and sulfate reduction was shown to occur in similar sediments from John Evans Glacier in the high Arctic under anaerobic conditions[27]. Reports on stable isotopes of sulfur and oxygen also support subglacial sulfate reduction beneath Arctic[101] and Antarctic glaciers[97].

Although the direct release of methane from subglacial environments has not been measured, there is evidence that methanogenesis occurs: methane has been shown to accumulate in anaerobic enrichment cultures that were derived from below the John Evans Glacier in Canada[27]. Molecular signatures have also been detected in subglacial sediments from Robertson Glacier in Canada including 16S rRNA and methyl coenzyme M reductase gene sequences for methanogenic archaea of the euryarchaeal order of Methanosarcinales[102]. Below the Russell Glacier in Greenland, 16S reverse-transcribed RNA sequences related to the euryarchaeal order Methanosarcinales and Methanomicrobiales were detected[103]. A significant concern for the atmosphere and climate is the fate of subglacial carbon, which is estimated to be between 418 Pg and 610 Pg[104]. In fact, one study suggests that the concentration of methane in the Antarctic may be of the same magnitude as estimates for Arctic permafrost[105].

Subglacial environments are geochemically diverse; community composition is determined by a variety of factors, including the environment that existed before glaciation, the energy sources or minerals available in the bedrock and the possible presence of a geothermal energy source. Betaproteobacteria seem to dominate most freshwater subglacial ecosystems sampled to date[98] (FIG. 3). Blood Falls, a subglacial outflow from the Taylor Glacier in Antarctica (FIG. 1), is a highly saline subglacial environment that is thought to have a marine origin[97,106]. Consistent with this view, it is dominated by Gammaproteobacteria related to marine phylotypes[95]. A volcanic subglacial lake below the Vatnajökull ice cap in Iceland that receives limited geothermal input has low microbial diversity and is dominated by a species of Epsilonproteobacteria related to *Sulphuricurvum* spp.[107] (FIG. 3).

Gene sequences related to known chemolithoautotrophic phylotypes have also been reported in subglacial environments. For example, 13% of the sequences retrieved from subglacial Lake Whillans were most similar to genes described in *Candidatus* Nitrotoga arctica, a bacterium that gains energy from reduced nitrogen, iron or sulfur compounds[91]. In addition, the most abundant 16S rRNA gene detected in Blood Falls was related to the 16S rRNA gene from the bacterium *Thiomicrospira arctica*, which is a chemolithoautotrophic sulfur oxidizer[95]. Functional genes for chemolithoautotrophy, including those encoding ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), a key enzyme in the Calvin cycle, have also been retrieved from subglacial environments[108]. Quantification and sequencing of these gene transcripts suggest the prevalence of bacteria related to *Candidatus* Sideroxydans lithoautotrophicus, an iron- and sulfide-oxidizing autotroph that is also abundant in subglacial Lake Whillans[91]. These data indicate that the oxidation of reduced forms of nitrogen, sulfur and iron drive subglacial chemolithoautotrophy (FIG. 2a).

In Blood Falls, sequences related to *Geopsychrobacter electrodiphilus* and *Desulfocapsa sulfoexigens* are abundant[95]. These bacteria are known to use a diverse repertoire of metabolic modes but commonly reduce Fe(III) to Fe(II), which is soluble (FIG. 2a). Blood Falls gets its name from the copious amounts of iron released in the subglacial liquid from below the Taylor Glacier (3.3 mM Fe(II)). This iron has a non-zero isotopic signature ($\delta^{56}\text{Fe} = -2.60$ %), which is indicative of iron reduction by bacterial respiratory processes[97]. Subglacial environments have only recently been recognized as an additional source of iron to the Southern Ocean alongside atmospheric deposition and melting icebergs and sea ice. Modest discharge along the coastal margins from a system like Blood Falls represents a concentrated, but significant, iron pulse[109]. A recent study estimated that

Box 3 | Sampling icy life

Collecting samples from sea ice, glacial and subglacial environments remains a technological challenge owing to the remoteness and lack of infrastructure in polar regions but also because of difficulties analyzing microbial processes *in situ* at ecologically relevant spatiotemporal scales in the ice matrix. Most microbiological assays must be applied to melted ice, which does not capture the *in situ* physicochemical conditions of the unmelted ice. Thus, it remains unclear how sea ice communities will respond to ice thinning and retreat. Offshore sea ice sampling requires the use of ice-breaking research vessels and helicopters, but even these platforms rarely have access during the long dark winter months, resulting in seasonal undersampling.

