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Minireview

MINIREVIEW

Alpine soil microbial ecology in a changing world

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One sentence summary: We review important contemporary studies related to high-alpine microbial ecology associated with the impact of climate change.

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ABSTRACT

Climate change has a disproportionally large impact on alpine soil ecosystems, leading to pronounced changes in soil microbial diversity and function associated with effects on biogeochemical processes at the local and supraregional scales. However, due to restricted accessibility, high-altitude soils remain largely understudied and a considerable heterogeneity hampers the comparability of different alpine studies. Here, we highlight differences and similarities between alpine and arctic ecosystems, and we discuss the impact of climatic variables and associated vegetation and soil properties on microbial ecology. We consider how microbial alpha-diversity, community structures and function change along altitudinal gradients and with other topographic features such as slope aspect. In addition, we focus on alpine permafrost soils, harboring a surprisingly large unknown microbial diversity and on microbial succession along glacier forefield chronosequences constituting the most thoroughly studied alpine habitat. Finally, highlighting experimental approaches, we present climate change studies showing shifts in microbial community structures and function in response to warming and altered moisture, interestingly with some contradiction. Collectively, despite harsh environmental conditions, many specially adapted microorganisms are able to thrive in alpine environments. Their community structures strongly correlate with climatic, vegetation and soil properties and thus closely mirror the complexity and small-scale heterogeneity of alpine soils.

Keywords: climate change; soil microbiome; warming; mountains

INTRODUCTION

Mountains cover 25% of the world's land surface and are distributed across all latitudes and longitudes (Barry 2008a). They are an important water source, providing 60%–80% of the world's fresh water supply. Mountainous regions are also of significant economic interest, harboring major forest reserves and mineral resources and enabling the production of hydropower (Huss 2011). Moreover, because they are largely protected from human influences, owing to restricted accessibility, and encompass a wide range of climatic gradients within a small area, mountain areas are hotspots of biodiversity (Körner 2003; Pauli *et al.* 2015). Alpine ecosystems are largely characterized by low temperatures and comprise various habitats including soils, bare rocks, permafrost, glaciers and snow. In mountain environments, microbes play a crucial role in soil development and all major elemental cycles affecting plant establishment, growth and survival at the local scale, as well as the greenhouse gas balance at the global scale. Microbial activity and diversity strongly depend on temperature and other climatic variables, which are projected to be significantly altered by the end of this century as part of ongoing global change (Bardgett *et al.* 2008; Classen *et al* 2015). However, owing to difficulties with access and transport logistics, high mountains remain largely understudied with regard to microbial ecology. In this review, we focus on the alpine and nival vegetation zones, defined as terrain above the treeline, and hereafter refer to these two zones collectively as 'alpine'. Taking into account similarities and differences between alpine

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and arctic ecosystems, we discuss (i) geographical and pedological features shaping mountainous soil ecosystems as microbial habitats in the context of climate change, (ii) current literature on alpine microbial ecology and (iii) climate change studies on the alpine soil microbiome, highlighting current experimental approaches.

CLIMATE CHANGE IN THE ALPINE ENVIRONMENT

Geographical controls on mountain climate

In order to study the impact of climate change on the soil microbiome in mountain regions and to compare findings with arctic environments and between different mountain areas, it is crucial to understand the main drivers of mountain climate. Mountain regions are distributed all over the world and harbor a complex topography, leading to considerable heterogeneity of mountain climate, both across regions and locally within a region (Gruber and Haeberli 2009). An overview of geographical controls on mountain climate is given in Fig. 1. One important factor influencing mountain climate is latitude, with lower temperatures and less solar radiation at high latitudes than at lower latitudes, as well as varying seasonal and diurnal patterns of incoming solar radiation across different latitudes (Barry 2008b; Margesin 2012). These latitudinal effects account for the main climatic differences between high latitude arctic habitats and cold high altitude mountain habitats located in temperate or equatorial regions. However, there is an overlap between arctic and alpine ecosystems, and as mountains exist across all latitudes they should be contemplated along latitudinal gradients rather than in discrete zones. Another geographical control on mountain climate is related to altitude. Air temperature decreases with altitude by 6°C per 1000 m on average (Barry 2008b), whereas UV-radiation radiation increases by roughly 10% per 1000 m (Calbo *et al.* 2005; Schulz *et al.* 2013). Due to this altitude-dependent temperature decrease, alpine regions, similar to arctic regions, are largely comprised of low-temperature dominated ecosystems. In alpine regions, however, sharp altitudinal gradients lead to the presence of a large range of climatic conditions on a small spatial scale (Haeberli and Gruber 2009). Thus, a 1000 m increase in altitude occurring over a horizontal distance of few kilometers roughly corresponds to the same temperature change as a 1000 km increase in latitude (Diaz, Grosjean and Graumlich 2003; Nagy and Grabherr 2014). In addition, soil temperature is strongly influenced by the presence of snow cover, which insulates the ground from fluctuations in air temperature (Geiger, Aron and Todhunter 2003; Phillips and Schweizer 2007). Precipitation also increases with altitude, although this trend may be reversed above the cloud zone and may be controlled by other more complex relationships in the tropics (Barry 2008b; Nagy and Grabherr 2014). Local mountain climate is also strongly influenced by topographic effects related to slope aspect and angle and depressions versus ridges, which affect incoming solar radiation, air flow, heat transfer, precipitation and hydrological processes (Geiger, Aron and Todhunter 2003; Barry 2008b). Owing to orographic enhancement, the windward side of mountain regions receives more precipitation than lowlands, whereas a rain shadow effect leads to reduced precipitation on the leeward side, for example on the Tibetan Plateau (Browning and Hill 1981). A large amount of precipitation is another main climatic feature of many mountain regions that is in contrast to the Arctic, which typically receives less than 500 mm per year (Serreze and Barry 2005).

Projected change in alpine climate

With climate change, global temperatures have risen by 0.85°C during the period from 1880 to 2012 (Hartmann *et al.* 2013). By 2100, another increase by 1°C–3.7°C is expected on average, with stronger warming over land than over ocean (Collins *et al.* 2013). In the Arctic, warming is projected to amount to 2.2–2.4 times the global average (Collins *et al.* 2013). Similarly, an increased sensitivity of mountain regions to climate change has been proposed (Diaz, Grosjean and Graumlich 2003; Schröter *et al.* 2005), with some studies reporting stronger warming at high than at low altitudes, although the reverse relationship or no difference has been reported elsewhere (Rangwala and Miller 2012). Precipitation is projected to increase with warming on a global average, but with large spatial variation reinforcing contrasts between humid and arid regions (Collins *et al.* 2013). In the Arctic, precipitation is expected to increase significantly (IPCC 2013), whereas no consistent patterns of precipitation change are expected to occur in mountain regions. However, both in the Arctic and in high altitude regions, snowfall is expected to decline with warming and be replaced by rain, implicating significant impacts on soil temperature due to modification of thermal insulation by snow (Phillips and Schweizer 2007). All these climatic alterations will have profound effects on the biotic components of alpine ecosystems. Microbial activity and diversity have been shown to depend on both temperature and moisture (Bardgett *et al.* 2008; Zumsteg *et al.* 2013; Classen *et al.* 2015). Thus, by affecting the structure and functioning of soil microbial communities, climate change will lead to changes in all major element cycles, implicating changes in soil nutritional status and productivity, plant survival and biotic interactions.

ALPINE SOILS, MICROBIAL LIFE AND IMPLICATIONS FOR C- AND N-CYCLING

Soil formation in alpine environments

As in lowland ecosystems, the main drivers of soil development in alpine environments are climate, biological factors, parent material, topography and time. Similar to in arctic environments, soil development in mountain regions is largely restricted by harsh climatic conditions (Townsend, Vitousek and Trumbore 1995; King *et al.* 2011). Climatic variables such as temperature and moisture affect weathering type and rate. While in cold and arid areas physical fracturing of rocks is dominant, a warmer and moister climate is more favorable for chemical and biological processes (Thorn *et al.* 2001, 2011). Mountain regions harbor a complex topography, which influences soil formation processes. On the one hand, microclimatic conditions related to topography strongly affect biological activity as well as physical and chemical processes (Bridges and Van Baren 1997). On the other hand, slope angle and length have a critical control on soil development: most mountain soils develop from material transported along slopes rather than directly from the bedrock underneath. Thus, soils on steep slopes are prone to erosion, while soils on gentle slopes rather experience deposition from steeper areas. Soil stability largely depends on comprehensive vegetation cover forming a tight root network (Körner 2003).

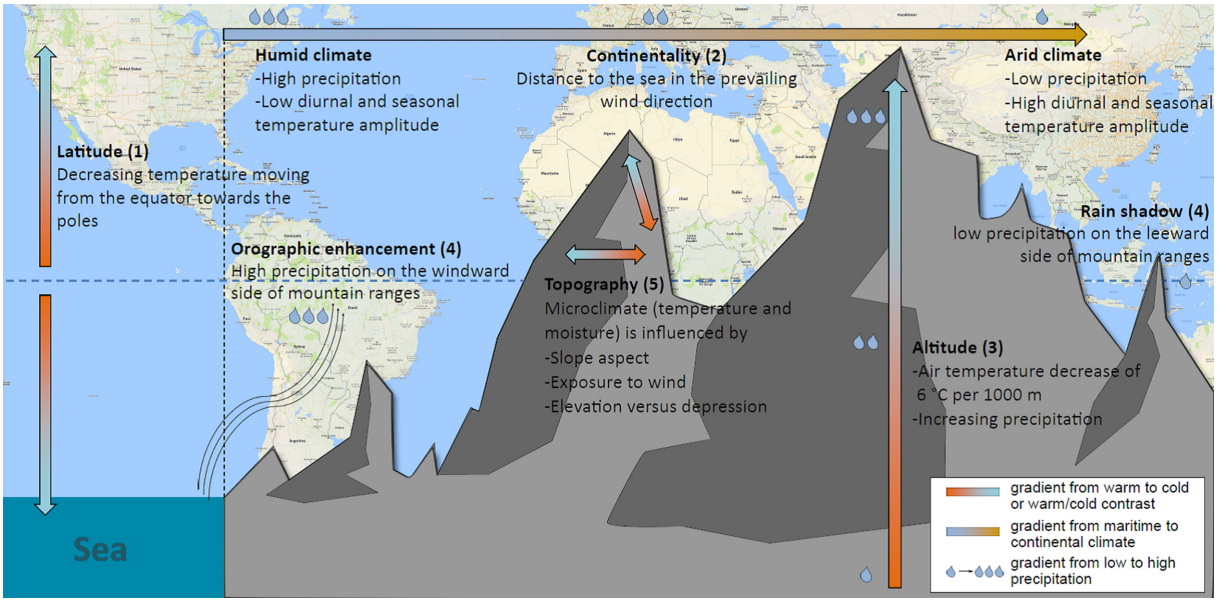


Figure 1. Geographical controls on mountain climate. Mountain climate is controlled by a complex combination of global geographical drivers such as latitude (1) and continentality (2) as well as mountain-specific topographic effects. The latter include altitude (3), orographic enhancement versus rain shadow (4) as well as microclimatic effects (5) associated with for example 'slope aspect and angle', 'exposure to wind' and 'elevation versus depression'. Climate is an important driver of soil formation processes and strongly influences the ecology of plants and microorganisms. Thus, the heterogeneity of mountain climate is closely mirrored in vegetation patterns, soil properties and microbial community structures. Map from maps.google.com

Due to unfavorable climatic conditions, relatively young geological age and interruption of soil-forming processes by erosion, most mountain soils are developed incompletely. The formation of well-defined soil horizons is the consequence of stable conditions over a long period, which rarely occurs in mountains. Thus, mountain soils typically are shallow, rocky, infertile and immature with poorly developed horizons (Price and Harden 2013). Mountain soils, as opposed to lowland soils, feature a very high local-scale heterogeneity that closely reflects the complex topography associated with different microclimatic regimes present in these environments (Whittaker *et al.* 1968; Messerli 1973). Major soil types occurring in the alpine and nival zones of mid-latitude mountains include Entisols, Inceptisols, Mollisols, Histosols and permafrost affected soils (Price and Harden 2013).

A considerable part of high-alpine soils is affected by permafrost (ground that remains frozen for at least two consecutive years). Alpine permafrost covers an area of 3.3 million km^2 and high latitude permafrost covers 23 million km^2, corresponding to 2.3% and 15% of the earth's land surface, respectively (Bockheim and Munroe 2014). Compared with arctic permafrost soils, alpine permafrost soils have a deeper active layer (mostly >2 m), higher mean annual soil temperatures (>−2°C) (Christiansen *et al.* 2010; Zhao *et al.* 2010; Vaughan *et al.* 2013) and a much lower density of soil organic carbon (SOC) (Hugelius *et al.* 2014), as well as a smaller water content, which significantly influences soil temperature (Bockheim and Munroe 2014; Bockheim 2015). However, 30% of mountain permafrost soils can be classified as cryosols, defined by an active layer <1 m and occurring mostly at latitudes >55°N or 55°S or at high altitudes (e.g. 5100 m on the Tibetan Plateau and 4900 m in the central Andes). A detailed comparison of alpine and arctic permafrost soils is depicted in Fig. 2.

Alpine glaciers are disintegrating rapidly in response to climate change, exposing large expanses of barren bedrock (Vaughan *et al.* 2013). Chronosequences along successively exposed glacier forefields have been widely used as a model for soil formation, as the different stages of soil development are present simultaneously within a relatively short spatial gradient (Walker *et al.* 2010; Schulz *et al.* 2013; Bradley, Singarayer and Anesio 2014). Glacier forefields thus represent the best studied alpine habitat with regard to microbial ecology. Recently deglaciated soils are poor in organic C (less than 10 mg g^{-1} (Bradley, Singarayer and Anesio 2014) and nutrients and are completely plant free. Thus, C- and nutrient cycling solely depend on microorganisms that acquire C and N from ancient organic matter (OM), deposition and fixation (Bardgett *et al.* 2007). Microbial activity eventually forms soil that is sufficiently fertile for plant colonization, which increases along the chronosequence. Plant establishment shapes further ecosystem development by interacting with the soil microbiome and allocating OM in the form of litter and root exudates (Schulz *et al.* 2013). The speed of soil development, and thus primary succession, in glacier forefields varies strongly across different latitudes, altitudes and climate systems. For example, in Patagonia a glacier forefield was forested after less than fifty years (Fernández-Martínez *et al.* 2016), while high-latitude and high-altitude glacier forefields may still be completely devoid of plants after more than 100 years (Kazemi, Hatam and Lanoil 2016). An overview of microbial succession and soil formation in glacier forefields is given in Fig. 3.

Microbial life in alpine environments

Similar to in arctic regions, low temperatures that frequently drop below 0°C and snow cover for most of the season crucially limit biological, chemical and physical processes and thus microbial life in mountain soils (Zumsteg *et al.* 2013). For a long time, microbes were thought to be inactive at subzero temperatures. However, microbial activity has been shown to occur at temperatures as low as −39°C (Panikov *et al.* 2006), and several mechanisms of adaptation to low temperatures

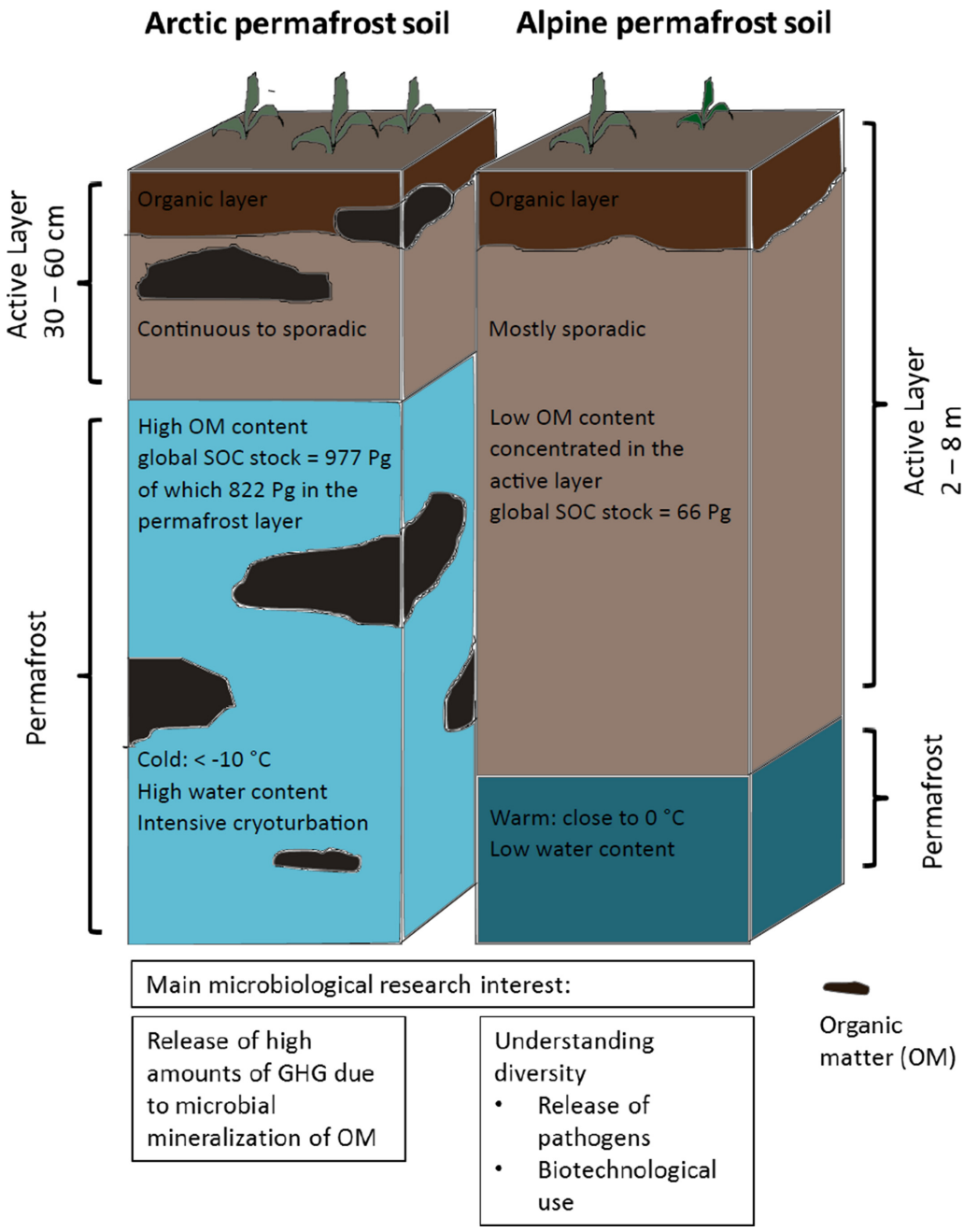


Figure 2. Comparison of arctic and alpine permafrost soils. Owing to differences in prevalent climatic regimes and topographic effects influencing heat flow and water run-off, arctic and alpine permafrost soils have pronounced differences in their properties. Compared with alpine permafrost soils, arctic permafrost soils have a shallower active layer, lower temperatures and higher water content. They are therefore subjected to intensive cryoturbation, leading to the accumulation of large amounts of OM deep in the permafrost layer. Alpine permafrost soils, on the other hand, are mostly well drained and less cryoturbated and therefore feature much smaller amounts of OM. Despite subzero temperature conditions, both arctic and alpine permafrost soils harbor a considerable microbial diversity. The fundamentally different soil properties in arctic and alpine permafrost are associated with different research interests with regard to microbial ecology: for arctic permafrost soil, a major focus lies on the microbial degradation of OM, which becomes increasingly bioavailable with permafrost thaw and might lead to high emissions of greenhouse gases. For alpine permafrost soil, the potential release of pathogens from thawing permafrost, as well as the exploitation of a large unknown, cold-adapted microbial diversity for biotechnological purposes, are paramount. Abbreviations: GHG = Greenhouse gas, SOC = soil organic carbon

have been identified (De Maayer *et al.* 2014; Nikrad, Kerkhof and Häggblom 2016). These mechanisms encompass a variety of specially adapted cellular components ensuring that cellular membranes remain fluid, that enzymes function with low thermal energy available and that damage to the cell by ice nuclei is prevented (Bakermans 2008; Jansson and Tas 2014). Liquid water is essential as a solvent for enzymes and membranes as well as for enabling substrate diffusion (Bakermans 2008), and thus microbial activity in frozen systems such as permafrost or glacier ice is limited to small unfrozen amounts of water often containing high concentrations of salts, exopolymeric substances and/or particulate matter (D'Amico *et al.* 2006).

