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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.

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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].

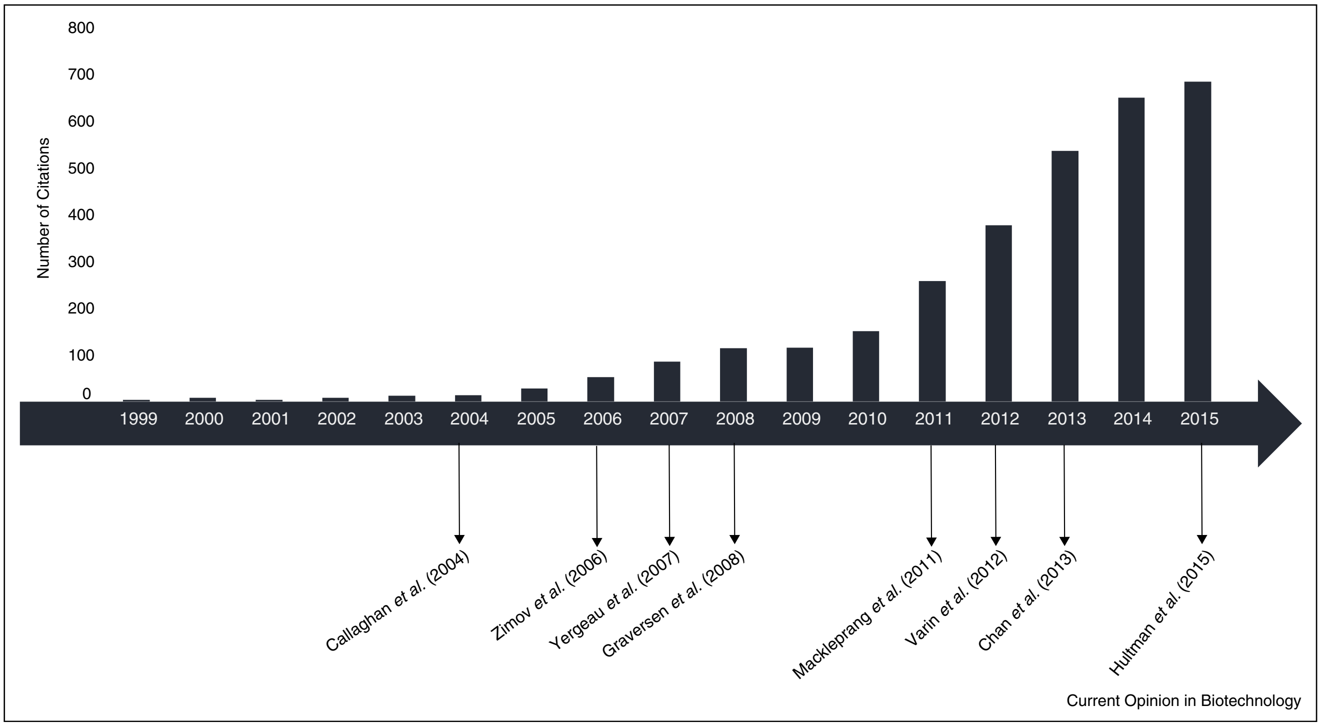
A major consequence of climate change in cold environments is the thawing of submerged and surface ice, which alters the hydrology of the systems and may have adverse effects on microbial processes [6•]. In cold environments, microorganisms (bacteria, archaea and fungi) are major constituents of the 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