Microbial diversity and functional capacity in polar soils

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Global change is disproportionately affecting cold environments (polar and high elevation regions), with potentially negative impacts on microbial diversity and functional processes. In most cold environments the combination of low temperatures, and physical stressors, such as katabatic wind episodes and limited water availability result in biotic systems, which are in trophic terms very simple and primarily driven by microbial communities. Metagenomic approaches have provided key insights on microbial communities in these systems and how they may adapt to stressors and contribute towards mediating crucial biogeochemical cycles. Here we review, the current knowledge regarding edaphic-based microbial diversity and functional processes in Antarctica, and the Artic. Such insights are crucial and help to establish a baseline for understanding the impact of climate change on Polar Regions.

Introduction

The Congress of Parties (COP) 21 meeting in Paris (November 2015) highlighted the urgency of global climate change, and the critical need to reduce global average temperatures through curbing greenhouse gas emissions [1]. Nowhere are the effects of global change more apparent than in cold environments (polar and alpine regions), which are subject to accelerated rates of warming compared to other ecosystems [2•,3]. Climatic models have predicted that temperatures in high latitude regions of the Northern Hemisphere are likely to increase by between 0.3°C and 4.8°C before the end of the twenty first century [4]. There is also evidence that regions in the Southern Hemisphere have experienced the fastest warming globally, with average increases of as much as 2.4°C in the last fifty years [5].

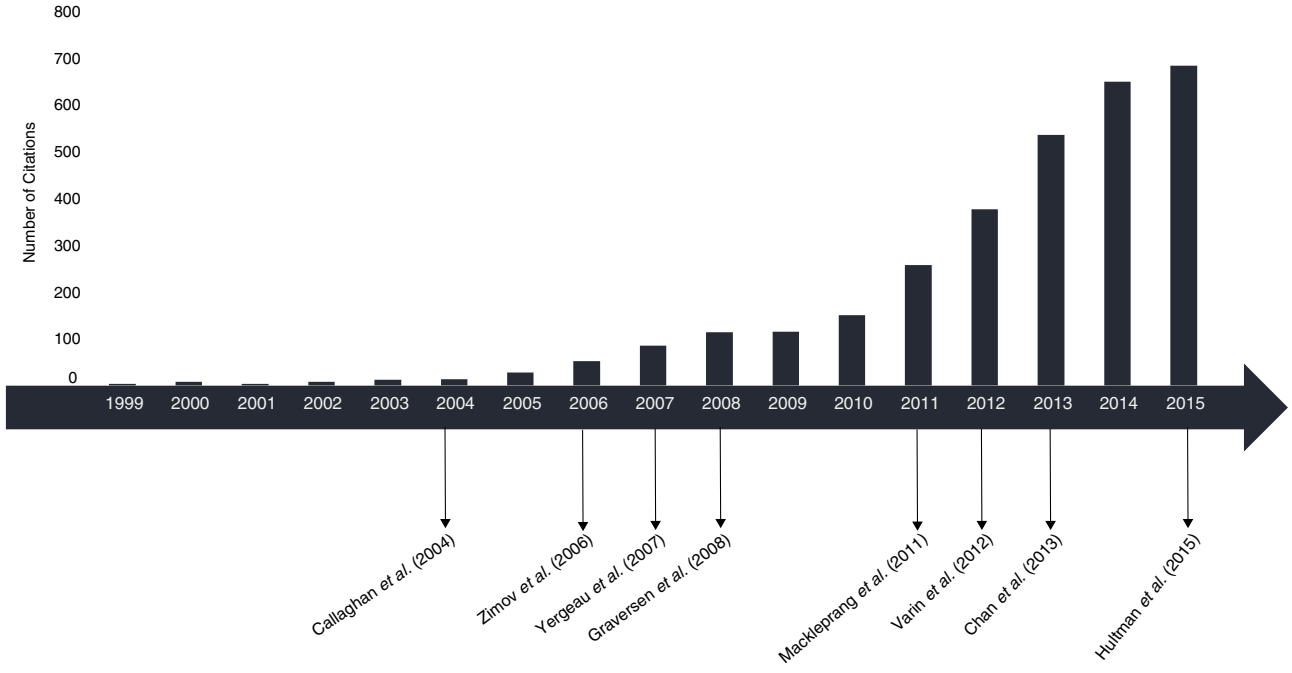
A major consequence of climate change in cold environments is the thawing of submerged and surface ice, which alters the hydrology of the systems and may have adverse effects on microbial processes [6•]. In cold environments, microorganisms (bacteria, archaea and fungi) are major constituents of the total biomass, and are estimated to mediate the cycling of key biogeochemical elements such as nitrogen and carbon, with potentially important implications for the productivity of these systems [7]. Although the precise contribution of microbial processes to global change processes are not well known, there are efforts to incorporate biological processes into Earth systems models with the realization that they may be crucial in regulating soil organic matter (SOM) [8••]. For instance, permafrost (defined as ground which remains frozen for at least two years) in cold environments stores roughly 1600 Pg of carbon, which if released would significantly contribute towards increasing global CO_2 levels [9]. The current contribution of microbial communities to constraining carbon losses in permafrost and the influence on CO_2 levels remains virtually unknown. In contrast, the responses and adaptations of macro-organisms to climate change are reasonably well understood [10,11]. Overall, there is still a dearth of knowledge regarding the effects of anthropogenic processes on cold environments and how these effects may impact on important microbial derived ecosystem services.