As plant life is increasingly restricted by climatic conditions at higher altitudes, organic matter decreases strongly with

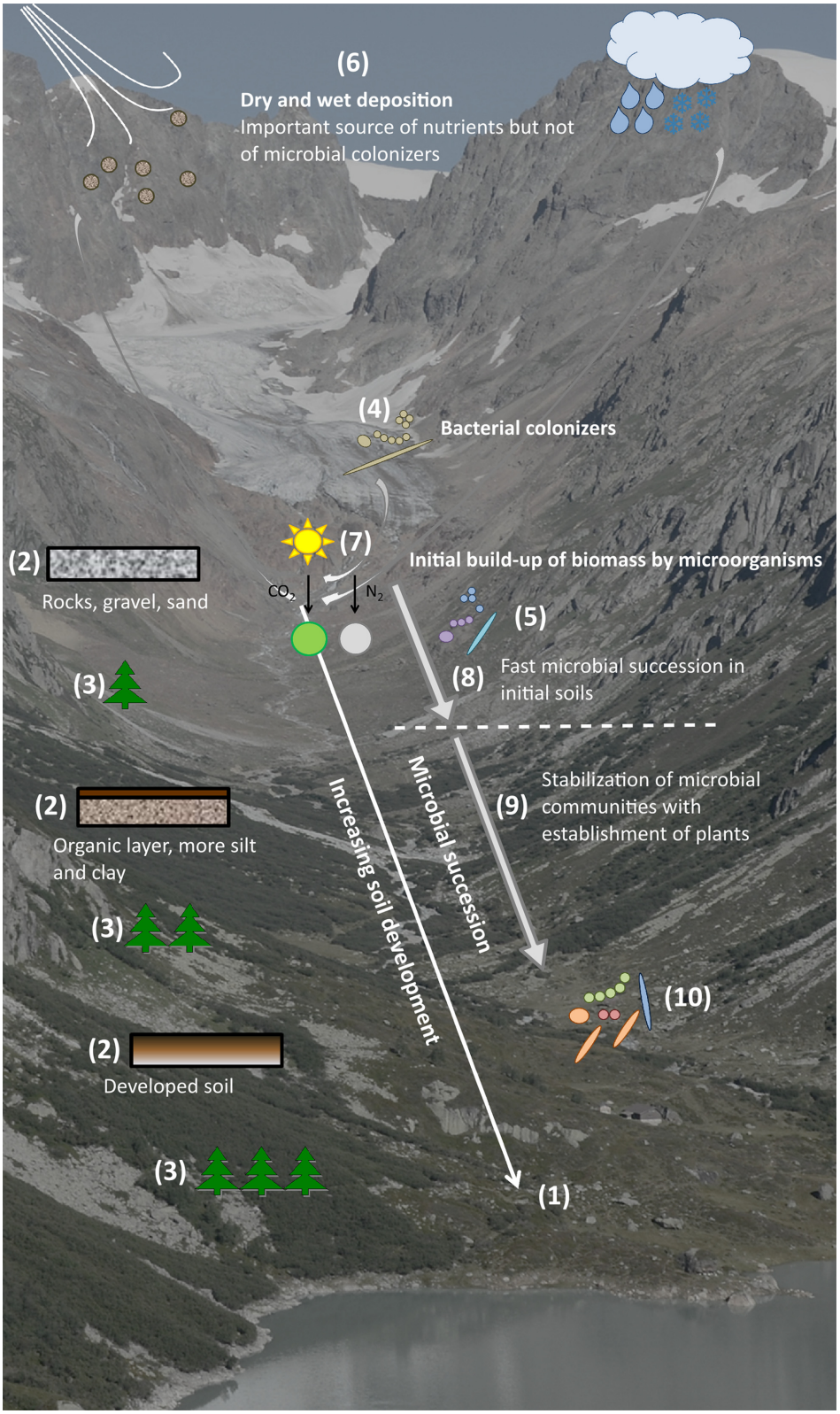


Figure 3. Microbial succession and soil formation in glacier forefields. As glaciers increasingly retreat with climate change, barren bedrock is exposed and colonized by pioneer microorganisms. This process gives rise to soil formation in a successional manner (1), with an increase in organic matter (OM), fine soil fractions (2) and vegetation cover (3). Bacterial colonizers arise mainly from endogenous glacial sources (4) whereas for fungi, the assemblage of which is driven more by environmental filtering, an unambiguous provenance has not been identified. Microbial colonizers (5), such as metabolically versatile bacteria and psychrophilic yeasts, contribute to the initial build-up of biomass, using C and N from ancient OM, deposition (6) and by fixation (7). Further nutrients may be obtained from weathering. In the initial stages, microbial communities undergo a fast succession (8) that is stabilized in later stages with the establishment of plants (9) and is shaped by interactions within the rhizosphere of plants. In these stages microbial communities are characterized by bacteria and fungi able to degrade complex, plant-derived organic compounds (10). Photo credit: Beat Stierli, WSL

increasing altitude (Egli *et al.* 2004, 2009). Thus, high-alpine soil microorganisms have to cope with oligotrophic, severely nutrient-limited conditions. Moreover, coarse-textured, shallow soils with a low water retention capacity and limited plant cover provide little protection against environmental stressors, such as high UV-radiation and fluctuations in temperature and moisture, that might influence microbial community structures (Ciccazzo *et al.* 2014; Rime *et al.* 2015). Despite these hostile environmental conditions, many specially adapted microorganisms are able to thrive in mountain environments (Margesin 2012; Rime *et al.* 2015, Rime, Hartmann and Frey 2016a). As a mechanism of protection against the above-named environmental stressors and in order to enable biological weathering and nutrient acquisition, microbes in alpine environments with limited vegetation are frequently aggregated in biofilms, leading to the formation of biological soil crusts (Schulz *et al.* 2013).

The significance of microbial life for C- and N-cycling in alpine environments

Soil microorganisms contribute critically to biogeochemical cycles, both at the regional and at the supraregional scale (Schimel and Schaeffer 2012; Rousk and Bengtson 2014). Recently, mountain regions have received increasing attention with regard to their contribution to terrestrial C-storage (Hagedorn *et al.* 2010a; Chang *et al.* 2014; Liu *et al.* 2016). As key players in all major element cycles, microbes are indispensable in the equation of global C-budgets. With enhanced rates of warming in mountain regions compared with the global average, similar to in the Arctic, biogeochemical cycles might be more critically altered in mountain regions compared with in lowland areas (Theurillat and Guisan 2001; McGuire *et al.* 2009). As a direct response to elevated temperature, all biogeochemical reactions can be expected to be accelerated leading to an increase in both ecosystem input and output (e.g. photosynthesis and respiration). However, besides temperature, microbial reactions depend on a plethora of environmental factors such as other climatic variables (e.g. moisture), substrate availability, nutrient availability, biotic interactions and soil physicochemical properties. All these factors are expected to covary with temperature or to be indirectly modulated by temperature effects. Thus, net C- and N-budgets depend on complex interactions and feedbacks between biological, physical and chemical factors (Davidson and Janssens 2006). In a comprehensive global study on warming experiments, Crowther *et al.* (2016) found a strong dependence of the warming response of SOC stocks on the initial SOC concentration irrespective of climate and soil properties. Based on the results from this study, nival zone soils containing very low C-stocks (Ohtsuka *et al.* 2008) can be expected to become C-sinks with warming. This hypothesis is further supported by space for time substitution studies where increased primary production outweighs increases of respiration and increased losses by leaching (e.g. Guelland *et al.* 2013). Conversely, in alpine grassland soils, SOC density mostly lies in the range projected to become a C-source (Ohtsuka *et al.* 2008; Yang *et al.* 2016a; Chen *et al.* 2017). Nonetheless, Chen *et al.* (2017) reported an increase in SOC in alpine grassland on the Tibetan plateau with global warming between 2002 and 2011. For N-cycling, in a global meta-study, Bai et al. (2013) reported increased net N-mineralization and nitrification with a concurrent increase of soil inorganic and plant N-pools in response to warming. These warming impacts varied strongly across different ecosystems but are generally in accordance with a study in an alpine treeline ecosystem reporting increased N-mineralization and an increase of plant available N upon warming (Dawes *et al.* 2017). Similar to C-cycling, for extremely oligotrophic alpine environments, chronosequence studies suggest that total soil N will increase with warming owing to increased primary production in the long term. However, precise, reliable predictions about the amount and the temporal progression of C- and N-cycling changes in response to warming can be only made understanding the complex biotic and abiotic interactions concurring with direct warming effects of which microbial ecology is an indispensable component. An overview of C- and N-cycling in alpine environments in response to global warming is given in Fig. 4.

STRUCTURAL AND FUNCTIONAL DIVERSITY OF THE ALPINE SOIL MICROBIOME

Microbial diversity and function along altitudinal gradients

Despite harsh environmental conditions, similar to arctic soils, mountain soils harbor a considerable microbial diversity (Rime *et al.* 2015; Frey *et al.* 2016). While plant and animal diversity decreases with increasing altitude, owing to the extreme climatic conditions at higher altitudes, microbes seem to be more versatile and adapted to growing in these inhospitable, cold habitats and thus follow different distribution patterns than plants and animals along altitudinal transects (Bryant *et al.* 2008; Fierer *et al.* 2011; Shen *et al.* 2014). In the Arctic, mainly latitudinal gradients have been used to study the effect of the prevalent climate on soil microbial alpha-diversity, community structures and function (Sjögersten *et al.* 2003; Yergeau *et al.* 2007). Conversely, in the alpine and nival zone of mountain environments, most studies have been conducted along altitudinal transects in order to elucidate the patterns of species distributions and functional diversity in relation to altitude-dependent climatic variation, which crucially shapes alpine ecosystems. An overview of studies on microbial ecology in alpine ecosystems is given in Table 1a, and Fig. 5 shows a summary of main findings along climatic gradients in alpine environments. Some of these studies involved investigations of bacterial (Lipson 2007; Shen *et al.* 2013; Yuan *et al.* 2014; Lazzaro, Hilfiker and Zeyer 2015; Shen *et al.* 2015; Wang *et al.* 2015), archaeal (Singh, Takahashi and Adams 2012; Wang *et al.* 2015) or fungal (Lazzaro, Hilfiker and Zeyer 2015; Liu *et al.* 2015) community structure, abundance or phylogenetic relationships. Others focused on specific functional groups such as autotrophs (Guo *et al.* 2015), ammonia oxidizers (Zheng *et al.* 2014; Yuan *et al.* 2015) and denitrifiers (Zheng *et al.* 2014) or on total functional diversity using GeoChip (Yang *et al.* 2014; Yue *et al.* 2015).

Investigating microbial diversity based on phylogenetic marker genes, Liu *et al.* (2015) reported a decreasing alpha-diversity of arbuscular mycorrhizal fungi with increasing altitude (4149–5033 m a.s.l.) on the east slope of Mt. Mila, Tibetan Plateau, China, while no trend was observed on the west slope. Similarly, Shen *et al.* (2015) found a decreasing alpha-diversity of bacteria with increasing altitude along a 2000–2500 m a.s.l. transect on the north slope of Changbai mountain, China. For archaea, Singh, Takahashi and Adams (2012) reported a peak in alpha-diversity at mid-altitudes along a 1000–3760 m a.s.l. gradient on Mt. Fuji, Japan. Wang *et al.* (2015) reported that the ratio of bacterial to archaeal gene copy numbers decreased with altitude on Mt. Shegyla, Tibetan Plateau, China (3106–4479 m a.s.l. transect), while gene copy numbers of bacteria and archaea showed

Table 1. Overview of studies on soil microbial ecology in mountain ecosystems.

Geographical location	Altitude (m)	Climate	Soil	Sampling sites and approaches	Microbial parameters	Main findings	Reference
(A) Soil microbial ecology studies in mountain ecosystems (since 2006)							
Colorado Rocky Mountains	3500	near 0 °C (soil)	pH 4.3–5.3, SOC 5%–30%	alpine tundra wet meadow soil, seasonal sampling, depth profile	Bacteria, archaea; T-RFLP; cloning and Sanger sequencing	Shift of communities with depth; high abundance of uncultivable Chloroflexi	Costello and Schmidt (2006)
Peruvian Andes	5000	−5 to 25 °C (surface soil T); 1000 mm (P)	Bare soils, 0 to 20 years old; SOC 0.1%	Glacier forefield	Bacteria; cloning and Sanger sequencing,	Bacterial community structure changed with soil age; Comamonadaceae dominated youngest soils and N_2-fixing cyanobacteria at all stages	Nemergut *et al.* (2007)
Scandes, Sweden	980	−2°C (T); 850 mm (P)	–	Alpine tundra, seasonal sampling	PLFA	Shift of PLFA patterns with snowmelt; decrease of fungi:bacteria ratio; second shift across growing season	Björk *et al.* (2008)
Colorado Rocky mountains	2460–3380	13.7 to 21.6 °C (soil T in July)	pH 5.5–7.0; SOC 2.0%–3.9% (2–4 cm depth)	Elevation gradient	Acidobacteria; cloning and Sanger sequencing	Bacterial diversity decreases from lowest to highest elevations	Bryant *et al.* (2008)
Peruvian Andes	5000	−5 to 25 °C (surface soil T; 1000 mm (P)	Bare soils, 0 and 4 years old; SOC 0.1%; pH 7.5	Glacier forefield	Bacteria; cloning and Sanger sequencing, enyzmes, SIR	Diverse cyanobacterial community dominated early stages of soil formation	Schmidt *et al.* (2008)
Swiss Alps, Damma glacier	2100	1.8 °C (T); 2400 mm (P)	pH 4.7–4.9; SOC 0.1%–8.0% (0–10 cm depth)	Glacier forefield	Diazotrophic communities; cloning and Sanger sequencing of *nifH* genes	Soil age and the presence of pioneer plants influence the composition of free-living diazotrophs	Duc *et al.* (2009)
Colorado Rocky mountains, Nepal	3800 (Colorado); 5500 (Nepal);	–	SOC: 1.9%–3.3% (10 cm depth)	Unvegetated soils	Fungi; cloning and Sanger sequencing	Chytridiomycota dominate fungal communities in high-elevation soils	Freeman *et al.* (2009)
Austrian Alps	2300–2530	−3.8 to −2.1 °C (air T); 2.8 to 6.8 °C (soil T); 1915 to 2250 mm (P)	pH 4.4–5.9 (5 cm depth)	Aspect; soils at south and north slopes	Bacteria, fungi, PLFA, culturing, dehydrogenase activity	Microbial activity decreases with altitude; number of cells decrease with altitude	Margesin *et al.* (2009)

Table 1. Continued

Geographical location	Altitude (m)	Climate	Soil	Sampling sites and approaches	Microbial parameters	Main findings	Reference
French Alps	3200	–	SOC 8.7%–15.7% (10 cm depth;	Alpine tundra soils	Bacteria, fungi; cloning and Sanger sequencing	Strong heterogeneity in community structures; spatial variations are stronger than seasonal variations	Zinger *et al.* (2009)
Tianshan Mountains, China	3523	5 °C max. T in summer; 36 mm (P)	–	Alpine tundra soils	xylanase genes; cloning and Sanger sequencing	High xylanase gene diversity related to Actino- and Proteobacteria	Wang *et al.* (2010)
Swiss Alps, Damma glacier	2100	1.8 °C (T); 1900 mm (P)	pH 4.0–6.2; SOC 0.1%–8.0% (0–10 cm depth)	Glacier forefield	Bacteria, fungi, archaea; T-RFLP, PLFA	Microbial communities change along chronose-quence	Bernasconi *et al.* (2011)
Swiss Alps, Damma glacier	2100	1.8 °C (T); 2400 mm (P)	pH 4.0–6.2; SOC 0.1%–8.0% (0–10 cm depth)	Glacier forefield	N-cycling communities; N-cycling genes (e.g. *nifH*), qPCR, enyzmes	High abundance of *nifH* genes in transient soils (50–70 soil age); nitrification and denitrification activity high at older soils where plants dominated	Brankatschk *et al.* (2011)
Swiss Alps, Damma glacier	2100	1.8 °C (T); 1900 mm (P)	pH 4.0–6.2; SOC 0.1%–8.0% (0–10 cm depth)	Glacier forefield	Bacteria; Bacterial growth rates (leucine incorporation)	Bacterial growth in older soils was limited by the lack of C	Göransson, Venterink and Baath (2011)
Mountains of Ladakh, India	3700–5970	–	pH 6.4–8.8, SOC 1.7%–3.3%, TN 0.6–1.0%	Altitudinal gradient	Phototrophic microbial communities, epifluorescene microscopy	Phototrophs dominated by cyanobacteria; 28 morphotypes; communities depend on altitude, mountain range, vegetation and soil properties	Řeháková, Chlumská and Doležal (2011)
French Alps	2227–2818	–	pH 4.8–8.0; SOC 2.8%–34.8% (10 cm depth;	Alpine tundra soils	Bacteria, archaea, fungi; cloning and Sanger sequencing	Microbial communities exhibit non-random spatial patterns	Zinger *et al.* (2011)
Swiss Alps	2100	July–August: 7.9–11.1 °C (T)	pH 6.9–7.4; SOC 0.1–6.0 (0–5 cm depth)	Glacier forefield	T-RFLP, cloning and Sanger sequencing; Bacteria	Actinobacteria and Firmicutes show seasonal changes in abundance and composition	Lazzaro, Brankatschk and Zeyer (2012)

