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REVIEW ARTICLE

Microbial communities and primary succession in high altitude mountain environments

Sonia Ciccazzo[1] · Alfonso Esposito[1] · Luigimaria Borruso[1] · Lorenzo Brusetti[1]

Abstract In high mountain environments, microbial communities are key players of soil formation and pioneer plant colonization and growth. In the last 10 years, many researches have been carried out to highlight their contribution. Bacteria, fungi, archaea, and algae are normal inhabitants of the most common habitats of high altitude mountains, such as glacier surfaces, rock wall surfaces, boulders, glacier waters, streams, and mineral soils. Here, microbial communities are the first colonizers, acting as keystone players in elemental transformation, carbon and nitrogen fixation, and promoting the mineral soil fertility and pioneer plant growth. Especially in high mountain environments, these processes are fundamental to assessing pedogenetic processes in order to better understand the consequences of rapid glacier melting and climate change. This review highlights the most important researches on the field, with a particular view on mountain environments, from glaciers to pioneer plant growth.

Keywords Microbial community · Rhizosphere · Soil formation · Glacier · Moraine · Pioneer plants · Alps

Introduction

The ecological research of ecosystem development in the foreland of a receding glacier represents a pivotal topic to highlight the primary successional stages. Since a glacier chronosequence is characterized by a set of sites with the same parent material and substrates (Walker et al. 2010), time is substituted by space, and the distance from the retreating glacier is used as a proxy for soil age. Under this vision, the mineral soil closer to the glacier terminus is usually vegetation free and heterogeneously composed of distinct geological and pedological morphotypes, i.e., recent sandy deposit, exposed rock materials, erosion channels, floodplains, and mudslides with low amounts of carbon, nitrogen and other nutrients. Up until a few years ago, plant establishment was normally considered the first step of primary succession (Odum 1969; Connell and Slatyer 1977; Chapin et al. 1994). Now it is well known that a rich microbial community is able to colonize freshly exposed substrates, a long time before lichens, nonvascular, and vascular plants (Sigler et al. 2002; Sigler and Zeyer 2002, 2004; Nicol et al. 2005; Bardgett et al. 2007; Nemergut et al. 2007; Schmidt et al. 2008). Hence, microbial colonization is the first step of a cascade of processes that deal with the formation of a fertile soil where complex vegetation communities grow and develop (Fig. 1). Consequently, bacteria, archaea, fungi, and algae are crucial and fundamental actors capable of enriching mineral soil of nitrogen and carbon (Jumpponen et al. 2002; Nicol et al. 2006; Zumsteg et al. 2012; Frey et al. 2013). On the other side, microbial respiration, methanogenesis, denitrification and anammox act as opposite processes, leading to a loss of nutrients and organic matter. In this complex equilibrium, microorganisms have to continuously answer to the habitat change and to the inter-kingdom and trans-kingdom intra-species competition, through their ecological behavior and developmental strategies. Here we review the processes of primary succession on high mountain environments in temperate regions from the viewpoint of microbial communities, and in particular, their contribution in the colonization of mineral soil and pioneer plants.

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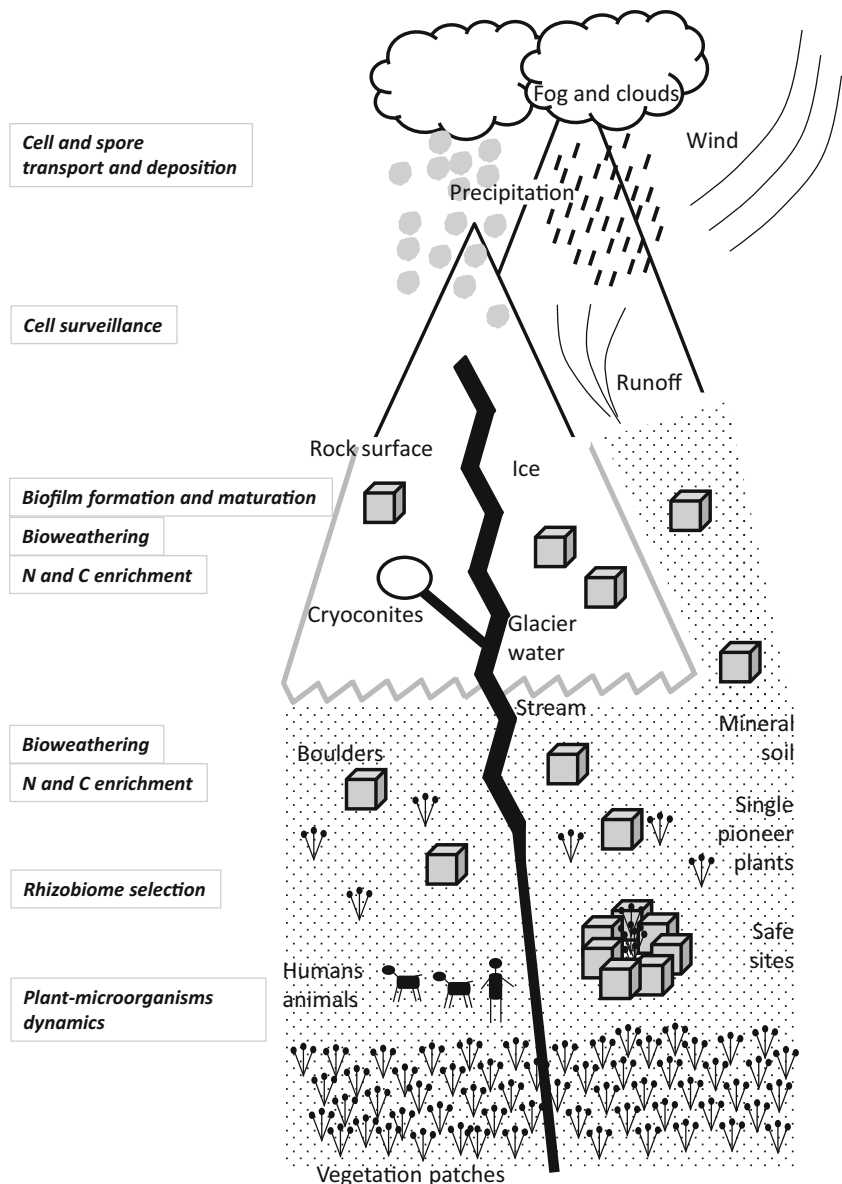
Colonization of glacier surface by microorganisms

Glacier surfaces can easily be colonized by microorganisms from the atmosphere by water precipitation (rainfall, snowfall), water deposition (clouds, fog, icy crystals), wind or even dust deposition (Sattler et al. 2001; Jumpponen 2003; Segawa et al. 2005). The presence of an active bacterial community in clouds has been shown, where bacteria can be present at density of 1500 cells/cm^3 (Sattler et al. 2001). These microorganisms can persist at the above-ground level, as shown at high altitude sites by Bowers and coworkers (2012). Bacterial abundances and community compositions of airborne microorganisms varied significantly according to the season. A richer community with bacteria normally associated with leaves and soil surfaces was found in spring and autumn, due to the input from the surrounding areas at lower altitude.

Snowflakes can contain up to about 10,000 bacterial cells/cm^3 (Sattler et al. 2001). An additional important input of microorganisms is from far territories, such as the arid Sahara desert in the case of the European Alps (Kellogg and Griffin 2006). Sandy storms from the Sahara to alpine glaciers carry several types of microbial cells, both in viable and quiescent form (Chuvochina et al. 2011, 2012). These cells are physically attached to and protected by microparticles of clay-sized minerals, such as illite and smectite. Strains affiliated with Actinobacteria, α-Proteobacteria, Deinococcus-Thermus, Cyanobacteria, and Bacteroidetes widely distributed in the Sahara desert were able to adapt themselves to the alpine environment on Monte Bianco Glacier (Chanal et al. 2006).

Even high mountain lakes could act as direct interceptors of airborne bacteria (Hervàs and Casamayor 2009). After a Saharan storm event in June 2004, the bacteria inhabiting the top

of the air–water interface in a remote high mountain lake in the Pyrenees were more similar to the collected airborne bacteria than those of the underlying waters. Other important vectors of bacteria on glacier surfaces, especially in the Alps and other strongly human-impacted glacier areas, are humans (tourism) and livestock (mostly sheep and goat farming) (Lee et al. 2011), but these sources have not been well documented up to the present. And similarly, the contribution of wild animals crossing glaciers areas, such as birds, insects and other animals, is not well studied.

Surveillance, growth and activities of microorganisms on glaciers

Once on a glacier surface, microbial cells have to forego extreme environmental conditions, which can also change greatly during the daytime and along the seasons. Extremely cold temperatures chill microbial cells, causing injuries in the cell wall and in membranes, provoking cell lysis. Consequently, ice cores have been shown to harvest microbial communities (Branda et al. 2010; Lutz et al. 2015) that differ from those of the surrounding liquid water (Psenner and Sattler 1998; Priscu and Christner 2004). Due to the presence of solutes, glacier melt waters have a lower freezing point compared to pure water, resulting in a reticulate network of micron-sized liquid water veins embedded in the ice core. The size of the veins decreases with decreasing temperature. On Earth, it ranges from ~10 μm at −2 to ~1 μm at −50 °C (Price 2000). When rocky particles are also embedded, a layer of liquid water is formed on the mineral surface, including microbial cells attached to the particle. The freezing point of aqueous solutions is lower than that of pure water; therefore, most of the solutes during the process of formation of ice are left out from the crystal reticulate, resulting in a higher concentration. This is a favorable environment for microorganisms to survive and metabolize in, although at a lower rate. The range of microorganisms found in ice melt water is between 10^4 and 10^{10} CFU/ml (Price et al. 2010). Liquid water on glacier surface also derives from rock surface warming. Under sunlight, rock surfaces can reach relatively high temperatures, promoting snow and ice melt. For instance, in Antarctica, summer temperatures normally range between −15 and 0 °C, but temperatures beneath rock particles can reach 17–20 °C many hours per day (Mevs et al. 2000). In this habitat, microorganisms must forego difficulties due to UV irradiation, which may damage macromolecules and cause the cell to die, as well as nutrient scarcity. However, some microbial species seem to be able to resist into the glacier core, or even to answer to the harsh environmental constraints by growing and propagating in glacial ice or in soil permafrost. Such microorganisms have very limited sources of nutrients and it has been hypothesized that they use the resources almost entirely to repair macromolecular damages,

enabling them to survive for several hundreds of thousands of years (Miteva et al. 2004; Miteva and Brenchely 2005; Price 2007; Dieser et al. 2010; Buzzini et al. 2012; Hamilton et al. 2013). On the other side, bacterial cells are protected from chilling by the covering snow, since snow cover assures constant and not-extremely cold temperatures (Schmidt and Lipson 2004). Finally, glacier surfaces can have a sized habitat where nutrients, such as organic dust brought by wind (Okin et al. 2004; Duarte et al. 2006; Thevenon et al. 2009) or by animals, or ancient carbon pools (Bardgett et al. 2007; Singer et al. 2012; Hågvar and Ohlson 2013; Hood et al. 2015), are more available.

Temperatures below 0 °C pose one main challenge to life: the availability of liquid water, and the concentration of solutes in the cytosol resulting from the sequestration of water molecules to ice crystals. The resulting effect of lower water activity, ionic imbalance and desiccation leads to cell death (Russell et al. 1990). Cold denaturation of proteins occurs at temperatures below −15 °C (Franks 1994). Low temperatures are perceived by microorganisms as an increased rigidity of the membrane, and in the last instance, as an upregulation of genes for cold-shock proteins, fatty acid desaturase (which increase membrane fluidity, increasing unsaturation of the hydrophobic tails of the lipidic double layer), cold-active enzymes, catalase, superoxide dismutase and several other enzymes or proteins involved in replication, transcription and translation (Shivaji and Prakash 2010). An interesting adaptation of psychrophilic bacteria is their ability to produce proteins that protect them from the formation of ice crystals in the cytosol and the immediate extracellular environment (Kawahara 2002). Another key role is played by exopolymers (EPS), which are involved in the mechanism of attachment to mineral particles, and in protection from dehydration and low/high temperatures exposure, and are constituted primarily by high molecular weight exose and pentose sugars. EPS are secreted as mucous slime and create a suitable environment for living, and such slime has been found in high abundance in Arctic and Antarctic (Krembs et al. 2002; Mancuso Nichols et al. 2005).

