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REVIEW

A review of the ecology, ecophysiology and biodiversity of microalgae in Arctic soil crusts

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Abstract Biological soil crusts have been extensively studied in arid lands of temperate regions, particularly semi-arid steppes and warm deserts. Arctic soil crusts have received some attention, but they are far less studied than their temperate counterparts. While the tundra zone of Arctic regions has an abundant cover of lichens, mosses and low-growing vascular plants, the High Arctic semi-arid and arid deserts have a much reduced but still very significant cover of biological soil crust dominated by microalgae. This review discusses what is known about Arctic soil crusts with the intention of stimulating study of this sensitive ecosystem. Arctic soil crusts are considered to be one of the most extreme habitat types on earth. Low temperatures and lack of water associated with a wide spectrum of disturbances have a dramatic effect on chemical and physical soil ecological properties (salinity, pH, conductivity and gas content). Microalgae are the keystone microbial species in polar crusts, being significant primary producers, fixing atmospheric nitrogen and secreting polysaccharides that bind soil aggregates together, thereby reducing erosion and water runoff. The biological diversity of soil crust microalgae in the Arctic is high. Soil crusts of the Arctic semi-arid and arid deserts provide a special opportunity to study the environmental factors controlling the diversity, distribution and abundance of the microalgae in the absence of anthropogenic disturbance. However, anthropogenic disturbances and climate change are occurring in the Arctic, and even more transformations are expected in the near future. Therefore, the ecological study of Arctic ecosystems, including biological soil crusts, is a matter of urgency.

Keywords Soil crust · Arctic · Cyanobacteria and eukaryotic microalgae

Introduction

Biological soil crusts of arid and semi-arid regions have been studied over the past 35 years. Deserts and semi-arid steppes of temperate regions have received the most attention, where soil crusts have been found to have several key environmental roles, including soil stabilization and the subsequent protection from erosion by wind and water, nitrogen fixation, contribution to soil organic matter, influence on hydrology and infiltration of rain water, increasing soil temperature and affecting the mineral nutrient supply to vascular plants. Extensive work has also been conducted on the disturbance ecology of crusts, including both the impact of various types of disturbance and the recovery or succession following the cessation of the disturbance. Researchers have also been interested in the diversity of all major crust constituents (lichens, mosses, cyanobacteria, eukaryotic microalgae, fungi and

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heterotrophic prokaryotes). The literature dealing with crusts was reviewed in detail by Belnap and Lange (2001).

Our understanding of the biological soil crusts of polar desert and polar semi-desert regions is far less expansive. Green and Broady (2001) provided a review of the biological soil crusts of Antarctica, but at the time of this review much less was known about the ecosystem function of polar crusts. There has been considerable progress in expanding our understanding of polar biological soil crusts since these seminal reviews, for example, the recent review of soil crusts in Antarctica (Büdel and Colesie 2014). Recent reviews in Arctic terrestrial ecosystems are limited to Stewart et al. (2014) where the authors focused on atmospheric nitrogen exchanges. In addition, the recent article (Pointing et al. 2015) provides information about the biogeography of photoautotrophs in the Arctic and Antarctica.

The purpose of this article is to provide a current review of the biological soil crusts of Arctic semi-arid and arid deserts with a focus on the microalgal community. Here, we use the term “microalgae” to combine both prokaryotic cyanobacteria and eukaryotic microalgae.

Extent and components of Arctic soil crusts

Soil crusts of the Northern Hemisphere are mainly represented in the High Arctic (Fig. 1) and cover the territories of the European, Russian and Canadian Arctic as well as Greenland.

As shown in Fig. 1, the Arctic desert and semi-desert biome covers large parts of the High Arctic. However, in respect to area, the Canadian Arctic Archipelago and northeast part of the America contain most of this biome. The Canadian Arctic archipelago and neighboring coastal areas of Greenland constitute an immense geographical region dominated by polar deserts and semi-deserts (Bliss et al. 1984). The area differs in altitude, substratum and other ecological characteristics. In the spring, polar desert soils are supplied by a surge of meltwater, usually followed by longer periods of drought during summer (Elster 2002; Elster and Benson 2004). Thus, the microalgal communities are subject to seasonal extremes of inundation and desiccation, hypo- and hypersalinity, seasonal and diurnal temperature fluctuations, frequent freeze-thaw cycles and, ultimately, deep-freeze temperatures up to −34 °C in winter (Láska et al. 2012).

Even though polar desert occupies 15–20 % of the surface area of the Arctic, only a limited number of studies deal with the Arctic biological soil crust ecosystem (Liengen 1999; Elster et al. 1999; Kaštovská et al. 2005, 2007; Patova and Beljakova 2006; Breen and Lèvesque 2006, 2008; Yoshitake et al. 2007, 2010, 2014; Andreyeva 2009; Pushkareva and Elster 2013; Steven et al. 2013; Inoue et al. 2014; Pushkareva et al. 2015; Shi et al. 2015). Most of the studies describing microalgal communities in Arctic soil crusts are based on morphology (Elster et al. 1999; Kaštovská et al. 2005, 2007; Patova and Beljakova 2006; Andreyeva 2009; Pushkareva and Elster 2013). A few studies have applied modern molecular methods for microalgal identification, but most of these studies present data for the whole microbial community without a detailed assessment of microalgae (Schutte et al. 2010; Knelman et al. 2012; Steven et al. 2013; Pushkareva et al. 2015). In Table 1, we summarize the microalgal species that have been found in Arctic soil crusts. Greenland is excluded because of the lack of information on crusts of this large and important island.

