Chapter 8
Cyanobacteria in Cold Ecosystems

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8.1   Introduction

Perennially cold environments in which temperatures remain below 5°C are common throughout the biosphere (Margesin and Häggblom 2007). In these habitats, the persistent cold temperatures are often accompanied by freeze–thaw cycles, extreme fluctuations in irradiance (including ultraviolet radiation), and large variations in nutrient supply and salinity. As a result of these constraints, polar and alpine environments

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contain a reduced biodiversity, with prokaryotes contributing a major component of the total ecosystem biomass as well as species richness. Cyanobacteria are of particular interest because they often represent the predominant phototrophs in such ecosystems. Current research shows that a diverse range of cyanobacteria can be found in polar and alpine habitats, and that they show a remarkable ability to tolerate the abiotic stresses that prevail in these cold environments. Their presence was already observed during the early explorations of the polar regions at the end of the nineteenth century (Vincent 2007).

The widespread distribution in cold habitats of communities dominated by cyanobacteria, particularly in ice-based environments, makes them of great interest for the reconstruction of microbial life and diversification on early Earth (Vincent et al. 2004b). These ice-based habitats with their sustainable microbial communities are potential analogues for biotopes present during the major glaciation events of the Precambrian. The fossil record suggests that cyanobacteria would have been present throughout these Proterozoic events, and perhaps during earlier periods of global cooling (Schopf 2000). Polar microbes, including cyanobacteria, are also of interest to astrobiologists studying the prospect of life beyond our planet. Antarctica has been proposed as an analogue to an early stage of Mars where liquid water occurred and where life could have evolved at a similar time to the development of cyanobacteria on early Earth (Friedmann 1986).

In this chapter, we first introduce the taxonomical status and the general characteristics of cyanobacteria. We then examine cyanobacterial diversity in Antarctic, Arctic and alpine habitats, focusing on the molecular approaches. The ecophysiological traits of cyanobacteria that allow them to survive and often thrive in such cold environments are also presented. We conclude this review by consideration of the biogeographical distribution of polar cyanobacteria, an active topic of current research.

8.2   Taxonomy and diversity

Cyanobacteria are Gram-negative oxygenic photosynthetic bacteria that, according to the fossil record, achieved most of their present morphological diversity by two billion years ago (Schopf 2000). Cyanobacteria were initially described as algae in the eighteenth century and the first classification system was based on the International Code of Botanical Nomenclature as described by Oren (2004). In the botanical taxonomy, two major works can be noted. Firstly, Geitler (1932) produced a flora that compiled all European taxa, which already encompassed 150 genera and 1,500 species based on the morphology. Secondly, the recent revisions by Anagnostidis and Komárek (e.g., Komárek and Anagnostidis 2005) aimed to define more homogeneous genera, still based on the morphology. After the prokaryotic nature of cyanobacteria became more obvious on the basis of ultrastructural and molecular studies, it was proposed that their nomenclature should be governed by the International Code for Nomenclature of Bacteria (Stanier et al. 1978).

Currently, the phylum of Cyanobacteria encompasses 5 subsections (corresponding to the 5 orders in the botanical classification) in the Bergey's Manual of Systematic Bacteriology (Castenholz 2001):

  I. Chroococcales (unicellular);
 II. Pleurocapsales (large cells subdividing into smaller baeocysts);
III. Oscillatoriales (simple filamentous);
IV. Nostocales (filamentous, non-branching heterocyst-forming);
 V. Stigonematales (filamentous, branching, heterocyst-forming).

To date, only a few names of cyanobacterial taxa have been validly published according to bacterial rules, reflecting not only technical difficulties but also the confusion due to the existence of two nomenclatural systems (Oren 2004). Current taxonomical studies on cyanobacteria are now adopting a polyphasic approach, which combines genotypic studies with morphological and phenotypic analyses.