If microbial cells survive on glacier surfaces after environmental selection, they can grow and metabolize. It has been shown that ice cores from Tsanfleuron Swiss Glacier had a bacterial charge evaluated at between 9.3×10^5 and 5.9×10^6 CFU/ml (Sharp et al. 1999), while for Guliya Glacier (China), charges were between 1×10^4 and 5×10^5 CFU/ml (Christner et al. 2000). The growth rate of microorganisms in the glacier system is strongly affected by temperature, oxygen and nutrient availability. Microclimatic factors can impact the efficiency of colonization success (Lipson 2007). For instance, UV radiation and freeze-thaw cycles can select microorganisms able to produce protective secondary metabolites such as pigmentations (Sterflinger et al. 2012; Selbmann et al. 2014).

Several taxa of specialized psychrophilic microorganisms have been often found on glacier surfaces, even in an active form, showing that glaciers are far from being only passive deposits, and that after ice melting, glacier waters are already enriched with a complex microbial community (Branda et al. 2010; Margesin and Miteva 2011; Buzzini et al. 2012; Schmidt et al. 2012; de Garcia et al. 2012; Turchetti et al. 2013). Of course, spore formers can be found in the surveillance, but non-spore-forming microorganisms can also be frequently found. For instance, the psychrophilic bacterial species *Cryobacterium psychrophilum*, *Variovorax paradoxus* and *Janthinobacterium lividum* are specialized members of the snow biota,distributed worldwide in polar environments and high mountains (Segawa et al. 2005). An increasing number of psychrophilic yeasts strains has recently been reported in the Antarctic and non-Antarctic cryosphere (Jumpponen 2003; Buzzini et al. 2012; Schmidt et al. 2012; Selbmann et al. 2014).

Many polar and alpine cryospheric areas, such as Greenland (Lutz et al. 2014), Svalbard (Müller et al. 2001), the European Alps (Remias et al. 2005), the Rocky Mountains (Thomas and Duval 1995), Antarctica (Fujii et al. 2010; Remias et al. 2013), Alaska (Takeuchi 2013) and the Himalayas (Yoshimura et al. 2006), are colonized by colorful snow algae that are also primary support for other snow and ice microbial communities as carbon and nutrient sources (Lutz et al. 2014). Using a high-throughput sequencing approach for microbial communities of all major Icelandic glaciers (Lutz et al. 2015), a limited number of snow algal taxa (*Chloromonas polyptera*, *Raphidonema sempervirens* and two uncultured Chlamydomonadaceae) were detected as supporting a rich community comprised of other micro-eukaryotes, bacteria and archaea.

Moreover, on the glacier surface there are several different habitats where microorganisms can survive, grow and multiply. Of the most interesting are the cryoconite holes; namely, cylindrical melt holes on the glacier surface filled by liquid water and small stones. Cryoconites are enriched for hydrocarbons and other nutrients, as well as nitrogen compounds and rock mineral elements, helping the development of a relatively rich microbial community. Cryoconite microbial communities could act as efficient recyclers of allochthonous carbon and nutrients similar to microbe–mineral aggregates from other icy environments (Varin et al. 2010). Edwards et al. (2013), provided the first metagenomic study of alpine cryoconite microbial diversity of Rotmoos Glacier in the Austrian Alps. The cryoconite microbial community was dominated by Proteobacteria, Bacteroidetes and Streptophytes. Functional gene analysis of N, Fe, S and P cycling showed an acquisitive trend and a nitrogen cycle based upon efficient ammonia recycling. Carbon cycles are also dominated by anoxygenic photosynthetic bacteria, oxyphototrophic Cyanobacteria and eukaryotic microalgae, which easily colonize cryoconite holes (Kaštovská et al. 2007) as well as patches of snow (Sawstrom et al. 2002; Stibal et al. 2008a, b). This kind of complex community can even sustain the growth and reproduction of animals, as demonstrated for Tardigrada, cold-resistant animals often found in these habitats (Kaczmarek et al. 2012).

Since it is well known that mountain glaciers are collectors of persistent pollutants such as pesticides, herbicides, halogenates and artificial radionuclides (Tieber et al. 2009), glacier environments are getting more attention from different points of view. The high natural mineral content (usually heavy metals or natural radioactive elements) led to the selection of bacteria resistant to metals and other toxic elements, thanks to cellular efflux pumps. Truly, antibiotic resistant bacteria can be easily found in glacier environments, associated with cryoconites (Brusetti et al. 2008) or ice cores (Segawa et al. 2013). In particular, while Brusetti et al. (2008) found uncharacterized ampicillin-resistant bacterial isolates in the Midtre Lowenbreen Glacier cryoconites (Svalbard Islands), Segawa and coworkers showed a great variability of antibiotic resistance genes from both clinical and agricultural origins in at least 17 glaciers worldwide.

Another important and dynamic sink of microorganisms in high-altitude environments, which can be referred to as glacier habitats both for microbial colonization and processes, are the ice covers and snowpacks on mountain lakes (Felip et al. 1999). The bacterial communities of the slush layers of an alpine lake (Redon, Pyrenees) in winter during growth of the snowpack, and in spring during the melting phase, were characterized. In winter, the microbial community was especially related to the autochthonous planktonic bacteria beneath the ice, whereas in spring, the microbial community was more similar to those from the cryosphere and probably were derived by remote aerosol deposition (Llorens-Marès et al. 2012).

Colonization of rock surface by microorganisms

High mountain landscapes are dominated by boulders, small stones and mountain rock faces. These are normally distributed surroundings, on and below glaciers. Rains and melt waters flow down rock surfaces, wetting microbial biofilms and weathering the lithic substrate. Detached minerals as well as mobilized ions flow down, enriching the downstream mineral soil or watercourse. When bare rocks are colonized, the microbial community composition varies according to the type of rock substrate (Marnocha and Dixon 2014). These microorganisms live in a biofilm form. On solid mineral surfaces exposed to the atmosphere, a biofilm creates suitable conditions for the life of microorganisms (Gorbushina 2007). Within biofilms, there are consortia of different prokaryotic phyla, but also eukaryotes such as algae and fungi. Biofilm formation

leads to the creation of microenvironments suitable for bacterial growth. Usually, environmental niches within the biofilm may be quite different from the ambient condition: a different pH, different aerobic conditions, and a relatively favorable temperature and humidity. This allows for the development of complex microbial communities that increase the rate of rock weathering and soil formation, favoring the establishment of pioneer macro-organisms such as mosses and lichens (Gorbushina 2007). Such organisms eventually constitute the dead organic matter that will be decomposed by decomposers in the mineral soil.

Indeed, temperature on a stone surface is strongly dependent on the surface exposure (north or south), weather (cloudy, cloudiness, rainy, etc.), season, and on the day/night cycle (McFadden et al. 2005). For example, in November 2001 at 4500 m a.s.l. on the southern face of Zumstein Peak (Italy/Switzerland), the maximal and minimal temperatures recorded by rock surface sensors were +17 and −20 °C, respectively. On the other hand, on the northern face of the same peak, temperatures were −6 and −22 °C, respectively (Gruber et al. 2003). Temperature fluctuations are also important; daily temperature fluctuations on rock surfaces are often twice that of the air temperature fluctuations (McFadden et al. 2005), reaching to even about 30 °C or more (Gruber et al. 2003; McFadden et al. 2005). Moreover, the daily fluctuations depends on the rock mineral composition and color, i.e., blackish rocks such as oxidized iron rocks, black rock varnish or mica phyllosilicates minerals can absorb more light energy, reaching relatively high temperatures under the sun (Mevs et al. 2000). Rock varnish is a dark-red or blackish colored coating that is formed on the surfaces of the rocks (Potter and Rossman 1977). There is little knowledge about this geological formation: it involves iron and manganese oxide precipitate that forms deposits on the surfaces of rocks, together with clay and small particulate matter. Up to now, the role of microbial communities in the formation of rock varnish is a matter of debate (Dorn 2007). Siliceous acidic boulders in Match Valley (Italy), coated with an iron and manganese-rich rock varnish or totally uncoated, hosted Cyanobacteria, Chloroflexi, Proteobacteria and, along with minor taxa, *Solirubrobacterales*, *Conexibaxter* and *Rhodopila*. Taxa like *Edaphobacter* sp. had a marked spatial variation according to the sampling site. A highly oxidative Fe and Mn-rich varnish environment seemed to favor an anoxigenic autotrophy on rock coating (Esposito et al. 2015). Despite the harsh environmental conditions of high mountain rock surfaces, autotrophs (Duc et al. 2009a, b) and heterotrophs (Tscherko et al. 2003; Bardgett et al. 2007) may follow a succession, playing crucial roles in ecosystem development. Microorganisms can carry out mineral bioweathering of bedrock surfaces (Gorbushina and Broughton 2009) due to enzymatic reactions, pH reduction or release of oxalate, cianide, gluconic acid, siderophores, and chelating molecules, which react with the rocks (Mavris

et al. 2010; Styriakova et al. 2012). Free living fungi and growing lichens could carried out mineral bioweathering due to mechanical actions of the lithic substrates (Gorbushina 2007). It should be mentioned that not all those processes are deterministic. Sometimes, microorganisms secrete those compounds just as a by-product of their metabolism, and sometimes a siderophore/chelating molecule secreted by a microorganism could be used by cells of other species. This results in a very complex network of interactions that can end up with the dissolution of rock and the development of biofilms on its surface. Bacterial strains belonging to *Arthrobacter*, *Janthinobacterium*, *Leifsonia* and *Polaromonas* or isolated from biofilms on rock substrates were able to dissolve granite, plagioclase and feldspar, thanks to oxalic acid excretion. Oxalic acid is highly corrosive against mineral rocks, dissolving the metal ligands by acidification of the mineral surface (Welch et al. 1999; Welch and Ullman 1999). Oxalic acid can be also accumulated in large amount when microorganisms are organized in biofilm, reducing the pH; free ions can wear oxygen away from minerals, weakening the chemical bond between the metal ion and the rock surface. The dissolved elements were incorporated in the biofilm matrix, which become a hotspot of nutrients on the bare bedrock. Moreover, cryptoendolithic Cyanobacteria could improve bioweathering during the process of photosynthesis, because of the substrate alkalization (Budel et al. 2004).

There is evidence of the pivotal role of cyanobacteria within endolithic microecosystems of acid biofilms on granite rocks in extreme environments such as Antarctica (de los Ríos et al. 2003), as well as the biogenic weathering role exerted by lithobiontic bacteria on deglaciated granite of Damma Glacier (Central Alps) (Frey et al. 2010; Lapanje et al. 2012). Independent of existing pores or fissures, homogeneous carbonates rocks could be colonized by algae and ascomycetes, which act as lithobiontic organisms favoring endolithic processes (Hoppert et al. 2004).

Three pioneering fungal species, isolated from granitic sediments in the forefields of Damma Glacier, have the capability to exude citrate, malate, and oxalate to dissolve granite powder, increasing the concentration of macro and micro nutrients (Ca, Mg, P, Fe, Mn) in solution (Brunner et al. 2011). A follow-up batch of experiments showed a different pattern of organic acid release dependent on various carbohydrate sources in the same study area, including glucose, cellulose, pectin, pollen, and cell remnants of cyanobacteria, fungi, and algae (Brunner et al. 2014).

All these microbial activities facilitate the release of mineral cations essential for microbial growth. Of course, the activity of microorganisms is strongly influenced by humidity and temperature. Environmental fluctuations can exert a strong pressure on microbial communities influencing enzymatic activities. Chemical composition and acidity of the bedrock (Mummey et al. 2005) are also important for the accessibility of mineral

elements that favor microbial life. Siliceous rocks, broken as a result of the combination freeze-thaw cycle (McFadden et al. 2005), release mineral elements such as apatite (phosphorous source) useful for microbial growth, whereas calcareous rocks, dissolved by chemical weathering, usually do not release useful elements for microorganisms. Microbial community composition in a natural alpine apatite deposit (Piatto della Miniera, Switzerland) showed a specific bacterial community dominated by Acidobacteria, Chloroflexi, Actinobacteria, Rhizobiales and Firmicutes, while the non-apatite samples surroundings had a higher relative abundance of Actinobacteria and Chloroflexi (Ragot et al. 2013). The different bacterial compositions could also be explained by the different bioavailable elements from the surfaces.

Recently through 454 pyrosequencing, a great number of lithoautotrophic bacteria, autotrophic methane producing archaea and heterotrophic eukarya in the subglacial environment of Robertson Glacier (Canada) were found, allowing the researchers to suggest their active contribution to the global carbon cycle over extended periods of time (Hamilton et al. 2013).