The dominant components in the soil cyanobacterial community are filamentous forms (Table 1). Representatives from the orders Chroococcales, Pseudanabaenales, Oscillatoriales and Nostocales are the most species-diverse groups found in Arctic soil crusts (Kaštovská et al. 2005, 2007; Patova and Beljakova 2006; Pushkareva and Elster 2013; Pushkareva et al. 2015). *Nostoc* spp. are widely dispersed in all types of soil crusts and primarily inhabit the soil surface (Yeager et al. 2004; Řeháková et al. 2011; Hu et al. 2012; Bastida et al. 2014). Arctic habitats with high humidity, such as areas around streams, pools, lakes, waterfalls and snow fields, have soils frequently covered by a thick layer of *Nostoc* spp. (Pushkareva and Elster 2013). A high abundance of *Nostoc* spp. might also be explained by decreased nitrogen availability in the soil crusts (Zielke et al. 2005; Stewart et al. 2012). Notably absent from Arctic soils are the genera *Oculatella* and *Hassallia*, which are common in desert soil crusts from temperate and tropical regions (Flechtner et al. 2008; Patzelt et al. 2014; Osorio-Santos et al. 2014).

The extreme conditions of polar regions strongly affect the diversity of eukaryotic microalgae. Coccoid green algae (Chlorophyta) are the most abundant eukaryotic group in Arctic soil crusts (Lange 2001; Andreyeva 2009; Pushkareva and Elster 2013; see Table 1) represented by Chlorophyceae and Trebouxiophyceae (Elster et al. 1999; Andreyeva 2009). Some soils are wet and acidic and support sacoderm desmids as well (see Table 1, Zygnematophyceae). In addition to the coccoid taxa, filamentous taxa can be important as well (e.g., *Klebsormidium*, *Xanthonema* and *Tribonema*; see Elster 2002). Representatives of the stramenopile (heterokont) class Xanthophyceae are also abundant in polar regions (Table 1).

In the Russian Arctic the soil crust ecosystem is well described in tundra zones. However, accessibility to this literature is difficult because most of the papers are in Russian language and consequently the findings of Russian