The relationship between microbial biodiversity and functional processes remains ambiguous in most ecosystems, but particularly in low productivity systems [12,13]. Such knowledge is vital, given the known status of microbial communities as the main drivers of biogeochemical processes in polar ecosystems.

Microbial diversity in cold environments

Early approximations suggested that a gram of soil may harbour up to 10 billion microorganisms [14], possibly representing as many as 10^4 different microbial species [15]. Regardless of the actual figures, microorganisms are highly abundant and, thanks in part to culture independent methods and the so-called 'omic' approaches, we now have realistic estimates of the true depth of microbial diversity, and their functional capacity. Through application of metagenomic approaches (Figure 1), it is now known that most extreme environments harbour lower levels of microbial diversity (species richness and relative

Figure 1



Overview of studies published between 1999 and 2015, which focus on cold environments (Arctic and Antarctic). Key studies based on the average number of citations are shown.

abundance), than more 'benign' ecosystems [16,17]. This is thought to be due to the requirement for specific physiological adaptations, which allow organisms to exploit the combination of physical and biochemical stressors, but result in simplified ecosystems dominated by a relatively few taxa [18,19].

In contrast to many other extremophilic biomes, cold environments appear to have a higher level of spatial heterogeneity [20–22]. Within cold regions, both soils and permafrost niches appear to be dominated by bacterial (mainly Proteobacterial, Actinobacterial and Acidobacterial), archaeal (mostly Euryarchaeota) and fungal (dominated by Ascomycota) lineages [7,23,24,25••] (Table 1). While these studies have provided a comprehensive, and reasonably consistent, survey of microbial diversity at the specific sites sampled, few of these studies have any temporal component; that is, they are single time-point analyses which provide, at best, a baseline for future assessments of the effects of environmental change.

A recent (and unique) analysis of the temporal and spatial trends in Arctic heartland soils reported a change in microbial community structure in response to simulated climate change, with a general shift from *r*- to *K*-selected taxa [21]. Interestingly, the application of network analysis suggested that *Burkholderia* species might be keystone species in Arctic soils [21]. This is consistent with previous observations that *Burkholderia* taxa may confer cold tolerance to plant species exposed to low temperatures [26]. Interestingly, cold adapted *Burkholderia* species have also been recovered from coastal regions of the Ross Sea in Antarctica [27]. Copiotrophic α- and β-Proteobacteria were more responsive to shifts in nutrient status in Arctic soils than other taxa [28], supporting their proposed role as keystone taxa. Whether similar microbial community structural changes might be expected in oligotrophic Antarctic desert soils remains uncertain.

Actinobacteria are prominent colonists of cold soil biotopes and have been linked to a range of functional processes such as stress response and nitrogen cycling [29,30,31•]. Recent draft genomes of Actinobacterial isolates from cold soil environments have provided some new insights into the metabolic adaptation of these bacteria to cold environments [32,33]. Actinobacteria are capable of maintaining metabolic activity and DNA repair processes [34] at low temperatures, critical adaptations to survival in polar soil habitats where the seasonal metabolic window is limited [7] and DNA damage from freeze–thaw, desiccation and associated oxidative processes and radiation damage is all thought to be one of the major impositions on survival [35]. A seminal study, which applied metatranscriptomics, metagenomics and

Table 1

Some of the most significant studies focused on soil and permafrost from Antarctica and the Arctic