Pioneer colonization of mineral soils and sediments by microorganisms

Whatever the mechanism behind stone and bedrock degradation, mineral elements and microfragments are deposited in what will be converted in an oligotrophic soil. Water from glacier, from springs, or from atmospheric precipitations bring more nutrient and wet the system. Of course, soil moisture and texture that affect water and gas fluxes could be responsible for nutrient availability. During the warmer seasons, water may come out through the glacier moraine springs. This water may have different properties according to its underground path. A long storage in an aquifers usually results in an enrichment of ions due to the contact of water with the inner surface, leading to weathering of the bedrock (Blaine McCleskey et al. 2012). Different bedrock may enrich water with different ions, leading to different chemical properties in the corresponding water spring. Water springs in high mountains constitute a hotspot for conservation issues. This is due to the unique nature of their three dimensional ecotones, which makes them very sensitive to environmental changes (Barquin and Scarsbrook 2008). Several studies have been done on high alpine water springs, but very seldom have those studies focused on prokaryotes. Most of the microorganisms studied are eukaryotes (diatoms and macroinvertebrates above all) or cyanobacteria (Cantonati et al. 2006). The change of chemical parameters influences the rate of organic matter originating from a terrestrial versus a microbial source (Hood et al. 2005; Judd et al. 2006). Glacier retreat alters the relative contribution of melt water to the streams: as glacier runoff

decreases, the water inputs from ground water increase. Eventually, the whole nutritional state of the high mountain environment will change.

In this system, microorganisms are the key players of sediment fertilization and soil neogenesis, thanks to several different metabolic activities. Respiration, dehydrogenase activity, dimethylsulfoxide reduction and ammonification generally increase along a chronosequence from the youngest to the oldest soil, and higher values are usually seen at the end of growing seasons, indicating distinct seasonal changes (Hofmann et al. 2013). When relatively high temperatures are also available on the soil surface, a noticeable methanogenic activity can be observed. In this sense, archaea can be considered an important group in these environments, but unfortunately they have not been thoughtfully studied. Few studies have been done, underlining that methane release is generally low in the primary soil, but it increases slightly as soil formation proceeds, reaching higher values at the end of the growing seasons. But, in general, in mature mineral soils, methanotrophy greatly exceeds methanogenesis, and the net methane consumption distinctly increases along the chronosequence (Hofmann et al. 2013).

Organic carbon may come from ancient deposits under ice cover (Bardgett et al. 2007), glacier water (cryoconites, meltwater, biofilms) or rock surfaces (biofilms, varnish), but it may come from elsewhere, such as wind deposition of allochthonous organic matter, i.e., plant and algal litter, organic deposition from living invertebrates and animals, natural or anthropogenic soot, pollution, or even dead animals and plants (Hodkinson et al. 2003). Unfortunately the contribution of such kinds of organic carbon inputs has never been studied with a multidisciplinary approach. Another carbon source is represented by both fungal and algal biomass (Frey et al. 2013). It has been recently been shown that some strains of *Flavobacterium* sp., Acidobacteria, and Proteobacteria can be fed by this source of nutrients (Zumsteg et al. 2013). Acidobacteria seem to be negatively related to the carbon mineralization process, and they are thought to be essential actors in the balance of the carbon cycle in high mountain environments (Zumsteg et al. 2013).

Nitrogen fixation by microorganisms and nitrogen deposition by the atmosphere (rain, pollutants, dust) are the only two processes to improve the amount of available nitrogen in the sandy moraines. Nitrogen fixation activity is low during the earliest pre-plant stages (Duc et al. 2009a, b), as confirmed by the low abundance of the marker gene *nifH* found in those environments. Nevertheless, nitrogen deposition, and decomposition and mineralization of the organic matter could be the most important nitrogen transformation process (Brankatschk et al. 2011).

Mineral soils and glacier stream sediments host a remarkably high microbial diversity, as shown in several researches (Nicol et al. 2005; Branda et al. 2010; Buzzini

et al. 2012; Frey et al. 2013; Wilhelm et al. 2013). Among the most common bacterial phyla, Acidobacteria seem to be more common in mineral soil with low carbon and nitrogen content, and neutral or alcaline pH, whereas Bacteroidetes seem to colonize acidic soil with organic matter supplied by mosses. Moreover, Acidobacteria seem to decrease their genetic diversity by function of the altitude (Bryant et al. 2008). High mountain mineral soils host new taxa, sometimes strictly correlated to the carbon and nitrogen cycles (Ganzert et al. 2011). Some of these phyla can constitute significant percentages of the overall diversity, such as the bacterial phylum AD3 on the Tibetan Plateau between 4042 and 4477 m a.s.l. (Wang et al. 2015). Surprisingly, these authors also found also an extraordinary percentage of archaeal ribosomal genes (up to 80 % of the total archaeal communities) belonging to the marine group MBGA. Interestingly, this finding can be explained with the very recent uplifting of the Tibetan Plateau from the ocean (less than 7 million years ago). If this hypothesis is true, the past history of the bedrock (in terms of lithology and of microbiology) is also important. The past history of mineral soil substrate is also important for fungal colonization: soil fungal communities of Lyman Glacier from sites adjacent to the glacier terminus (very young substrate) and from sites adjacent to the terminal moraine (old substrate) were analyzed (Jumpponen 2003). Stochastic events and airborne spore deposition seem to strongly influence the diversity and distribution of the early fungal communities dominated by three fungal phyla, whereas old-substrate-hosted fungi were widely distributed among Ascomycetes and Hymenomycetes. But authors noted a significant unexpected presence of biotrophic fungi such as Taphrinomycetes, Urediniomycetes (the rust fungi), Ustilaginomycetes (the smut fungi), and other unknown groups, due to random aerial deposits or to dormant spore banks already present in the older substrate.

Cyanobacteria and eukaryotic microalgae may also be a significant source of organic carbon not only in arctic environments (Mataloni et al. 2000; Freeman et al. 2009), but also in alpine glacier forefields (Frey et al. 2013). Significant differences in the cyanobacterial and green algal communities according to three different successional stages of the Damma Glacier forefield were found (Frey et al. 2013). Oscillatoriales dominated in bare soils, whereas Nostoc sp. dominated in sparsely vegetated soils. The algal phylotypes of the Trebouxiophyceae, living as symbiotic partners in lichens, had widespread distribution in all the sites. Moreover, both cyanobacteria and microalgae represented a source of organic matter and were contributors of carbon in the nutrient-deficient deglaciated soils (Frey et al. 2013).

Microbial communities in primary vegetation successions

According to the vegetation succession theory, pioneer plants are the first colonizers of incoherent mineral soil, and, through a complex dynamical process, they lead to a plant community stable association. This process is based on an orderly and continuing replacement of one plant community by another one. The ecological development is affected by several environmental and physical factors, such as local microclimate changes, mudslides, and anthropogenic modifications. An ecological succession is mainly due to two contrasting physiological behaviors: r-selection and K-selection. The r/K selection theory is based on the Verhulst model of population dynamics where the two parameters r (maximum growth rate of a population N) and K (carrying capacity of the environmental site) are important and have consequences on the rate of population growth dN/dt (Odum 1963) through the formula $dN/dt=rN(1-N/K)$. Ecologists typically distinguish r-strategists and K-strategists: The first case is composed of species that accentuate growth rate, producing a great amount of offspring and exploiting less competitive niches, whereas K-strategists maximize K, with a more careful use of the natural resources and a stronger adaptability to live in highly competitive niches and invest more time and energy in fewer offspring.

While the r/K theory is well known in plant and animal ecology, in microbial ecology it is rarely studied due to the extraordinary complexity of microbial cell behavior. Surveillance, growth and reproduction are affected by different environmental factors and by the presence of competitors. Nevertheless, microbiologists consider microbial species able to growth in laboratory conditions on carbon-rich media as a r-strategists, while K-strategists are microbial species rarely isolated or intrinsically not culturable (Garland et al. 2001; Sigler and Zeyer 2002). Consequently, bacterial genera such as Bacillus and Pseudomonas are believed to be r-strategists, while Acidobacteria and most of the Actinobacteria are considered K-strategists (Philippot et al. 2013).

Microbial ecologists tried to apply the r/K selection theory to the primary succession in high mountain environments. Ohtonen et al. (1999) firstly used molecular techniques to study microbial community composition in unvegetated sites, and in mycorrhized and non-mycorrhized pioneer plants from 20-year-old to 80-year-old soils in a primary succession along the forefield of Lyman Glacier (Washington, United States). They measured microbial biomass with three independent methods. Biomass increased over the successional time from unvegetated soil to vegetated soils, due to a different community composition and to a community shift from bacterial-dominated to fungal-dominated communities.

Hence, during the early stages of succession, the microbial community is not able to incorporate all the carbon substrate into its biomass, and thereby it increases the respiration process. The later-stage microbial community is not able to reach high rates of respiration, being mostly linked to K-strategy, and remains in an "energy-saving state", accumulating carbon in the biomass. In this case, fungi are K-strategists acting as an important carbon-sink of this habitat. These results had been confirmed by Jumpponen et al. (2002), who obtained important evidence on the soil fungal community in non-vegetated areas of the Lyman Glacier forefield. On Damma Glacier and Rotfirn Glacier (Switzerland), the development of microbial populations from the youngest to oldest soil was mainly due to the increase in microbial abundance and activity, confirming the previous result of Ohtonen et al. (1999) on Lyman Glacier (Sigler and Zeyer 2002). Following a different model of microbial community succession, the composition of all the microbial communities from Damma Glacier were significantly different, whereas on the Rotfirn Glacier moraine, the diversity of microbial communities was quite similar. Moreover, the authors applied the ecological r/K selection to the microbial succession, labeling microbial culturability as r-strategy (Garland et al. 2001). Opportunistic microorganisms able to grow on non-selective medium were dominant during the first 10 years of succession due to stress tolerance strategies against the harsher environmental conditions (Sigler and Zeyer 2004). Microbial activity increased to a maximum in the 70-year soil, while it decreased or reached a plateau in the 100-year soil. A shift from r-strategists to K-strategists occurred in the late successional stages, and a metabolically more efficient population that invests few resources into reproduction was settled (Ohtonen et al. 1999; Schipper et al. 2001; Sigler and Zeyer 2004).

Other studies about the same alpine environment were conducted, and they highlighted different aspects of the primary colonization. The bacterial community composition of mineral soils from siliceous or calcareous parental materials seems not to be determined by bedrock type, being otherwise dominated by ubiquitous bacterial taxa, generally adapted to the oligotrophic conditions (Lazzaro et al. 2009). This was confirmed by transplantation experiments of siliceous soil to calcareous soils to assess possible shifts in bacterial community structure and diversity (Meola et al. 2014). The natural growth dynamics of the bacterial populations did not change after the transplantation, and bacterial communities from bare soil, despite their simple species composition, could efficiently and dynamically answer to the changed environmental conditions. α-Proteobacteria were not affected by seasonal dynamics and the related physico-chemical variations, while Actinobacteria and Firmicutes showed marked changes in abundance and composition.

Bacterial, archaeal, fungal, and algal communities on rock substrates from fine granite sand near the glacier terminus, to the well-developed soils covered with complex vegetation, were studied to have a simultaneous picture of the microbial population (Nemergut et al. 2007; Schütte et al. 2009). The Shannon diversity index for Bacteria was high and constant along the forefield according to Schütte et al. (2009), but was in contrast to Nemergut et al. (2007), who detected increasing diversity along the chronosequence. Different factors such as climatic conditions, soil texture, bedrock composition and soil age could influence the bacterial community structure. Proteobacteria, Actinobacteria, Firmicutes and Cyanobacteria were abundant in young soil, whereas Acidobacteria colonized especially old soils. To assess the dynamics of bacterial populations that could be limited by selection processes along the gradients of chemical and biological parameters, two-dimensional sampling was performed in the same oligotrophic forefields (Hammerli et al. 2007). Sites of different age and vegetation showed significant differences in soil properties, such as pH, ammonium concentration, and total organic carbon, although those variations were not particularly high, as expected. Strains of the genus Pseudomonas were tested for adaptation in transfer experiments from young to old soils and vice versa. The isolated strains did not show a significant specific interaction with their local environment with a limited local expansion of soil bacteria. Environmental constraints, such as exclusion due to competition, different migration behavior of bacteria from young and old soil, or the ability of early colonizing bacteria to survive under the glacier ice, could be effective factors for the lack of local adaptation (Hammerli et al. 2007).