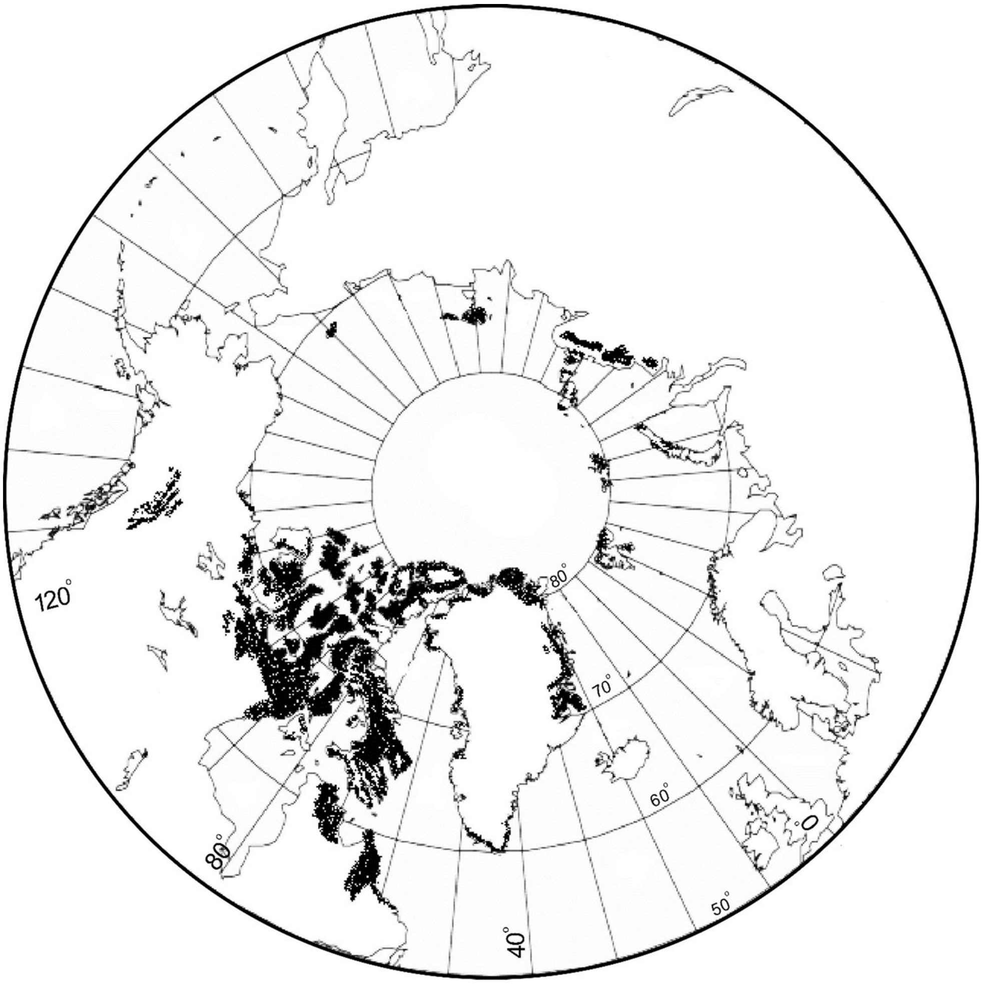

Fig. 1 Map of the High Arctic. Polar semi-desert and desert are colored *black* and represent areas where biological soil crust development is most widespread. In particular geographical areas more than 65°N, high elevation (more than 400–1000 m a.s.l.), lack of precipitation (less than 250 mm), mean air temperature lower than −10 to −15 °C, soil temperature regime (hypergolic) and continentality (eucontinental, hypercontinental), the polar desert and semi-desert with biological soil prevail (see more in the Soil Atlas of the Northern Circumpolar Region, Jones et al. 2009). The highest area with a biological soil crust is located in the Canadian High Arctic (southern part of Nunavut and Canadian Arctic Archipelago). A lesser extent of soil crust is also located in the northeast sea shore of Greenland, northern part of Svalbard, Franz Josef Land, Severnaya Zemlya Archipelago, and higher altitude in Taymyr Peninsula and New Siberian Islands. The southern limit is located in the southeast part of North America (Newfoundland and Labrador, Baffin Island, north part of Hudson Bay)

scientists are poorly known. The most important representatives of mosses in the Russian Arctic are *Rhacomitrium lanuginosum*, *Ditrichum flexicaule* and *Dicranoweisia crispula* (Matveeva 1979; Afonina and Matveyeva 2003). The lichen flora is dominated by the genus *Cetraria* (*C. delisei*, *C. islandica* var. *polaris*, *C. laevigata*, *C. elenkinii*) (Matveeva 1979; Zhurbenko and Matveyeva 2006). To the best of our knowledge, cyanobacterial species composition of soil crusts in the Russian Arctic was described only on Bolshevik Island, Severnaya Zemlya Archipilago (Patova and Beljakova 2006; see Table 1).

Andreyeva (2009) identified nine species of Chlorophyta from Alexandra Land (Franz Josef Land) and 22 species from Bolshevik Island (Table 1). Common genera for both regions are *Chlamydopodium* sp. and *Chlorococcum* sp.

Ecological factors affecting the polar soil crust ecosystem

Soil crust communities can occur in almost all types of soil, and many biotic and abiotic parameters influence their development (soil geological properties, climate, presence of vascular plants, and animal and human intervention) (Langhans et al. 2009; Fischer and Subbotina 2014; Huang et al. 2014; Pushkareva et al. 2015).

Table 1 Microalgal genera reported in biological soil crusts, based on seven studies of these communities in the Arctic

	Russian Arctic (Bolshevik Island, Alexandra Land)^{a,b}	European Arctic (Svalbard)^{a,c,d,e}	Canadian Arctic (Ellesmere Island, Ellef Ringens Island)^{a,f}
Cyanobacteria			
Chroococcales			
Aphanocapsa	+		
Aphanothece	+		
Chlorogloea		+	
Chroococcus	+	+	+
Cyanosarcina			+
Gloeocapsa	+	+	+
Gloeocapsopsis	+		
Gloeothece	+		
Rhabdoderma	+		
Synechococcus			+
Synechocystis	+		
Pseudanabaenales			
Geitlerinema		+	
Komvophoron		+	
Leptolyngbya	+	+	+
Phormidesmis		+	
Pseudanabaena		+	
Schizothrix			+
Oscillatoriales			
Microcoleus		+	+
Oscillatoria	+		
Phormidium	+	+	+
Symploca	+		
Symplocastrum	+		
Nostocales			
Anabaena	+	+	
Calothrix	+	+	
Cylindrospermum	+		
Dichothrix	+		
Nodularia		+	
Nostoc	+	+	+
Scytonema	+	+	
Stigonema	+		
Tolypothrix	+	+	
Trichormus		+	
Stramenopila			
Xanthophyceae			
Botrydiopsis			+
Heterococcus			+
Monodopsis			+
Xanthonema			+
Chlorophyta			
Chlorophyceae			
Actinochloris			+
Ascochloris			+
Asterococcus			+

Table 1 continued

	Russian Arctic (Bolshevik Island, Alexandra Land)[a,b]	European Arctic (Svalbard)[a,c,d,e]	Canadian Arctic (Ellesmere Island, Ellef Ringens Island)[a,f]
Bracteacoccus	+	+	+
Borodinellopsis			+
Chlamydocapsa	+		+
Chlamydopodium	+		+
Chlamydomonas			+
Chlorolobion			+
Chlorococcum	+	+	+
Chloromonas			+
Chlorosarcina			+
Chlorosarcinopsis		+	+
Chlorosphaeropsis			+
Coccobotrys			+
Coleochlamys		+	
Deasonia			+
Dictyochloris			+
Dictyococcus			+
Diplosphaera			+
Ettlia			+
Gloeococcus		+	+
Gloeocystis		+	+
Halochlorella	+	+	+
Hormotila		+	
Hormotilopsis			+
Macrochloris	+		+
Monoraphidium			+
Mychonastes	+	+	+
Nautococcus			+
Neochloris			+
Neochlorosarcina		+	+
Neospongiococcum			+
Palmellopsis	+		+
Planktosphaeria			+
Pleurastrum			+
Radiosphaera	+		+
Scotiellopsis	+		+
Spongiochloris	+		+
Tetracystis	+	+	+
Trebouxiophyceae			
Chlorella	+	+	+
Choricystis		+	
Coccomyxa	+	+	
Dictyochloropsis			+
Dictyosphaerium			+
Elliptochloris			+
Keratococcus	+		+
Leptosira			+
Muriella	+	+	+
Muriellopsis	+		+