Early studies on the diversity and biogeographical distribution of cyanobacteria were based on the identification of the organisms entirely on the basis of morphological criteria. Cyanobacteria often have quite simple morphologies and some of these characters exhibit plasticity with environmental parameters, so that their taxonomic usefulness can be limited. Moreover, a number of botanical taxa have been delimited based on minute morphological differences (e.g., sheath characteristics, slight deviations in cell dimensions or form), and many authors have shown that the genetic diversity does not always coincide with that based on morphology (e.g., Rajaniemi et al. 2005; Taton et al. 2006b). To address these problems, studies on environmental samples (natural mixed assemblages of microorganisms) are typically based at present on clone libraries or DGGE (Denaturing Gradient Gel Electrophoresis) using molecular taxonomic markers, most often the 16S rRNA gene. The obtained 16S rRNA sequences are compared and generally grouped into OTUs (Operational Taxonomic Units) or phylotypes on the basis of their similarity (e.g., 97.5% similarity for Taton et al. 2003, or 98% for de la Torre et al. 2003). With such similarity values, each OTU might correspond to one or more bacterial species but is clearly distinct from other OTUs at the species level (Stackebrandt and Göbel 1994). This therefore provides a conservative estimate of the diversity, following bacterial criteria.

8.3   General characteristics

Cyanobacteria possess photosystems I and II, which are located on thylakoid membranes (except in the genus *Gloeobacter*). The cells usually have a characteristic blue-green coloration due to the phycocyanin (blue), allophycocyanin (blue) pigments in addition to chlorophyll *a*, although some species may additionally contain phycoerythrin that colors the cells red. In a few taxa, other chlorophylls have been observed, including chlorophylls *b* and *d* (Miyashita et al. 1996; Castenholz 2001). Some cyanobacteria are also able to fix atmospheric nitrogen. Furthermore, cyanobacteria have various storage bodies for carbon, nitrogen, phosphate and the enzyme

ribulose 1,5-biphosphate carboxylase/oxygenase (RubisCO) (Castenholz 2001). Cyanobacteria are also known to produce a great variety of secondary metabolites with diverse activities. To date, 600 bioactive molecules have been described, most of which have been found in the Oscillatoriales and Nostocales orders (Welker and von Döhren 2006).

8.4   Antarctic habitats

Studies on the molecular cyanobacterial diversity in Antarctica, using a culture-independent approach, have focused on the following regions to date: the Prydz Bay region (Bowman et al. 2000; Smith et al. 2000; Taton et al. 2006a), the McMurdo Dry Valleys (Priscu et al. 1998; Gordon et al. 2000; Christner et al. 2003; de la Torre et al. 2003; Taton et al. 2003; Smith et al. 2006; de los Rios et al. 2007), the McMurdo Ice Shelf (Jungblut et al. 2005) and the Antarctic Peninsula region (Hughes and Lawley 2003; Hughes et al. 2004). Strains have been isolated from the same regions, as well as from the Dronning Maud Land (Rudi et al. 1997; Vincent et al. 2000; Smith et al. 2000; Billi et al. 2001; Nadeau et al. 2001; Casamatta et al. 2005; Taton et al. 2006b; Comte et al. 2007).

8.4.1   Ice-based habitats

Cyanobacteria dominate microbial consortia formed in ice-based habitats such as cryoconite holes and meltwater ponds. Cryoconite (literally "cold rock dust") gives rise to vertical, cylindrically-formed holes in the ice surface that contain a thin layer of sediment overlain by water. The formation of these habitats is initiated through the absorption of solar radiation by the sediment and the subsequent ablation of the surrounding ice (Wharton et al. 1985). Studies of these holes on the Canada Glacier, McMurdo Dry Valleys, show that they contain cyanobacteria as well as hetero-trophic bacteria, eukaryotic micro-algae and colorless protists, and even metazoans such as rotifers, nematodes and tardigrades (Mueller et al. 2001).

An analysis of 16S rRNA sequences from the Canada Glacier cryoconite communities showed the presence of cyanobacteria phylogenetically related to *Chamaesiphon* (96.2% 16S rRNA sequence similarity) (Christner et al. 2003), a genus that is known to occur in the periphyton that forms over rocks in European mountain streams. Other polar sequences in this lineage (ca. 96% similarity) originated from the ice cover of Lake Bonney (Priscu et al. 1998) and a deglaciated glacier area in the Peruvian Andes (Nemergut et al. 2007). A second group of sequences is 99.2% similar to a clone from a meltwater in Livingston Island (Antarctic Peninsula) (unpublished data) and the third sequence group is 99.7% similar to clones from lake Fryxell, lakes in the Prydz Bay area and the Antarctic Peninsula. Notably, sequences of the third group are also 99.2% similar to one sequence from the Peruvian Andes (Nemergut et al. 2007).