Table 1. Continued

Geographical location	Altitude (m)	Climate	Soil	Sampling sites and approaches	Microbial parameters	Main findings	Reference
Different regions (Himalayas, Rocky, Andes)	3660–6330	–	pH 4.2–7.2; SOC 0.03%–1.9% (0–4 cm depth)	Plant-free high-alpine soils	Fungi; cloning and Sanger sequencing	Diversity is little at high altitudes with some yeasts (Filobasidiales) and Doth-ideomycetes; zoosporic fungi (e.g. Spizel-lomycetales) are dominant after snow melt	Schmidt, Naff and Lynch (2012)
Mount Fuji, Japan	1000–3760	–	–	Elevation gradient; different vegetation zones; mountain summit at north face	Archaea; 454 pyrosequenc-ing	Archaeal diversity decreases with elevation; mesophilic archaea common at high altitude	Singh, Takahashi and Adams (2012)
Tibetan Plateau	3000–3600	2.0 to 4.0 °C (T); 850 mm (P)	pH 5.8–6.6 (0–25 cm depth); SOC 4.2%–17.4%	Elevation gradient; grassland	Microbial biomass, enzyme activity	Soil thawing increases microbial biomass; collapse of soluble organic nutrient pool with decline of enzymatic activity	Tan *et al.* (2012)
Swiss Alps, Damma glacier	2100	1.8 °C (T); 1900 mm (P)	pH 4.0–6.2; SOC 0.1–8.0 (0–10 cm depth)	Glacier forefield	Bacteria, fungi, archaea; T-RFLP, cloning and Sanger sequencing	Bacterial diversity does not change with soil age; Euryarchaeota dominate young soils while Thau-marchaeota dominate older soils	Zumsteg *et al.* (2012)
Robson Glacier, Canada, glacier forefield	3954	1.0 °C (T); 881 mm (P)	pH 6.9–7.4; SOC 0.07–4.73 (0–7.5 cm depth)	Glacier forefield	Bacteria, fungi; PLFA, respiration, enzymes	No change of PLFA profiles along chronose-quence; fungal activity increases with time since deglaciation	Hahn and Quideau (2013)
Tibetan Plateau	5300–5900	–	pH 7.5–8.5; SOC 2.0%–12.0% (2–4 cm depth)	Elevation gradient; biological soil crust; alpine and subnival zone	Cyanobacteria; Microscopy	High phototrophic biomass in the biological soil crusts	Janatkova *et al.* (2013)
Changbai Mountains, China	530–2200	−4.8 to 2.9 °C (T); 632 to 1154 mm (P)	pH 3.9–5.4 (0–10 cm depth); SOC 4.0%–11.0%	Elevation gradient	Bacteria; 454 pyrosequenc-ing	No bacterial diversity gradient with elevation	Shen *et al.* (2013)
Norway Alps	1230	–	SOC 9.9%–32.6%	Environmental gradient from ridge to snowbed	Fungi; 454 pyrosequenc-ing	Distinct gradient in fungal community structure	Yao *et al.* (2013)

Table 1. Continued

Geographical location	Altitude (m)	Climate	Soil	Sampling sites and approaches	Microbial parameters	Main findings	Reference
Tibetan Plateau	3400–4813	−1.7 °C (T); 560 mm (P)	pH 6.1–7.4 (0–15 cm depth); SOC 9%–21%	Altitudinal gradient; grassland	C- and N-cycling genes; Geo-Chip (DNA)	Microbial communities are structured by altitude, C, N and pH; high functional gene diversity (e.g. carbon degradation)	Zhang *et al.* (2013b)
Italian Alps	2400	7.3 °C (T growing season), 550 mm (P)	pH 4.3; SOC 0.6%–19%, TN 0.05%–0.98%	Glacier forefield; Rhizosphere and bulk soil; protected sites versus barren soil	bacteria, DGGE, ARISA	Floristic composition structures bacterial communities along transect; plant species effect on bacterial communities	Ciccazzo *et al.* (2014)
Swiss Alps	400–2535	–	–	Elevation gradient; grassland; large scale study (213 locations)	Fungi; 454 pyrosequencing	Fungal richness and shannon diversity index increase with elevation	Pellissier *et al.* (2014)
Southern Patagonia	7–615	–	SOC 4%–7%, TN 0.8%–1.4%	Altitudinal transect at upper and lower border of three vegetation belts	Soil microbial community structures and biomass (PLFA and SSCP)	Increase of C:N ratio induces shift from bacteria-dominated to fungal-dominated communities	Thébault *et al.* (2014)
Tibetan Plateau	3200–3800	−1.7 °C (T); 560 mm (P)	pH 7.4 (0–10 cm depth)	Altitudinal gradient; grassland	C- and N-cycling genes; Geo-Chip (DNA)	Microbial gene diversity changes with elevation; increase of cold stress genes with elevation	Yang *et al.* (2014)
Tibetan Plateau	4400–5210	−1.6 to 3.7°C (T); 227 to 420 mm (P)	pH 5.4–7.0 (0–20 cm depth); SOC 1.1%–17.1%	Altitudinal gradient along south-facing slope; grassland and steppe	Bacteria; T-RFLP, cloning and Sanger sequencing	Precipitation change rather than temperature change was the main driving force of community structure	Yuan *et al.* (2014)
Tibetan Plateau	3650	1.2 °C (T); 672 mm (P)	pH 5.3 (0–15 cm depth); SOC 7.1%–14.1%	Grassland	Ammonia-oxidizers (AOB, AOA) and denitrifiers; cloning and Sanger sequencing, qPCR	Grazing increases AOB and AOA abundance	Xie *et al.* (2014)
Tibetan Plateau	3105–4556	−4.6 to 4.0 °C (T); 1134 mm (P)	pH 3.9–5.4 (0–15 cm depth); SOC 2.6%–9.2%	Altitudinal gradient along south-facing slope; grassland	Bacteria, fungi; PLFA, CLPP	Microbial biomass decreases with elevation; fungi:bacteria ratio decreases with elevation	Xu *et al.* (2014)

Table 1. Continued

Geographical location	Altitude (m)	Climate	Soil	Sampling sites and approaches	Microbial parameters	Main findings	Reference
Tibetan plateau	4628	continental highland climate	pH 7.9–8.7; SOC 1.8%–3.3%	different types of alpine meadow	Bacteria; 454 pyrosequencing	Different community structures among different meadow types; Proteobacteria and Acidobacteria dominated	Zhang *et al.* (2014)
Tibetan Plateau	4400–5100	−1.6 to 3.7 °C (T); 227 to 420 mm (P)	pH 5.3–7.0 (0–10 cm depth); SOC 1.6%–10.7%	Elevation gradient; grassland	Autotrophic communities; T-RFLP, cloning and Sanger sequencing of *cbbL* genes and Rubisco activity	*CbbL* gene abundance and Rubisco enzyme activity increased with elevation; *CbbL* community structures shifted along the transect with soil temperature, water content, nutrients and plant diversity as the main drivers	Guo *et al.* (2015)
Swiss Alps	1930–2519	1.2 °C (T); 1600 mm (P)	pH 3.8–6.5 (0–15 cm depth); SOC 5.7%–27.5%	Elevation gradient; alpine meadows; glacier forefield; seasonal variations for 14 months	Bacteria, fungi; T-RFLP; Illumina MiSeq	Season has a strong impact on microbial community structures	Lazzaro, Hilfiker and Zeyer (2015)
Tibetan Plateau	4149–5033	−1.5 °C (T); 444 mm (P)	pH 4.1–5.1 (0–15 cm depth); SOC 3.1%–10.2%	Elevation gradient; eastern and western slope; mountainous grassland	AMF fungi; cloning and Sanger sequencing	52 OTUs; elevation patterns of AMF diversity	Liu *et al.* (2015)
Swiss Alps Damma glacier	2100	1.8 °C (T); 1900 mm (P)	pH 4.0–6.2; SOC 0.1%–8.0% (0–10 cm depth)	Glacier forefield	Bacteria, archaea, fungi; 454 pyrosequencing	Contrasting microclimatic conditions along the depth gradient in unvegetated soils; convergence of depth-related differences of community structures in later stages (homogenization due to the impact of plants)	Rime *et al.* (2015)
Changbai Mountain, China,	2000–2500	−4.8 °C (T); 1154 mm (P)	pH 5.5 (0–10 cm depth); SOC 4.0%–11.0%	Elevation gradient	Bacteria; 454 pyrosequencing	Bacterial communities differ with elevation; richness decreases with elevation	Shen *et al.* (2015)

Table 1. Continued

Geographical location	Altitude (m)	Climate	Soil	Sampling sites and approaches	Microbial parameters	Main findings	Reference
Tibetan Plateau	3106–4479	−4.6 to 4.0 °C (T); 1134 mm (P)	pH 4.6–6.4 (0–10 cm depth); SOC 1.8%–6.6%	Elevation gradient along three vertical climate zones, grassland	Bacteria, archaea; 454 pyrosequencing	Decreasing diversity patterns along elevation gradient; ratio of bacterial to archaeal gene abundance is negatively correlated with elevation	Wang *et al.* (2015)
Tibetan Plateau	4400–5200	−1.6 to 3.7 °C (T); 227 to 420 mm (P)	pH 5.4–7.0 (0–20 cm depth); SOC 1.1%–17.1%	Elevation gradient; grassland; different soil depths (surface, subsoils)	Ammonia oxidizers (AOB, AOA), *amoA* genes; cloning and Sanger sequencing	Bacterial *amoA* genes increase with altitude, whereas archaeal *amoA* genes on surface soils decrease with altitude	Yuan *et al.* (2015)
Tibetan Plateau	4600–5900	−8.2 °C (T); 50 to 80 mm (P)	pH 7.5–8.9; SOC 2.0%–3.9% (2–4 cm depth)	Soil crusts; arid cold desert	Cyanobacteria; eukaryotic microalgae; culturing; Sanger sequencing	soil P and Mg are the most important predictors for community composition with elevation	Capkova *et al.* (2016)
California (White mountains)	3100–3800	−1.7 to 0.9 °C (T); 327 to 456 mm (P)	pH 5.9–6.2; SOC 1.7%–2.6%	subalpine to alpine meadow	Bacteria, archaea; Illumina MiSeq	Native range expansions (sagebrush) affect soil microbial communities	Collins *et al.*(2016)
Swiss Alps	2960	−3.0 °C (T); 2500 mm (P)	pH 4.6–7.4; SOC <0.1%	Active layer and permafrost soils on southern and northern slopes	Bacteria, archaea, fungi, Illumina MiSeq	Alpine permafrost harbours a diverse and largely uncharacterized microbiome; members of the bacterial candidate superphylum Patescibacteria are characteristic for permafrost soils	Frey *et al.* (2016)
Carpathians and Alps	2200–2700	–	pH 4.5–6.8; SOC 1.2%–2.0%	Alpine grasslands; acidic versus calcareous grassland	Bacteria, Fungi; Ilumina MiSeq	Plant as a driver of fungal communities; influence of human activity on microbial assemblages	Geremia *et al.* (2016)
Yukon, Canada;	2214	−7.3 °C (T); 155 mm (P)	pH 7.8–8.9; SOC 0.6–35.3 (0–10 cm depth)	Glacier forefield	Bacteria; Ion Torrent sequencing	Deterministic assembly; drastic change from subglacial to proglacial environments	Kazemi, Hatam and Lanoil (2016)

Table 1. Continued

Geographical location	Altitude (m)	Climate	Soil	Sampling sites and approaches	Microbial parameters	Main findings	Reference
Tibetan Plateau	4500	−2.1 °C (T); 406 mm (P)	pH 7.6–8.9 (0–10 cm depth); SOC 2.0%–4.2%	Grassland	Bacteria, fungi; Ilumina MiSeq	Grazing altered bacterial and fungal community structures and relative abundance of pathogenic fungi; shift to Doth-ideomycetes	Li *et al.* (2016b)
Italian Alps	2705–3054	–	pH 5.2–6.4 (0–10 cm depth); SOC 0.3%–11.8%	Alpine meadows (patterned ground); elevation gradient	Bacteria, archaea, fungi; DGGE, cloning and Sanger sequencing, qPCR	Lowest bacterial and archaeal abundance in highest elevation; lithology affects community structure	Mania *et al.*(2016)
European Alps	2000	2.4 °C (T); 1050 mm (P)	pH 4.1 (0–10 cm depth); SOC 30%	Altitudinal gradient from submontane to alpine vegetation zones	Bacteria, archaea, fungi; Ilumina MiSeq	Bacterial and fungal relative abundance increases with altitude	Siles and Margesin (2016)
Tibet	3368	8 °C (T), 608 mm (P)	–	Fire-affected alpine meadow	Microbial communities, PLFA, Biolog EcoPlate	Fire affects C-utilization patterns, increase in total PLFAs and bacterial PLFAs in burnt soil	Wang *et al.* (2016)
Colorado Rocky mountains	3500	−3.7 °C (T)	pH 4.5–5.5; SOC 86–138 mg g^{-1}; TN 7.3–10.9 mg g^{-1}	N- and P-fertilization along plant species and moisture gradient	Bacteria; Ilumina MiSeq	Plant richness and P and N treatment drive microbial community structures; impact of N on microbes via direct and indirect (plant, pH) effects	Yuan *et al.* (2016)
Tibetan Plateau	5210–6029	–	pH 7.0–8.5 (0–10 cm depth); SOC 0%–5%	Elevation gradient; alpine and subnival zone	Cyanobacteria; microscopy	Plant diversity decreases whereas cyanobacteria abundance increases with elevation; cyanobacteria are generally more abundant and diverse in bare than vegetated soils	Řeháková *et al.* (2017)

Table 1. Continued

(B) Climate change experiments (e.g. soil transplantation, OTCs, heating cables, laboratory incubation) on microbial ecology in mountain ecosystems

Geographical location	Altitude (m)	Climate	Soil	Experimental approach	Microbial parameters	Main findings	Reference
Scotland	Low-alpine	4.3 °C (air T), 5.3 °C (soil T), 980 mm (P)	pH 4.3; SOC 14.3%, TN 0.56%, TP, 1.09% (2–8 cm)	Warming (OTCs), N-deposition, fire in factorial design; low-alpine heath for 22 months	Litter decomposition (native and standard litter) enzymes, bacterial and fungal diversity by T-RFLP	Changes of litter decomposition, enzyme activity, and microbial community structures in response to treatments; coupling between plant and microbial communities	Papanikolaou *et al.* (2010)
Tibetan Plateau	3200	−2.0 °C (T); 500 mm (P)	pH 7.6 (0–10 cm depth); SOC 7.3%–8.6%	Simulated warming by infrared heater for 3 years; grassland	Methanotrophs (*pmoA* gene fragments); cloning and Sanger sequencing	Warming does not change community composition; methane oxidation activity increases	Zheng *et al.* (2012)
Swiss Alps, Damma glacier	2100	1.8 °C (T); 1900 mm (P)	pH 5.5–7.1; SOC 0.08%–0.12% (0–10 cm depth)	Reciprocal soil transfer for 16 months; glacier forefield	Bacteria, fungi; T-RFLP, cloning and Sanger sequencing; growth rates, enzymes	Microbial activity responds from warmer to drier site; bacterial and fungal communities respond in both directions	Zumsteg *et al.* (2013)
Tibetan Plateau	4635	−3.8 °C (T); 221 mm (P)	pH 8.0 (0–15 cm depth); SOC 7.8%–8.8%	Infrared heaters aboveground for 15 months (soil warming +1 and +2°C); grassland	Bacteria; 454 pyrosequencing	Short-term warming leads to shifts in community structure; Actinobacteria increase while Acidobacteria decrease	Xiong *et al.* (2014)
Tibetan Plateau	3200–3800	0.4 to 4.0 °C (T); 500 mm (P)	pH 7.4 (0–10 cm depth); SOC 11.3%	2-year reciprocal elevation translocation (upward and downward); grassland	Ammonia-oxidizers (AOB, AOA) and denitrifiers; clone library and Sanger sequencing	AOB react more sensitively to warming than AOA (abundance increase by warming)	Zheng *et al.* (2014)
Tibetan Plateau	3000–3600	3.0 °C (T); 850 mm (P)	pH 5.3–5.8 (0–10 cm depth); SOC 4.5%–15.0%	Soil transplantation along transect; temperature increase, air: 2.0 °C; soil: 1.5 °C	Microbial biomass, enzyme activity in different soil depths	Warming has stronger effects on microbial biomass in the organic than mineral layer	Guo *et al.* (2015)
Tibetan Plateau	3200–3800	−1.7 °C (T); 570 mm (P)	pH 7.2–8.0 (0–10 cm depth)	Soil transplantation downward and upward along elevation gradient; grassland	Bacteria; 454 pyrosequencing	Warming leads to change of origin community; communities become similar to destination communities	Rui *et al.* (2015)

Table 1. Continued

(B) Climate change experiments (e.g. soil transplantation, OTCs, heating cables, laboratory incubation) on microbial ecology in mountain ecosystems

Geographical location	Altitude (m)	Climate	Soil	Experimental approach	Microbial parameters	Main findings	Reference
Tibetan Plateau	3200–3800	−1.7 °C (T); 570 mm (P)	pH 7.3 (0–20 cm depth)	Soil transplantation along elevation gradient; grassland	C- and N-cycling genes; Geo-Chip	Decrease of C- and N-cycling genes with warming	Yue *et al.* (2015)
Tibetan Plateau	3200–3800	−3.8 °C (T); 291 mm (P)	pH 7.9 (0–20 cm depth), 8.8% SOC	Laboratory incubations; temperature increase from 10 to 40°C for 28 days; grassland	Bacteria; MiSeq sequencing, enzymes, CLPP, turnover rates	Increased turnover rates; change in bacterial community structure, CLPP and enzymes with increased temperature	Wu *et al.* (2015)
Tibetan Plateau	4500–4750	−3.8 °C (T); 383 mm (P)	pH 7.4 (0–15 cm depth); SOC 2.5%–5.0%	OTCs for 3 years (approx. 1.4 C warming on average); grassland / steppe	Bacteria, fungi; PLFA profiles at different soil depths	Soil depth-related changes of microbial biomass and community structures	Zhang *et al.* (2015a)
Tibetan Plateau	3200	−2.0 °C (T); 500 mm (P)	pH 7.4 (0–20 cm depth); SOC 7.3%–8.6%	Infrared heaters for 3 years; grassland	Bacteria; 454 pyrosequencing	Warming increases alpha-diversity; composition is resistant to warming after 3 years	Li *et al.* (2016a)
Tibetan Plateau	4500–4750	−4.0 °C (T); 620 mm (P)	pH 7.4 (0–5 cm depth); SOC 2.5%–6.0%	OTCs for 3 years (approx. 2.0 C warming on average); enhanced rainfall (+ 20%); grassland, steppe	Bacteria, fungi; Ilumina MiSeq	Enhanced rainfall rather than warming reduces microbial diversity; alpine steppe more resistant than alpine meadow	Zhang *et al.* (2016a)
Tibetan Plateau	3200	−1.8 to −0.8 °C (T); 351 mm (P)	pH 7.8 (0–5 cm depth); SOC 9.2%–11.1%	Infrared heaters for 1 year (approx. 2.0 C warming on average); grassland	Bacteria, fungi; 454 pyrosequencing	Short-term warming did not change bacterial community structures (relative abundance of Betaproteobacteria increased)	Zhang *et al.* (2016b)

Abbreviations: T = Annual mean temperature; P = Annual mean precipitation; OTC = Open top chamber; SOC = Soil organic carbon; PLFA = Phospholipid fatty acids; T-RFLP = Terminal restriction fragment length polymorphism; DGGE = Denaturing gradient gel electrophoresis; SSCP = Single strand conformation polymorphism; ARISA = Automated ribosomal intergenic spacer analysis; CLPP = Community-level physiological profiles; SIR = Substrate induced respiration; AMF = arbuscular mycorrhizal fungi; pmoA = particulate methane monooxygenase gene; amoA = ammonia monooxygenase gene; nifH = nitrogen reductase gene; AOB = Ammonia oxidizing bacteria; AOA = Ammonia-oxidizin archaea; Rubisco = ribulose-1,5-bisphosphate carboxylase/oxygenase; cbbL = gene coding for *RubisCO* large subunit; TN = Total nitrogen; qPCR = quantitative polymerase chain reaction

no clear trend along the transect. Lazzaro, Hilfiker and Zeyer (2015) observed the lowest bacterial and fungal gene copy numbers at the highest site of an altitudinal transect in the Swiss Alps (1930–2519 m a.s.l.).