Table 1 continued

	Russian Arctic (Bolshevik Island, Alexandra Land)[a,b]	European Arctic (Svalbard)[a,c,d,e]	Canadian Arctic (Ellesmere Island, Ellef Ringens Island)[a,f]
Myrmecia	+	+	+
Parietochloris	+		
Pseudococcomyxa	+	+	+
Schizochlamydella			+
Stichococcus		+	+
Trebouxia		+	+
Streptophyta			
Klebsormidiophyceae			
Klebsormidium		+	+
Zygnemophyceae			
Actinotaenium			+
Cosmarium			+
Cylindrocystis		+	+
Mesotaenium			+

Diatoms are not reported, but likely they could be detected with proper methodology

[a] Andreyeva (2009), [b] Patova and Beljakova (2006), [c] Kaštovská et al. (2005, 2007), [d] Pushkareva and Elster (2013), [e] Pushkareva et al. (2015), [f] Elster et al. (1999)

Excellent examples of Arctic semi-desert soil crust can be found in the northern part of Petunia Bay, Billefjorden, Central Svalbard (78°39′22″–78°44′36″N latitude, 16°22′12″–16°49′27″E longitude) (Fig. 2a, b). The highest ground cover is produced by *Dryas octopetala* and the lowest by the *Papaver dahlianum* (Prach et al. 2012). In semi-desert crusts of this area the soil surface can be consolidated by microalgae alone (Fig. 2d, f), a mixture of lichens and cyanobacteria (Fig. 2c, e), or in especially well-established crusts by a rich community of micro- or even macro-lichens (Fig. 2g, h). Such types of crusts are typical in many High Arctic areas (Belnap et al. 2001; Stewart et al. 2011b; Pushkareva et al. 2015).

In more humid habitats, the freeze-thaw cycles, occurring in soils, produce pinnacled and rolling crusts where mosses dominate (Belnap and Lange 2001; Belnap 2008). Water saturation occurs only for a short period of time during snow melt in dry, unstable soils, most frequently in steep slopes at higher elevation. Here, for most of the summer season, water is available only as water vapor from more frequent cloud occurrence. The crusts in these unstable dry soils are dominated by free-living microalgae, which usually become lichenized in less disturbed, more stable habitats (Colesie et al. 2014a). The biological crusts in temperate deserts decrease water evaporation from soil (Xiao et al. 2010; Lichner et al. 2013). This may be true for polar crusts as well, particularly those that are light-colored and do not attain elevated temperatures because of higher albedo (Fig. 3). In polar regions, the melting of snow and ice during the spring and summer periods increases the availability of liquid water (Láska et al. 2011); thus, the highest microalgal biomass presence in the Arctic is usually at the time of summer snowmelt (Elster et al. 1999).

Svalbard is a representative example of the yearly course of soil surface temperature and volumetric water content at a depth of about 2–3 cm below the surface of the soil (Fig. 3). In the Arctic semi-desert (northern part of Petunia Bay, Billefjorden, Central Svalbard) most of the year is both too cold and too dry for the growth of microalgae (October through June, Fig. 3), but both the temperature and moisture at the site shown are quite amenable to the growth of microalgae, lichens and mosses from July through September, with moisture likely being the more limiting factor (Fig. 3).

Soil texture greatly influences biological crust communities in polar regions (Colacevich et al. 2009). In contrast to deep soil, the soil crust has a greater proportion of silt and clay on or just below the surface (Breen and Lèvesque 2008). Thin clay particles adhere to the mucilaginous sheath of microalgae in the soil crust. These particles have a negative charge, which allows them to bind plant micronutrients, which have a positive charge. This process increases soil fertility (Belnap and Lange 2001; Breen and Lèvesque 2008). A more stable and softer soil texture such as gypsum and silty loams increases the diversity of microalgae, lichens and mosses (Belnap et al. 2001). The presence of unstable and coarse soils negatively influences the abundance and diversity of the structural organisms of soil crusts in the Arctic (Kaštovská et al. 2005). However, filamentous cyanobacteria can be quite abundant in the