Another important class of ice-based habitat is the meltwater ponds that form on ice shelves. These contain liquid water during the summer months, but completely freeze over in winter. The biota of these habitats must therefore contend with extreme temperature changes, freezing and desiccation stress, and high salinities. The ponds on the McMurdo Ice Shelf have low nutrient concentrations, especially nitrogen, due to the marine origin of the sediments (Hawes et al. 1993), and their characteristics are described by Wait et al. (2006). Thick benthic cyanobacterial mats comprise a diverse community of Nostocales and Oscillatoriales as well as other bacterial phyla and microeukaryotes (Howard-Williams et al. 1989; Nadeau et al. 2001; Jungblut et al. 2005). In one of these mats, the presence of microcystin was detected (Jungblut et al. 2006).

8.4.2   Soils and rock

Cyanobacteria are often the primary colonizers of permafrost soils in areas where meltwater flushes occur through snow melt or retreated glaciers. In the Dry Valleys of Antarctica, the soils are old, weathered and have low carbon and nutrient concentrations (Vincent 1988). Thus, the colonization by cyanobacteria increases soil stability and nutrient concentrations through, for example, nitrogen fixation. Terrestrial dark crusts are found throughout Antarctica and are commonly dominated by cyanobacteria (e.g., Broady 1996; Mataloni and Tell 2002; Adams et al. 2006).

Cyanobacteria are also often identified in biofilms below and within the rocks where the microclimate gives protection against environmental stresses such as high UV radiation, temperature extremes, desiccation and physical removal by wind. They can be found in depth below the rock surface depending on the optical characteristics of the rocks and the level of available photosynthetically active radiation (PAR). Depending on the spatial location of the communities, they are hypolithic (beneath rocks), endolithic (in pore spaces of rocks), chasmoendolithic (in cracks and fissures of rocks), or cryptoendolithic (in the pore space between mineral grains forming sedimentary rocks) (Vincent 1988; Hughes and Lawley 2003).

Molecular analysis of such communities revealed a few cryptoendolithic cyanobacterial sequences in beacon sandstone of the Dry Valleys (de la Torre et al. 2003), and in granite boulders of Discovery Bluff (de los Rios et al. 2007). Interestingly, in the latter study, one 16S rRNA sequence was related (98.9%) to a DGGE band from Swiss dolomite (Sigler et al. 2003) and the second sequence is identical to one hypolithic sequence from quartz rocks in the Vestfold Hills (Smith et al. 2000). This group of sequences also has affinities (93.5% similarity) to the chlorophyll *d* containing *Acaryochloris marina* (Miyashita et al. 1996) and de los Rios et al. (2007) hypothesized that some cryptoendoliths could possess this pigment and that its particular absorption spectrum would be beneficial in environments with little light. Another well-known cryptoendolithic cyanobacterium belongs to the genus *Chroococcidiopsis* and was found in sandstones of the Dry Valleys (Friedmann 1986). It is remarkably resistant to desiccation and has close relatives in hot deserts (Fewer et al. 2002).

8.4.3 Ponds, lakes, rivers and streams

Similar to their presence in ice-based habitats, cyanobacteria form large bio-mass accumulations in Antarctic ponds, lakes, rivers and streams (Vincent 1988). They often form thick, cohesive, highly pigmented mats that coat the benthic environments. A large variety of lake types are present in Antarctica and span a wide range of environmental conditions (Gibson et al. 2006). Many of them are covered with ice for most of the year or even have a perennial ice cover. Studies on perennially ice-covered Lake Hoare in the McMurdo Dry Valleys have shown that PAR irradiance exerts an overall control on microbial photosynthetic production, composition and mat structure (Vopel and Hawes 2006). Other characteristics such as nutrients and salinity also influence the cyanobacterial diversity (Gibson et al. 2006). The diversity and function of the microbial lake communities have been reviewed by Ellis-Evans (1996). At the molecular level, Taton et al. (2003, 2006a, 2006b) showed a large cyanobacterial diversity in the benthic mats from five different Antarctic lakes in two regions (see Sect. 8.7). Cyanobacteria also form biofilms and microbial mats in rivers and streams (Vincent 1988).