All studies assessing bacterial, fungal or archaeal community structures revealed distinct compositions along altitudinal transects, which mostly spanned 500–1500 m of altitudinal distance (Table 1a). Hence, microbial community structures mirror the drastic change in environmental conditions related to altitude that occur over short distances in mountain environments. Both climatic variables such as temperature and precipitation and soil and vegetation properties were identified as drivers of microbial community structures. The former can be expected to exert direct effects on the microbial communities, while the latter two can be expected to be related with climatic variables and among each other via biological and chemical feedbacks. As the main environmental drivers of bacterial community composition along such transects, soil physicochemical properties (total C (Shen *et al*. 2015), total N (Shen *et al*. 2015), C:N ratio (Shen *et al*. 2015), dissolved organic C (Shen *et al*. 2015), pH (Shen *et al*. 2013)), nutrients and moisture (Shen *et al*. 2013), temperature (Rui *et al*. 2015), precipitation (Yuan *et al*. 2014) and vegetation (species and biomass (Rui *et al*. 2015)) were identified. Likewise, fungal community structures were shown to be strongly driven by soil organic matter content, pH, soil nutrients, plant diversity and temperature (Lazzaro, Hilfiker and Zeyer 2015; Liu *et al*. 2015). For archaea, pH, clay, SOC, cation-exchange capacity, total N, moisture, NH_4^+, potassium and NO_3^- were identified as predictors of community structures (Singh, Takahashi and Adams 2012; Wang *et al*. 2015).

As soil properties and thus nutrient cycling and C-dynamics change with climatic conditions, recently, increasing attention has been directed towards changes in microbial functional diversity with altitude (Yang *et al*. 2014; Zheng *et al*. 2014; Guo *et al*. 2015; Yuan *et al*. 2015; Yue *et al*. 2015). Similar to findings for phylogenetic marker genes, functional gene abundance and functional gene alpha- and beta-diversity were shown to vary with altitude in these studies. The reactions catalyzed by the functional genes discussed in the following section are depicted in Fig. 4. Yang *et al*. (2014) addressed the functional diversity at four sites along an altitudinal gradient in the Tibetan grassland using the functional gene microarray tool GeoChip 4.0. They identified distinct functional communities along the gradient, with substantial variation in stress genes (e.g. cold shock genes) as well as N- and C-cycling genes: *amoA* (ammonia monooxygenase A, involved in nitrification, catalyzing oxidation of ammonium nitrite that can be converted to nitrate in a subsequent reaction) was decreased at higher altitudes, consistent with lower amounts of the substrate of this reaction (ammonium). Genes involved in denitrification (reduction of nitrate via nitrite and nitrous oxide) as well as the substrate NO_3^- showed the reverse trend. Abundance of the *Rubisco* (ribulose-1,5-bisphosphate carboxylase/oxygenase, involved in CO_2-fixation) gene as well as several genes involved in starch and cellulose degradation was lower at the lowest site compared to the other sites which might indicate lower CO_2-fixation activities as well as lower degradation of organic matter. However, care should be taken making inferences about processes, as functional genes detected at the DNA level are not necessarily active. Soil pH, temperature, NH_4^+ and vegetation diversity accounted for 81.4% of all microbial community variation. Out of this,15.8%, 16.4% and 19.9% were explained by climatic variables, soil properties and vegetation properties alone, respectively. Using the altitudinal transect as a proxy for warming, the authors predicted that climate change will affect microbial community structure and function with a particularly large impact on microbial N-cycling genes and thus N-dynamics. The importance of N-cycling in alpine soils was further highlighted in a study by Yuan *et al*. (2015), where archaeal *amoA* (ammonia monooxygenase A) abundance decreased with increasing altitude in the surface soil but remained stable at lower depths along a transect from 4400–5200 m a.s.l. in the Nyainqentanglha mountains on the Tibetan Plateau. Conversely, bacterial *amoA* increased with increasing altitude at all depths indicating lower transformation rates of ammonium to nitrate by archaea and higher transformation rates by bacteria at higher altitudes. The environmental factors best explaining patterns of bacterial and archaeal *amoA* abundance and community composition were soil pH and precipitation. Guo *et al*. (2015) hypothesized that microbial autotrophic CO_2-fixation plays a critical role in C-cycling in alpine environments with limited vegetation. Therefore, the authors investigated *cbbL* (ribulose bisphosphate carboxylase large chain) gene abundance and diversity along an altitudinal gradient on the Tibetan Plateau. They found increasing gene copy numbers and Rubisco enzyme activity with increasing altitude pointing towards increased CO_2-fixation activities at higher altitudes. *CbbL* community structures shifted along the transect, and this change was driven by changes in soil temperature, water content, nutrients and plant diversity. These communities were dominated by bacterial autotrophs affiliated with Rhizobiales, Burkholderiales and Actinomycetales. In agreement with these findings several authors detected increasing phototrophic biovolume with increasing altitude in the Himalaya (Řeháková, Capková and Dvorsky 2011; Janatkova *et al*. 2013; Capkova *et al*. 2016).

In addition to investigating altitudinal patterns, several studies addressed the impact of topography, such as slope aspect, on microbial diversity (Zumsteg *et al*. 2013; Liu *et al*. 2015; Frey *et al*. 2016). These studies revealed that microbial community structures, as well as their relationship with altitude, may vary drastically with slope aspect within short distances (Table 1a). Similarly strong contrasts were found among a moisture gradient in an alpine meadow (Yuan *et al*. 2016). Thus, these findings highlight that the complex topography and consequently the considerable small-scale heterogeneity of mountain soils is reflected in microbial alpha- and beta-diversity. Furthermore, the strong mutual influence between microbes and plants was stressed in alpine environments (Ciccazzo *et al*. 2014; Geremia *et al*. 2016; Collins at al. 2016) that might be particularly pronounced in these nutrient poor ecosystems that are exposed to strongly fluctuating environmental conditions (Ciccazzo *et al*. 2014; Rime *et al*. 2015). Moreover, soil microbial functional as well as structural diversity was shown to vary fundamentally with soil depth (Costello and Schmidt 2006; Rime *et al*. 2015; Yuan *et al*. 2015), but this information has barely been taken into account in other existing studies. Furthermore, seasonal variation has been shown to exert a substantial influence on alpine soil microbial communities (Costello and Schmidt 2006; Lipson 2007; Gou *et al*. 2015; Lazzaro, Hilfiker and Zeyer 2015) yet this remains another understudied topic in alpine soil microbial ecology.

Collectively, soil microbial community structures in alpine environments closely mirror the complexity and heterogeneity of these habitats. Due to the scarcity of studies, limitations in methodology and the pronounced heterogeneity of environmental conditions in these habitats (both from a local and from a global point of view), soil microbial alpha- and beta-diversity and especially the significance of diversity with regard to biogeochemical processes and microbial ecosystem services remain poorly understood.

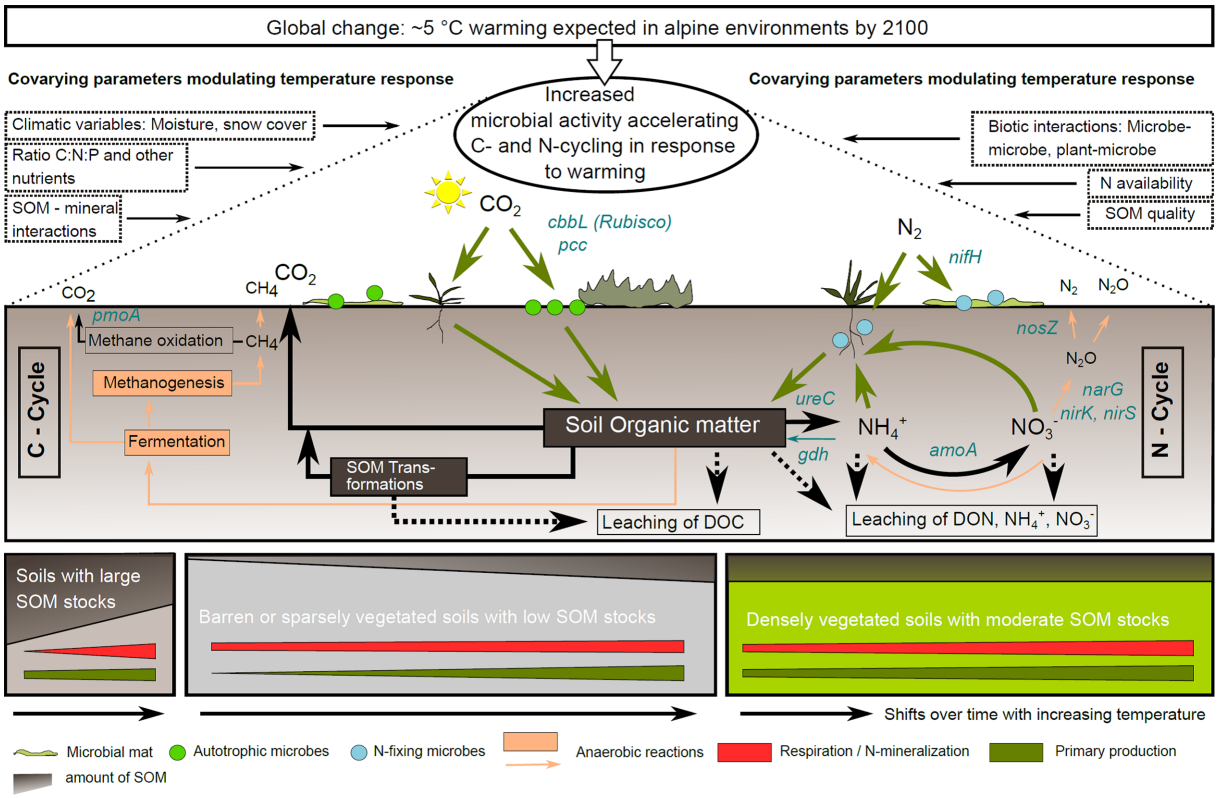


Figure 4. Top part: With global warming the activity of alpine microorganisms will increase leading to profound alterations in all reactions of the C- and N-cycle, respectively: Microbial activity will lead to elevated mineralization of SOM but also assimilation of SOM by plants as well as C- and N-fixing microbes might be enhanced under warming conditions (Addition to the SOM-pool is depicted with green arrows, depletion or transformation is depicted in black with anaerobic reactions in peach-colored; environmental conditions favoring anaerobic reactions rarely occur in alpine environments. Anaerobic reactions are therefore represented with thinner arrows; microbial enzymes discussed in the section on current literature in microbial ecology are depicted in petrol-blue next to the reaction they catalyze). All N-cycling reactions can be expected to be accelerated with warming including N_2- fixation and nitrification among aerobic reactions as well as dissimilatory nitrate ammonification, denitrification and anammox (anaerobic ammonium oxidation) among anaerobic reactions. As mountain environments are subject to considerable hydrological activity, significant amounts of both C and N drain with the soil solution, which might be reinforced by warming. Mineralization of organic matter, methanogenesis and denitrification lead to the emission of the GHG CO_2, CH_4 and N_2O, which is counteracted by photosynthesis, methane oxidation and reduction of N_2O to N_2, respectively. With the current state of knowledge, it is not possible to conclusively evaluate how the balance among different C- and N-cycling reactions and thus uptake and emission of greenhouse gases will shift in response to climate change in alpine environments. Direct warming impacts on alpine soil microorganisms will be modulated moreover by concurrent changes in moisture and snow cover regimes, changes in soil physicochemical properties, substrate availability as well as changes in biotic and abiotic interactions. In addition, increasing microbial mineralization of SOM will lead to a shift in SOM quality towards more recalcitrant compounds accompanied by a shift of microbial degrader communities. Thus, net uptake and emission of CO_2 may not follow a linear relationship with increasing temperature. **Bottom part:** Based on space for time substitution approaches such as along altitudinal gradients or glacier forefield chronosequences, alpine environments as a whole can be expected to act as C and N-sink due to increased plant productivity under warmer conditions. This especially holds true for barren or sparsely vegetated soils with low C and N content where increased plant growth and primary production clearly outweigh increases in soil respiration. For densely vegetated soils such as alpine meadow also both primary production and soil respiration are expected to increase with warming which might roughly compensate each other. However, due to the complex interactions driving C- and N-cycling under warming that are described above, the exact outcome of shifts in C- and N-fluxes remains unclear in densely vegetated soils. Conversely, soils sequestering large amounts of organic material which is largely protected from microbial degradation under current climatic conditions such as permafrost or peat soils, are expected to become significant sources of GHG. However, such soils hardly occur in alpine environments and can be therefore considered rather insignificant in terms of supraregional C and N-budgets. Abbreviations: SOM = soil organic matter, DOC = dissolved organic carbon, DON = dissolved organic nitrogen, GHG = greenhouse gas, amoA = ammonia monooxygenase A, nirK, NirS = nitrite reductase K, S, narG = nitrate reductase G, nosZ = nitrous oxide reductase Z, nifH = nitrogenase H, ureC = urease C, gdh = glutamate dehydrogenase, pmoA = particulate methane monooxygenase A, pcc = Propionyl-CoA carboxylase, cbbL (Rubisco) = ribulose bisphosphate carboxylase large chain

Mountain permafrost soils

Arctic permafrost sequesters large C-stocks that might become subject to microbial degradation under warmer conditions, triggering a positive feedback to climate change due to the release of greenhouse gases arising from mineralization of organic matter (Schuur, McGuire and Schadel 2015). Therefore, recently, increasing effort has been put into investigating the arctic permafrost microbiome and its response to thaw using a variety of omics tools (Yergeau *et al.* 2010; Mackelprang *et al.* 2011; Hultman *et al.* 2015). The extent of alpine permafrost is much smaller and organic matter is mostly confined to the upper 30–40 cm of the soil profile, which is part of the active layer and not the permafrost layer (Bockheim and Munroe 2014). Hence, concern about the emission of high levels of greenhouse gases with permafrost thaw is much less valid for alpine soils, and thus they have received far less attention than arctic soils.

The majority of studies on alpine permafrost has been conducted on the Tibetan Plateau in China, which harbors the largest area of mountain permafrost. Microbial studies on Chinese permafrost have been reviewed by Hu *et al.* (2015). They reported large cell numbers (up to 10^7–10^9 cells per g soil), detected by epifluorescence microscopy, that decrease

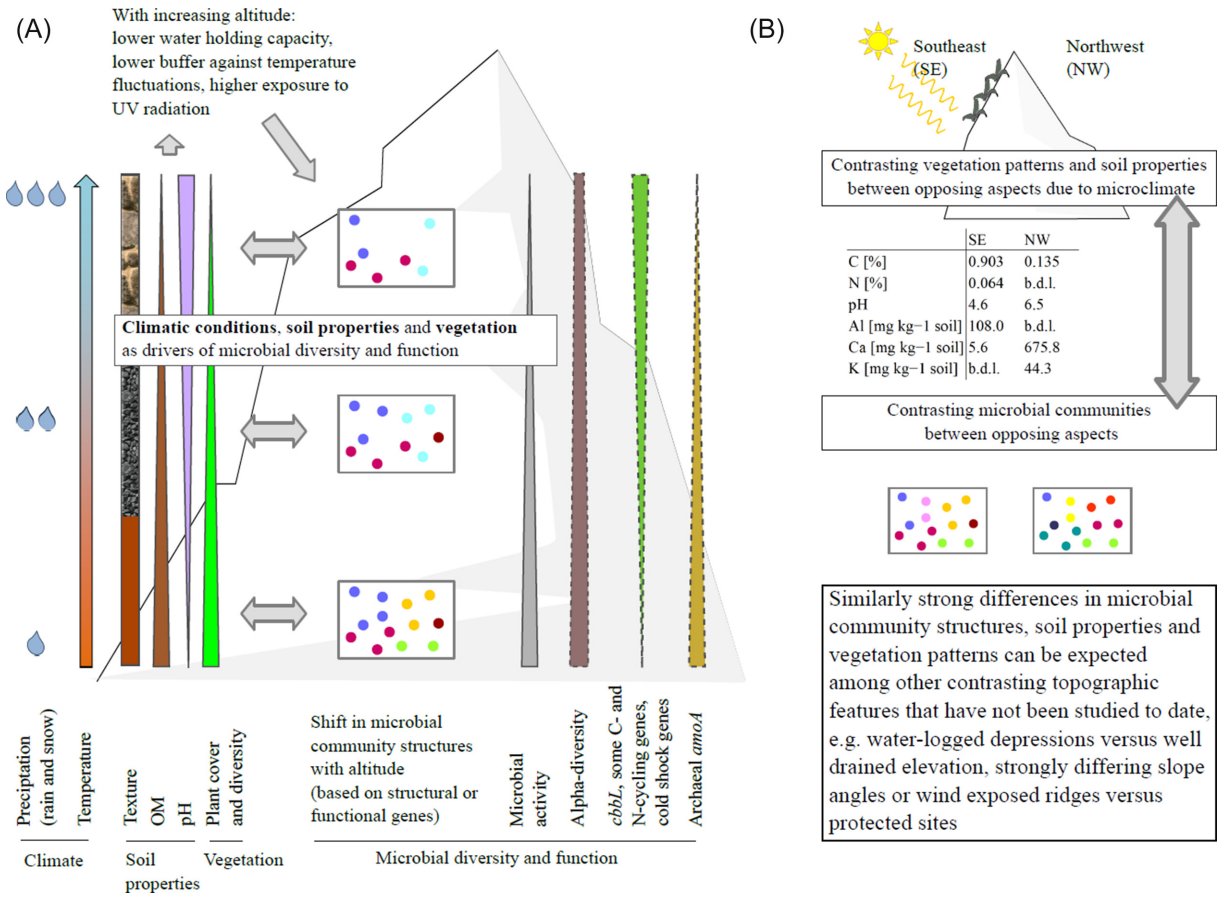


Figure 5. Shift in microbial community structures, soil properties and plant diversity with altitude and aspect. Microbial community structures and functions vary along altitudinal gradients, which are associated with strong changes in climatic regimes (**A**). Simultaneously, vegetation patterns and soil properties (texture, organic matter content and pH) have been identified as important drivers of microbial community structures. Topographic features and their related microclimatic regimes similarly have strong effects on the soil microbiome, which is shown here for the example of slope aspect on the mountain ridge 'Muot da Barba Peider' located at 2960m a.s.l. in the Swiss Alps (**B**). Here, within less than 50 m horizontal distance, C- and N-content, pH and texture vary fundamentally between the northwest- and the southeast-exposed sides. These differences are closely reflected in contrasting bacterial and fungal community structures between the two expositions. Abbreviatons: B.d.l. = below detection limit; cbbL = ribulose bisphosphate carboxylase large chain; amoA = ammonia monooxygenase gene A, OM = organic matter

with increasing depth, and they documented a wide spectrum of isolates from Chinese permafrost that are comparable with those from permafrost in the Arctic. Moreover, studies assessing the non-culturable diversity in Chinese permafrost revealed substantially different bacterial community composition across different geographical regions, with the most frequently detected phyla being Proteobacteria, Actinobacteria, Firmicutes, Acidobacteria and Bacteroidetes, as well as several candidate phyla (Hu *et al.* 2015). Bacterial and fungal community structures varied across different permafrost-affected habitats, which could be related to various environmental parameters such as vegetation type, moisture, C:N ratio and pH (Zhang *et al.* 2013a; Zhang *et al.* 2014). Bacterial isolates affiliated with Actinobacteria, Firmicutes, Proteobacteria and Cytophaga-Flavobacterium-Bacteroides (CFB) phylum were found in alpine permafrost (Hu *et al.* 2015). Bai *et al.* (2006) analyzed the cultural bacterial diversity in a 3-m alpine permafrost core from the Tianshan mountains, China, recovering 91 isolates. The isolates grew on oligotrophic medium and were mostly psychotrophs (cold-tolerant with growth optimum >15°C) comprising only two psychrophils (growth optimum <15°C). This is in agreement with temperature adaptation in various arctic and antarctic permafrost isolates, which are mostly psychrotrophic rather than psychrophilic (Gilichinsky 2003; Steven, Niederberger and Whyte 2009). These findings are also in line with the hypothesis that bacteria mostly have a growth optimum well above the annual mean temperature (Rousk and Baath 2011). The most abundant and diverse isolates in alpine permafrost culturable populations belong to the genera *Arthrobacter* (Bai *et al.* 2006; Zhang *et al.* 2007). Arthrobacters are ubiquitous in many low temperature environments (Margesin *et al.* 2004; Frey *et al.* 2010; Lapanje *et al.* 2012). The dominance of Actinobacteria, to which *Arthrobacter* belongs, in permafrost soil has been attributed to their ability to form resting stages, the so-called cysts (Soina *et al.* 2004). Zhao *et al.* (2011) moreover isolated novel bacterial strains from permafrost in the Tianshan mountains China that may represent new species within the genus *Chryseobacterium*.