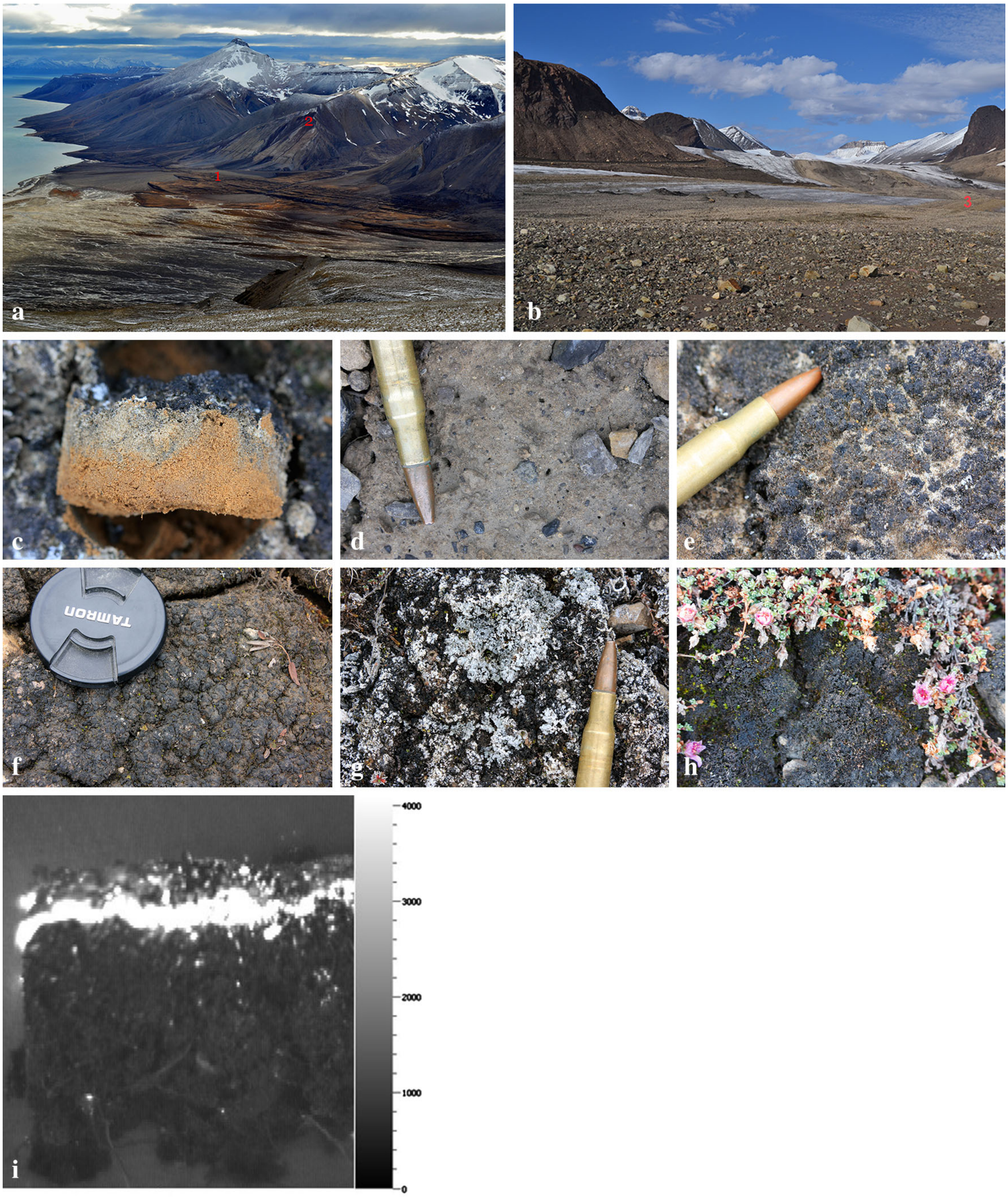

Fig. 2 Northern part of Petunia Bay, Billefjorden, Central Svalbard, Arctic semi-desert soil crust (**a**). Close-up images (**d**, **e**, **f**, **g**, **h**) show development of a soil crust community from quite young bare habitat in front of the Horbye Glacier (**b**, **d**) up to more developed (**e**, **f**) and partially covered by vascular plants and lichenized soil crust types (**g**, **h**). *Arrows* in images **a** and **b** show the top of Mummien Peak (1), a raised marine terrace that is characteristic of the early Holocene shoreline of Svalbard (2) and front of the Horbye Glacier (3). Cross-sections of a soil crust and its surface (**c**, **i**) show algal presence and photosynthetic activity in surface layers. An image (**i**) taken with the FluorCam 700MF fluorescence imaging camera (Photon Systems Instruments, Czech Republic) has a distinct whitish layer demonstrating the photosynthetically active area of soil crust. The *vertical scale* demonstrates relative units of imaging fluorometry

coarse type of soil crust (Pushkareva et al. 2015). Well-developed soil crusts with a high density of soil crust organisms, mainly microalgae, lichens and mosses, are usually dark in color (Yoshitake et al. 2007), but sometimes the surface can be paler because of certain lichen species, for example, *Ochrolechia frigida* (Inoue et al. 2014). In dark-colored well-developed biological crusts, there are more available mineral nutrients (such as phosphorus and/or nitrogen) and organic carbon (Chae et al. 2016; Pushkareva et al. 2015). In contrast, a poorly

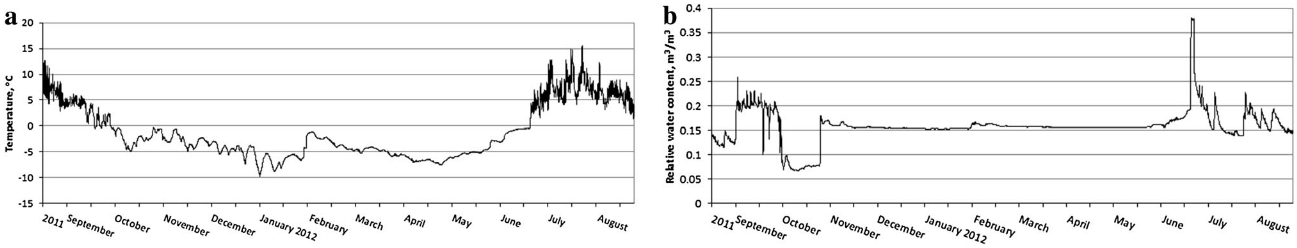

Fig. 3 Soil temperature (**a**) and volumetric water content (**b**) at a depth of 2 cm below the surface from the Herbye glacier foreland (northern part of Petunia Bay, Billefjorden, Central Svalbard) in the period from August 2011 to August 2012

developed light-colored soil surface is associated with a low biomass of major soil crust organisms followed by lower photosynthetic activity and lower pigment content (Chae et al. 2016; Pushkareva et al. 2015).