Niche/habitat	Location	Reference	Region
Contaminated soils	Northwest Territories, Canada	Akbari *et al.* [36]	Arctic
Permafrost	McGill Arctic Research Station, Expedition Fjord, Canada	Allan *et al.* [46]	Arctic
Wetland sediment	Brøgger Peninsula, Svalbard, Norway	Blake *et al.* [67]	Arctic
Permafrost	EML watershed, Healy, Alaska	Deng *et al.* [23]	Arctic
Soil	Canada, Alaska and European Arctic	Feng *et al.* [68]	Arctic
Soil	Svalbard Island, Norway	Ferrari *et al.* [69]	Arctic
Active layer soils	Western Canadian Arctic, Herschel Island & Yukon Coast	Frank-Fahle *et al.* [70]	Arctic
Soil	Abisko, Northern Sweden	Hill *et al.* [21]	Arctic
Peat soils	Spitsbergen, Norway	Høj *et al.* [2•]	Arctic
Permafrost	Fairbanks Alaska	Hultman *et al.* [25••]	Arctic
Soil	Toolik Lake region, Brooks Range, Alaska	Koyama *et al.* [28]	Arctic
Permafrost	McGill Arctic Research Station, Expedition Fjord, Canada	Lau *et al.* [22]	Arctic
Tundra soil	Barrow, Alaska	Lipson *et al.* [66]	Arctic
Snow pack	Svalbard, Norway	Maccario *et al.* [71]	Arctic
Permafrost	Fairbanks, Alaska	Mackelprang *et al.* [42••]	Arctic
Soil	Malla Nature Reserve, Kilpisjarvi, Finland	Männistö *et al.* [37]	Arctic
Soil	McGill Arctic Research Station, Expedition Fjord, Canada	Martineau *et al.* [65]	Arctic
Soil	Toolik Lake region, Brooks Range, Alaska	Morgado *et al.* [72]	Arctic
Ectomycorrhizal	Isdammen, Svalbard, Norway	Mundra *et al.* [73]	Arctic
Soil Ascomycetes	Toolik Lake region, Brooks Range, Alaska	Semenova *et al.* [74]	Arctic
Tundra soil	Canada, Alaska and European Arctic	Shi *et al.* [75]	Arctic
Tundra soil	Raisduoddar, Norway	Stark *et al.* [76]	Arctic
Subglacial sediment	Canada, Greenland, Norway	Stibal *et al.* [77]	Arctic
Peat soils	Svalbard, Knudseheia, Norway	Tveit *et al.* [63]	Arctic
Microbial mats	Ward Ice Shelf, Markham Ice Shelf on Ellesmere Island	Varin *et al.* [78]	Arctic
Microbial mats	Ward Ice Shelf, Markham Ice Shelf on Ellesmere Island	Varin *et al.* [31•]	Arctic
Permafrost	Eureka, Canadian High Arctic	Yergeau *et al.* [58]	Arctic
Soil and lithobionts	McKelvey Valley	Chan *et al.* [30•]	Antarctica
Hypolith	Miers Valley	Cowan *et al.* [29]	Antarctica
Soil	Mitchell Peninsula & Browning Peninsula	Ferrari *et al.* [69]	Antarctica
Permafrost	University Valley	Goordial *et al.* [33]	Antarctica
Soil	Darwin Mountains	Guerrero *et al.* [32]	Antarctica
Soil	Miers Valley, Beacon Valley, Upper Wright Valley	Lee *et al.* [79]	Antarctica
Hypolith and soil	Miers Valley	Makhalanyane *et al.* [20]	Antarctica
Soil	Miers Lake, Buddha Lake, Miers Valley	Niederberger *et al.* [80]	Antarctica
Surface soil	Mars Oasis, Antarctic Peninsula	Pearce *et al.* [81]	Antarctica
Soil	Miers Valley, Marshall Valley, Garwood Valley, Shangri-La	Richter *et al.* [82]	Antarctica
Subglacial sediment	Lower Wright Glacier, McMurdo Dry Valleys	Stibal *et al.* [77]	Antarctica
Soil	Lake Fryxell, Taylor Valley	Van Horn *et al.* [6•]	Antarctica
Microbial mats	McMurdo Ice Shelf	Varin *et al.* [31•]	Antarctica
Chasmoendolith and soil	Miers Valley	Wei *et al.* [83]	Antarctica
Soil	Falklands Island, Signy Island, Anchorage Island	Yergeau *et al.* [38]	Antarctica

metaproteomics to permafrost, active layer and thermokarst bog soils [25••], demonstrated that Actinobacterial lineages were both numerically dominant and the most active members of the prokaryotic community in seasonally thawed soils [25••]. Actinobacteria also appear to be particularly resilient to both short- and long-term changes in environmental conditions [36]. Under the influence of diurnal temperature variations in oil contaminated sub-Arctic soils, Actinobacteria were consistently the most abundant taxa at all temperature regimes [36].