Ollivier *et al.* (2014) investigated bacterial diversity along a depth gradient in the active layer of two permafrost soils and one seasonally frozen soil as a model of future climatic conditions in permafrost soils on the Tibetan Plateau using T-RFLP profiling and quantitative PCR. Depth-related changes in diversity, which could mainly be related to C- and N-content, were much more pronounced in the seasonally frozen ground than in the active layer of the permafrost-affected soil. The authors contrasted these results with findings about permafrost soils from Siberia, where depth-associated changes in bacterial diversity occurred (Wagner, Kobabe and Liebner 2009), and argued that

these differences might be associated with waterlogged conditions present at the Siberian permafrost table but not at the Tibetan Plateau permafrost table.

The only study addressing microbial diversity in mountain permafrost outside of China was conducted recently in the European Alps by Frey *et al.* (2016). Here, on the mountain ridge 'Muot-da-Barba-Peider' in the eastern Swiss Alps, a unique experimental design was applied comparing a permafrost soil on the north-western (NW) slope of the ridge to the active layer as well as to a non-permafrost soil at the same depth on the south-eastern (SE) side, thus accounting for depth-related effects. Microbial community structures in the NW permafrost soil differed drastically both from the NW top soil and from the SE soil. Strikingly, from the permafrost soils, besides some well-established phyla such as Proteobacteria, Verrucomicrobia and Acidobacteria, the bacterial candidate phyla OD1, TM7, GN02 and OP11 forming the superphylum Patescibacteria were recovered, comprising one-third of the community (Frey *et al.* 2016). Likewise, fungi exhibited considerable taxonomic diversity, notably comprising 14% of sequences that could not be assigned beyond the kingdom level, indicating an undercharacterized fungal community in these permafrost environments. Among fungi, cold-adapted yeasts and lichenized fungi, in particular basidiomycetous *Rhodotorula*, *Cryptococcus*, *Mrakia* and *Leucosporidium*, as well as the ascomycetous *Lecidea*, *Acarospora* and *Umbilicaria* have been recovered. These fungal groups are common in permafrost-like habitats (Margesin and Miteva 2011; Zucconi *et al.* 2012; Zalar and Gunde-Cimerman 2014) and are known to undergo structural and functional adaptations to survive and be metabolically active under subzero, nutrient-poor conditions (Ozerskaya *et al.* 2009; Buzzini *et al.* 2012).

Overall, as with arctic permafrost soils, mountain permafrost soils harbor a surprisingly high diversity of microbes equipped with a variety of adaptation mechanisms to survive in harsh subzero, oligotrophic conditions (Margesin and Miteva 2011; Jansson and Tas 2014), although the number of existing studies is still very limited. The recovery of a large unknown bacterial and fungal diversity in alpine permafrost (Frey *et al.* 2016) points towards a limited understanding of the metabolic processes taking place in these environments and highlights the need for further studies exploring the genomic potential of permafrost soils, with regard to both ecological functions and possible biotechnological applications.

Mountain glacier forefields

Serving as a paradigm for soil formation in mountain regions, the forefields of receding glaciers remain the best-studied alpine habitat with regard to soil microbial ecology. With the rapid disintegration of alpine glaciers due to climate change, large expanses of barren bedrock are exposed where new ecosystems develop. In order to understand the contribution of glacier forefield ecosystems to both local and global C- and nutrient budgets, the study of microbial alpha- and beta-diversity as well as function is essential. Microbial ecology and soil development along glacier forefields have been recently reviewed by Schulz *et al.* (2013) and Bradley, Singarayer and Anesio (2014). Thus, this review will not go into detail on the topic of microbial ecology in glacier forefields but instead briefly summarize the main points and complement with some more recent findings. An overview is depicted in Fig. 3.

After retreat of a glacier, microbes constitute the initial colonizers of the exposed bedrock (Zumsteg *et al.* 2012; Rime *et al.* 2015). Microbial life is considered fundamental in stabilizing soils and shaping the physical and biological development of these ecosystems (Bernasconi *et al.* 2011). Microbes contribute importantly to the initial build-up of biomass, with potential sources of C and N being allochthonous deposition, input from landslides and avalanches, faunal and vegetal debris, ancient organic matter stored in the ground and autotrophic fixation (Schmidt *et al.* 2008; Brankatschk *et al.* 2011). The relative contributions of these different sources remain a matter of ongoing debate in both arctic and alpine glacier forefields (Stibal *et al.* 2008; Duc *et al.* 2009; Zumsteg *et al.* 2012; Frey *et al.* 2013; Rime, Hartmann and Frey 2016a; Rime *et al.* 2016b). Other nutrients, such as phosphorus and sulfur, may be obtained from the bedrock by weathering (Frey *et al.* 2010).

Microbial communities and soil geochemical properties were found to change in tandem along glacier forefields (Bernasconi *et al.* 2011). Microbial community compositions were reported to shift in response to increasing C-content in soils, decreasing soil pH and plant establishment (Zumsteg *et al.* 2012). Plant establishment was identified as a main driver of community structure by several authors (e.g. Blaalid *et al.* 2012; Knelman *et al.* 2012; Brown and Jumpponen 2014). Comparing bacterial and fungal compositions along the forefield of Lyman Glacier, Washington, USA, Brown and Jumpponen (2014) observed distinct succession patterns for bacteria and fungi. They highlighted that the presence rather than the type of vegetation influenced the soil microbiome, with a stronger impact in structuring soil bacterial communities compared with fungal communities. However, Kazemi, Hatam and Lanoil (2016) reported stabilization of microbial community structures already before the establishment of plants at Duke River Glacier, Yukon, Canada. The authors found that sites along two transects perpendicular to the glacier snout clustered into three main stages, with an early and an intermediate stage devoid of vegetation and a third stage coinciding with the advent of plants.

In addition to documenting spatiotemporal patterns along a chronosequence, Rime *et al.* (2015) addressed the vertical distribution of microbial communities along a chronosequence in the forefield of the Damma glacier, Switzerland. The authors observed strong depth-related differences of microbial community structures in recently deglaciated soils, while soils became increasingly homogenous along the depth-profile with increasing soil age. This pattern was hypothesized to be governed by analogous changes of environmental conditions with depth along the chronosequence, respectively: the surfaces of unvegetated soils are strongly exposed to environmental stressors such as UV-radiation producing a strong contrast between the surface and deep soil that is alleviated in more vegetated soils due to protection of the soil surface by plant cover. Microclimatic conditions as an important driver of microbial community structures in glacier forefields were also pointed out by Lazzaro, Gauer and Zeyer (2011) as well as Zumsteg *et al.* (2013). Moreover, in vegetated soils, interactions with the rhizosphere rather than inherent soil properties and microclimatic conditions might be the primary driver of microbial community structures. In accordance with this interpretation, the surface of barren and sparsely vegetated soils was characterized by species able to resist high UV-exposure and fluctuations in temperatures and soil moisture, such as *Phormidium* sp. (Cyanobacteria), *Sphingobacteriales* sp. (Bacteroidetes) and *Rhodotorula* sp. (Basidiomycota). Conversely, more densely

vegetated stages of soil development were marked by bacterial representatives able to use complex C-compounds (e.g. *Candidatus Solibacter* sp.), specialist lignocellulolytic ascomycetes (e.g. *Geoglossum* sp.) and ectomycorrhizal basidiomycetes (e.g. *Laccaria* sp.) in all depths. These findings additionally stress the significance of plants in structuring microbial communities in glacier forefields. Besides soil physicochemical properties and vegetation cover, bedrock mineralogy was also found to significantly impact microbial community structures in recently deglaciated soils (Carson *et al.* 2007; Lazzaro, Abegg and Zeyer 2009).

A major breakthrough in understanding the initial colonization of proglacial areas was achieved by Rime, Hartmann and Frey (2016a). The authors identified endogenous glacial habitats as the main source of bacterial colonizers, while exogenous sources (snow, wet and dry deposition) played a minor role. As opposed to bacteria, fungal communities exhibited very distinct community structures among all habitats when community structures in these potential precursor habitats were compared with recently deglaciated soils. From the observed patterns, the authors postulated that bacterial community assembly in recently deglaciated soils is driven by stochastic events and priority effects, while fungal community assembly is more controlled by deterministic processes associated with a low dispersal capacity and environmental filtering (Brown and Jumpponen 2014; Rime, Hartmann and Frey 2016a). Moreover, in a stable isotope probing approach, Rime *et al.* (2016b) showed that prokaryotic C-utilizers were similar among distinct stages of soil development, indicating that differences in environmental conditions do not influence the composition of the active prokaryotic C-utilizer populations during soil development. Conversely, fungal populations involved in the utilization of organic C-sources differed clearly among different stages of soil development. These findings support the hypothesis of stochastic versus deterministic assemblage patterns along proglacial chronosequences for bacterial and fungal communities, respectively.

Glacier forefields constitute the first alpine microbial habitat where comprehensive interdisciplinary studies have been conducted, allowing for elucidation of larger ecological relationships between microbial and plant succession as well as biogeochemical cycles (Bernasconi *et al.* 2011; Schulz *et al.* 2013; Bernasconi 2014). A major knowledge gap has been identified in the microbial succession on freshly deglaciated soils, especially in the context of the initial build-up of microbial biomass and the utilization of potential C- and N-sources. Moreover, glacier forefields are characterized by a profound geomorphological heterogeneity, and unconsolidated rock material is reworked frequently by glacial advances, landslides and streams, the effect of which has been largely neglected in studies on microbial ecology using a chronosequence approach (Bernasconi *et al.* 2011; Bradley, Singarayer and Anesio 2014). In addition, as for all alpine environments, studies on glacier forefields are restricted to very few sites, and biogeographical approaches might help to understand overall ecological patterns at a supraregional scale in the context of global gradients such as climatic latitudinal gradients. Finally, as considerable expanses of glaciated areas become exposed with climate change (Vaughan *et al.* 2013), in parallel with a substantial increase in biological activity, microbial ecology in glacier forefields should in future be studied more thoroughly with regard to the balance of uptake and losses of C and N.

THE EFFECT OF CLIMATE CHANGE ON THE ALPINE SOIL MICROBIOME

Experimental approaches to study the impact of climate change

Current approaches to study the effect of climate on soil microbial diversity and function can be divided into field-based and laboratory microcosm studies. As a field-based approach, comparative studies of soils along natural climatic gradients and related topographic features, including gradients of altitude, latitude, precipitation and stages of permafrost thaw, may be conducted (Dunne *et al.* 2004; Bryant *et al.* 2008; Wang *et al.* 2015; Siles and Margesin 2016). Moreover, in order to study soil ecosystem development after glacial retreat, a chronosequence approach is applied frequently. As the glacier retreats successively over time, spatial patterns along a transect perpendicular to the glacier snout are assumed to reflect temporal changes in response to glacial retreat and thus global warming (Walker *et al.* 2010). A more manipulative approach frequently applied in plant ecology but also used in a few soil microbial studies is to transplant soil along such gradients in order to analyze adaptation of the soil microbiome to the environmental conditions at the target site and to reveal the driving forces behind that adaptation (Zumsteg *et al.* 2013). Moreover, temperature and other climatic variables can be manipulated directly in the field. For instance, temperature has frequently been elevated passively by the use of open top chambers (OTC) that trap natural heat (Bokhorst *et al.* 2011; Lamb *et al.* 2011; Yergeau *et al.* 2012; Zhang *et al.* 2015a; Rousk, Michelsen and Rousk 2016). Alternatively, temperature may be actively manipulated by the use of underground heating wires or infrared radiators (Aronson and McNulty 2009; Hagedorn, Mulder and Jandl 2010b; Schindlbacher *et al.* 2011). Precipitation can be reduced by the use of roofs or increased by the use of sprinklers (Beier *et al.* 2012). Increased snow accumulation can be achieved using snow fences to trap drifted snow (Morgado *et al.* 2016; Ricksetts *et al.* 2016) or reduced by shoveling manually or by the application of a warming treatment, for instance by the use of dark cloth covers (for a review, see Wipf and Rixen 2010). Laboratory incubation experiments, on the other hand, permit analyses of climatic parameters under controlled conditions, avoiding the confounding effect of natural fluctuations (Wu *et al.* 2015). However, as a disadvantage, laboratory incubations implicate largely artificial conditions only partially reflecting the natural environment. In microcosms, the impact of climate-related parameters such as temperature, moisture, light regime and freeze-thaw cycles can be analyzed. An overview of climate change studies in alpine environments is given in Table 1b. Approaches to study the impact of climate change in alpine environments are summarized and discussed in Table 2.

Soil transplantation experiments along natural climatic gradients

As climatic parameters such as temperature and precipitation change with altitude, altitudinal transects may be used to study the effect of climate on the soil microbiome. Indeed, temperature and precipitation have been identified as important drivers of microbial community structures along altitudinal gradients (Yuan *et al.* 2014; Liu *et al.* 2015; Rui *et al.* 2015; Ren *et al.* 2018). Thus, assuming that altitudinal patterns along transects reflect temporal changes with global warming, one might hypothesize that the differences in microbial community structures and

Table 2. Experimental approaches to study the impact of climate change on soil microbial ecology

Field approaches: Field approaches reflect best natural conditions, but are associated with covarying environmental variables such as e.g. climatic variables and soil physicochemical properties (natural gradients) and subject to natural fluctuations obscuring treatment effects (natural gradients, experimental manipulation)

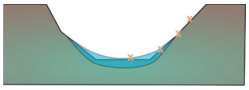
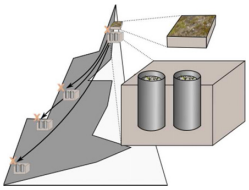
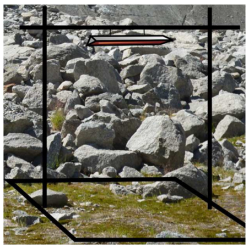
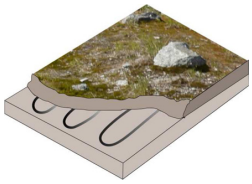
	Method	Figure/Description	Pro	Contra
Studies along natural gradients	Descriptive comparison: Most simple approach, but most complex to separate target climatic variable from covarying factors			
	Temperature gradients	Transects along temperature gradients (e.g. altitudinal, latitudinal, slope aspect)	• Little effort • Gradients over large range possible • Multiple sampling points along gradient enable investigation of gradual response	• Covarying environmental factors • Natural fluctuations • Indirect approach, assumes that spatial gradient reflects development over time
	Chronosequences	Space for time substitution (e. g. after glacier retreat, used extensively to study soil ecosystem development)		
	Moisture gradients			
	Soil transplantation: More direct approach compared to descriptive approach, actively exposing soils to presumable future conditions, but still associated with complex covariation patterns; Relatively cheap and easy to perform in remote environments			
	Intact cores or monoliths		• Active exposure of soils to "future conditions" • Preserves soil structure and vegetation	• Conditions at target site subject to fluctuations • Immigration of microbes from target site • Artefacts (different conditions within core)
	Loose soil		• Active exposure of soils to "future conditions" • Easy to obtain soil • Easy to transport soil in bags	• As for core transplantation • Strong creation of artefacts (disruption of soil structure, removal of plants =>suitable controls indispensable)
Field manipulation of climatic parameters	Temperature manipulations			
	Open top chambers (trapping natural heat)		• Cheap, easy to install • No energy supply needed	• Small temperature increase • Warming depends on ambient temperature • Artefacts (e. g. change of gas concentrations)
	Overhead infrared lights		• Reflects best "natural" warming (heating from above) • Controlled amount of heating	• Expensive • Energy supply needed (especially difficult in remote areas)

Table 2. Continued

	Method	Figure/Description	Pro	Contra
Field approaches: Field approaches reflect best natural conditions, but are associated with covarying environmental variables such as e.g. climatic variables and soil physicochemical properties (natural gradients) and subject to natural fluctuations obscuring treatment effects (natural gradients, experimental manipulation)				
	Soil warming cables		• Relatively cheap • Controlled amount of heating	• Heating from below, temperature gradient away from cable • Disturbance of soil installing cables • Energy supply needed
	Moisture manipulations Roofs (=>reduction of precipitation input)		• Cheap, easy to install • No energy supply needed	• Treatment effect depends on ambient conditions • Accumulation of water from roofs in adjacent plots
	Irrigation	Installation of sprinklers	• Controlled amount of water added	• Expensive • Complex system, difficult to install in remote areas
	Snow cover manipulation Snow fences (accumulation of snow)		• Cheap, easy to install • No energy supply needed	• Treatment effect depends on natural snowfall
	Warming treatments	OTCs, infrared lights, soil warming cables or dark cloth covers	• See warming treatments	• See warming treatments
	Removal or accumulation with shovels		• Cheap, easy to perform	• Site needs to be accessible under harsh winter conditions • Frequent access needed
Laboratory approaches: Laboratory microcosm studies allow for investigation of the impact of climatic factors under very controlled conditions where only one variable at a time is modulated. However, it is questionable how well laboratory studies reflect field conditions and thus can be used to make predictions about natural ecosystems.				
Laboratory approaches:	Temperature incubations Temperature cycles Freeze-thaw cycles Moisture manipulation etc.	In incubators or climate chambers microcosm experiment can be set up and used to study the impact of climatic variables in a constant or cyclic treatment	• No expensive field campaigns needed once samples are collected • One parameter manipulated at a time • Defined amount of temperature / moisture / etc. manipulations • Proximity to laboratory facilities	• Massive change compared to field conditions (disruption of soil structure, removal of plants unless intact cores are used, no diurnal or seasonal temperature cycles, light input => change of primary production…)

function discussed above are similar to those that warming will cause in high alpine soils. In this scenario, high-altitude soil microbial communities would be expected to increasingly resemble those present at lower sites.