Dark-colored soil crusts better absorb long-wave radiation, which may increase the temperature of the soil surface (Stradling et al. 2002). Dark soils usually retain warmth for a longer time than light-colored soils and can positively influence the growth of biological soil crusts and vascular plants. Nevertheless, UV radiation can negatively affect Arctic soil crust organisms (Solheim et al. 2006). Microalgae can enter into a resting stage under such stressful conditions (Chen et al. 2003; Tashyreva and Elster 2012, 2015; Pichrtová et al. 2014). Motile cyanobacteria, such as *Microcoleus vaginatus*, *M. steenstrupii* and other filamentous cyanobacteria, typically occupy a position from 1 to 5 mm below the soil surface and thus can achieve a balance between receiving sufficient light for photosynthesis and avoiding harmful UV radiation and photooxidation (Castenholz and Garcia-Pichel 2000; Norris and Castenholz 2006). Non-motile cyanobacteria, such as the heterocytous genera *Scytonema*, produce dark yellowish pigmentation in their sheaths, which acts as a UV screen and darkens the soil surface associated with biological soil crusts (George et al. 2001).

Soil pH is a very important factor for the growth and diversity of microalgae. Soil crusts in temperate and tropical regions with a low pH (<7.0) are usually dominated by green algae (Johansen et al. 1993; Hastings et al. 2014), while the pH optimum for cyanobacteria is between 7.4 and 8.0 (Burja et al. 2002). Lower pH was found to promote higher microalgal abundance in Arctic soil crusts (Kaštovská et al. 2007). However, an increase of pH results in dominance of filamentous cyanobacteria (Pushkareva et al. 2015).

Organisms living on the soil surface are more easily exposed to and affected by wind compared to organisms inhabiting other parts of the ecosystem (Jia et al. 2012). Because of the sparse vegetation in polar regions, the soil crust organisms lack protection from the wind. Soil movements generated by freeze-thaw processes limit development of vascular plants, but likely are less limiting to microbial components of biological soil crusts (Jia et al. 2012). However, the responses of polar desert and/or semi-desert biological soil crust to wind are still largely unexplored.

Adaptation of soil crust microalgae to polar conditions

In polar soil crust ecosystems, microalgae have developed a wide range of adaptive strategies that allow them to avoid, or at least minimize, the injurious effects of extreme and fluctuating environmental conditions (Elster 2002). Soil microalgae are poikilohydric microorganisms (having no mechanism to prevent desiccation), but are extremely tolerant to drought and are able to quickly return to an active state upon rehydration. They can survive long periods of desiccation and strong fluctuations in temperature (Moquin et al. 2012; Pichrtová et al. 2014; Tashyreva and Elster 2015) and have very different life strategies with respect to their susceptibility to low temperatures and freezing. This could be because cyanobacteria and several microalgae (mainly terrestrial Chlorophyceae) do not contain vacuoles, which in many eukaryotic microalgae and plants are the cellular component responsible for water control. For example, in the marine polar ecosystem vacuoles have been recorded in microalgae quite frequently (Kirst 1990; Kirst and Wiencke 1995), while there is scarce information about the presence of vacuoles in polar soil microalgae. The external environment directly manages the metabolic activity of poikilohydric organisms by affecting the presence or absence of water in either liquid or vapor form. Cyanobacteria are particularly well adapted to the severe and changeable conditions involving cycles of desiccation, rehydration, low to high salinity and freeze-thaw episodes. High light intensity during freezing and desiccation has been shown to negatively influence the survival of *Leptolyngbya* spp. (George et al. 2001). In contrast, *Scytonema* spp. usually live on the surface of biological soil crusts, requiring the production of the UV-screen sheath pigment scytonemin (Quesada et al. 1999). However, the biomass of *Scytonema* sp. can decrease where mosses occur and compete for light (Lan et al. 2012).

Microalgae are the most important photosynthetic organisms of soil crusts in the polar regions (Elster 2002). However, they often have a low concentration of photosynthetic pigments per unit area (Elster et al. 1999) as a consequence of the harsh climatic and environmental conditions (Colacevich et al. 2009). Figure 2c, i shows photosynthetic organisms (mainly microalgae) living on the soil surface or slightly below it. Because of structural and functional differences in photosynthetic organelles, eukaryotic microalgae have higher rates of photosynthesis and lower resistance to freeze-thaw cycles than cyanobacteria (Šabacká and Elster 2006; Pichrtová et al. 2014). A good example of structural changes in cell morphology that provide resistance to freeze-thaw injuries was documented in a study of the annual development of mat-forming conjugating green algae, *Zygnema* sp. (Pichrtová et al., in press), showing that in summer *Zygnema* sp. cells contain stellate chloroplasts and large hyaline vacuoles. As summer progressed, *Zygnema* sp. produced pre-akinetes, overwintering cells, with high lipid content and reduced chloroplast lobes. Such cells have been found to be able to survive winter conditions and other extremes. However, features responsible for resistance against low temperature, cryoinjuries, desiccation and salinity stress are taxonomically specific at the species and ecoform levels (Elster and Benson 2004). Cyanobacteria, in contrast to eukaryotic microalgae, have lower rates of photosynthesis, but their biomass production is higher than their subsequent decomposition. Accumulation of cyanobacterial biomass in Arctic soil crust habitats is, in addition to the low rate of decomposition, influenced by low grazing pressure by invertebrates. However, these processes are still poorly understood, and accumulation of cyanobacterial biomass in particular polar habitats needs further research. For example, soil crusts dominated by *Nostoc* spp. rapidly rebuild (during several hours or days) after freezing and desiccation (Hawes et al. 1992). Extracellular polysaccharides in the sheath and colonial investments of cyanobacteria often persist in the environment and can serve to aggregate soil particles and stabilize the soil surface even after the cellular components of the soil have died (Elster and Benson 2004; Tashyreva and Elster 2015).