Along an age gradient of 20 years of an early successional soil in Southeastern Peru, evenness, phylogenetic diversity and number of phylotypes increased up to the oldest soil (Nemergut et al. 2007). Moreover, during the first 4–5 years of the succession, photosynthetic and nitrogen-fixing bacteria dramatically increased the amount of nutrients and organic matter many years before the occurrence of mosses, lichens and vascular plants (Schmidt et al. 2008). At 0 m from the glacier tongue, samples were dominated by Comamonadaceae, which probably came from glacier ice because they are widely distributed in cold environments such as glacier ice core (Sheridan et al. 2003) and Antarctic ice (Gordon et al. 2000). Some of those genera were N-fixing, but most were heterotrophs. In this case, microbial heterotrophs seemed to be the first colonizers and they were probably influenced by the same environmental factors that control other microbial communities.

In terms of cyanobacterial diversity, along a chronosequence from initial (0–10 year) and transient soils to the developed soils (110–120 year), transient and developed soils are quite heterogeneous in view to the ecological niches (Frey et al. 2013), whereas the developed soils host cyanobacteria ubiquitous in soil, rhizosphere, freshwater, mountain and endolithic habitats (Heath et al.

2010; Jungblut et al. 2010; Wong et al. 2010; Schmidt et al. 2011).

The differences could be explained by the spread of vegetation cover and by the physico-chemical characteristics of the soils. The developed soils present a finer texture, and consequently a higher store of organic matter, water contents and nutrient concentrations, than the initial bare soils or the transient sparsely vegetated soils (Frey et al. 2013). The vegetation cover results in less light for phototrophic microorganisms, and competition with vascular plants and root-associated microorganisms for nutrients. About algae, there are no significant differences in diversity along the chronosequence, maybe because recurring floods events due to melt-waters in summer cause the dispersal of algal cell across different soils.

Another alpine glacier recently studied is the forefield of the Weisskugel Glacier in Matsch Valley (Italy). A first insight into the bacterial communities associated with different environmental matrices showed distinct variations among sites: Acidobacteria mostly found in mineral soil; Proteobacteria in sediments, biofilms, and lichens; Cyanobacteria on rock surfaces; and Firmicutes and Bacteroidetes in biofilms (Esposito et al. 2013). Among the different environmental matrices of higher Matsch Valley, mineral soil showed the highest bacterial diversity in terms of taxa, even accounting for nitrogen fixing bacteria (Ciccazzo et al. 2014b).

All these overall data show that mineral soil of high mountain environments, before being reached by plant seeds, already has a high potential for soil fertilization and plant growth promotion. An extraordinary high diversity is locally available and strong environmental factors drive the final combination of the microbial taxa in each site at a microscopic scale. Once a seed randomly reaches the site, depending on the combination of microorganisms and of the chemical characteristics, it can germinate or be inhibited.

Microbial growth dynamics after pioneer plant growth

When the vegetation appeared along a primary succession, it could be influenced by environmental factors, ecological competition and mineral nutrient stress (Grime 2001). In this context, plants could be distinguished as competitors (low stress and low disturbance), stress tolerators (high stress, low disturbance), and ruderals (low stress, high disturbance).

Pioneer plants could play a crucial role in soil development with alteration of parent materials, slope stabilization, accumulation of litter and rhizodeposition. Microorganisms can convert rhizodeposits in other organic substrates, which can improve soil water retention capability to hold water and nutrients (Philippot et al. 2013). Moreover, plants supply sugars to microorganisms, which in turn supply fixed nitrogen to plants, and bioavailable phosphate. Plant growth promoting

rhizobacteria can also improve plant growth and health, protecting it from parasites (Singh et al. 2004). On the other hand, phytopathogenic microorganisms could be also selected by the plant, increasing their pathogenic efficiency, thanks to nutrients and minerals available in the rhizosphere.

Studies about the effect of pioneer plants on rhizobacterial community in alpine ecosystems were especially focused on single plants along a chronosequence, while studies about the effect of the overall plant cover regarded different ecological niches and pointed out the higher significance of environmental parameters on the microbial communities. Regarding single plants in high mountain environment, most of the studies have been conducted on pioneer autochthonous plants in Europe and in Northern America. Overall, these studies showed the rhizosphere effects exerted by each single plant species on their respective rhizobacterial communities, even if some contrasting results can be found. For instance, along the chronosequence of the Rotmoos Glacier in Austria, the first pioneer plants appeared within 14–20-year-old soils due to the specific adaptations to the environmental conditions. Plants in stable symbiosis with diazothrops occurred late up to the 48-year-old soils, due to the scarcity of phosphorous, essential for the nitrogen cycle. Moreover, the energy required for the maintenance of symbiosis is usually very high, and this is why stable symbiosis is more rare under critical environmental conditions (Merbach et al. 1999). Woody plants occasionally colonize very young soils, but, due to the low growth rates, they are often replaced by more competitive perennial herbs. During the succession, when the vegetation cover and plant diversity increase, heat stress affecting soil microorganisms is reduced, while soil moisture is maintained. Nutrient availability and root exudation increase microbial root colonization. The organic matter accumulates and K-strategists are favored against r-strategists. Moreover, the abundance and the activity of microorganisms increase during the succession due to the soil age and to the shift from annual vegetation to perennial vegetation. Actually, perennial plants are known to be able to exude more carbon, increasing the nutrient availability in the late successional stages (Bardgett et al. 1999).

In a recent work (Brown and Jumpponen 2014), the fungal and bacterial successions along the glacier forefield chronosequence of Lyman Glacier were studied through high-throughput sequencing, comparing establishing vegetation soils of four plant species with diverse mycorrhizal ecologies (*Abies lasiocarpa*, ectomycorrhizal; *Luetkea pectinata*, arbuscular mycorrhizal; *Phyllodoce empetriformis*, ericoid mycorrhizal; *Saxifraga ferruginea*, nonmycorrhizal) and non-vegetated soils. The biomass, the diversity and the distribution of both fungi and bacteria within the microbial communities were strictly related to the distance from glacier terminus. There were evidences of different drivers for fungal and bacterial trajectories. The presence of plants and not the plant species itself played a crucial role in structuring bacterial

communities along the chronosequence, and a minor role in structuring the fungal communities. Moreover, while only bacterial communities appeared to taxonomically converge during assembly (hence supporting determinism), fungal communities appeared to act oppositely, although many fungal taxa were non randomly distributed across the glacier foreland.

During the early succession, plant species could not select specific rhizobacterial communities, whereas pioneer plants on 15-year-old soils in Glacier Bay (Alaska) could select for specific rhizobacterial communities (Bardgett and Walker 2004; Knelman et al. 2012). In Glacier Bay, the vegetation succession is faster due to a different developmental pattern based on different climates (Matthews 1992). After 75 years, a plant species effect on the rhizobacterial communities was observed because of the increasing range of plant exudation patterns, which favors the selection of specific microbial communities characterized by higher microbial diversity. The perennial pioneer plant *Leucanthemopsis alpina*, characterized by extensive root development and longevity (Körner 1999), was chosen to assess the influence of a pioneer plant on the rhizobacterial community along a chronosequence of soil development (5, 50, and 70 years) in the forefield of the Damma Glacier (Edwards et al. 2006). The pioneer plant colonization creates hotspots where microbial growth and activity resulted to be higher than in adjacent bare soil of the same age. Interestingly, K-strategist bacteria colonized more efficiently the young soil where the plant was growing, while the r-strategists were commonly found in non-young soils, especially in the 50-year-old and 70-year-old soils. This was maybe due to the increased concentrations of labile nitrogen and carbon. The rhizobacterial communities associated with *L. alpina* depend on soil age and were clearly different from the interspace community in the young soils, but these differences tended to disappear in the older soils. The relative similarity of the profiles strongly reflected labile carbon and nitrogen availability. Variable results on *L. alpina* were found when Miniaci et al. (2007) studied the impact on biological and chemical–physical soil parameters of the pioneer plant within isolated patches. In this case, *L. alpina* rhizosphere could influence bacterial communities even 20 cm away from a plant. Different results were obtained when assessing the influence of *Poa alpina* on the soil microbial community in primary succession along four different stages of grassland development on the Rotmoos Glacier. In the pioneer stage, the rhizobacterial community was determined by the environmental conditions, whereas in the later stages, plants were selected for a specific microbial community related to soil properties and carbon supply (Tscherko et al. 2004). The selective role of pioneer plants, which counteracts resource scarcity of bare soils, was clearly confirmed by some studies about pioneer plants in high elevation alpine environments (Roy et al. 2013; Ciccazzo et al. 2014a, b).

Along an elevation gradient (2000–3000 m a.s.l.), the cushion pioneer plant *Silene acaulis* affected the microbial communities modifying soil properties on calcareous and siliceous bedrocks in the French Alps (Roy et al. 2013). The bedrock type outside the cushions strongly influenced the bacterial communities, whereas inside the cushions, the bacterial communities were highly similar in both types of bedrock. The fungal communities showed an opposite behavior. Outside the cushion, they were weakly influenced by the different bedrock types and inside the cushions, they varied with bedrock, elevation, soil nutrients, and water availability. In this case, by buffering soil pH and enhancing soil nutrient availability, the pioneer plant *S. acaulis* exerted a strong action opposite to lithology, to rock chemistry and to oligotrophy.

The same selective behavior was observed in *S. acaulis* and eleven other pioneer plant species when compared to bare soil samples in the alpine forefield of Weisskugel Glacier in Italy (Ciccazzo et al. 2014a, b). Within a sampling area of similar environmental parameters, the pioneer plants act as hotspots that counteract resource limitation and the harsh environmental conditions of the near bare soils, as confirmed by the rhizobacterial community structure being extremely different from those of the bare soils. The study also highlighted a clear plant species effect on the associated rhizobacterial community. Different plant species selected specific rhizobacterial communities (Ciccazzo et al. 2014b) mainly composed of Acidobacteria and Proteobacteria, while bare soils were characterized by a lower bacterial diversity with a predominance of Acidobacteria and Clostridia. Even the fungal communities of the rhizosphere of different alpine species were strictly related to the host identity for *Taraxacum ceratophorum, Taraxacum officinale*, and *Polemonium viscosum* (Becklin et al. 2012).

On the other hand, very little has been done to understand if the rhizosphere effect of single plants continues in more definite vegetation patches. This is possible studying safe-sites, i.e., little soil areas surrounded by boulders where few plant individuals can grow together, or vegetation plots. The study of the microbial communities associated with safe-sites showed another evidence of rhizobacterial community selection in a high altitude alpine environment. This has been emphasized by Ciccazzo et al. (2014a) for different floristic communities colonizing three safe-sites. The communities were composed of pioneer plants able to colonize niche where the soil formation processes happened thanks to the mitigated environmental conditions. The nitrogen and carbon content confirmed the different soil developmental stages of the three safe-sites. In this situation, not only were the rhizobacterial communities significantly different from the bare soils both in structure and diversity, but a gradient of increased diversity was also found according to the different safe-site developmental stages. The capability of individuals of the same pioneer plant species to select specific and highly similar

rhizobacterial community can be confirmed even if the plants grow strictly together with plants of different species.

Moving to vegetation patches in moraine environments, to the best of our knowledge, the only available data derive from Antactica. Here, along a latitudinal gradient, bacterial, fungal and nematode diversities of dense vegetation from different locations were comparable, whereas microbial diversity of "fell-field" vegetation decreased with increasing of latitude (Yergeau et al. 2007a, b). In permafrost vegetated soils characterized by meadow, steppe or desert steppe soil moisture, C/ N ratio and pH were main driving factors of the microbial diversity (Zhang et al. 2012). In high elevated arid grassland, a strong plant effect was demonstrated for the perennial bunchgrasses *Stipa*, *Hilaria* and for the invading annual grass *Bromus* (Kuske et al. 2002).

Microbial role in nutrient cycling in high mountain environments

Bacteria of mountain soils are key players in biogeochemical cycles on rock surfaces, incoherent sands, mineral soil, and pioneer plant rhizosphere. Particularly in plant rhizosphere, the exchange taking place between plants and microorganisms at the soil-root interface leads to stone micro-particles bioweathering and lisciviation, nitrogen and carbon enrichment, plant organic compound decomposition or mineralization, and soil pH modification. In an alpine oligotrophic environment, bacteria drive symbiotic or non-symbiotic nitrogen fixation, due to the nitrogenase enzyme able to reduce atmospheric nitrogen into soluble ammonium.