In merely descriptive studies, climatic variables such as temperature and precipitation covary with plant diversity and soil physicochemical properties, and associations are based solely on correlations. In order to corroborate the impact of prevalent environmental conditions on the soil microbiome, transplantation of soil along altitudinal gradients has been used as a more direct approach (Budge *et al.* 2011; Lazzaro, Gauer and Zeyer 2011; Zheng *et al.* 2014; Gou *et al.* 2015; Rui *et al.* 2015; Yue *et al.* 2015). In such studies, soils become experimentally exposed to their presumed future conditions. Zumsteg *et al.* (2013) used a reciprocal soil transplantation approach in an unvegetated glacier forefield to investigate adaptation of the soil microbiome to microclimatic conditions associated with contrasting slope aspects in a valley bottom (Table 1b). These studies revealed significant shifts in microbial community structures and functions in response to soil transplantation (Budge *et al.* 2011; Zumsteg *et al.* 2013; Zheng *et al.* 2014; Gou *et al.* 2015; Rui *et al.* 2015; Yue *et al.* 2015) that can be hypothesized to be induced in a similar manner by climate change. Similar to in descriptive studies of altitudinal gradients, temperature, moisture and vegetation patterns were identified as important drivers of microbial community structures and function in soil transplantation studies (Zumsteg *et al.* 2013; Zheng *et al.* 2014; Rui *et al.* 2015). For instance, in reciprocal soil transplantation experiment along an altitudinal gradient from 3200–3800 m a.s.l. on the Tibetan plateau, Rui *et al.* (2015) found that 13.6% of the variation in microbial community structures could be attributed, to temperature alone, 11.4% to soil properties alone and 7.9% to temperature, soil properties and plant biomass. Thus, these studies point out the importance of climatic parameters and thus the considerable effect of climate change on alpine soil microbial communities.

Soil transplantation experiments have also been used to study the impact of warming on microbial functional genes (Zheng *et al.* 2014; Yue *et al.* 2015). The reactions catalyzed by the functional genes discussed in the following section are shown in Fig. 4. Yue *et al.* (2015) mimicked warming by downward transplantation of soil along an altitudinal gradient in the Qilian mountains (Tibetan Plateau, China) ranging from 3200 to 3800 m a.s.l. Using GeoChip, they observed a decrease in C-degradation genes, especially such that are associated with degradation of recalcitrant substrates, e.g. cellobiase and exochitinase while the *pcc* gene (Propionyl-CoA carboxylase, involved in C-fixation) increased. This could be interpreted as lower degradation of organic matter with a simultaneous increase of CO_2-uptake from the atmosphere upon downward transplantation. The majority of N-cycling genes decreased with the exception of *narG* (nitrate reductase G, reduces nitrate to nitrite) and *gdh* (glutamate dehydrogenase). Decrease of *gdh* with concurrent increase of *ureC* (urease C) could point towards increased release of ammonia from organic matter. Concomitantly, total organic C, total N and ammonia as well as vegetation biomass increased upon warming. An increase of total N however cannot be explained by the observed changes in N-cycling genes at the DNA level as abundance of the N-fixation gene *nifH* (nitrogenase H) decreased upon warming, while at the same time N_2O emissions increased. Collectively, from their findings, the authors concluded that the alpine grassland soils harbor a negative feedback mechanism to increased microbial mineralization due to warming, thereby keeping the balance between C- and N-uptake and release constant despite warming. This interpretation was supported by relatively stable C-stocks in Tibetan grassland, whereas warming has been shown to cause C-loss due to enhanced microbial mineralization in other northern soils (Yue *et al.* 2015). As microbial N-cycling is expected to be significantly altered by climate change, Zheng *et al.* (2014) studied the abundance and diversity of N-cycling genes in response to reciprocal soil transplantation along an altitudinal gradient spanning 600 m of vertical distance in the Qilian mountains (Tibetan Plateau, China). They reported a significant increase in the abundance of the bacterial *amoA* gene (ammonia monooxygenase A, function: See above) upon downward soil transplantation, while the abundance of the archaeal *amoA* gene was less affected by soil transplantation. Moreover, the abundance of *nir*K (nitrite reductase K, converts nitrite to nitrous oxide, part of denitrification) was lower in the control transplants at the higher altitude and decreased upon upwards transplantation but did not react to downward transplantation. The abundance of *nir*S (nitrite reductase S) and *nos*Z (nitrous oxide reductase Z, converts nitrous oxide to molecular nitrogen, part of denitrification) remained unaffected. This could indicate enhanced transformation of NH_4^+ to NO_3^- in downward transplants but at the same time an increase of denitrification.

To the best of our knowledge, no transplantation experiments along altitudinal gradients have been conducted in the Arctic to date. However, the effects of transplantation along 500–1000 m altitudinal gradients on soil microbial community structures and function in alpine regions are comparable to the effects of soil transplantation along a latitudinal gradient from northern to southern Finland (Vanhala *et al.* 2011), indicating similarities in the responses of alpine and arctic microbial communities to climate change. Altitudinal gradients are associated with similar changes in climatic regime in the Arctic compared with in alpine regions and would therefore constitute a useful, easily applicable set-up for the study of climate change in arctic regions. Topographic effects, such as slope aspect, associated with changes in incoming solar radiation throughout the day are smaller in the Arctic compared with in temperate and tropical mountain regions because of smaller diurnal variations (Barry 2008b) but might still be used effectively to study adaptation of the soil microbiome to particular climatic conditions.

The number of soil transplantation studies in alpine environments is still very limited and mostly restricted to altitudinal gradients. Consequently, microbial community structures and function should be studied more intensively among contrasting topographic features in order to obtain a comprehensive understanding of alpine microbial ecology and associated biogeochemical fluxes (Zumsteg *et al.* 2013). To this end, soil transplantation constitutes a suitable experimental approach allowing assessments of adaptation to given environmental conditions. Moreover, contrasting slope aspects on mountain ridges provide an interesting experimental set-up to study climatic effects, as sharp microclimatic contrasts may be present over a very short distance, reducing the variability of other soil-forming factors compared with the variability occurring within gradients over larger spatial intervals such as altitudinal gradients (Frey *et al.* 2016). In addition, relative to slopes and valleys, ridges and summits are less affected by landslides and do not receive input from transported rock material, further stressing their suitability for climate studies with minimal confounding effects (Pauli *et al.* 2015).

Soil warming experiments

To avoid the confounding effects of covarying environmental variables along altitudinal transects, several studies have used experimental warming applied directly in the field (Zheng *et al.* 2012; Xiong *et al.* 2014; Zhang *et al.* 2015a; Zhang *et al.* 2015b; Li *et al.* 2016a; Zhang *et al.* 2016) or in a laboratory setting with a controlled climate (Wu *et al.* 2015). Warming treatments have been applied for between one and three years with the use of OTCs (Papanikolaou *et al.* 2010; Zhang *et al.* 2015a) or overhead infrared radiators (Xiong *et al.* 2014; Li *et al.* 2016a; Zhang *et al.* 2015b; Zhang *et al.* 2016). As climate change might also involve changes in precipitation regimes, Zhang *et al.* (2016) additionally manipulated (increased and decreased) precipitation. Most of these studies reported shifts in microbial (bacterial and fungal) community structures in response to warming (Papanikolaou *et al.* 2010; Xiong *et al.* 2014; Li *et al.* 2016a). However, Zhang *et al.* (2016) found that warming only had an effect on bacterial communities when combined with reduced or enhanced precipitation after one year; these changes were shown to be driven by changes in moisture, while fungi remained unaffected by warming, precipitation and combined treatments. These findings highlight that, besides warming, climate change may induce altered precipitation, which may critically affect the soil microbiome in arid mountain ranges such as the Tibetan Plateau. Moreover, Li *et al.* (2016a) proposed that microbial community structures will become more homogeneous over space in response to climate change, as they observed such patterns in response to experimental warming in the Qilian mountains (Tibetan Plateau, China). Direct effects of increased temperature, as well as indirect changes in soil and plant properties, have been revealed as drivers of microbial diversity in warming experiments (Xiong *et al.* 2014).

Besides diversity, microbial function and thus dynamics of nutrient cycling and greenhouse gas budgets might be strongly altered in response to climate change. Therefore, Zheng *et al.* (2012) investigated the methanotrophic community in response to infrared-induced warming in an alpine meadow soil at 3200 m a.s.l. on the Tibetan Plateau, China for three years. The abundance of the *pmoA* gene (particulate methane monooxygenase A, key enzyme involved in the oxidation of methane) and the potential CH_4-oxidation increased following warming treatment, while *pmoA* abundance was negatively correlated with moisture and NH_4-N-content. Conversely, methanotrophic community compositions were not affected by warming. These results suggest that enhanced methane oxidation might efficiently counteract a potential warming-induced increase in CH_4-emissions in these ecosystems. Another study on microbial function was conducted by Papanikolaou *et al.* (2010). The authors assessed enzyme activity and litter degradation as microbial functional traits in a low-alpine heath ecosystem in Scotland, revealing that these parameters were hardly affected after 22 months of warming by OTCs.

Functional warming responses of soil microbial communities have been also assessed in arctic environments, although studies are similarly scarce as in alpine environments. With regard to microbial C-cycling, most studies were conducted in organic matter rich, permafrost affected soils either in thaw-experiments or in anoxic incubations of water-logged active layers that result from permafrost thaw – soil properties as they are rarely found in alpine ecosystems complicating comparability of findings. Such studies reported increased CH_4- and CO_2-emission upon warming going along with shifts of microbial functional gilds involved in degradation of organic matter, methanogenesis and methane oxidation as analyzed using Geochip or metagenomics/metatranscriptomics (Tveit *et al.* 2015; Yang *et al.* 2016b; Yang *et al.* 2017). Lamb *et al.* (2011) conducted a long-term (16 years) field warming and fertilization experiment in tundra soils in the Canadian High Arctic using OTCs. Warming increased vegetation cover but surprisingly greenhouse gas fluxes, soil properties (SOC, dissolved organic nitrogen, NH_4^+, NO_3^-) as well as abundance of the microbial N-cycling genes *amoA* (ammonia monooxygenase A, function: see above) and *nosZ* (nitrous oxide reductase Z, function: see above) remained stable. In an N-fertilization treatment of geothermally warmed soils in subarctic Iceland, Daebeler *et al.* (2012) found that archaeal *amoA* was higher in fertilized and warmed plots, respectively, compared to the control plots, indicating that nitrification plays a more important role in the warmed and fertilized plot, respectively. However, soil physicochemical properties including NH_4^+-content did not change significantly and *amoA* community structures were better explained by pH and clay than warming and fertilization. This highlights the importance of intrinsic soil properties in driving microbial functional gilds and thus determining warming responses. Incubating these soils in microcosms at different temperatures, the authors reported that soils with warmer *in-situ* temperatures exhibited higher gross nitrification with a higher temperature optimum, with *in-situ* soil temperature and gross nitrification being strong predictors of archaeal *amoA* communities at the RNA level (Daebeler *et al.* 2017). Also N-fertilization as well as interactions between *in-situ* temperature and fertilization influenced N-transformation rates highlighting that prediction of N-cycling responses to warming requires the consideration of complex, dynamic interactions between intrinsic environmental conditions and adaptation of the soil microbiome. The only existing microcosm study on the effect of warming on alpine soil microbial communities was conducted by Wu *et al.* (2015). They applied a temperature gradient from 10°C to 40°C for 28 days on alpine meadow soils from sites at 4635 m a.s.l. on the Tibetan Plateau. After this period, pronounced changes were observed in bacterial community structures and C-utilization patterns (as assessed by the use of Ecoplate) at all temperatures. In addition, a subset of temperature treatments was sampled at several points throughout the incubation period, revealing that shifts in microbial community structures in response to elevated temperatures occurred in gradual manner over time.

Collectively, studies using experimental warming have suggested that the alpine soil microbiome might react significantly in response to global warming. In many studies, rather subtle changes were reported in response to temperature increase, which might be attributed to the relatively short duration of the experiments. For example, in arctic environments it has been shown that global warming affects soil microbial functions only on a decadal scale rather than in short-term experiments (Rinnan *et al.* 2007; Lamb *et al.* 2011). Similarly, alpine ecosystems might not react significantly over short time frames.

FUTURE PERSPECTIVES

Microbes have been shown to exhibit a surprisingly high diversity in cold alpine environments under harsh conditions where plant growth is largely restricted due to climatic restrictions and the paucity of nutrients (Bryant *et al.* 2008; Fierer *et al.* 2011; Rime *et al.* 2015). Thus, in these habitats microorganisms are the main ecosystem engineers governing C- and nutrient cycling. Microbial diversity and function have been shown to respond sensitively to warming (e.g. Rui *et al.* 2015; Li *et al.* 2016a) leading to

an acceleration of C- and N-cycling possibly associated with net losses from the system (Hagedorn *et al.* 2010a; Dawes *et al.* 2017). Conversely, for instance Yue *et al.* (2015) reported that some alpine grassland soils possess a feedback mechanism counteracting increased mineralization in response to warming ultimately keeping C- and N-stocks stable. Warming directly affects microbial activity and diversity, but simultaneously soil properties, quality of organic matter, soil nutrient status, vegetation properties and biotic interactions change, partially as they are directly affected by warming and partially in response to altered microbial activity. Such co-occurring effects and feedback mechanisms likely explain contrasting results with regard to C-stock changes and N-dynamics in response to warming in alpine environments. Microbial dynamics are an important component in this equation and a deeper understanding of microbial ecology will contribute to elucidate patterns of biogeochemical cycling in response to warming at the ecosystem level. With warming increased activity of microbial pioneers will likely facilitate expansion of plants to higher altitudes analogously to plant colonization along a glacier forefield chronosequence. Cryospheric microbial habitats such as glacial ice or permafrost soils are currently characterized by very low cell numbers and activity. Once these inhospitable habitats diminish, increasing microbial growth, activity and subsequent establishment of plants will likely lead to increased primary production as well as accelerated biogeochemical cycling on considerable land expanses. Environments currently dominated by ice and snow as well as harsh environmental conditions might become more hospitable and thus more similar to lowland environments, reducing the richness of microbial niches. Thus, reduction of the cryosphere could signify a considerable loss of microbial diversity such as observed for plant diversity in alpine environments with warming (Pauli, Gottfried and Grabherr 2003). Besides ecological consequences, melting of cryospheric components of alpine ecosystems also potentially entails the risk of releasing pathogens, and indeed potentially pathogenic microbes have been recovered from cold environments (Butinar, Spencer-Martins and Gunde-Cimerman 2007; Petrova *et al.* 2008; Legendre *et al.* 2014). This potential global change impact is especially relevant for alpine environments, as they are often closely associated with human populations that might be reached via air circulation or through hydrological processes.

To date microbial studies are extremely scarce and do not yet make it possible to draw comprehensive conclusions about large-scale ecological patterns and biogeochemical cycles. Especially if one considers the heterogeneity of alpine habitats that exist across all latitudes and climate systems, with regard to topography, climate, soil forming processes, vegetation patterns and microbial diversity, large datasets and studies with a fine spatial resolution are required if results should be upscaled to the supraregional level or compared with other cold-dominated environments such as the Arctic. Biogeographical approaches could be used to elucidate large-scale distribution and mechanisms of adaptation to the local ambient conditions in alpine habitats (Pellissier *et al.* 2014). Seasonality and depth-related patterns are further important factors shaping alpine microbial ecology that have been largely neglected to date. Changes in alpine soil microbial diversity and function in response to climate change occur in tandem with changes in soil physicochemical properties and vegetation patterns. Therefore, comprehensive interdisciplinary studies are needed to obtain a process-based understanding of microbial ecology at the ecosystem level and to disentangle covarying variables (Bernasconi 2014). Moreover, investigating shifts of symbiotic or competitive interactions among microorganisms in response to environmental conditions by the analysis of co-occurrence patterns could yield a more mechanistic understanding of microbial feedbacks to warming impacts (Foster and Bell 2012; Gokul *et al.* 2016). To date, most studies on alpine microbial diversity have used amplicon sequencing of phylogenetic marker genes providing information on microbial identity and community structures but not on microbial function. The application of metagenomic and metatranscriptomic approaches which have been successfully applied in arctic environments (Coolen and Orsi 2015; Hultman *et al.* 2015; Johnston *et al.* 2016), could significantly contribute to the identification of important microbial functional traits shaping ecosystem functioning in alpine environments. Thus, these techniques could help to corroborate the link between the microbial functional potential and biogeochemical dynamics. The high diversity of microbial taxa found in high-alpine soils opens a new and exciting microbial resource that might be exploited for biotechnological purposes. Cold-adapted enzymes from psychrophilic microorganisms require low thermal energy and catalyze biochemical reactions at low temperature with rates comparable to mesophilic enzymes at their optimum temperature. Of these properties, advantage could be taken in industrial processes providing environmentally friendly, energy-saving solutions avoiding the use of aggressive chemicals. Such approaches have been already successfully applied e.g. producing detergents or in food industry (Huston 2008). In addition, secondary metabolites from fungi are widely used e.g. as antibiotics, to date however mostly from warm environments (Frisvad 2008). Exploration of cold environments such as the Arctic and alpine regions could significantly extend the reservoir of substances with potential pharmaceutical applications. A particular characteristic of alpine environments are high levels of UV-radiation against which alpine microorganisms evolved protection mechanisms (Karsten and Holzinger 2014) including protective molecules which are currently tested for their potential in protecting human skin from UV-damage (Ariede *et al.* 2017). To utilize such microbial resources culture-independent tools such as metagenomics as well as isolation of cold-adapted microbes could be applied. The development of new isolation techniques, such as the high-throughput isolation chip (ichip, Nichols *et al.* 2010) and the improvement of sequencing techniques, might facilitate the isolation of microbes from high-alpine soil samples and thus exploitation of their biotechnological potential as well as understanding their ecological role.

Overall, recognition of the importance of alpine microorganisms has emerged only very recently, and therefore our current knowledge of alpine microbial ecology remains severely limited. However, especially in the context of climate change, increasing attention has been directed towards mountain environments. With the help of new molecular tools that have already been successfully employed in arctic environments, as well as more comprehensive large-scale studies, one can be optimistic that our knowledge about alpine microorganisms will soon grow towards a comprehensive ecological understanding including biotic and abiotic interactions at the local as well as at the regional scale.

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REFERENCES

Ariede MB, Candido TM, Jacome ALM *et al.* Cosmetic attributes of algae—a review. *Algal Res* 2017;**25**:483–7.

Aronson EL, McNulty SG. Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agric Forest Meteorol* 2009;**149**:1791–99.

Bai E, Li S, Xu W *et al.* A meta-analysis of experimental warming effects on terrestrial nitrogen pools and dynamics. *New Phytol* 2013;**199**:441–51.

Bai Y, Yang D, Wang J *et al.* Phylogenetic diversity of culturable bacteria from alpine permafrost in the Tianshan Mountains, northwestern China. *Res Microbiol* 2006;**157**:741–51.