Acidobacteria have been found to be common in a wide range of Arctic and Antarctic soil biotopes [20,25••,37,38], consistent with their known ability to compete in oligotrophic environments [38]. A recent study, which assessed the active bacterial communities of Arctic tundra, found a shift from SD1 to SD2 Acidobacterial lineages as a consequence of changing environmental conditions, suggesting a change in functional diversity [37]. In Antarctic soils, it has been observed that warming leads to a shift in the relative abundance of Alphaproteobacteria to Acidobacteria due to increased soil carbon turnover [38].

Archaea have also been observed in Arctic and Antarctic soils, albeit at very low abundance [39–41]. Low abundance levels are not necessarily indicative of the functional importance of these taxa, as the archaeal taxa identified are typically associated with unique functional properties, such as methanogenesis [42••]. In cold soil environments, archaeal diversity appears to increase with soil depth, probably due to the increased anaerobic status of deeper soils [43]. In both Antarctic and Arctic soils, *Thaumarchoeota* dominate, with a high abundance of *Nitrososphaerales* lineages [44–46]. It has been speculated

that *Thaumarchoeota* may be important heterotrophs in depauperate soils, where their capacity to utilise recalcitrant organic substrates such as methane, short-chained alkanes, chlorinated ethanes and aromatic hydrocarbons may contribute significantly to the energy balance of the community [47]. The observation that the relative abundance of methanogens increased significantly when permafrost thawed emphasises the significant of these taxa as contributors to climate change.

Although Proteobacteria, Actinobacteria and Acidobacteria are the most numerically abundant, Cyanobacteria are also significant colonists of cold soils [16]. Cyanobacteria, mostly affiliated to *Nostoc commune*, are prevalent in both Arctic and Antarctic soils and appear to drive most functional processes related to carbon and nitrogen cycling [48–50].

Free-living fungi are generally of limited abundance in Antarctic and Arctic soils [41,51], and are primarily restricted to lithobionts niches [7]. However, as for archaeal lineages, low apparent fungal abundance does not necessarily imply that these organisms are not important in a physiological context. The known capacity of fungi to degrade of recalcitrant polymeric substrates [52] may give these organisms a particularly important role in community heterotrophy [38].

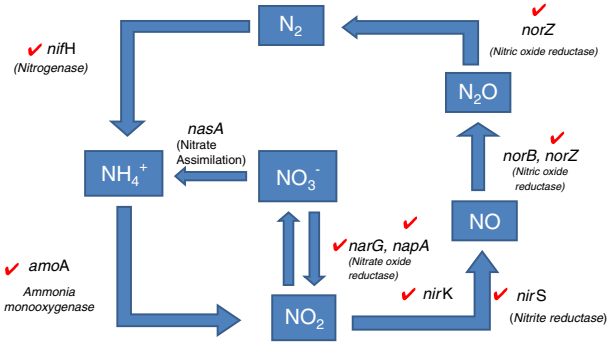
It has been proposed that one important consequence of increasing soil temperatures may be extended microbial growth periods. In some regions of the Arctic and Antarctic Peninsula, it is projected that ground cover may shift from mosses to vascular plants and active soil layers, where fungi are involved in soil organic carbon decomposition, may increase in volume [51]. However, this effect may be minimized in permafrost systems, where the proportion of genes assigned to fungal taxa is relatively small [25••]. A recent meta-analysis does suggest that warming of cold soils may substantially increase microbial abundance, which could significantly impact stored carbon [24]. In general, there is an urgent requirement for more extensive datasets on the effects of different climatic scenarios on microbial community composition and functional processes.

It has been speculated that viruses may play a very significant role in the microbial food webs of Arctic and Antarctic ecosystems, particularly by inducing species diversification and the consequent functionality [53]. However, very few studies have assessed the diversity of viruses in cold environments, let alone their functional roles. Of these published studies on polar habitats, mostly focus on lacustrine systems [54,55] with only very limited surveys of polar edaphic metaviromes [40,56]. The latter suggests that viruses in cold soil environments are highly diverse but are typically dominated by *Mycobacterium* phages [56]. The extent to which phages may influence metabolic processes in cold soil environments remains effectively unknown.