The most studied microorganisms involved in nitrogen fixation are rhizobia, often symbiotic nitrogen-fixing bacteria, commonly associated with legume host plants. Other bacteria of the genus *Frankia* sp. have an actinorrhizal symbiosis with nodular rhizosphere of plants such as *Alnus*, *Myricae*, *Betula*, or *Coriaria* (Benson and Silvester 1993; Kennedy et al. 1997; Simonet et al. 1999). There are also bacteria that can fix nitrogen in non-symbiotic association with plant. A great number of non-symbiotic bacteria help plant growth by feeding plant individuals a significant amount of nitrogen. β-Proteobacteria such as *Burkholderia* and *Herbaspirillum* are often associated with nitrogen fixation, although several strains can act as plant or even human pathogens (Hayat et al. 2010). The free-living diazotrophs *Azotobacter* sp. are more common in mature soils, where a significant amount of reduced sugars is available. Other non-symbiotic nitrogen-fixers are some strains of *Clostridium* (Kennedy et al. 2004) more common in anaerobic soils, such as high-mountain marshlands, ponds, and wet soils, which need a higher C/N ratio. *Azospirillum* is usually found in close associations with the family of Graminaceae (Kennedy et al. 2004), where it provides plants of nitrogen, but also promotes plant root-

growth by increasing water, mineral and nutrient uptake from the surrounding soil. Such asymbiotic nitrogen-fixers could be considered to be potential key players in nitrogen accumulation after glacier retreat, when mineral soil without pioneer plants has to be enriched with nutrients. Cyanobacteria are considered to be one of the most important bacterial taxa in deglaciated oligotrophic environments, since they can provide mineral soil with both fixed nitrogen (through nitrogen reduction) and fixed carbon (through oxygenic photosynthesis) (Fritzsheridan 1988; Chapin et al. 1991; Davey and Clarke 1991; Kaštovská et al. 2005). Due to the low concentration of nitrogen, which is not part of the mineral composition of the initial soil, the foreland of a retreated glacier also represents a unique habitat to study the asymbiotic nitrogen fixation to assess which are the main actors.

The first investigation of asymbiotic diazotrophic diversity in high altitude alpine soil was carried out by Duc et al. (2009a, b). Acetylene reduction tests showed nitrogen fixation along the chronosequence with higher activity in the rhizosphere, according to previous studies of the influence of rhizosphere on the associated bacterial community, that showed how exudation and reduction of environmental stress (i.e., plant cover effect) help bacterial diversity (Miniaci et al. 2007; Tscherko et al. 2004). Nitrate reductase activity in the early successional stage in Rotmoos Glacier moraine was found to be 23-times higher in rhizosphere of *P. alpina* than in bare soil (Deiglmayr et al. 2006). In the rhizosphere of *P. alpina*, with increase of soil age, the amount of nitrate decreased while ammonium increased. The authors explained that this observation was maybe due to nitrate immobilization by root or by microorganisms, rather than nitrification activities. Nitrifying microorganisms could be inhibited by heterotrophic bacteria in N-poor environments such as the glacier foreland (Bengtson and Bengtsson 2005), while nitrogen fixation and ammonification could guarantee the ammonium amount in these soils.

Although nitrogen fixation is a complex process that requires several proteins, the basis of the process is the nitrogenase reductase (*nifH*) gene. The highly conserved amino acid sequence of nifH protein allows the *nifH* gene to be a useful marker gene to assess diazotroph diversity in the environment. The diversity of *nifH* genes was generally found to be higher and with a broader environmental distribution in glacier moraines than in forest and agricultural soils (Widmer et al. 1999; Poly et al. 2001; Rösch and Bothe 2005). Actually in forest soils or in agricultural soils, *nifH* diversity was mainly due to Proteobacteria only. New *nifH* clusters or *nifH* genes referred to in Firmicutes were widely distributed in 8-year-old unvegetated soils in polar environments (Deslippe and Egger 2006). The most common *nifH* sequences were related to *Geobacter* sp., a taxon able to perform both oxic and anoxic metabolisms. Its physiologic plasticity is very useful to answer to environmental fluctuation between aerobic and anaerobic

conditions during wet periods (snow melting, rainfall). The nitrogen cycle of the glacial forefield on Anvers Island (Antarctic Peninsula) was dominated by heterotrophic diazotrophs and not by Cyanobacteria (Strauss et al. 2012), whereas previous studies on the Arctic environment showed the crucial role of Cyanobacteria species in nitrogen fixation (Zielke et al. 2002). The relative importance of Cyanobacteria, however, is still debated, since in many cases they represent only a minor part of the overall bacterial communities in mineral soils, even if the mineral soil is fully exposed to light (Esposito et al. 2013). Cyanobacterial communities of the Damma Glacier moraine were quite similar to the ones found in the biological soil crusts of the Chihuahuan Desert, but in Damma they were found to be not shaped in well-organized crusts. Maybe in this type of high-mountain environment, Cyanobacteria are mainly symbionts of mosses or lichens, as frequently occurrs in vegetation patches of mountain forelands (Solheim et al. 2004).

Comparing contrasting climatic conditions (wetter vs drier) of a chronosequence at Cordillera Darwin (Tierra del Fuego), Arróniz-Crespo et al. (2014) found that the epiphytic cyanobacteria genera, hosted by mosses, were correlated to the different stages of ecological succession rather than host species identity, and were capable of high rates of nitrogen fixation. Under wetter conditions, the moss-cyanobacteria associations at very early sites after glacier retreat (4–7 years) showed the highest N-fixation rates, whereas in drier climate, N-fixation on the same associations was also high, but reached the maximum at intermediate-aged sites (26–66 years).

Moreover, the nitrogen cycle in rhizosphere soil of *L. alpina* was characterized by quantifying functional genes involved in nitrogen fixation and mineralization, nitrification and denitrification at two time points along a chronosequence transect in Damma Glacier Valley (Töwe et al. 2010). The functional gene abundance did not change between time points, but they were more abundant in rhizosphere than in unvegetated soils. Since plants grown on 10-year-old soils were able to accumulated large amounts of nitrogen, plants on young soils were strongly more dependent on asymbiotic nitrogen fixation. The results were confirmed in situ by Brankatschk et al. (2011), who observed that early and transient successional stages were mostly dominated by N-fixation and organic matter mineralization, while nitrification and the following denitrification, which cause nitrogen loss, were increased in later successional stages, when plant cover and microbial associations were fully established.

Among macronutrients, the absence of phosphorus affects plant growth and productivity (Plassard and Dell 2010) remarkably. Nitrogen and phosphorus are linked to each other because nitrogen fixation depends on the available P and the P-solubilization processes depend strictly on the type of carbon source, nitrogen availability and temperature. The bioavailable form of phosphate is generally very low, due to P interactions with the soil. A large proportion of phosphate is quickly sequestered in insoluble forms. There are evidences of P-solubilizing microorganisms able to convert the insoluble phosphorus, such as the mineral P sources, to soluble forms by acidification, chelation, exchange reactions and polymeric substances formation (Delvasto et al. 2006). In a high mountain environment, the presence of P-solubilizing bacteria is generally less abundant, due to the natural harsher environmental conditions. In cold environments, psychrophilic bacterial species with optimal cold temperature ranges of P-solubilization processes have been recently isolated and characterized. For instance, from Himalaya, P-solubilizer psychrophilic strains belonging to *Kluyvera intermedia* (Pallavi and Gupta 2013) *Pseudomonas corrugata* (Pandey et al. 2002), *Pseudomonas putida* (Pandey et al. 2006), *Pseudomonas fragi*, *Pantoea dispersa*, *Exiguobacterium acetylicum*, and *Serratia marcenscens* (Selvakumar et al. 2008a, b, 2009a, b) have been isolated from acid oligotrophic soils. Although a comprehensive study of phenotypic behavior of P-solubilizing bacteria in mountain environment has never been attempted, the effect of temperature on P-solubilizing skills of naturally occurring psychrotolerant strains of *Pseudomonas fragi* (Selvakumar et al. 2009a) has been reported.

In many respects, the sulfur cycle parallels the nitrogen cycle, except for the input source, which for this element is volcanic rocks. In glacier forefields, bacteria could mobilize S from mineral substrates and make it bioavailable (Borin et al. 2010; Mapelli et al. 2011). This process could lead to an exceptional primary production in spots where abundant sulfur rocks are present.

Iron is an essential micro-element for life, and iron cations are present in the environment with two oxidation states: trivalent (ferric) and divalent (ferrous); at circumneutral pH, the divalent cation is more stable. In acidic environment, the bacterially mediated oxidation of ferrous iron prevails over the molecular oxidation, which normally occurs at circumneutral pH (Helmann 2014). Recent findings have disclosed the mechanisms that regulate iron uptake from bacteria. It appears that iron metabolism is regulated by manganese concentration (Puri et al. 2010). This finding highlights the interconnection among the cycles of different elements (Puri et al. 2010).

Microbial cycling of other elements as components of geochemical budgets is not yet well described, especially in cold climates (Marnocha and Dixon 2014). It should be pointed out that cycles of different elements are connected to each other. Some elements may be essential in the processes of transformation of other elements; for example, Mn and Fe are essential ions in photosynthesis (Vitousek et al. 2002).

Conclusions and perspectives

A number of studies have recently been published to highlight the colonization of microorganisms in high mountain environments, and the consequential contribution in soil formation and pioneer plant growth. Bacteria, archaea, fungi, and algae have been revealed as major biological factors in driving these processes, influenced by environmental factors such as soil pH, moisture and temperature. Once pioneer plants have grown, they can determine the shape of the rhizospheric microbial communities, driving their activities.

Unfortunately most of the high mountain areas are still not studied. Most of the data come from European Alps or U.S.A., while a quite limited number of papers consider Himalaya or the Andes. Several other mountain ranges have been rarely considered, such as Karakorum, Urals, Caucasus or Pamir in Asia, Southern Alps in New Zealand, Atlas and Kilimanjaro in Africa, and so on. Adding these areas will give us a broader vision of the environmental processes at the world scale, giving important information for the climate change consequences.

Moreover, very little is known on the functionality of these communities, especially for Acidobacteria and other common key players. Analysis of active microbial communities has rarely been done, due to the difficulties in extracting functional RNA from mineral soils and other kind of matrices. If the carbon and the nitrogen cycles in these environments have been studied by some research group, even if not fully considered, other cycles have never been investigated. In this context, the archaeal contribution is still poorly considered, and the contribution of several rare bacterial and archaeal phyla to biogeochemical cycles is completely unknown.

References

Arróniz-Crespo M, Pérez-Ortega S, De los Ríos A, Allan Green TG, Ochoa Hueso R, Casermeiro MA, de la Cruz MT, Pintado A, Palacios D, Rozzi R, Tysklind N, Sancho LG (2014) Bryophyte-Cyanobacteria associations during primary succession in recently deglaciated areas of Tierra del Fuego (Chile). PLOS One 9:e96081

Bardgett R, Walker L (2004) Impact of coloniser plant species on the development of decomposer microbial communities following deglaciation. Soil Biol Biochem 36:555–559

Bardgett R, Mawdsley J, Edwards S, Hobbs P, Rodwell J, Davies W (1999) Plant species and nitrogen effects on soil biological properties of temperate upland grasslands. Funct Ecol 13:650–660

Bardgett RD, Richter A, Bol R, Garnett MH, Baumler R, Xu XL, Lopez-Capel E, Manning DAC, Hobbs PJ, Hartley IR, Wanek W (2007) Heterotrophic microbial communities use ancient carbon following glacial retreat. Biol Lett 5:487–490

Barquin J, Scarsbrook M (2008) Management and conservation strategies for cold water springs. Aquat Conserv Mar Freshw Ecosys 18:580–591

Becklin KM, Hertweck KL, Jumpponen A (2012) Host identity impacts rhizosphere fungal communities associated with three alpine plant species. Microb Ecol 63:682–693

Bengtson P, Bengtsson G (2005) Bacterial immobilization and remineralization of N at different growth rates and N concentrations. FEMS Microbiol Ecol 54:13–19

Benson DR, Silvester WB (1993) Biology of *Frankia* strains actinomycete symbionts of actinorhizal plants. Microbiol Rev 57:293–319

Blaine McCleskey R, Clor L, Lownstern J, Evans W, Nordstrom D, Heasler H, Huebner M (2012) Solute and geothermal flux monitoring using electrical conductivity in the Madison, Firehole, and Gibbon rivers, Yellowstone National Park. Appl Geochem 27:2370–2381