Bakermans C. Limits for microbial life at subzero temperatures. In: Margesin R, Schinner F, Marx J-C *et al.* (eds). *Psychrophiles: From Biodiversity to Biotechnology*. Berlin, Heidelberg: Springer, 2008, 17–28.

Bardgett RD, Freeman C, Ostle NJ *et al.* Microbial contributions to climate change through carbon cycle feedbacks. *ISME J* 2008;**2**:805–14.

Bardgett RD, Richter A, Bol R *et al.* Heterotrophic microbial communities use ancient carbon following glacial retreat. *Biol Lett* 2007;**3**:487–90.

Barry RG. Geographical controls of mountain meteorological elements. In: Barry RG (ed). *Mountain Weather and Climate*. Cambridge: Cambridge University Press, 2008b;24–124.

Barry RG. Mountains and their climatological study. In: Barry RG (ed). *Mountain Weather and Climate*. Cambridge: Cambridge University Press, 2008a, 1–23.

Beier C, Beierkuhnlein C, Wohlgemuth T *et al.* Precipitation manipulation experiments—challenges and recommendations for the future. *Ecol Lett* 2012;**15**:899–911.

Bernasconi SM, Bauder A, Bourdon B *et al.* Chemical and biological gradients along the Damma glacier soil chronosequence, Switzerland. *Vadose Zone J* 2011;**10**:867–83.

Bernasconi SM. Measuring the critical zone: Lessons from the Damma glacier critical zone observatory. *Procedia Earth Planet Sci* 2014;**10**:38–45.

Björk RG, Björkman MP, Andersson MX *et al.* Temporal variation in soil microbial communities in Alpine tundra. *Soil Biol Biochem* 2008;**40**:266–68.

Blaalid R, Carlsen T, Kumar S *et al.* Changes in the root-associated fungal communities along a primary succession gradient analysed by 454 pyrosequencing. *Mol Ecol* 2012;**21**:1897–908

Bockheim JG, Munroe JS. Organic carbon pools and genesis of alpine soils with permafrost: a review. *Arctic, Antarctic, Alpine Res* 2014;**46**:987–1006.

Bockheim JG. Global distribution of cryosols with mountain permafrost: an overview. *Permafrost Periglac Process* 2015;**26**:1–12.

Bokhorst S, Huiskes A, Convey P *et al.* Microclimate impacts of passive warming methods in Antarctica: implications for climate change studies. *Polar Biol* 2011;**34**:1421–35.

Bradley JA, Singarayer JS, Anesio AM. Microbial community dynamics in the forefield of glaciers. *Proc Biol Sci/Roy Soc* 2014;**281**:1795.

Brankatschk R, Towe S, Kleineidam K *et al.* Abundances and potential activities of nitrogen cycling microbial communities along a chronosequence of a glacier forefield. *ISME J* 2011;**5**:1025–37.

Bridges EM, Van Baren JHV. Soil: an overlooked, undervalued and vital part of the human environment. *Environmentalist* 1997;**17**:15–20.

Browning KA, Hill FF. Orographic rain. *Weather* 1981;**36**:326–28.

Brown SP, Jumpponen A. Contrasting primary successional trajectories of fungi and bacteria in retreating glacier soils. *Mol Ecol* 2014;**23**:481–97.

Bryant JA, Lamanna C, Morlon H *et al.* Microbes on mountainsides: contrasting elevational patterns of bacterial and plant diversity. *Proc Natl Acad Sci USA* 2008;**105**:11505–11.

Budge K, Leifeld J, Egli M *et al.* Soil microbial communities in (sub)alpine grasslands indicate a moderate shift towards new environmental conditions 11 years after soil translocation. *Soil Biol Biochem* 2011;**43**:1148–54.

Butinar L, Spencer-Martins I, Gunde-Cimerman N. Yeasts in high Arctic glaciers: the discovery of a new habitat for eukaryotic microorganisms. *Antonie van Leeuwenhoek* 2007;**91**:277–89.

Buzzini P, Branda E, Goretti M *et al.* Psychrophilic yeasts from worldwide glacial habitats: diversity, adaptation strategies and biotechnological potential. *FEMS Microbiol Ecol* 2012;**82**:217–41.

Calbó J, Pagès D, González JA. Empirical studies of cloud effects on UV radiation: a review. *Rev Geophys* 2005;**43**:2.

Capkova K, Hauer T, Řeháková K *et al.* Some Like it High! Phylogenetic diversity of high-elevation cyanobacterial community from biological soil crusts of western Himalaya. *Microb Ecol 7* 2016;**1**:113–23.

Carson JK, Rooney D, Gleeson DB *et al.* Altering the mineral composition of soil causes a shift in microbial community structure. *FEMS Microbiol Ecol* 2007;**61**:414–23.

Chang X, Wang S, Cui S *et al.* Alpine Grassland Soil Organic Carbon Stock and Its Uncertainty in the Three Rivers Source Region of the Tibetan Plateau. *PLoS One*; 2014;**9**:e97140.

Chen L, Jing X, Flynn DFB *et al.* Changes of carbon stocks in alpine grassland soils from 2002 to 2011 on the Tibetan Plateau and their climatic causes. *Geoderma* 2017;**288**:166–74.

Christiansen HH, Etzelmüller B, Isaksen K *et al.* The thermal state of permafrost in the nordic area during the international polar year 2007–2009. *Permafrost Periglac Processes* 2010;**21**:156–81.

Ciccazzo S, Esposito A, Rolli E *et al.* Safe-site effects on rhizosphere bacterial communities in a high-altitude alpine environment, *BioMed Res Int* 2014.

Classen AT, Sundqvist MK, Henning JA *et al.* Direct and indirect effects of climate change on soil microbial and soil microbial-plant interactions: What lies ahead? *Ecosphere* 2015;**6**:1–21.

Collins CG, Carey CJ, Aronson EL *et al.* Direct and indirect effects of native range expansion on soil microbial community structure and function. *J Ecol* 2016;**104**:1271–83.

Collins M, Knutti R, Arblaster J *et al.* Long-term climate change: projections, commitments and irreversibility. In: Stocker TF, Qin D, Plattner G.-K. *et al.* (eds). *Climate Change 2013: The Physical Science Basis Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press, 2013;1029–36.

Coolen MJL, Orsi WD. The transcriptional response of microbial communities in thawing Alaskan permafrost soils. *Front Microbiol* 2015;**6**:197.

Costello EK, Schmidt SK. Microbial diversity in alpine tundra wet meadow soil: Novel. Chloroflexi from a cold, water-saturated environment. *Environ Microbiol* 2006;**8**:1471–86.

Crowther TW, Todd-Brown KEO, Rowe CW *et al.* Quantifying global soil carbon losses in response to warming. *Nature* 2016;**540**:104.

D'Amico S, Collins T, Marx JC *et al.* Psychrophilic microorganisms: challenges for life. *EMBO Rep* 2006;**7**:385–89.

Daebeler A, Abell G, Bodelier P *et al.* Archaeal dominated ammonia-oxidizing communities in Icelandic grassland soils are moderately affected by long-term N fertilization and geothermal heating. *Front Microbiol* 2012;**3**:352.

Daebeler A, Bodelier PLE, Hefting MM *et al.* Soil warming and fertilization altered rates of nitrogen transformation processes and selected for adapted ammonia-oxidizing archaea in subarctic grassland soil. *Soil Biol Biochem* 2017;**107**:114–24.

Davidson EA, Janssens IA. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 2006;**440**:165–73.

Dawes MA, Schleppi P, Hättenschwiler S *et al.* Soil warming opens the nitrogen cycle at the alpine treeline. *Global Change Biol* 2017;**23**:421–34.

De Maayer P, Anderson D, Cary C *et al.* Some like it cold: understanding the survival strategies of psychrophiles. *EMBO Rep* 2014;**15**:508–17.

Diaz HF, Grosjean M, Graumlich L. Climate variability and change in high elevation regions: past, present and future. *Climatic Change* 2003;**59**:1–4.

Duc L, Noll M, Meier BE *et al.* High diversity of diazotrophs in the forefield of a receding alpine glacier. *Microbial Ecol* 2009;**57**:179–90.

Dunne JA, Saleska SR, Fischer ML *et al.* Integrating experimental and gradient methods in ecological climate change research. *Ecology* 2004;**85**:904–16.

Egli M, Hitz C, Fitze P *et al.* Experimental determination of climate-change effects on above-ground and below-ground organic matter in alpine grasslands by translocation of soil cores. *J Plant Nutr Soil Sci* 2004;**167**:457–70.

Egli M, Sartori G, Mirabella A *et al.* Effect of north and south exposure on organic matter in high Alpine soils. *Geoderma* 2009;**149**:124–36.

Fernández-Martínez MA, Pointing SB, Pérez-Ortega S *et al.* Functional ecology of soil microbial communities along a glacier forefield in Tierra del Fuego (Chile). *Intl Microbiol* 2016;**19**:161–73.

Fierer N, McCain CM, Meir P *et al.* Microbes do not follow the elevational diversity patterns of plants and animals. *Ecology* 2011;**92**:797–804.

Foster Kevin R, Bell T. Competition, Not Cooperation, Dominates Interactions among Culturable Microbial Species. *Curr Biol* 2012;**22**:1845–50.

Freeman KR, Martin AP, Karki D *et al.* Evidence that chytrids dominate fungal communities in high-elevation soils. *Proc Natl Acad Sci United States Amer* 2009;**106**:18315–20.

Frey B, Buhler L, Schmutz S *et al.* Molecular characterization of phototrophic microorganisms in the forefield of a receding glacier in the Swiss Alps. *Environ Res Lett* 2013;**8**:1.

Frey B, Rieder SR, Brunner I *et al.* Weathering-associated bacteria from the Damma glacier forefield: physiological capabilities and impact on granite dissolution. *Appl Environ Microbiol* 2010;**76**:4788–96.

Frey B, Rime T, Phillips M *et al.* Microbial diversity in European alpine permafrost and active layers. *FEMS Microbiol Ecol* 2016;**92**:10.1093/femsec/fiw018.

Frisvad JC. Cold-adapted fungi as a source for valuable metabolites. In: Margesin R, Schinner F, Marx J-C *et al.* (eds). *Psychrophiles: From Biodiversity to Biotechnology*. Berlin, Heidelberg: Springer, 2008, 381–7.

Geiger R, Aron TRH, Todhunter P. *The Climate Near the Ground*. 6th edn, Lanham: Rowman and Littlefield Publishers, 2003.

Geremia RA, Puscas M, Zinger L *et al.* Contrasting microbial biogeographical patterns between anthropogenic subalpine grasslands and natural alpine grasslands. *New Phytologist* 2016;**209**:1196–207.

Gilichinsky D. Permafrost. *Encyclopedia of Environmental Microbiology*, New York: John Wiley & Sons, Inc, 2003.

Gokul JK, Hodson AJ, Saetnan ER *et al.* Taxon interactions control the distributions of cryoconite bacteria colonizing a High Arctic ice cap. *Mol Ecol* 2016;**25**:3752–67.

Gou X, Tan B, Wu F *et al.* Seasonal dynamics of soil microbial biomass C and N along an elevational gradient on the eastern Tibetan Plateau, China. *Plos One* 2015;**10**:e0132443.

Gruber S, Haeberli W. Mountain permafrost. In: Margesin R (ed). *Permafrost Soils*. Berlin, Heidelberg: Springer, 2009, 33–44.

Guelland K, Hagedorn F, Smittenberg RH, *et al.* Evolution of carbon fluxes during initial soil formation along the forefield of Damma glacier, Switzerland. *Biogeochemistry* 2013;**113**:545–561.

Guo G, Kong W, Liu J *et al.* Diversity and distribution of autotrophic microbial community along environmental gradients in grassland soils on the Tibetan Plateau. *Appl Microbiol Biotechnol* 2015;**99**:8765–76.

Göransson H, Venterink HO, Baath E. Soil bacterial growth and nutrient limitation along a chronosequence from a glacier forefield. *Soil Biol Biochem* 2011;**43**:1333–40.

Haeberli W, Gruber S. Global warming and Mountain Permafrost. In: Margesin R (ed). *Permafrost Soils*. Berlin, Heidelberg: Springer Berlin Heidelberg, 2009;205–18.

Hagedorn F, Martin M, Rixen C *et al.* Short-term responses of ecosystem carbon fluxes to experimental soil warming at the Swiss alpine treeline. *Biogeochemistry* 2010a;**97**:7–19.

Hagedorn F, Mulder J, Jandl R. Mountain soils under a changing climate and land-use. *Biogeochemistry* 2010b;**97**:1–5.

Hahn AS, Quideau SA. Shifts in soil microbial community biomass and resource utilization along a Canadian glacier chronosequence. *Can J Soil Sci* 2013;**93**:305–18.

Hartmann DL, Klein Tank AMG, Rusticucci M *et al.* Observations: atmosphere and surface. In: Stocker TF, Qin D, Plattner G.-K. *et al.* (eds). *Climate Change 2013: The Physical Science Basis Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press, 2013;159–54.

Hugelius G, Strauss J, Zubrzycki S *et al.* Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps. *Biogeosciences* 2014;**11**:6573–93.

Hultman J, Waldrop MP, Mackelprang R *et al.* Multi-omics of permafrost, active layer and thermokarst bog soil microbiomes. *Nature* 2015;**521**:208–12.

Huss M. Present and future contribution of glacier storage change to runoff from macroscale drainage basins in Europe. *Water Resour Res* 2011;**47**:7.

Huston AL. Biotechnological aspects of cold-adapted enzymes. In: Margesin R, Schinner F, Marx J-C *et al.*, (eds). *Psychrophiles:*

From Biodiversity to Biotechnology Berlin, Heidelberg: Springer, 2008;347–363.

Hu W, Zhang Q, Tian T *et al*. The microbial diversity, distribution, and ecology of permafrost in China: a review. *Extremophiles* 2015;**19**:693–705.

IPCC Annex I: atlas of global and regional climate projections In: Stocker TF, Qin D, Plattner G-K *et al*. (eds). *Climate Change 2013: The Physical Science Basis Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press, 2013;1311–94.

Janatkova K, Řeháková K, Dolezal J *et al*. Community structure of soil phototrophs along environmental gradients in arid Himalaya. *Environ Microbiol* 2013;**15**:2505–16.

Jansson JK, Tas N. The microbial ecology of permafrost. *Nat Rev Microbiol* 2014;**12**:414–25.

Jiang N, Li Y, Zheng C *et al*. Characteristic microbial communities in the continuous permafrost beside the bitumen in Qinghai-Tibetan Plateau. *Environ Earth Sci* 2015;**74**:1343–52.

Johnston ER, Rodriguez-R LM, Luo C *et al*. Metagenomics reveals pervasive bacterial populations and reduced community diversity across the Alaska tundra ecosystem. *Front Microbiol* 2016;**7**:579.

Karsten U, Holzinger A. Green algae in alpine biological soil crust communities: acclimation strategies against ultraviolet radiation and dehydration. *Biodivers Conserv* 2014;**23**:1845–58.

Kazemi S, Hatam I, Lanoil B. Bacterial community succession in a high-altitude subarctic glacier foreland is a three-stage process. *Mol Ecol* 2016;**25**:5557–67.

King A, Karki D, Nagy L *et al*. Microbial biomass and activity in high elevation (>5100 meters) soils from the Annapurna and Sagarmatha regions of the Nepalese Himalayas. *Himal J Sci* 2011;**6**:11–8.

Knelman JE, Legg TM, O'Neill SP *et al*. Bacterial community structure and function change in association with colonizer plants during early primary succession in a glacier forefield. *Soil Biol Biochem* 2012;**46**:172–80.

Körner C. Plant ecology at high elevations. In: Körner C (ed). *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*, Berlin, Heidelberg: Springer, 2003;1–7.

Lamb EG, Han S, Lanoil BD *et al*. A High Arctic soil ecosystem resists long-term environmental manipulations. *Global Change Biol* 2011;**17**:3187–94.

Lapanje A, Wimmersberger C, Furrer G *et al*. 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* 2012;**63**:865–82.

Lazzaro A, Abegg C, Zeyer J. Bacterial community structure of glacier forefields on siliceous and calcareous bedrock. *Eur J Soil Sci* 2009;**60**:860–70.

Lazzaro A, Brankatschk R, Zeyer J. Seasonal dynamics of nutrients and bacterial communities in unvegetated alpine glacier forefields. *Appl Soil Ecol* 2012;**53**:10–22.)

Lazzaro A, Gauer A, Zeyer J. Field-scale transplantation experiment to investigate structures of soil bacterial communities at pioneering sites. *Appl Environ Microbiol* 2011;**77**:8241–48.

Lazzaro A, Hilfiker D, Zeyer J. Structures of microbial communities in alpine soils: seasonal and elevational effects. *Front Microbiol* 2015;**6**:1330.

Legendre M, Bartoli J, Shmakova L *et al*. Thirty-thousand-year-old distant relative of giant icosahedral DNA viruses with a pandoravirus morphology. *Proc Natl Acad Sci* 2014;**111**:4274–79.

Lipson DA. Relationships between temperature responses and bacterial community structure along seasonal and altitudinal gradients. *FEMS Microbiol Ecol* 2007;**59**:418–27.

Liu L, Hart MM, Zhang J *et al*. Altitudinal distribution patterns of AM fungal assemblages in a Tibetan alpine grassland. *FEMS Microbiol Ecol* 2015;**91**:fiv078.

Liu S, Zhang F, Du Y *et al*. Ecosystem carbon storage in Alpine Grassland on the Qinghai Plateau. *PLOS One* 2016;**11**:e0160420.

Li Y, Lin Q, Wang S *et al*. Soil bacterial community responses to warming and grazing in a Tibetan alpine meadow. *FEMS Microbiol Ecol* 2016a;**92**:10.1093/femsec/fiv152.

Li Y, Wang S, Jiang L *et al*. Changes of soil microbial community under different degraded gradients of alpine meadow. *Agr Ecosyst Environ* 2016b;**222**:213–22.

Mackelprang R, Waldrop MP, DeAngelis KM *et al*. Metagenomic analysis of a permafrost microbial community reveals a rapid response to thaw. *Nature* 2011;**480**:368–71.

Mania I, D'Amico M, Freppaz M *et al*. Driving factors of soil microbial ecology in alpine, mid-latitude patterned grounds (NW Italian Alps). *Biol Fertility Soils* 2016;**52**:1135–48.

Margesin R, Jud M, Tscherko D *et al*. Microbial communities and activities in alpine and subalpine soils. *FEMS Microbiol Ecol* 2009;**67**:208–18.

Margesin R, Miteva V. Diversity and ecology of psychrophilic microorganisms. *Res Microbiol* 2011;**162**:346–61.

Margesin R, Schumann P, Spröer C *et al*. Arthrobacter psychrophenolicus sp. nov., isolated from an alpine ice cave. *Int J Syst Evolut Microbiol* 2004;**54**:2067–72.

Margesin R. Psychrophilic microorganisms in Alpine Soils. In: Lütz C (ed). *Plants in Alpine Regions: Cell Physiology of Adaption and Survival Strategies*. Vienna: Springer, 2012;187–98.

McGuire AD, Anderson LG, Christensen TR *et al*. Sensitivity of the carbon cycle in the Arctic to climate change. *Ecol Monogr* 2009;**79**:523–55.

Messerli B. Problems of vertical and horizontal arrangement in the high mountains of the extreme arid zone (central Sahara). *Arctic Alpine Res* 1973;**5**:A139–47.