In addition to the benthic communities, cyanobacteria are also found in the water column of lakes, and picoplanktonic forms often dominate the plankton. The abundance of planktonic picocyanobacteria is dependent on nutrient availability and light (Vincent 2000), The 16S rRNA sequences of Synechococcus-like picocyanobacteria were obtained from lakes in the Vestfold Hills (Lakes Ace, Pendant, Clear). They appeared to be related, but distinct from other *Synechococcus* genotypes such as *Synechococcus* PS840 from the Russian marine coast (Waleron et al. 2007).

8.4.4 Marine ecosystems

The abundance of picocyanobacteria decreases markedly from temperate latitudes to the polar regions (Marchant et al. 1987; Fouilland et al. 1999). This decrease is assumed to be due to temperature-limitation (Marchant et al. 1987) as well as continuous losses due to grazing, advection and mixing (Vincent 2000). The 16S rRNA sequences of picocyanobacteria retrieved at the Subantarctic Front (51°S) were closely related to temperate oceanic *Synechococcus*, as WH8103 and WH7803 (Wilmotte et al. 2002).

8.5 Arctic habitats

Most available studies have so far focused on the Canadian Arctic, whereas no information is yet available from the Russian Arctic.

8.5.1   Ice-based habitats

Similar to the South Polar Region, ice shelves as well as glaciers provide a variety of habitats for cyanobacteria in addition to other biota (Säwström et al. 2002; Mueller et al. 2005). However, the total area of ice shelves is lower than in Antarctica, where 40% of coastline is fringed by ice shelves. Furthermore, the recent break up of the Ward Hunt Ice Shelf (Mueller et al. 2003) signals the massive reduction of these habitats through global warming. Arctic ice-based habitats can be differentiated into cryoconite holes, meltwater ponds and sediment patches without continuous coverage by water. Microbial mats can be prolific (Vincent et al. 2004a), but are less developed than in Antarctica, and this may be due to the increased grazing pressure in the Arctic (Vincent 2000).

8.5.2   Lakes, streams and ponds

Cyanobacteria play an important role in Arctic lakes, ponds and streams and have been well studied in the Canadian High Arctic (Bonilla et al. 2005).The most common groups are Oscillatoriales and Nostocales, with some Chroococcales. The benthic microbial mats in lakes often have a cohesive layering, which is established through an extra polysaccharide matrix and often have a characteristic pigment stratification (Bonilla et al. 2005). Planktonic picocyanobacterial communities of these lakes comprise mainly *Synechococcus* (Vincent 2000) and can be separated into fresh and saline ecotypes (unpublished data). In these lakes, primary production is only nutrient limited in the planktonic communities, whereas the microenvironments of the benthic mats result in increased nutrient availability and sufficiency (Bonilla et al. 2005).

8.5.3   Soils and rock

Terrestrial cyanobacteria in the Arctic are also major primary colonizers of soils and can be found within soil crusts, symbiotic in lichens and within rocks. They are an important source of nitrogen for the nutrient limited soils of the Arctic (Zielke et al. 2005). Cryptoendolithic communities are common in sandstone outcrops of Eureka, Ellesmere Island, and consist of similar cyanobacterial morphotypes as in Antarctic rocks (Omelon et al. 2006). However, their diversity seems higher than in comparable habitats of the Dry Valleys. This may be due to higher average temperatures, higher humidity due to close spatial distance to open water, and longer periods with available liquid water relative to the McMurdo Dry Valleys. Hypolithic cyanobacteria are commonly observed under opaque rocks subjected to periglacial movements (Cockell and Stokes 2004).

8.5.4 Marine ecosystems

In the Arctic marine environment, similar to the Southern Ocean, picocyanobacteria are rare, in contrast with their abundance in temperate and tropical oceans. A study of their molecular diversity in the Beaufort Sea showed that the picocyano-bacteria were affiliated with freshwater and brackish *Synechococcus* lineages, but not to the oceanic ones. Their origin, therefore, seemed allochthonous, as the Arctic Sea is much influenced by large riverine inputs (Waleron et al. 2007).

8.6 Alpine habitats

8.6.1 Streams and lakes

In alpine streams, water chemistry, geochemical conditions, hydraulic conditions and permanence of flow are the key factors defining taxonomic diversity. Cyanobacteria have been found as part of microbial mats, epiphytic on mosses and endosymbiotic in lichens in stream habitats of many alpine regions, but there are no specific studies on their molecular diversity or adaptations (McClintic et al. 2003; Rott et al. 2006). Nutrient concentrations show large variations during the year with peaks in late winter and autumn. PAR and UV radiation also range from low levels in presence of ice and snow cover to high levels during summer months, creating a need for protective mechanisms to survive. Rott et al. (2006) have described different colonization patterns for several cyanobacterial morphotypes in alpine streams.