Only a few technologies such as under-ice remotely operated vehicles (ROVs) enable non-invasive *in situ* studies of sea ice microbial habitats; most of these are limited to snapshot studies in time. On land, there are several well-established glacier observatories, such as the NASA Earth Observatory or the World Glacier Inventory at the National Snow and Ice Data Center, where the main focus is the changing mass of ice sheets. Time-series observations of the microbial colonization of glacial ice, and its role in biogeochemical cycling and ice melt, are still lacking. Sampling subglacial environments requires drilling through thick ice to obtain samples. In Antarctica, drilling platforms require transport via airplanes or tractors to access the remote locations. Subglacial Lake Whillans was the first such successful feat in Antarctica. A key aim is to obtain uncompromised samples for microbial studies from the enclosed liquid reservoirs; one current approach is to filter drilling water and treat it with UV radiation, combined with the use of sterilized probes. Guidelines have been established by the scientific community and funding agencies to protect these unique ecosystems and to ensure that contaminating microorganisms and chemicals from drilling equipment are not inadvertently introduced[145]. Probes designed to melt through ice and collect samples or instruments deployed down boreholes are also sterilized prior to deployment, similar to the planetary protection approach of a space mission[146–148].

that subglacial iron flux is comparable to wind-driven flux (~0.06–0.17 Tg Fe per year)[110]. Such bioavailable iron leaking from Antarctic subglacial environments may contribute to sustaining primary productivity in the iron-limited Southern Ocean[111,112].

Genomic analyses of ice bacteria

Genomic analyses of microorganisms from cryosphere habitats considered in this Review have mostly been conducted on bacteria from sea ice. Among the best characterized of these bacteria is strain 34H of *C. psychrerythraea*. Although originally isolated from subzero Arctic sediments, this Gammaproteobacterium has since been found in sea ice from both poles. It can grow at temperatures as low as −12 °C and a corresponding ice-brine salinity of 16%; in these conditions it can also support the proliferation of bacteriophages[35,113,114] (BOX 2). Genomic evidence showing that *C. psychrerythraea* encodes genes from both bacteriophages[71] and distant organisms[115] provides support to the emerging concept that lateral gene transfer has been a key contributor to the adaptation of bacteria, in particular sea ice bacteria, to life in ice[116]. *C. psychrerythraea* 34H can also swim at temperatures as low as −12 °C in viscous solution[39], providing it with the ability to relocate within the interior brine network of sea ice. It also contributes to the viscosity of its surroundings by releasing cold-active extracellular hydrolytic enzymes[117] to acquire nutrients and by overproducing EPS after becoming enclosed into the ice matrix[118]. The capsular polysaccharides of strain 34H may explain the colonization of sea ice by *Colwellia* spp., as these polysaccharides are decorated with the amino acid threonine in a pattern that makes their structures mimic ice-binding proteins[119,120]. Although *C. psychrerythraea* 34H grows fastest in the saline conditions of seawater, it survives the briniest of sea ice conditions by using compatible solutes such as glycine betaine, which are known to protect against hyperosmotic shock[44,115]. Its genome encodes not only proteins aiding the transport of compatible solutes but also an abundance of proteins involved in the export of various other compounds across its PUFA-enriched membrane and EPS-coated surface[71]. Experimental work has shown that these functions are relevant to survive the temperature and salinity fluctuations that characterize sea ice through the seasons[44,118]. Analyses of the predicted proteome of this bacterium have revealed trends in its amino acid sequences that are consistent with those of known cold-adapted enzymes, such as increased polar residues (particularly serine), substitution of aspartate for glutamate and decreased charged residues on the surface of proteins. Genomic analyses of other sea ice bacteria, such as *P. irgensii*[65], *Psychroflexus torquis*[116] and *Marinomonas primoryensis*[121], have also shown that they display many of these genomic traits, which suggests that they are signatures of bacteria adapted to life in sea ice.

Ice-binding proteins
Proteins used by microorganisms to prevent or limit the growth of ice structures within or outside of their body fluids, by, for example, adhering to the ice or otherwise inhibiting ice crystal growth or recrystallization.

In addition to genomic studies of ice-adapted bacteria obtained in pure culture, a limited number of metagenomic analyses have been carried out on sea ice and glacial ice samples. A metagenomic study of bacterial communities in frost flowers on the surface of new sea ice revealed genes involved in biogeochemical processes relevant to air–ice interactions, including genes for mercury reduction, dimethylsulfide uptake, dimethylsulfoniopropionate catabolism, glycine betaine turnover and halocarbon production[74]. For supraglacial habitats, the few metagenomic analyses that have been carried out revealed bacterially dominated habitats and genes that confirm ice-adaptive traits identified in genomic studies, such as the formation of cryoprotectants and the maintenance of membrane fluidity using PUFAs[84,122]. Initial analyses of functional genes in subglacial habitats clearly show a positive correlation between genes and the diversity of energy sources available. For example, in the sulfate-rich sediments of subglacial Lake Whillans, numerous genes relevant for microbial sulfur cycling were detected[123]. These findings provide evidence for the potential for members of active microbial communities in glaciers and ice sheets to interact with each other and with their environment[22].