Metabolic capacity in cold temperature environments

Recent metagenomic studies have significantly contributed to our understanding of the functional capacity of microorganisms in cold soil environments [22,30•], through the identification of genes and pathways implicated in key biogeochemical cycles. The genes of nitrogen cycling have been extensively studied in both Arctic and Antarctic soils [57,58], primary by targeting the nitrogenase (*nif*H) gene (Figure 2). The capacity for diazotrophy is widespread in these soils, and appears to be linked primarily, but not exclusively, to cyanobacterial lineages [30•,57,58]. Genes implicated in nitrite oxidation and ammonia oxidation, the *nxr*A and *amo*A genes, respectively, have also been reported in Arctic and Antarctic soil metagenomes [30•,58]. In Arctic soils, *amo*A genes with homology to those found in archaea (Thaumarchaeota) appear to dominate [59], while ammonia oxidation genes in Antarctic soils are primarily of bacterial origin [30•]. Denitrification, a process which generates the 'greenhouse' gas N_2O and for which the *nar*G gene is the genetic marker, is mostly linked to Actinobacteria and Proteobacteria in both Arctic and Antarctic soils [39,60]. However, PCR-dependent and metagenomic gene surveys have suggested that the nitrogen cycle is severely truncated in these soils, with key enzymes implicated in some crucial steps (such as dissimilatory nitrate reductase and nitrous oxide reductases) either present at very low abundance or undetectable [30•]. The abundance of genes linked to the nitrogen cycle appears to be strongly influenced by available soil moisture [61]. A likely consequence of increasing moisture input (i.e. from melting ice) may be higher rates of nitrogen cycling (and denitrification), which may further contribute to global warming.

Figure 2



Simplified nitrogen cycle in cold soils. Red ticks indicate marker genes amplified from Antarctic and Arctic soils.

The nitrogen and carbon cycling are intimately associated through feedback mechanisms [62]. However, due to the sheer number of genes and processes involved in the carbon cycling, it is challenging to understand how these complex processes may be impacted by global change. The methane cycle is probably the most studied of carbon cycle-related processes and has been shown to occur extensively in Arctic [25••,63] and Antarctic [64] soils. The balance of methanogenesis and methylotrophy dictates, in part, the carbon source/sink ratio [43]. *In situ* measurements suggests that polar soils are a net source of CO_2 emissions, but a sink for methane [43]. However, there is evidence that increased soil temperatures (thaw) increased methanogen diversity in both active layer and permafrost soils [43], coupled with substantial increases in methane production [63]. Changes in methane productivity were linked to a shift from formate- and H_2-using Methanobacteriales to Methanomicrobiales and from the acetotrophic *Methanosarcinaceae* to *Methanosaetaceae* [63]. In Arctic soils, methanogenesis is driven principally by *Euryarchaeota*, based on detection of *mcr*ABG genes, although homologous genes assigned to α- and γ-proteobacterial taxa also appear to be ubiquitous [22,65]. Methanogenic processes appear to be dominant in peat soils in the Arctic while methanogens are less abundant in permafrost soils [66]. Very little is known with respect to the distribution and abundance of methanogens in Antarctic soils, with the majority of positive reports derived from lacustrine biotopes. The highly aerobic nature of the upper horizons of Antarctic desert soils probably explains the typical failure to detect methanogenic archaeal phylotypic signals in metagenomic surveys of these biotopes. However, it is reasonable to predict that a warming climate may lead to more anaerobic soil conditions, which could ultimately result in these soils becoming net methane producers.

Conclusion and future directions

There can be little doubt that the application of metagenomics has greatly enhanced the understanding of microbial diversity and functional capacity in cold desert biotopes. Clearly, microbial communities in cold habitats are highly diverse and demonstrate the capacity for a very wide range of functional processes. However, there are clear gaps in the available knowledge.

Firstly, there is an inequity in available data, with the majority of comprehensive metagenomic studies focused on Arctic soil biotopes. Comparatively, very little is known of the microbial diversity and functional capacity of Antarctic permafrost. In order to better understand the impact of regional climate change processes on Antarctic edaphic systems, there is a need for a greater focus on the dominant ice-free areas, particularly the Antarctic Peninsula. Such studies should include a range of 'omics' methods; in order simultaneously assess microbial diversity, the functional fraction of the population and functional capacity of the ecosystem. The weakness of these modern methods is, of course, their focus on functional capacity and their failure to quantify actual process rates. There is therefore also a critical need for more extensive *in situ* and *ex situ* analyses of key process kinetics and their responses to different microclimatic regimes.

Secondly, there is little information available on the interactions between organisms and trophic tiers in polar soil ecosystems. Interactions between microinvertebrates, bacteria, archaea, fungi and viruses may all significantly influence the balance between species biodiversity and ecosystem functioning. Such studies are technically challenging, even *ex situ*, and particularly difficult under the physical and logistic constraints of the Polar Regions.

Finally, it is ultimately necessary to integrate taxonomic and functional data into climatic models to understand both the role of climate in dictating changes in the soil microbial community structure and function and the contributions of these communities to climate-linked processes. Here, a complex combination of diversity, abundance and rate data is required, data which are, at the current stage, largely lacking.

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