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Mini-review

Structure and function of alpine and arctic soil microbial communities

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Abstract

Cultivation-independent molecular phylogenetic techniques are now widely employed to examine environmental microbial diversity; however, the relationship between microbial community structure and ecosystem function is unclear. This review synthesizes cultivation-independent views of microbiological diversity with our current understanding of nutrient dynamics in alpine and arctic soils. Recently, we have begun to explore connections between microbial community structure and function in soils from the alpine Niwot Ridge LTER site in Colorado, USA, whose ecology has been extensively investigated for over 50 years. We examined the diversity of bacterial, eucaryal, and archaeal small subunit rRNA genes in tundra and talus soils across seasons in the alpine. This work has provided support for spatial and seasonal shifts in specific microbial groups, which correlate well with previously documented transitions in microbial processes. In addition, these preliminary results suggest that the physiologies of certain groups of organisms may scale up to the ecosystem level, providing the basis for testable hypotheses about the function of specific microbes in this system. These studies have also expanded on the known diversity of life, as these soils harbor bacterial and eucaryotic lineages that are distantly related to other known organisms. In contrast to the alpine, microbial diversity in the arctic has been little explored; only three published studies have used molecular techniques to examine these soils. Because of the importance of these systems, particularly to the global C cycle, and their vulnerability to current and impending climate change, the microbial diversity of these soils needs to be further investigated.

Keywords: 16S rRNA; Biogeochemistry; Cold; Snow

1. Introduction

High altitude and latitude ecosystems are experiencing the effects of human-induced environmental change, and many predictions suggest that future changes are likely to be both larger in magnitude and have greater impacts on these systems. Specifically, increasing rates of nitrogen deposition threaten alpine regions [8,63]; and these areas may experience N saturation at comparatively low levels of excess nitrogen [61]. Soils from arctic environments, on the other hand, play important roles in the global C cycle because they contain a disproportionately large reservoir of soil carbon [45]. This large C pool is vulnerable to climate change, as higher temperatures will put these stocks of soil carbon at risk of mineralization via increases in microbial respiration, and may provide potential positive feedbacks to warming [30–32,56]. However, the effects of both climate change and alterations in the N cycle on the nutrient cycling, and therefore microbiology, of arctic and alpine systems is poorly understood.

Historically, the microbiology of these soils has been investigated in the snow-free season only, because it was assumed that low temperatures and frozen soil prohibited microbial activity during the winter. More recent studies demonstrate that microbial processes continue in snow-covered soils, and that a significant portion of yearly decomposition (reviewed in [51]) and production of microbially derived trace gases [7,19,42,65] occurs in subnival soil. Microbial activity continues because snow insulates soil,

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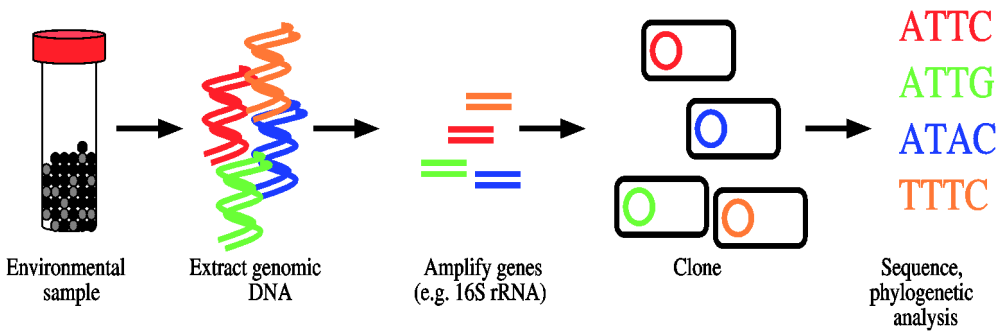

Fig. 1. Summary of the cultivation-independent molecular phylogenetic method.

protecting the microbial community from harsh winter conditions. A deep snowpack can sustain soil temperatures at or around 0 °C, maintaining the presence of liquid water. In addition, although most soil water freezes at 0 °C, soil particles can have liquid water films at temperatures below −10 °C [47], which can support microbial growth even at very cold temperatures. In fact, microbial metabolism has been detected at soil temperatures as low as –20 °C [10]. Previously regarded as a dormant time for microbial communities, evidence is mounting that snow-covered soils are teeming with active microbial life.

Cultivation-dependent experiments show that microbes that are capable of life at low temperatures are phylogenetically widespread, and include many types of Bacteria, Eucarya and Archaea [13]. However, it is well known that the vast majority of organisms cannot be cultured using traditional techniques [1]. The advent of molecular phylogenetic methods has provided a powerful tool with which to examine microbial diversity without the biases and limitations associated with culture-based methods. Here, DNA is extracted from environmental samples, and genes (typically small subunit [SSU] rRNA) are amplified (Fig. 1). These genes are cloned, sequenced, and subjected to phylogenetic analyses, revealing the types of organisms that comprise the community. These molecular-based views of species diversity are then combined with phenotypic information from cultivation studies in an attempt to predict the functional attributes of the organisms in these environments [44]. These approaches are becoming increasingly commonplace; the Genbank database now includes sequences for over 88 000 16S rRNA genes from environmental samples.