Morgado LN, Semenova TA, Welker JM *et al*. Long-term increase in snow depth leads to compositional changes in arctic ectomycorrhizal fungal communities. *Global Change Biol* 2016;**22**:3080–96.

Nagy L, Grabherr G. *The Biology of Alpine Habitats*. Oxford: Oxford University Press, 2014.

Nemergut DR, Anderson SP, Cleveland CC *et al*. Microbial community succession in an unvegetated, recently deglaciated soil. *Microb Ecol* 2007;**53**:110–22.

Nichols D, Cahoon N, Trakhtenberg EM *et al*. Use of Ichip for high-throughput in situ cultivation of "uncultivable" microbial species. *Appl Environ Microbiol* 2010;**76**:2445–50.

Nikrad MP, Kerkhof LJ, Häggblom MM. The subzero microbiome: microbial activity in frozen and thawing soils. *FEMS Microbiol Ecol* 2016;**92**:fiw081

Ohtsuka T, Hirota M, Zhang X *et al*. Soil organic carbon pools in alpine to nival zones along an altitudinal gradient (4400–5300 m) on the Tibetan Plateau. *Polar Sci* 2008;**2**:277–85

Ollivier J, Yang S, Dörfer C *et al*. Bacterial community structure in soils of the Tibetan Plateau affected by discontinuous permafrost or seasonal freezing. *Biol Fertilty Soils* 2014;**50**:555–59.

Ozerskaya S, Kochkina G, Ivanushkina N *et al*. Fungi in Permafrost. In: Margesin R (ed). *Permafrost Soils*. Berlin, Heidelberg: Springer, 2009;85–95.

Panikov NS, Flanagan PW, Oechel WC *et al*. Microbial activity in soils frozen to below −39°C. *Soil Biol Biochem* 2006;**38**:785–94.

Papanikolaou N, Britton AJ, Helliwell RC *et al.* Nitrogen deposition, vegetation burning and climate warming act independently on microbial community structure and enzyme activity associated with decomposing litter in low-alpine heath. *Global Change Biol* 2010;**16**:3120–32.

Pauli H, Gottfried M, Grabherr G. Effect of climate change on the alpine and nival vegetation of the Alps. *J Mountain Ecol* 2003;**7**:9–12

Pauli HG, Lamprecht A, Niessner S *et al.* *The GLORIA Field Manual–Standard Multi-Summit Approach, Supplementary Methods and Extra Approaches*. Vienna: GLORIA-Coordination, Austrian Academy of Sciences & University of Natural Resources and Life Sciences, 2015.

Pellissier L, Niculita-Hirzel H, Dubuis A *et al.* Soil fungal communities of grasslands are environmentally structured at a regional scale in the Alps. *Mol Ecol* 2014;**23**:4274–90.

Petrova MA, Gorlenko ZM, Soina VS *et al.* Association of the strA-strB genes with plasmids and transposons in the present-day bacteria and in bacterial strains from permafrost. *Russ J Genet* 2008;**44**:1116–20.

Phillips M, Schweizer J. Effect of mountain permafrost on snowpack stability. *Cold Regions Sci Technol* 2007;**47**:43–9.

Price LW, Harden CP. Mountain soils. In: Price MF, Byers AC, Friend DA *et al.* (eds). *Mountain Geography*. Berkeley: University of California Press 2013;167–82.

Rangwala I, Miller JR. Climate change in mountains: a review of elevation-dependent warming and its possible causes. *Climatic Change* 2012;**114**:527–47.

Ren C, Zhang W, Zhong Z *et al.* Differential responses of soil microbial biomass, diversity, and compositions to altitudinal gradients depend on plant and soil characteristics. *Sci Total Environ* 2018;**610–611**:750–58.

Ricketts M, Poretsky R, Welker J *et al.* Soil bacterial community and functional shifts in response to altered snowpack in moist acidic tundra of northern Alaska. *Soil* 2016;**2**:459–74

Rime T, Hartmann M, Brunner I *et al.* Vertical distribution of the soil microbiota along a successional gradient in a glacier forefield. *Mol Ecol* 2015;**24**:1091–108.

Rime T, Hartmann M, Frey B. Potential sources of microbial colonizers in an initial soil ecosystem after retreat of an alpine glacier. *ISME J* 2016a;**10**:1625–41.

Rime T, Hartmann M, Stierli B *et al.* Assimilation of microbial and plant carbon by active prokaryotic and fungal populations in glacial forefields. *Soil Biol Biochem* 2016b;**98**:30–41.

Rinnan R, Michelsen A, Baath E *et al.* Fifteen years of climate change manipulations alter soil microbial communities in a subarctic heath ecosystem. *Global Change Biol* 2007;**13**:28–39.

Rousk J, Baath E. Growth of saprotrophic fungi and bacteria in soil. *FEMS Microbiol Ecol* 2011;**78**:17–30.

Rousk J, Bengtson P. Microbial regulation of global biogeochemical cycles. *Front Microbiol* 2014;**5**:103.

Rousk K, Michelsen A, Rousk J. Microbial control of soil organic matter mineralization responses to labile carbon in subarctic climate change treatments. *Global Change Biol* 2016;**22**:4150–61.

Rui J, Li J, Wang S *et al.* Responses of bacterial communities to simulated climate changes in alpine meadow soil of the Qinghai-Tibet Plateau. *Appl Environ Microbiol* 2015;**81**:6070–77.

Schimel JP, Schaeffer SM. Microbial control over carbon cycling in soil. *Front Microbiol* 2012;**3**:348.

Schindlbacher A, Rodler A, Kuffner M *et al.* Experimental warming effects on the microbial community of a temperate mountain forest soil. *Soil Biol Biochem* 2011;**43**:1417–25.

Schmidt SK, Naff CS, Lynch RC. Fungal communities at the edge: ecological lessons from high alpine fungi. *Fungal Ecol* 2012;**5**:443–52.

Schmidt SK, Reed SC, Nemergut DR *et al.* The earliest stages of ecosystem succession in high-elevation (5000 metres above sea level), recently deglaciated soils. *Proc Biol Sci/Roy Soc* 2008;**275**:2793–802.

Schröter D, Cramer W, Leemans R *et al.* Ecosystem service supply and vulnerability to global change in Europe. *Science* 2005;**310**:1333–37.

Schulz S, Brankatschk R, Dümig A *et al.* The role of microorganisms at different stages of ecosystem development for soil formation. *Biogeosciences* 2013;**10**:3983–96.

Schuur EAG, McGuire AD, Schadel C. Climate change and the permafrost carbon feedback. *Nature* 2015;**520**:171–79.

Serreze MC, Barry RG. Physical characteristics and basic climatic features. In: Serreze MC, Barry RG (eds). *The Arctic Climate System*. Cambridge: Cambridge University Press, 2005;17–54.

Shen C, Liang W, Shi Y *et al.* Contrasting elevational diversity patterns between eukaryotic soil microbes and plants. *Ecology* 2014;**95**:3190–202.

Shen C, Ni Y, Liang W *et al.* Distinct soil bacterial communities along a small-scale elevational gradient in alpine tundra. *Front Microbiol* 2015;**6**:582.

Shen C, Xiong J, Zhang H *et al.* Soil pH drives the spatial distribution of bacterial communities along elevation on Changbai Mountain. *Soil Biol Biochem* 2013;**57**:204–11.

Siles JA, Margesin R. Abundance and diversity of bacterial, archaeal, and fungal communities along an altitudinal gradient in alpine forest soils: what are the driving factors? *Microb Ecol* 2016;**72**:207–20.

Singh D, Takahashi K, Adams JM. Elevational patterns in Archaeal Diversity on Mt. Fuji. *PLoS One* 2012;**7**:e44494.

Sjögersten S, Turner BL, Mahieu N *et al.* Soil organic matter biochemistry and potential susceptibility to climatic change across the forest-tundra ecotone in the Fennoscandian mountains. *Global Change Biol* 2003;**9**:759–72.

Soina VS, Mulyukin AL, Demkina EV *et al.* The structure of resting bacterial populations in soil and subsoil permafrost. *Astrobiology* 2004;**4**:345–58

Steven B, Niederberger TD, Whyte LG. Bacterial and Archaeal Diversity in Permafrost. In: Margesin R (ed). *Permafrost Soils*. Berlin, Heidelberg: Springer 2009;59–72.

Stibal M, Tranter M, Benning LG *et al.* Microbial primary production on an Arctic glacier is insignificant in comparison with allochthonous organic carbon input. *Environ Microbiol* 2008;**10**:2172–78.

Tan B, Wu F-z, Yang W-q *et al.* Soil biochemical dynamics at three elevations during the soil thawing period, Eastern Tibetan Plateau: Nutrient availabilities, microbial properties and enzyme activities. *Afr J Microbiol Res* 2012;**6**:4712–21.

Theurillat JP, Guisan A. Potential impact of climate change on vegetation in the European Alps: a review. *Climatic Change* 2001;**50**:77–109.

Thorn CE, Darmody RG, Dixon JC. Rethinking weathering and pedogenesis in alpine periglacial regions: some Scandinavian evidence. *Geol Soc, Lond, Special Publications* 2011;**354**:183–93.

Thorn CE, Darmody RG, Dixon JC *et al.* The chemical weathering regime of Kärkevagge, arctic–alpine Sweden. *Geomorphology* 2001;**41**:37–52.

Thébault A, Clément JC, Ibanez S *et al.* Nitrogen limitation and microbial diversity at the treeline. *Oikos* 2014;**123**:729–40.

Townsend AR, Vitousek PM, Trumbore SE. Soil organic matter dynamics along gradients in temperature and land use on the island of Hawaii. *Ecology* 1995;**76**:721–33.

Tveit AT, Urich T, Frenzel P *et al.* Metabolic and trophic interactions modulate methane production by Arctic peat microbiota in response to warming. *Proc Natl Acad Sci USA* 2015;**112**:E2507–16.

Vanhala P, Karhu K, Tuomi M *et al.* Transplantation of organic surface horizons of boreal soils into warmer regions alters microbiology but not the temperature sensitivity of decomposition. *Global Change Biol* 2011;**17**:538–50.

Vaughan DG, Comiso JC, Allison I *et al.* Observations: Cryosphere. In: Stocker TF, Qin D, Plattner G-K *et al.* (eds). *Climate Change 2013: The Physical Science Basis Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press 2013;317–82.

Wagner D, Kobabe S, Liebner S. Bacterial community structure and carbon turnover in permafrost-affected soils of the Lena Delta, northeastern Siberia. *Can J Microbiol* 2009;**55**:73–83.

Walker LR, Wardle DA, Bardgett RD *et al.* The use of chronosequences in studies of ecological succession and soil development. *J Ecol* 2010;**98**:725–36.

Wang C, Wang G, Wang Y *et al.* Fire Alters Vegetation and Soil Microbial Community in Alpine Meadow. *Land Degrad Develop* 2016;**27**:1379–90.

Wang G, Wang Y, Yang P *et al.* Molecular detection and diversity of xylanase genes in alpine tundra soil. *Appl Microbiol Biotechnol* 2010;**87**:1383–93.

Wang JT, Cao P, Hu HW *et al.* Altitudinal distribution patterns of soil bacterial and archaeal communities along Mt. Shegyla on the Tibetan Plateau. *Microb Ecol* 2015;**69**:135–45.

Whittaker RH, Buol SW, Niering WA *et al.* A soil and vegetation pattern in the Santa Catalina Mountains, Arizona. *Soil Sci* 1968;**105**:440–50.

Wipf S, Rixen C. A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. *Polar Res* 2010;**29**:95–109.

Wu JF, Xiong JB, Hu CJ *et al.* Temperature sensitivity of soil bacterial community along contrasting warming gradient. *Appl Soil Ecol* 2015;**94**:40–8.

Xie Z, Le Roux X, Wang C *et al.* Identifying response groups of soil nitrifiers and denitrifiers to grazing and associated soil environmental drivers in Tibetan alpine meadows. *Soil Biol Biochem* 2014;**77**:89–99.

Xiong J, Sun H, Peng F *et al.* Characterizing changes in soil bacterial community structure in response to short-term warming. *FEMS Microbiol Ecol* 2014;**89**:281–92.

Xu M, Li X, Cai X *et al.* Soil microbial community structure and activity along a montane elevational gradient on the Tibetan Plateau. *Eur J Soil Biol* 2014;**64**:6–14.

Yang R-M, Zhang G-L, Yang F *et al.* Precise estimation of soil organic carbon stocks in the northeast Tibetan Plateau. *Nat Sci Rep* 2016a;**6**:21842.

Yang Y, Gao Y, Wang S *et al.* The microbial gene diversity along an elevation gradient of the Tibetan grassland. *ISME J* 2014;**8**:430–40.

Yang Z, Wullschleger SD, Liang L *et al.* Effects of warming on the degradation and production of low-molecular-weight labile organic carbon in an Arctic tundra soil. *Soil Biol Biochem* 2016b;**95**:202–11.

Yang Z, Yang S, Van Nostrand JD, *et al.*, Microbial community and functional gene changes in Arctic tundra soils in a microcosm warming experiment. *Frontiers in Microbiology* 2017;**8**:1741.

Yao F, Vik U, Brysting *et al.* Substantial compositional turnover of fungal communities in an alpine ridge-to-snowbed gradient. *Mol Ecol* 2013;**22**:5040–52.

Yergeau E, Bokhorst S, Kang S *et al.* Shifts in soil microorganisms in response to warming are consistent across a range of Antarctic environments. *ISME J* 2012;**6**:692–702.

Yergeau E, Hogues H, Whyte LG *et al.* The functional potential of high Arctic permafrost revealed by metagenomic sequencing, qPCR and microarray analyses. *ISME J* 2010;**4**:1206–14.

Yergeau E, Newsham KK, Pearce DA *et al.* Patterns of bacterial diversity across a range of Antarctic terrestrial habitats. *Environ Microbiol* 2007;**9**:2670–82.

Yuan X, Knelman JE, Gasarch E *et al.* Plant community and soil chemistry responses to long-term nitrogen inputs drive changes in alpine bacterial communities. *Ecology* 2016;**97**:1543–54.

Yuan Y, Si G, Li W *et al.* Altitudinal Distribution of ammonia-oxidizing archaea and bacteria in alpine grassland soils along the south-facing slope of Nyqentangula Mountains, central Tibetan Plateau. *Geomicrobiol J* 2015;**32**:77–88.

Yuan Y, Si G, Wang J *et al.* Bacterial community in alpine grasslands along an altitudinal gradient on the Tibetan Plateau. *FEMS Microbiol Ecol* 2014;**87**:121–32.

Yue H, Wang M, Wang S *et al.* The microbe-mediated mechanisms affecting topsoil carbon stock in Tibetan grasslands. *ISME J* 2015;**9**:2012–20.

Zalar P, Gunde-Cimerman N. Cold-adapted yeasts in arctic habitats. In: Buzzini P, Margesin R (eds). *Cold-adapted Yeasts: Biodiversity, Adaptation Strategies and Biotechnological Significance*. Berlin, Heidelberg: Springer, 2014;49–74.

Zhang B, Chen SY, Zhang JF *et al.* Depth-related responses of soil microbial communities to experimental warming in an alpine meadow on the Qinghai-Tibet Plateau. *Eur J Soil Sci* 2015a;**66**:496–504.

Zhang G, Niu F, Ma X *et al.* Phylogenetic diversity of bacteria isolates from the Qinghai-Tibet Plateau permafrost region. *Can J Microbiol* 2007;**53**:1000–10.

Zhang K, Shi Y, Jing X *et al.* Effects of short-term warming and altered precipitation on soil microbial communities in alpine grassland of the Tibetan plateau. *Front Microbiol* 2016a;**7**:1032.

Zhang NL, Wan SQ, Guo JX *et al.* Precipitation modifies the effects of warming and nitrogen addition on soil microbial communities in northern Chinese grasslands. *Soil Biol Biochem* 2015b;**89**:12–23.

Zhang W, Wu X, Liu G *et al.* Tag-encoded pyrosequencing analysis of bacterial diversity within different alpine grassland ecosystems of the Qinghai-Tibet Plateau, China. *Environ Earth Sci* 2014;**72**:779–86.

Zhang X, Xu S, Li C *et al.* The soil carbon/nitrogen ratio and moisture affect microbial community structures in alkaline permafrost-affected soils with different vegetation types on the Tibetan plateau. *Res Microbiol* 2014;**165**:128–39.

Zhang XF, Zhao L, Xu SJ *et al.* Soil moisture effect on bacterial and fungal community in Beilu River (Tibetan Plateau) permafrost soils with different vegetation types. *J Appl Microbiol* 2013a;**114**:1054–65.

Zhang Y, Dong S, Gao Q *et al.* Climate change and human activities altered the diversity and composition of soil microbial community in alpine grasslands of the Qinghai-Tibetan Plateau. *Sci Total Environ* 2016b;**562**:353–63.

Zhang Y, Lu Z, Liu S *et al*. Geochip-based analysis of microbial communities in alpine meadow soils in the Qinghai-Tibetan plateau. *BMC Microbiol* 2013;**13**:78.

Zhao L, Wu Q, Marchenko SS *et al*. Thermal state of permafrost and active layer in Central Asia during the international polar year. *Permafrost Periglac Processes* 2010;**1**:198–207.

Zhao Q, Bai Y, Zhang G *et al*. *Chryseobacterium xinjiangense* sp. nov., isolated from alpine permafrost. *Int J Syst Evolut Microbiol* 2011;**61**:1397–401.

Zheng Y, Yang W, Hu HW *et al*. Ammonia oxidizers and denitrifiers in response to reciprocal elevation translocation in an alpine meadow on the Tibetan Plateau. *J Soils Sediment* 2014;**14**:1189–99.

Zheng Y, Yang W, Sun X *et al*. Methanotrophic community structure and activity under warming and grazing of alpine meadow on the Tibetan Plateau. *Appl Microbiol Biotechnol* 2012;**93**:2193–03.

Zinger L, Coissac E, Choler P *et al*. Assessment of microbial communities by graph partitioning in a study of soil fungi in two alpine meadows. *Appl Environ Microbiol* 2009;**75**:5863–70.

Zinger L, Lejon DPH, Baptist F *et al*. Contrasting diversity patterns of crenarchaeal, bacterial and fungal soil communities in an alpine landscape. *PLoS One* 2011;**6**:e19950.

Zucconi L, Selbmann L, Buzzini P *et al*. Searching for eukaryotic life preserved in Antarctic permafrost. *Polar Biol* 2012;**35**:749–57.

Zumsteg A, Baath E, Stierli B *et al*. Bacterial and fungal community responses to reciprocal soil transfer along a temperature and soil moisture gradient in a glacier forefield. *Soil Biol Biochem* 2013;**61**:121–32.

Zumsteg A, Luster J, Göransson H *et al*. Bacterial, archaeal and fungal succession in the forefield of a receding glacier. *Microb Ecol* 2012;**63**:552–64.

Řeháková K, Capková K, Dvorsky M *et al*. Interactions between soil phototrophs and vascular plants in Himalayan cold deserts. *Soil Biol Biochem* 2017;**115**:568–78.

Řeháková K, Chlumská Z, Doležal J. Soil cyanobacterial and microalgal diversity in dry mountains of Ladakh, NW Himalaya, as related to site, altitude, and vegetation. *Microb Ecol* 2011;**62**:337–46.