Borin S, Ventura S, Tambone F, Mapelli F, Schubotz F, Brusetti L, Scaglia B, D'Acqui L, Solheim B, Turicchia S, Marasco R, Hirnichs K, Baldi F, Adani F, Daffonchio D (2010) Rock weathering creates oases of life in a high arctic desert. Environ Microbiol 12:293–303

Bowers RM, McCubbin IA, Haller AG, Fierer N (2012) Seasonal variability in airborne bacterial communities at a high-elevation site. Atmos Environ 50:41–49

Branda E, Turchetti B, Diolaiuti G, Pecci M, Smiraglia C, Buzzini P (2010) Yeast and yeast-like diversity in the southernmost glacier of Europe (Calderone glacier, Apennines, Italy). FEMS Microbiol Ecol 72:354–369

Brankatschk R, Towe S, Kleineidam K, Schloter M, Zeyer J (2011) Abundances and potential activities of nitrogen cycling microbial communities along a chronosequence of a glacier forefield. ISME J 6:1025–1037

Brown SP, Jumpponen A (2014) Contrasting primary successional trajectories of fungi and bacteria in retreating glacier soils. Mol Ecol 23:481–497

Brunner I, Plötze M, Rieder S, Zumsteg A, Furrer G, Frey B (2011) Pioneering fungi from the Damma glacier forefield in the Swiss Alps can promote granite weathering. Geobiology 9:266–279

Brunner I, Goren A, Schlumpf A (2014) Patterns of organic acids exuded by pioneering fungi from a glacier forefield are affected by carbohydrate sources. Environ Res Lett 9:025002

Brusetti L, Glad T, Borin S, Myren P, Rizzi A, Johnsen PJ, Carter P, Daffonchio D, Nielsen KM (2008) Low prevalence of bla$_{TEM}$ genes in Arctic environments and agricultural soil and rhizosphere. Microb Ecol Health Dis 20:27–36

Bryant JA, Lamanna C, Morlon H, Kerkhoff AJ, Enquist BJ, Green JL (2008) Microbes on mountainsides: Contrasting elevational patterns of bacteria and plant diversity. Proc Natl Acad Sci U S A 105:11453–11457

Budel B, Weber B, Kuhl M, Pfanz H, Sultemeyer D, Wessels D (2004) Reshaping of sandstone surfaces by cryptoendolithic cyanobacteria: bioalkalization causes chemical weathering in arid landscapes. Geobiology 2:261–268

Buzzini P, Branda E, Goretti M, Turchetti B (2012) Psychrophilic yeasts from worldwide glacial habitats: diversity, adaptation strategies and biotechnological potential. FEMS Microbiol Ecol 82:217–241

Cantonati M, Gerecke R, Bertuzzi E (2006) Springs of the Alps—sensitive ecosystems to environmental change: From biodiversity assessments to long-term studies. Hydrobiologia 562:59–96

Chanal A, Chapon V, Benzerara K, Barakat M, Christen R, Achouak W, Barras F, Heulin T (2006) The desert of Tataouine: an extreme environment that hosts a wide diversity of microorganisms and radiotolerant bacteria. Environ Microbiol 8:514–525

Chapin DM, Bliss LC, Bledsoe LJ (1991) Environmental-regulation of nitrogen-fixation in a high arctic lowland ecosystem. Can J Bot 69: 2744–2755

Chapin FS, Walker LR, Fastie CL, Sharman LC (1994) Mechanisms of primary succession following deglaciation at Glacier Bay Alaska. Ecol Monog 64:149–175

Christner BC, Mosley-Thompson E, Thompson LG, Zagorodnov V, Sandman K, Reeve JN (2000) Recovery and identification of viable bacteria immured in glacial ice. Icarus 144:479–485

Chuvochina MS, Marie D, Chevaillier S, Petit JR, Normand P, Alekhina IA, Bulat SA (2011) Community variability of bacteria in alpine snow (Mont Blanc) containing Saharan dust deposition and their snow colonisation potential. Microbes Environ 26:237–247

Chuvochina MS, Alekhina IA, Normand P, Petit JR, Bulat SA (2012) Three events of Saharan dust deposition on the Mont Blanc glacier associated with different snow-colonizing bacterial phylotypes. Microbiology 80:125–131

Ciccazzo S, Esposito A, Rolli E, Zerbe S, Daffonchio D, Brusetti L (2014) Safe-sites effects on rhizosphere bacterial communities in a high-altitude alpine environment. BioMed Res Int ID:480170

Ciccazzo S, Esposito A, Rolli E, Zerbe S, Daffonchio D, Brusetti L (2014b) Different pioneer plant species select specific rhizosphere bacterial communities in a high mountain environment. Springer Plus 3:391

Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. Am Nat 111:1119–1144

Davey MC, Clarke KJ (1991) The spatial distribution of microalgae on fellfield soils. Antarctic Sci 3:257–263

De Garcia V, Brizzio S, van Broock MR (2012) Yeasts from glacial ice of Patagonian Andes, Argentina. FEMS Microbiol Ecol 82:540–550

De los Ríos A, Wierzchos J, Sancho LG, Ascaso C (2003) Acid micro-environments in microbial biofilms of antarctic endolithic microecosystems. Environ Microbiol 4:231–237

Deiglmayr K, Philippot L, Tscherko D, Kandeler E (2006) Microbial succession of nitrate-reducing bacteria in the rhizosphere of *Poa alpina* across a glacier foreland in the Central Alps. Environ Microbiol 8:1600–1612

Delvasto P, Valverde A, Ballester A, Igual JM, Munoz JA, Gonzalez F, Blázquez ML, Garcia C (2006) Characterization of brushite as a re-crystallization product formed during bacterial solubilization of hy-droxyapatite in batch cultures. Soil Biol Biochem 38:2645–2654

Deslippe JR, Egger KN (2006) Molecular diversity of *nifH* genes from bacteria associated with High Arctic dwarf shrubs. Microb Ecol 51: 516–525

Dieser M, Nocker A, Priscu J, Foreman CM (2010) Viable microbes in ice: Application of molecular assays to McMurdo Dry Valley lake ice communities. Antarct Sci 22:470–476

Dorn RI (2007) Rock varnish. In: Nash DJ, McLaren SJ (eds) Geochemical sediments and landscapes. Blackwell, London, pp 246–297

Duarte CM, Dachs J, Llabres M, Alonso-Laita P, Gasol JM, Tovar-Sanchez A, Sañudo-Wilhelmy SA, Agustí S (2006) Aerosol inputs enhance new production in the subtropical northeast Atlantic. J Geophys Res-Biogeosc 111:1–8

Duc L, Neuenschwander S, Rehrauer H, Wagner U, Sobek J, Schlapbach R, Zeyer J (2009a) Development and experimental validation of a *nifH* oligonucleotide microarray to study diazotrophic communities in a glacier forefield. Environ Microbiol 11:2179–2189

Duc L, Noll M, Meier BE, Burgmann H, Zeyer J (2009b) High diversity of diazotrophs in the forefield of a receding alpine glacier. Microb Ecol 57:179–190

Edwards IP, Bürgmann H, Miniaci C, Zeyer J (2006) Variation in micro-bial community composition and culturability in the rhizosphere of *Leucanthemopsis alpina* (L.) Heywood and adjacent bare soil along an alpine chronosequence. Microb Ecol 52:679–692

Edwards A, Pachebat JA, Swain M, Hegarty M, Hodson AJ, Irvine-Fynn TDL, Rassner SME, Sattler B (2013) A metagenomic snapshot of taxonomic and functional diversity in an alpine glacier cryoconite ecosystem. Environ Res Lett 8:035003

Esposito A, Ciccazzo S, Borruso L, Zerbe S, Daffonchio D, Brusetti L (2013) A three-scale analysis of bacterial communities involved in rocks colonization and soil formation in high mountain environ-ments. Curr Microbiol 67:472–479

Esposito A, Ahmed E, Ciccazzo S, Sikorski J, Overmann J, Holmström SJM, Brusetti L (2015) Comparison of rock varnish bacterial com-munities with surrounding non-varnished rock surfaces: Taxon-specific analysis and morphological description. Microb Ecol. doi: 10.1007/s00248-015-0617-4

Felip M, Camarero L, Catalan J (1999) Temporal changes of microbial assemblages in the ice and snow cover of a high mountain lake. Limnol Oceanogr 44:973–987

Franks F (1994) Protein destabilization at low temperatures. Adv Protein Chem 46:105–139

Freeman KR, Pescador MY, Reed SC, Costello EK, Robeson MS, Schmidt SK (2009) Soil CO_2 flux and photoautotrophic community composition in high elevation, 'barren' soils. Environ Microbiol 11: 674–686

Frey B, Rieder SR, Brunner I, Ploetze M, Koetzsch S, Lapanje A, Brandl H, Furrer G (2010) Weathering associated bacteria from the Damma glacier forefield: physiological capabilities and impact on granite dissolution. Appl Environ Microbiol 76:4788–4796

Frey B, Bühler L, Schmutz S, Zumsteg A, Furrer G (2013) Molecular characterization of phototrophic microorganisms in the forefield of a receding glacier in the Swiss Alps. Environ Res Lett 8:015033

Fritzsheridan RP (1988) Physiological ecology of nitrogen-fixing blue-green-algal crusts in the upper-subalpine life zone. J Phycol 24:302–309

Fujii M, Takano Y, Kojima H, Hoshino T, Tanaka R, Fukui M (2010) Microbial community structure, pigment composition, and nitrogen source of red snow in Antarctica. Microb Ecol 59:466–475

Ganzert L, Lipski A, Hubberten HW, Wagner D (2011) The impact of different soil parameters on the community structure of dom-inant bacteria from nine different soils located on Livingston Island South Shetland Archipelago Antarctica. FEMS Microbiol Ecol 76:476–491

Garland JL, Cook KL, Adams JL, Kerkhof L (2001) Culturability as an indicator of succession in microbial communities. Microb Ecol 42: 150–158

Gorbushina AA (2007) Life on the rocks. Environ Microbiol 9: 1613–1631

Gorbushina AA, Broughton WJ (2009) Microbiology of the atmosphere-rock interface. Ann Rev Microbiol 63:431–450

Gordon DA, Priscu J, Giovannoni S (2000) Origin and phylogeny of microbes living in permanent Antarctic lake ice. Microb Ecol 39: 197–202

Grime JP (2001) Plant strategies vegetation processes and ecosystem properties. Wiley Blackwell London Ed

Gruber S, Peter M, Hoelzle M, Woodhatch I, Haeberli W (2003) Surface temperatures in steep Alpine rock faces—A strategy for regional-scale measurement and modeling. Proc 8th Int Conf Permafrost 1: 325–330

Hågvar S, Ohlson M (2013) Ancient carbon from a melting glacier gives high ^{14}C age in living pioneer invertebrates. Sci Rep 3:2820

Hamilton TL, Peters JW, Skidmore ML, Boyd ES (2013) Molecular evidence for an active endogenous microbiome beneath glacial ice. ISME J 7:1402–1412

Hammerli A, Waldhuber S, Miniaci C, Zeyer J, Bunge M (2007) Local expansion and selection of soil bacteria in a glacier forefield. Eur J Soil Sci 58:1437–1445

Hayat R, Safdar Ali S, Amara U, Khalid R, Ahmed I (2010) Soil beneficial bacteria and their role in plant growth promotion: a review. Ann Microbiol 60:579–598

Heath MW, Wood SA, Ryan KG (2010) Polyphasic assessment of freshwater benthic mat-forming cyanobacteria isolated from New Zealand. FEMS Microbiol Ecol 73:95–109

Helmann JD (2014) Specificity of metal sensing: iron and manganese homeostasis in *Bacillus subtilis*. J Biol Chem 289:28112–28120

Hervàs A, Casamayor EO (2009) High similarity between bacterioneuston and airborne bacterial community compositions in a high mountain lake area. FEMS Microbiol Ecol 67:219–228

Hodkinson ID, Coulson SJ, Webb NR (2003) Community assembly along proglacial chronosequences in the high Arctic: vegetation and soil development in north-west Svalbard. J Ecol 91:651–663

Hofmann K, Reitschuler C, Illmer P (2013) Aerobic and anaerobic microbial activities in the foreland of a receding glacier. Soil Biol Biochem 57:418–426

Hood E, Williams MW, McKnight DM (2005) Sources of Dissolved Organic Matter (DOM) in a Rocky Mountain stream using chemical fractionation and stable isotopes. Biogeochemistry 74:231–255

Hood E, Battin TJ, Fellman J, O'Neel S, Spencer RGM (2015) Storage and release of organic carbon from glaciers and ice sheets. Nat Geosci 8:91–96