Soil crust microalgae, due to a diverse range of ecological and physiological life strategies, manifest an ability to tolerate stressful conditions. There are three main strategies for survival in polar soil crust habitats: avoidance of stress, protection from stress and forming partnerships with other organisms. Water availability and state (liquid-ice-vapor) connected with all types of mechanical disturbances or instability are decisive factors that determine whether avoidance, protection or formation of a partnership prevails. In conditions where there is a more regular occurrence of water in the liquid form, avoidance or protection is more common. In contrast, protection or forming of partnerships is quite common in habitats where water in liquid form occurs only for a limited time or where water is primarily available only in vapor form (Elster 2002).

Some soil crust microalgae are motile in vegetative and/or reproductive cell stages. Mobility can facilitate avoidance of the most stressful conditions and propel the organism to a more favorable environment. Motile microalgae can also react to a wide spectrum of environmental conditions (soil properties, temperature, moisture). The mucilage protects them against fluctuations in water status by inhibiting water loss from cells. When soil is wet, the mucilage of cyanobacteria swells and trichomes migrate out of their sheaths (Hu et al. 2012). After each migration, new sheath material is formed, thus extending the filament length. Repeated swelling leaves a complex network of empty sheath material, which maintains the soil structure after the organisms have become dehydrated and decreased in size.

Other strategies for survival in severe conditions are the development of resting (dormant) vegetative stages as well as reproductive stages that affect an organism's ability to adapt to seasonal environmental fluctuations (Tashyreva and Elster 2012, 2015). We have already mentioned production of pre-akinetes in Arctic populations of *Zygnema* sp. (Pichrtová et al. 2014). In contrast, *Phormidium* sp. (Oscillatoriales, Cyanobacteria) forms perennial populations, with a high proportion of cells able to survive winter without specialized cells being produced (Tashyreva and Elster 2016). This is a very important adaptive feature for living in polar conditions. Physiological changes preceding dormancy include accumulating high concentrations of soluble carbohydrates that substitute for water molecules during dehydration (Elster and Benson 2004). These intracellular carbohydrates stabilize the structure and function of macromolecules, membranes and cellular organization. The presence of protective sugars in cells enables vitrification of cytoplasm on drying and supports the formation of a high-viscosity, metastable glassy state. This preserves cell viability during dry frozen storage by immobilizing cellular constituents and suppressing deleterious chemical or biochemical reactions that threaten survival (Sun and Leopold 1994).

An important feature of soil crust communities in polar regions is the production of life-form associations such as mutualistic symbiosis, which offer protection against unstable extreme conditions on the soil surface layer. They are traditionally defined as the living together of two or more unlike organisms to the benefit of all partner organisms. The life associations that commonly occur in the polar terrestrial environment, with the exception of physical protection, also have physiological and metabolic advantages.

The most frequent and most ecologically important association in the polar terrestrial environment is the association of microalgae with fungi in lichens (Bjerke 2011; Inoue et al. 2011, 2014). Fungal hyphae are frequent components of the cryptogamic crust. Through their filamentous hyphae, fungi in crusts contribute to soil stability by aggregating soil particles (Abed et al. 2012). This symbiosis helps to protect them from low temperatures and water fluctuations (Stewart et al. 2011b). Lichens that use green algae as photobionts are usually dominant in polar soil crusts. Lichens that have the green alga *Trebouxia* sp. as the photobiont are known to be extremely cold-resistant in the dry as well as hydrated states (Leal 2000), and several lichen species are known to be able to attain significant net photosynthetic rates at subzero temperatures.

Another important and common example of association in Arctic soil crusts is epiphytic occurrence of cyanobacteria on moss surfaces (Stewart et al. 2011b). Probably, the benefit for cyanobacteria in this kind of association may be the supply of carbohydrates and protection against desiccation and UV radiation while mosses can get nitrogen fixed from the cyanobacteria (Zielke et al. 2005).

Ecological role of microalgae in soil crusts

Soil crust organisms are involved in important processes of polar soil ecosystems such as nitrogen fixation, moisture retention, stabilizing of soil and increasing of soil organic carbon (Breen and Lévesque 2008; Stewart et al. 2012, 2014; Büdel and Colesie 2014; Chae et al. 2016). Stabilization of the soil surface by soil crust organisms helps to protect the soil from erosion through both aggregation of the soil and speeding the rate of water infiltration (Colesie et al. 2014b). By increasing surface roughness, they reduce runoff and, as a consequence, increase infiltration and the amount of water stored for plant use. Cyanobacteria secrete polysaccharides that bind soil, thus influencing the soil stability, erosion, runoff and growth of soil crust components such as lichens (Colesie et al. 2014a).