Cyanobacteria in alpine freshwater lakes can be found as benthic and planktonic communities. Plankton communities are mostly comprised of *Synechococcus* morphotypes and their abundance is correlated to nutrient availability, particularly nitrogen and phosphorus. Benthic communities were studied by Mez et al. (1998), and Sommaruga and Garcia-Pichel (1999). Interestingly, the presence of cyanotoxins was demonstrated by Mez et al. (1998).

8.6.2 Rocks and soils

Cyanobacteria are also dominant components of alpine soil crusts, and rock-associated communities as described for endolithic communities of dolomite rocks in the Swiss Alps (Sigler et al. 2003) and soils from recently deglaciated areas in the Peruvian Andes (Nemergut et al. 2007). The 16S rRNA sequences obtained from the Alpine dolomite layers show high similarities with Antarctic cryptoendo-liths (see Sect. 8.4.2), or up to 97.7% similarity with the Andean cyanobacteria (Nemergut et al. 2007), or appear novel (less than 93% similarity with database sequences). Other Andean soil sequences are related to the sequences of *Chamaesiphon* PCC7430 (ca. 96% sequence similarity), of diverse *Nostoc* strains

(a.o. 97.4–98.5 % with the Antarctic ANT.L52B.1), of the Antarctic *Leptolyngbya frigida* ANT.LH52.2 (98.5%) and ANT.LH52B.3 (99.6%), or are quite different from database sequences and thus represent a novel diversity.

8.7 Ecophysiology

8.7.1 Coping with the cold

In general, high latitude and high altitude cyanobacteria tend to be cold-tolerant (psychrotrophs), with suboptimal growth under low temperatures, rather than psychrophiles that grow optimally at low temperature (Tang and Vincent 1999). They have a variety of mechanisms that allows them to tolerate and continue to grow, albeit often at slow rates, in the cold and to tolerate freeze–thaw conditions (Vincent 2007). To maintain membrane fluidity at low temperatures, polyunsaturated fatty acids with decreased chain-lengths are incorporated into the membrane. In addition, the production of compatible solutes (e.g., trehalose) helps to reduce the freezing point of the intracellular fluid. This strategy also reduces cell desiccation as less water is needed to retain the osmotic equilibrium (Welsh 2000). Furthermore, extracellular compounds such as polymeric substances can reduce ice nucleation around the cells (Vincent 2007). Cyanobacteria must also withstand prolonged seasonal dormancy phases in frozen and liquid water. Freeze-dried cyanobacterial mats in Antarctica have been shown to resume photosynthesis within minutes to hours after rethawing (Vincent 2007).

8.7.2 Osmotic stress

Typical hypersaline environments are saline ponds and lakes and brine channels in the sea ice (Vincent 1988). Sudden increases in salt concentration are counterbalanced by a rapid accumulation of salts to maintain the osmotic equilibrium. Long-term survival strategies involve uptake of inorganic ions, to balance the extracellular ion concentrations, as well as the production of organic osmolytes (Oren 2000).

8.7.3 High and low irradiance

UV radiation and high energy PAR can induce photo-inhibition, phycobiliprotein degradation, chlorophyll-bleaching and DNA damage, or the production of reactive oxygen species, and the net damage may be exacerbated at low temperatures (Vincent 2007). Cyanobacteria have evolved a variety of DNA repair mechanisms, such as excision repair and photo-reactivation, to cope with UV induced DNA damage (Castenholz

and Garcia-Pichel 2000). However, these processes are reduced at lower temperatures. Furthermore, the cyanobacteria produce photoprotective screening and quenching pigments (gloeocapsin, scytonemin, mycosporine), and many Antarctic cyanobacteria seem to avoid radiation by migrating to deeper layers within the microbial mats (Castenholz and Garcia-Pichel 2000). High concentrations of scytonemin can lead to a black coloration in many cyanobacterial mats and soil crusts (Vincent 2007).