Hoppert M, Flies C, Pohl W, Günzl B, Schneider J (2004) Colonization strategies of lithobiontic microorganisms on carbonate rocks. Environ Geol 46:421–428

Judd KE, Byron CC, Kling GW (2006) Variation in dissolved organic matter controls bacterial production and community composition. Ecology 87:2068–2079

Jumpponen A (2003) Soil fungal community assembly in a primary successional glacier forefront ecosystem as inferred from rDNA sequence analyses. New Phytol 158:569–578

Jumpponen A, Trappe JM, Cázares E (2002) Occurrence of ectomycorrhizal fungi on the forefront of retreating Lyman Glacier (Washington, U.S.A.) in relation to time since deglaciation. Mycorrhiza 12:43–49

Jungblut AD, Lovejoy C, Vincent WF (2010) Global distribution of cyanobacterial ecotypes in the cold biosphere. ISME J 4:191–202

Kaczmarek L, Zawierucha K, Smykla J, Michalczyk L (2012) Tardigrada of the Revdalen (Spitsbergen) with the descriptions of two new species: *Bryodelphax parvuspolaris* (Heterotardigrada) and *Isohypsibius coulsoni* (Eutardigrada). Polar Biol 35:1013–1026

Kaštovská K, Elster J, Stibal M, Šantrůčková H (2005) Microbial assemblages in soil microbial succession after glacial retreat in Svalbard (High Arctic). Microb Ecol 50:396–407

Kaštovská K, Stibal M, Sabacka M, Cerna B, Santruckova H, Elster J (2007) Microbial community structure and ecology of subglacial sediments in two polythermal Svalbard glaciers characterized by epifluorescence microscopy and PLFA. Polar Biol 30:277–287

Kawahara H (2002) The structures and functions of ice crystal-controlling proteins from bacteria. J Biosci Bioeng 94:492–496

Kellogg CA, Griffin DW (2006) Aerobiology and the global transport of desert dust. Trends Ecol Evol 21:638–644

Kennedy IR, Pereggerk LL, Wood C, Deaker R, Glichrist K, Katupitiya S (1997) Biological nitrogen fixation in non-leguminous field crop: facilitating the evolution of an effective association between *Azospirillum* and wheat. Plant Soil 194:65–79

Kennedy IR, Choudhury ATMA, Kecskés ML (2004) Non-symbiontic bacterial diazotrophs in crop-farming systems: can their potential for plant growth promotion be better exploited? Soil Biol Biochem 36:1229–1244

Knelman JE, Legg TM, O'Neill SP, Washenberger CL, Gonzalez A, Cleveland CC, Nemergut DR (2012) Bacterial community structure and function change in association with colonizer plants during early primary succession in a glacier forefield. Soil Biol Biochem 46:172–180

Körner C (1999) Alpine plant life. Springer-Verlag, Berlin

Krembs C, Eicken H, Junge K, Deming JW (2002) High concentrations of exopolymeric substances in Arctic winter sea ice: Implications for the polar ocean carbon cycle and cryoprotection of diatoms. Deep Sea Res I 49:2163–2181

Kuske CR, Ticknor LO, Miller ME, Dunbar JM, Davis JA, Barns SM, Belnap J (2002) Comparison of soil bacterial communities in rhizospheres of three plant species and the interspaces in an arid grassland. Appl Environ Microbiol 68:1854–1863

Lapanje A, Wimmersberger C, Furrer G, Brunner I, Frey B (2012) Pattern of elemental release during the granite dissolution can be changed by aerobic heterotrophic bacterial strains isolated from Damma glacier (Central Alps) deglaciated granite sand. Microbial Ecol 6:865–882

Lazzaro A, Abegg C, Zeyer J (2009) Bacterial community structure in glacier forefields on calcareous and siliceous bedrock. Eur J Soil Sci 60:860–870

Lee YM, Kim SY, Jung J, Kim EH, Cho KH, Schinner F, Margesin R, Hong SG, Lee HK (2011) Cultured bacterial diversity and human impact on alpine glacier cryoconite. J Microbiol 49:355–362

Lipson DA (2007) Relationships between temperature responses and bacterial community structure along seasonal and altitudinal gradients. FEMS Microbiol Ecol 59:418–427

Llorens-Marès T, Auguet JC, Casamayor EO (2012) Winter to spring changes in the slush bacterial community composition of a high-mountain lake (Lake Redon, Pyrenees). Environ Microbiol Rep 4:50–56

Lutz S, Anesio AM, Jorge Villar SE, Benning LG (2014) Variations of algal communities cause darkening of a Greenland glacier. FEMS Microbiol Ecol 89:402–414

Lutz S, Anesio AM, Edwards A, Benning LG (2015) Microbial diversity on Icelandic glaciers and ice caps. Front Microbiol 6:307

Mancuso Nichols CA, Guezennec J, Bowman JP (2005) Bacterial exopolysaccharides from extreme marine environments with special consideration of the southern ocean, sea ice, and deep-sea hydrothermal vents: a review. Mar Biotechnol 7:253–271

Mapelli F, Marasco R, Rizzi A, Baldi F, Ventura S, Daffonchio D, Borin S (2011) Bacterial communities involved in soil formation and plant establishment triggered by pyrite bioweathering on arctic moraines. Microb Ecol 61:438–447

Margesin R, Miteva V (2011) Diversity and ecology of psychrophilic microorganisms. Res Microbiol 162:346–361

Marnocha CL, Dixon JC (2014) Bacterially facilitated rock-coating formation as a component of the geochemical budget in cold climates: An example from Kärkevagge, Swedish Lapland. Geomorphology 218:45–51

Mataloni G, Tell G, Wynn-Williams DD (2000) Structure and diversity of soil algal communities from Cierva Point (Antarctic Peninsula). Polar Biol 23:205–211

Matthews JA (1992) The ecology of recently-deglaciated terrain: a geoecological approach to glacier forelands and primary succession. Cambridge University Press, Cambridge

Mavris C, Egli M, Plotze M, Blum JD, Mirabella A, Giaccai D, Haeberli W (2010) Initial stages of weathering and soil formation in the Morteratsch proglacial area (Upper Engadine Switzerland). Geoderma 155:359–371

McFadden LD, Eppes MC, Gillespie AR, Hallet B (2005) Physical weathering in arid landscapes due to diurnal variation in the direction of solar heating. Geol Soc Am Bull 117:161–173

Meola M, Lazzaro A, Zeyer J (2014) Diversity, resistance and resilience of the bacterial communities at two alpine glacier forefields after a reciprocal soil transplantation. Environ Microbiol 16:1918–1934

Merbach W, Mirus E, Knof G, Remus R, Ruppel S, Russow R, Gransee A, Schulze J (1999) Release of carbon and nitrogen compounds by plant roots and their possible ecological importance. J Plant Nutr Soil Sci 162:373–383

Mevs U, Stackebrandt E, Schumann P, Gallikowski CA, Hirsch P (2000) *Modestobacter multiseptatus* gen nov sp nov a budding actinomycete from soils of the Asgard Range (Transantarctic Mountains). Int J Syst Evol Microbiol 50:337–346 Microbiol Ecol 67:219–228

Miniaci C, Bunge M, Duc L, Edwards I, Bürgmann H, Zeyer J (2007) Effects of pioneering plants on microbial structures and functions in a glacier forefield. Biol Fertil Soil 44:289–297

Miteva VI, Brenchely JE (2005) Detection and Isolation of ultrasmall microorganisms from a 120,000-year-old Greenland glacier ice core. Appl Environ Microbiol 71:7806–7818

Miteva VI, Sheridan PP, Brenchely JE (2004) Phylogenetic and physiological diversity of microorganisms isolated from a deep Greenland glacier ice core. Appl Environ Microbiol 70:202–213

Müller T, Leya T, Fuhr G (2001) Persistent snow algal fields in Spitsbergen: field observations and a hypothesis about the annual cell circulation. Arct Antarct Alp Res 123:42–51

Mummey DL, Rillig MC, Holben WE (2005) Neighboring plant influences on arbuscular mycorrhizal fungal community composition as assessed by T-RFLP analysis. Plant Soil 271:83–90

Nemergut DR, Anderson SP, Cleveland CC, Martin AP, Miller AE, Seimon A, Schmidt SK (2007) Microbial community succession in an unvegetated recently deglaciated soil. Microb Ecol 53:110–122

Nicol GW, Tscherko D, Embley TM, Prosser JI (2005) Primary succession of soil crenarchaeota across a receding glacier foreland. Environ Microbiol 7:337–347

Nicol GW, Tscherko D, Chang L, Hammesfahr U, Prosser JI (2006) Crenarchaeal community assembly and microdiversity in developing soils at two sites associated with deglaciation. Environ Microbiol 8:1382–1393

Odum EP (1963) Ecology. Holt Rinchart Winston Ed NY

Odum EP (1969) The strategy of ecosystem development. Science 164:262–270

Ohtonen R, Fritze H, Pennanen T, Jumpponen A, Trappe J (1999) Ecosystem properties and microbial community changes in primary succession on a glacier forefront. Oecologia 119:239–246

Okin GS, Mahowald N, Chadwick OA, Artaxo P (2004) Impact of desert dust on the biogeochemistry of phosphorus in terrestrial ecosystems. Global Biogeochem Cycles 18:GB2

Pallavi KP, Gupta PC (2013) A psychrotolerant strain *Kluyvera intermedia* solubilizes inorganic phosphate at different carbon and nitrogen source. Bioscan 8:1197–1201

Pandey A, Palni LMS, Mulkalwar P, Nadeem M (2002) Effect of temperature on solubilization of tricalcium phosphate by *Pseudomonas corrugata*. J Sci Ind Res 61:457–460

Pandey A, Trivedi P, Kumar B, Palni LMS (2006) Characteristics of a phosphate solubilizing and antagonistic strain of *Pseudomonas putida* (B0) isolated from a sub-alpine location in the Indian central Himalaya. Curr Microbiol 53:102–107

Philippot L, Raaijmakers JM, Lemanceau P, van der Putten WH (2013) Going back to the roots: the microbial ecology of the rhizosphere. Nature Microbiol Rev 11:789–799

Plassard C, Dell B (2010) Phosphorus nutrition of mycorrhizal trees. Tree Physiol 30:1129–1139

Poly F, Ranjard L, Nazaret S, Gourbière F, Jocteur Monrozier L (2001) Comparison of *nifH* gene pools in soils and soil microenvironments with contrasting properties. Appl Environ Microbiol 67:2255–2262

Potter RM, Rossman GR (1977) Desert varnish: the importance of clay minerals. Science 196:1446–1448

Price PB (2000) A habitat for psychrophiles in deep antarctic ice. Proc Nat Acad Sci 97:1247–1251

Price PB (2007) Microbial life in glacial ice and implications for a cold origin of life. FEMS Microbiol Ecol 59:217–231

Price MN, Dehal PS, Arkin AP (2010) FastTree 2—Approximately maximum-likelihood trees for large alignments. PLoS One 5:e9490

Priscu JC, Christner BC (2004) Earth's icy biosphere. In: Bull A (ed) Microbial diversity and prospecting. ASM Press, Washington, pp 130–145

Psenner R, Sattler B (1998) Life at the freezing point. Science 280:2073–2074

Puri S, Hohle TH, O'Brian MR (2010) Control of bacterial iron homeostasis by manganese. Proc Nat Acad Sci 107:10691–10695

Ragot S, Zeyer J, Zehnder L, Reusser E, Brandl H, Lazzaro A (2013) Bacterial community structures of an alpine apatite deposit. Geoderma 202–203:30–37

Remias D, Lütz-Meindl U, Lütz C (2005) Photosynthesis, pigments and ultrastructure of the alpine snow alga *Chlamydomonas nivalis*. Eur J Phycol 40:259–268

Remias D, Wastian H, Lütz C, Leya T (2013) Insights into the biology and phylogeny of *Chloromonas polyptera* (Chlorophyta), an alga causing orange snow in Maritime Antarctica. Antarct Sci 25:1–9

Rösch C, Bothe H (2005) Improved assessment of denitrifying N_2-fixing and total-community bacteria by terminal restriction fragment length polymorphism analysis using multiple restriction enzymes. Appl Environ Microbiol 71:2026–2035

Roy J, Albert CH, Ibanez S, Saccone S, Zinger L, Choler P, Clément JC, Lavergne S, Geremia RA (2013) Microbes on the cliff: alpine cushion plants structure bacterial and fungal communities. Front Microbiol 4:64