A major feature of cyanobacteria is the ability of heterocystous species to fix atmospheric nitrogen (Solheim et al. 2006; Maqubela et al. 2009; Stewart et al. 2011a). They start to fix nitrogen as soon as the temperature in the thallus rises above 0 °C. In addition to accumulation of organic carbon and other elements in cells, nitrogen fixation is one of the most important ecological contributions to cyanobacteria-rich Arctic soil crusts. Nitrogen-fixing bacteria (including cyanobacteria) are a significant source of fixed nitrogen for plants and edaphic heterotrophic microorganisms. Both free-living forms and those associated with species of vascular plants have been reported as being important nitrogen sources in High Arctic locations (Zielke et al. 2005; Breen and Lѐvesque 2006). In nature, nitrogen-fixing cyanobacteria are abundant in areas deficient in nitrogen.

Nitrogen fixation depends on the water availability, temperature, soil chemistry and other parameters (Zielke et al. 2005; Kvíderová et al. 2011). For example, soil crusts with a sandy cover can contain higher concentrations of nitrogen compared with non-sand-covered soil crusts (Williams and Eldridge 2011). However, the relation of the rate of nitrogen fixation and texture and the type of soil substrate has not yet been studied. Phosphate limitation can negatively affect nitrogen fixation by decreasing the rate of photosynthesis and consequently inhibiting nitrogenase by reducing the photosynthates required for the energy-intensive process of nitrogen fixation (Hartley and Schlesinger 2002; Stewart et al. 2011a).

Cyanobacteria are often responsible for the majority of carbon fixed in Arctic soils, providing fixed carbon to soil crusts, which likely subsidizes food webs there (Yoshitake et al. 2010; Darby et al. 2010). In addition, the abundance of cyanobacteria increases with crust development, resulting in a higher carbon concentration in well-developed soil crusts rather than in poorly developed ones (Kaštovská et al. 2007; Pushkareva et al. 2015).

Endemism or cosmopolitanism?

The question about endemism of polar terrestrial microorganisms is still unsettled (Lawley et al. 2004; Casamatta et al. 2005; Rybalka et al. 2009; Strunecký et al. 2012) because many isolates found in the Arctic and the Antarctic share similar morphology with microalgae from other geographic regions. Microorganisms can be transported by dispersed vectors such as atmospheric circulation, ocean currents, animals (particularly migratory birds) and humans (Lawley et al. 2004; Strunecký et al. 2010). However, recent molecular analyses have not detected totally identical genotypes between particular species of polar regions and other locations (Lawley et al. 2004; Rybalka et al. 2009; Schmidt et al. 2011; Strunecký et al. 2010, 2012). It is very possible that the unique challenges of polar ecosystems prevent establishment by most microbial introductions and that the microorganisms inhabiting these regions have become specially adapted.

The increase in scientific and tourist activities in polar regions has a potentially huge impact on the geographical distribution of microalgae genotypes. Anthropogenic activities promote species movement and their subsequent reproduction and spread at the new locations (Walther et al. 2002). Newly transported genotypes may adversely interfere with indigenous species and endanger their subsistence. Human presence in all polar regions has increased, thereby extending threats to biodiversity. However, up to now we have had very limited information about anthropogenic impacts on the geographical distribution of microalgae. There is a complete lack of data on alien microalgae dispersal and their subsequent occupation of particular localities and habitats. With the concomitant rapid climate change occurring in polar areas (particularly the Arctic and northwest Antarctic Peninsula region), the locally adapted species may lose their competitive advantage and be displaced by invasive species (Frenot et al. 2005). However, recent research on the dispersal of morphologically simple airborne eukaryotic microalgae, *Klebsormidium* (Streptophyta), *Chlorella* and *Stichococcus* (Chlorophyta), to polar regions showed ubiquitous distribution on a global scale (Hodač et al., in press; Ryšánek et al., in press). Almost 80 % of all Arctic *Klebsormidium* strains were included within the cosmopolitan superclade B sensu Rindi et al. (2011). Similarly, Hodač et al. (in press) found that psychrotolerant strains of *Chlorella* and *Stichococcus* are without exception conspecific (or closely related) with strains originating from the temperate zone. A warming climate can promote immigration of alien species into the polar regions and could cause shifts in species abundance and distribution. The combined effects of invasive species and climate change on the biodiversity of soil organisms could modify the polar ecosystem.

Conclusion

This article gives a brief overview of the microalgal ecology, physiological ecology and biodiversity of soil crust ecosystems in polar regions with a focus on Arctic soil crusts. Low temperature, low availability of liquid water and instability are characteristic for these terrestrial ecosystems. A combination of ecological properties, including geochemical and physical factors, light availability, grazing pressure by invertebrates, anthropogenic impacts and invasive species, influences various microalgal processes in soil crust ecosystems. The severe conditions influence the diversity, abundance and ecological manifestation of organisms in soil crusts. Soil microalgae have developed diverse ecological and physiological life strategies and behaviors that help them to avoid stressful conditions in the upper soil layer. Survival strategies in these microorganisms (similar to organisms living in temperate and tropical regions) have occurred because of the considerable evolutionary pressures experienced and an exceptionally long period of predictably unpredictable climatic conditions. Study of the community composition and main processes in Arctic soil crusts is necessary for better prediction of the future climate change.

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