Conclusions and outlook

This Review describes our current knowledge of microbial life in ice through a comparison of the key characteristics, functions and traits of microbial communities and microorganisms in sea ice, glacial and subglacial habitats. Scaling up the average bacterial cell abundances of the different icy habitats based on their total volume, it is estimated that approximately 10^{25}–10^{28} cells currently reside in ice, subglacial habitats and permafrost (TABLE 1). Given that phylogenetic analyses of frozen environments are still in their infancy, it is likely that an unknown number of taxa from the microbial domains of life are still awaiting discovery.

This Review highlights that across all icy habitats, microbial life is abundant at the interface between ice and liquid, where energy sources such as sunlight and reduced chemical compounds are available. Microbial biomass can be maintained by high concentrations of cryoprotective EPS that influence the physicochemical habitat of the microorganisms and increase their retention within the ice. Little is known about the viability of cells in the massive ice sheets of Greenland and Antarctica, the potential for undiscovered (macroscale) hydrological networks within them, and whether the underlying basal sediments can function as a microbial habitat. Future work may substantially increase current estimates of the abundance and activity of cells in ice, as well as enhance current estimates of the role of these cells in biogeochemical cycles[110].

Almost all bacterial phyla have representatives that inhabit ice, with Proteobacteria being the most abundant and diverse phylum[84,124] (FIG. 3). Bacterial communities in ice generally differ from those in water (seawater, freshwater or meltwater). The most striking differences between all cryosphere communities are in the Actinobacteria-dominated permafrost[12], the Alphaproteobacteria-dominated seawater, the Flavobacteria- and Gammaproteobacteria-dominated sea-ice communities, and the Betaproteobacteria-dominated snow, glacial ice and subglacial Lake Whillans (FIG. 3). The origin of the ice (seawater, freshwater or snow), its age, and the seasonality and the availability of light and nutrients, seem to be the key factors structuring the microbial communities of the cryosphere.

Where sunlight is available, diverse eukaryotic phototrophs thrive in ice: the surface of glaciers and ice sheets is usually dominated by the algal order Desmidiales[77], snow by the algal genus *Chlamydomonas*[78] and sea ice by diatoms[34]. These phototrophic eukaryotes seem to be better adapted to life in ice than cyanobacteria, which are largely absent from sea ice for reasons that are not yet well understood. The reported production of ice-binding proteins by a range of psychrophilic eukaryotic algae[125] may explain the success of phototrophic eukaryotes in this habitat compared with cyanobacteria, if such proteins provide a competitive advantage.

Today, the cryosphere is shrinking rapidly owing to climate warming, which has a substantial impact on these icy ecosystems in terms of the loss of habitats and changes in key biogeochemical functions[2]. The current rate of change has substantially modified the dimensions, and reduced the volume, of the sea ice habitats and has altered the timing of melting and freezing. Shrinkage of glaciers is also accelerating, with the loss of large masses occurring, especially where glaciers and ice streams flow from the ground (known as the grounding line) and start floating, releasing ice into the sea[126]. Assessing the natural dynamics and ecological baselines of ice ecosystems, and the causes and consequences of the observed ecological variations over spatial and temporal scales, is a major task for current and future research on life in ice.

Key questions in sea ice microbiology concern the effects of warming, sea ice retreat and loss of multi-year ice on future productivity, ecological functioning and the biological diversity of polar seas[37,49]. Reduction in albedo is considered to be one of the main drivers of ice melting and surface runoff[127]: in surface glacial environments, the accumulation of cells and particles alter the albedo of the ice, as do melt ponds on the surface of sea ice, leading to an increase in melting that functions as a positive feedback mechanism to warming. Climate change and anthropogenic influences are expected to warm the atmosphere, ocean and soils, and to extend the melt season, the equilibrium line of ice and the transport of nutrients from industrial activity to polar regions, all potentially increasing microbial activity on supraglacial and other surface-ice habitats, leading to increased melting. The warming of ice streams from the base near the grounding line by circumpolar deep water is also a key concern for the rising sea level[128].

In subsurface environments, intriguing questions remain about the origin, age and diversification of microbial communities, some of which may have been enclosed by ice over geological time without contact with the Earth's surface. Because the surfaces of numerous celestial bodies beyond the Earth are covered in ice and may be habitable (for example, Jupiter's moon Europa, Saturn's moon Enceladus and the polar regions of Mars), continued exploration of life in ice is relevant for the field of astrobiology[33]. Assessing the dynamics of the microbial communities of Earth's cryosphere and their contributions to the wider ecosystem remains a key challenge in microbial ecology and biogeochemistry.

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Competing interests statement

The authors declare no competing interests.

FURTHER INFORMATION

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