Russell NJ, Harrisson P, Johnston IA, Jaenicke R, Zuber M, Franks F, Wynn-Williams D (1990) Cold adaptation of microorganisms. Philos Trans R Soc London B 326:595–611

Sattler B, Puxbaum H, Psenner R (2001) Bacterial growth in supercooled cloud droplets. Geophys Res Lett 28:239–242

Sawstrom C, Mumford P, Marshall W, Hodson A, Laybourn-Parry J (2002) The microbial communities and primary productivity of cryoconite holes in an Arctic glacier (Svalbard 79 degrees N). Polar Biol 8:591–596

Schipper LA, Degens BP, Sparling GP, Duncan LC (2001) Changes in microbial heterotrophic diversity along five plant successional sequences. Soil Biol Biochem 33:2093–2103

Schmidt SK, Lipson DA (2004) Microbial growth under the snow: Implications for nutrient and allelochemical availability in temperate soils. Plant Soil 259:1–7

Schmidt SK, Reed SC, Nemergut DR, Grandy AS, Cleveland CC, Weintraub MN, Hill AW, Costello EK, Meyer AF, Neff JC, Martin AM (2008) The earliest stages of ecosystem succession in high-elevation (5000 meters above sea level) recently deglaciated soils. Proc R Soc B 275:2793–2802

Schmidt SK, Lynch RC, King AJ, Karki D, Robeson MS, Nagy L, Williams MW, Mitter MS, Freeman KR (2011) Phylogeography of microbial phototrophs in the dry valleys of the high Himalayas and Antarctica. Proc R Soc B 278:702–708

Schmidt SK, Naff CS, Lynch RC (2012) Fungal communities at the edge: ecological lesson from high alpine fungi. Fungal Ecol 5:443–452

Schütte UM, Abdo Z, Bent SJ, Williams CJ, Schneider GM, Solheim B, Forney LJ (2009) Bacterial succession in a glacier foreland of the High Arctic. ISME J 2:1258–1268

Segawa T, Miyamoto K, Ushida K, Agata K, Okada N, Kohshima S (2005) Seasonal change in bacterial flora and biomass in mountain snow from the Tateyama Mountains Japan analyzed by 16S rRNA gene sequencing and Real-Time PCR. Appl Environ Microbiol 71:123–130

Segawa T, Takeuchi N, Rivera A, Yamada A, Yoshimura Y, Barcaza G, Shinbori K, Motoyama H, Kohshima S, Ushida K (2013)

Distribution of antibiotic resistance genes in glacier environments. Environ Microbiol Rep 5:127–134

Selbmann L, Zucconi L, Onofri S, Cecchini C, Isola D, Turchetti B, Buzzini P (2014) Taxonomic and phenotypic characterization of yeasts isolated from worldwide cold rock-associated habitats. Fungal Ecol 118:61–71

Selvakumar G, Kundu S, Joshi P, Sehar N, Gupta AD, Mishra PK, Gupta HS (2008a) Characterization of a cold tolerant plant growth promoting bacterium Pantoea dispersa 1A, isolated from a sub alpine soil in the North Western Indian Himalaya. World J Microb Biot 24:955–960

Selvakumar G, Mohan M, Kundu S, Gupta AD, Joshi P, Sehar N, Gupta HS (2008b) Cold tolerance and plant growth promotion potential of Serratia marcescens strain SRM (MTCC 8708) isolated from flowers of summer squash (Cucurbita pepo). Lett Appl Microbiol 46:171–175

Selvakumar G, Joshi P, Sehar N, Mishra PK, Bisht JK, Gupta HS (2009a) Phosphate solubilization and growth promotion by Pseudomonas fragi CS11RH1 (MTCC 8984) a psychrotolerant bacterium isolated from a high altitude Himalayan rhizosphere. Biologia 64:239–245

Selvakumar G, Joshi P, Sehar N, Mishra PK, Kundu S, Gupta HS (2009b) Exiguobacterium acetylicum strain 1P (MTCC 8707) a novel bacterial antagonist from the North Western Indian Himalayas. World J Microb Biot 25:131–136

Sharp M, Parkes J, Cragg B, Fairchild IJ, Lamb H, Tranter M (1999) Widespread bacterial populations at glacier beds and their relationship to rock weathering and carbon cycling. Geology 27:107–110

Sheridan PP, Miteva VI, Brenchley JE (2003) Phylogenetic analysis of anaerobic psychrophilic enrichment cultures obtained from a Greenland glacier ice core. Appl Environ Microbiol 69:2153–2160

Shivaji S, Prakash JSS (2010) How do bacteria sense and respond to low temperature? Arch Microbiol 192:85–95

Sigler WV, Zeyer J (2002) Microbial diversity and activity along the forefields of two receding glaciers. Microb Ecol 45:397–407

Sigler WV, Zeyer J (2004) Colony-forming analysis of bacterial community succession in deglaciated soils indicates pioneer stress-tolerant opportunists. Microb Ecol 48:316–323

Sigler WV, Crivii S, Zeyer J (2002) Bacterial succession in glacial forefield soils characterized by community structure activity and opportunistic growth dynamics. Microb Ecol 44:306–316

Simonet P, Navarro E, Rouvier C, Reddell P, Zimpfer J, Dommergues Y, Bardin R, Combarro P, Hamelin J, Domenach AM, Gourbiére F, Prin Y, Dawson JO, Normand P (1999) Co-evolution between Frankia populations and host plants in the family Casuarinaceae and consequent patterns of global dispersal. Environ Microbiol 1:525–533

Singer GA, Fasching C, Wilhelm L, Niggeman J, Steier P, Dittmar T, Battin TJ (2012) Biogeochemically diverse organic matter in Alpine glaciers and its downstream fate. Nat Geosci 5:710–714

Singh BK, Millard P, Whiteley AS, Murrell JC (2004) Unravelling rhizosphere-microbial interactions: opportunities and limitations. Trends Microbiol 12:386–393

Solheim B, Wiggen H, Røberg S, Spaink HP (2004) Associations between arctic cyanobacteria and mosses. Symbiosis 37:169–187

Sterflinger K, Tesei D, Zakharova K (2012) Fungi in hot and cold deserts with particular reference to microcolonial fungi. Fungal Ecol 5:453–462

Stibal M, Tranter M, Benning LG, Rehak J (2008a) Microbial primary production on an Arctic glacier is insignificant in comparison with allochthonous organic carbon input. Environ Microbiol 8:2172–2178

Stibal M, Tranter M, Telling J, Benning LG (2008b) Speciation phase association and potential bioavailability of phosphorus on a Svalbard glacier. Biogeochemistry 90:1–13

Strauss SL, Garcia-Pichel F, Day TA (2012) Microbial colonization of a recently exposed glacial foreland on Anvers Island, Antarctic Peninsula. Polar Biol 35:1459–1471

Styriakova I, Mockovciakova A, Styriak I, Kraus I, Uhlik P, Madejova J, Orolinova Z (2012) Bioleaching of clays and iron oxide coatings from quartz sands. Appl Clay Sci 61:1–7

Takeuchi N (2013) Seasonal and altitudinal variations in snow algal communities on an Alaskan glacier (Gulkana glacier in the Alaska range). Environ Res Lett 8:035002

Thevenon F, Anselmetti FS, Bernasconi SM, Schwikowski M (2009) Mineral dust and elemental black carbon records from an Alpine ice core (Colle Gnifetti glacier) over the last millennium. J Geophys Res 114:D17102

Thomas WH, Duval B (1995) Sierra Nevada, California, USA, snow algae: snow albedo changes, algal-bacterial interrelationships, and ultraviolet radiation effects. Arctic Alp Res 27:389–399

Tieber A, Lettner H, Bossew P, Hubmer A, Sattler B, Hofmann W (2009) Accumulation of anthropogenic radionuclides in cryoconites on Alpine glaciers. J Environ Radioact 100:590–598

Töwe S, Albert A, Kleineidam K, Brankatschk R, Dümig A, Welzl G, Munch JC, Zeyer J, Schloter M (2010) Abundance of microbes involved in nitrogen transformation in the rhizosphere of Leucanthemopsis alpina (L.) Heywood grown in soils from different sites of the Damma Glacier forefield. Microb Ecol 60:762–770

Tscherko D, Rustemeier J, Richter A, Wanek W, Kandeler E (2003) Functional diversity of the soil microflora in primary succession across two glacier forelands in the Central Alps. Eur J Soil Sci 54:685–696

Tscherko D, Hammesfahr U, Marx MC, Kandeler E (2004) Shifts in rhizosphere microbial communities and enzyme activity of Poa alpina across an alpine chronosequence. Soil Biol Biochem 36:1685–1698

Turchetti B, Goretti M, Branda E, Diolaiuti G, D'Agata C, Smiraglia C, Onofri A, Buzzini P (2013) Influence of abiotic variables on culturable yeast diversity in two distinct Alpine glaciers. FEMS Microbiol Ecol 86:327–340

Varin T, Lovejoy C, Jungblut AD, Vincent WF, Corbeila J (2010) Metagenomic profiling of Arctic microbial mat communities as nutrient scavenging and recycling systems. Limnol Oceanogr 55:1901–1911

Vitousek PM, Cassman K, Cleveland C, Crews T, Field CB, Grimm NB, Howarth RW, Marino R, Martinelli L, Rastetter EB, Sprent JI (2002) Towards an ecological understanding of biological nitrogen fixation. Biogeochemistry 57–58:1–45

Walker LR, Wardle DA, Bardgett RD, Clarkson BD (2010) The use of chronosequences in studies of ecological succession and soil development. J Ecol 98:725–736

Wang JT, Cao P, Hu HW, Li J, Han LL, Zhang LM, Zheng YM, He JZ (2015) Altitudinal distribution patterns of soil bacterial and archaeal communities along Mt. Shegyla on the Tibetan Plateau. Microb Ecol 69:135–145

Welch SA, Ullman WJ (1999) The effect of microbial glucose metabolism on bytownite feldspar dissolution rates between 5 degrees and 35 degrees C. Geochim Cosmochim Acta 63:19–20

Welch SA, Barker WW, Banfield JF (1999) Microbial extracellular polysaccharides and plagioclase dissolution. Geochim Cosmochim Acta 63:1405–1419

Widmer F, Shaffer BT, Porteous LA, Seidler RJ (1999) Analysis of nifH gene pool complexity in soil and litter at a Douglas fir forest site in the Oregon Cascade Mountain Range. Appl Environ Microbiol 65:374–380

Wilhelm L, Singer GA, Fasching C, Battin TJ, Besemer K (2013) Microbial biodiversity in glacier-fed streams. ISME J 7:1651–1660

Wong FKY, Lacap DC, Lau MCY, Aitchison JC, Cowan DA, Pointing SB (2010) Hypolithic microbial community of quartz pavement in the high-altitude tundra of central Tibet. Microb Ecol 60:730–739

Yergeau E, Bokhorst S, Huiskes AHL, Boschker HTS, Aerts R, Kowalchuk GA (2007a) Size and structure of bacterial fungal and nematode communities along an Antarctic environmental gradient. FEMS Microbiol Ecol 59:436–451

Yergeau E, Newsham KK, Pearce DA, Kowalchuk GA (2007b) Patterns of bacterial diversity across a range of Antarctic terrestrial habitats. Environ Microbiol 9:2670–2682

Yoshimura Y, Kohshima S, Takeuchi N, Seko K, Fujita K (2006) Snow algae in a Himalayan ice core: new environmental markers for ice-core analyses and their correlation with summer mass balance. Ann Glaciol 43:148–153

Zhang XF, Zhao L, Xu SJ Jr, Liu YZ, Liu HY, Cheng GD (2012) Soil moisture effect on bacterial and fungal community in Beilu River (Tibetan Plateau) permafrost soils with different vegetation types. J Appl Microbiol 114:1054–1065

Zielke M, Ekker AS, Olsen RA, Spjelkavik S, Solheim B (2002) The influence of abiotic factors on biological nitrogen fixation in different types of vegetation in the high Artic, Svalbard. Arct Antarc Alp Res 34:293–299

Zumsteg A, Luster J, Göransson H, Smittenberg R, Brunner I, Bernasconi S, Zeyer J, Frey B (2012) Bacterial, archaeal and fungal succession in the forefield of a receding glacier. Microb Ecol 63:552–564

Zumsteg A, Schmutz S, Frey B (2013) Identification of biomass utilizing bacteria in a carbon-depleted glacier forefield soil by the use of ^{13}C DNA stable isotope probing. Environ Microbiol Rep 5:424–437