Conversely, phototrophs in polar and alpine regions must also contend with low irradiances caused by prolonged snow and ice cover. The cyanobacteria utilize highly efficient light capturing complexes, with photosynthetic quantum yields close to the theoretical maximum (Hawes and Schwartz 2001; Vincent 2007).

8.8   Biogeography

The question of endemism and distribution of cyanobacterial taxa is still a topic of much debate. A long-standing theory of microbial distribution is that "everything is everywhere, but the environment selects" and that local habitats select for specific microbial flora that is globally distributed (Baas-Becking 1934). Castenholz (1992) noted the slow rates of speciation in the cyanobacteria together with their large dispersal abilities, and this, in combination with the relatively young age of most polar ice-free environments, suggests that endemism is likely to be rare amongst polar cyanobacteria. Morphological identifications seemed to support this hypothesis. However, such characterization is limited due to morphological plasticity (see Sect. 8.2). In addition, Komárek (1999) noted that a number of identifications of Antarctic cyanobacteria had been made with flora written for temperate countries without taking into account their ecology, which could give the false impression that mostly cosmopolitan taxa were found on this continent. Indeed, by avoiding such 'force-fitting', Komárek (1999) has found about 60% of endemic species amongst the 68 morphospecies found in various microbiotopes of ice-free areas of King George Island.

Several features of Antarctica suggest that endemism may be possible there, although it has yet to be demonstrated convincingly (Vincent 2000): (1) Antarctica has been more isolated than other parts of the world for several million years; (2) dispersal processes which favour local species are more efficient than long-range dispersal processes; and (3) there has probably been strong environmental selection for adaptive strategies. As a step towards addressing this question, the molecular characterization of cultured and uncultured cyanobacterial diversity has been carried out in a number of Antarctic biotopes (see Sect. 8.4). The results from these studies suggest the presence of OTUs/phylotypes with cosmopolitan and bipolar distributions, but also the presence of some genotypes that seem to be restricted to specific Antarctic sites. However, there is never complete 16S rRNA sequence identity for bipolar or cosmopolitan organisms that are members of the same OTU. The use of ITS sequences, which

are more variable than the 16S rRNA, could increase the resolution of the distributional patterns (Taton et al. 2006a).

Taton et al. (2003, 2006a, 2006b) have analyzed the molecular diversity in Lake Fryxell (Dry Valleys), four coastal lakes in the Prydz Bay area (East Antarctica) and two meltwater samples from Livingston Island (Antarctic Peninsula). Using clone libraries based on 16S rRNA sequences, a total of 63 OTUs were detected, of which 44 were only found in Antarctica (70%). This suggests a high degree of endemism, even if a portion of this uniqueness could be due to geographic gaps in the database. A higher proportion of the cosmopolitan genotypes are found in several Antarctic regions (47% compared to 16% for the potentially endemic sequences). Thus, if they were able to disseminate and colonize habitats in different continents, this could be due to resistance capacities that are also helpful to spread to different Antarctic regions. Furthermore, there appears to be an on-going exchange between freshwater and terrestrial biotopes (Gordon et al. 2000), which could also explain why temperature flexibility (psychrotrophy, see Sect. 8.7.1) is more common than psychrophily in cyanobacteria. Another conclusion is that each new sample brings new genotypes and this suggests that much diversity still awaits discovery.

8.9 Conclusions

Cyanobacteria evolved under the harsh conditions of the Precambrian, and their modern representatives retain a remarkable ability to adapt to and survive within extreme conditions. They dominate terrestrial and freshwater cold ecosystems of the Arctic, Antarctic and alpine regions, even though they do not seem to be specifically adapted to optimal growth at low temperatures. They play a major ecological role as they often are primary colonizers of substrates and major primary producers in these ecosystems.

The application of molecular tools in combination with classic morphological techniques has begun to provide new insights into the real diversity of cyanobacteria and their biogeographical distribution in cold environments. Our survey of recent studies suggests complex distributional patterns of cyanobacteria, with cosmopolitan, endemic, and habitat-specific genotypes. This ongoing research will help to identify specific geographical areas that have unique microbial communities. However, many more studies are needed to unravel the enormous diversity of cyanobacteria and to better define their biogeographical patterns in cold environments. This is an urgent task in view of the climatic changes that will undoubtedly alter the structure and functioning of microbial communities in polar and alpine ecosystems.

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