However, while linking populations and processes has been a major focus of macroecology, there is debate about whether or not information on the structure of microbial communities is informative at the ecosystem level. For example, Andren et al. [2] suggested that ecosystems act to average out microbial species effects, implying that microbial populations do not easily scale-up to explain processes. Finlay et al. [14] further argued that all possible niches are always filled in an environment, so microbial diversity has no direct role in ecosystem function. In addition, Kemp and Aller [20] contended that exploring microbial diversity may be intractable given the present state of technology. Finally, other work suggests that horizontal gene transfer is pervasive in microbial communities (e.g. [39]), and there is an indirect relationship between phenotypes and phylogenies (e.g. [34]), further complicating the value of community studies in microbial ecology.

Recently, we have begun to explore the possible connections between microbial community structure and ecosystem function at the intensively studied Niwot Ridge Long-Term Ecological Research (LTER) site in Colorado, USA (reviewed in [6]). Our preliminary results suggest that the physiologies of certain groups of organisms may scale up to the ecosystem level, providing the basis for testable hypotheses about the function of certain microbes in this system. For example, this work has provided support for spatial and seasonal shifts in specific microbial groups, probably in response to changes in substrate availability and temperature ([26,28,33,48], Costello and Schmidt, in preparation). Some of these community shifts correlate with well-documented process-level transitions in these alpine systems. These studies have also expanded on the known diversity of life, as these soils harbor bacterial and eucaryotic lineages that are distantly related to other known organisms, leaving many open questions about the functions of these novel microbes in alpine soils. In contrast to the alpine, arctic tundra soil microbial diversity has been little-explored and, to our knowledge, only three studies that employed cultivation-independent techniques have been published.

This review attempts to synthesize molecular phylogenetic views of microbiological diversity with our current understanding of nutrient dynamics in alpine and arctic soils. Although much work has also been done on the microbiology of Antarctic soils, they are beyond the scope of this review. We acknowledge that PCR-based studies are not directly quantitative; rather they provide rough pictures of the microbial diversity in these soils. Here, we emphasize seasonal and spatial variation as well as the complexity of alpine and arctic systems. Because much of the work that we summarize has been done in the alpine tundra at the high elevation Niwot Ridge LTER site, we begin with a discussion of the ecology of this system.

2. Niwot Ridge LTER

The Niwot Ridge LTER site is located in the Front Range of the Colorado Rocky Mountains. Major ecosystems on Niwot Ridge transition along an elevation gradient, and range from subalpine forest (elevation $\sim$ <3400 m), to alpine tundra (elevation $\sim$ 3550 m), to talus slopes and glaciated regions (elevation $\sim$ 3750 m). Precipitation averages 930 mm yr^{-1} and approximately 80% of this occurs as snow [9]. Differences in topography, wind exposure, and plant cover significantly redistribute precipitation and lead to markedly different snow-cover and moisture regimes across the landscape [53]. This variation in snow-cover structures differences in plant communities, biogeochemistry, soil development, and nutrient transport [53].

Work at the Niwot Ridge LTER site has primarily focused on the wet and dry soils of the tundra, as well as the talus soils. Dry meadow tundra soils are windswept and thus have less snow-cover and longer plant growing seasons. These environments are dominated by the tussock-forming sedge *Kobresia myosuroides* (e.g., [27]). In contrast, wet meadow soils receive snow-melt throughout much of their short plant growing seasons, and are dominated by *Carex scopulorum* (e.g., [36]). In general, plant productivity, soil organic matter and microbial activity are higher in the wet meadow than in the dry meadow tundra soils [15]. The talus soils on Niwot Ridge are found on steep slopes between unconsolidated boulders, are snow-covered for approximately nine months of the year, and can be vegetated or barren (e.g., [22]). Talus soils are remarkably variable; organic matter ranges between 6 and 250 g kg^{-1} soil [22].

2.1. Alpine tundra

Alpine tundra soils commonly experience profound seasonal cycles that are characterized by shifts in microbial communities, processes and soil nutrient availability (Fig. 2). These systems have relatively short, snow-free growing seasons, when plants are photosynthetically active and competitive in the uptake and immobilization of available nitrogen [25]. The corresponding summer microbial communities are probably fast-growing organisms that feed on labile root exudates [26]. As summer transitions to fall, drier soils and cooler temperatures lead to the beginning of plant senescence, and the microbial community shifts to a population that is capable of degrading more recalcitrant compounds, such as polymers and phenolics found in plant litter. Winter's lower temperatures and snow-cover stimulate the cold-adapted microbial community, which feeds on moribund plant litter and mineralizes and immobilizes nitrogen from plant material [29]. Winter is an extremely active time for the microbial community, and the highest levels of microbial biomass are seen under snowpack [29]. Spring snow-melt triggers a crash in the microbial biomass and a concordant pulse of nitrogen, probably from lysed microbial cells [29]. Much of this nitrogen is then taken up by plants, and the growing season begins anew.

In addition to significant seasonal variation in the structure and function of the microbial communities, these soils

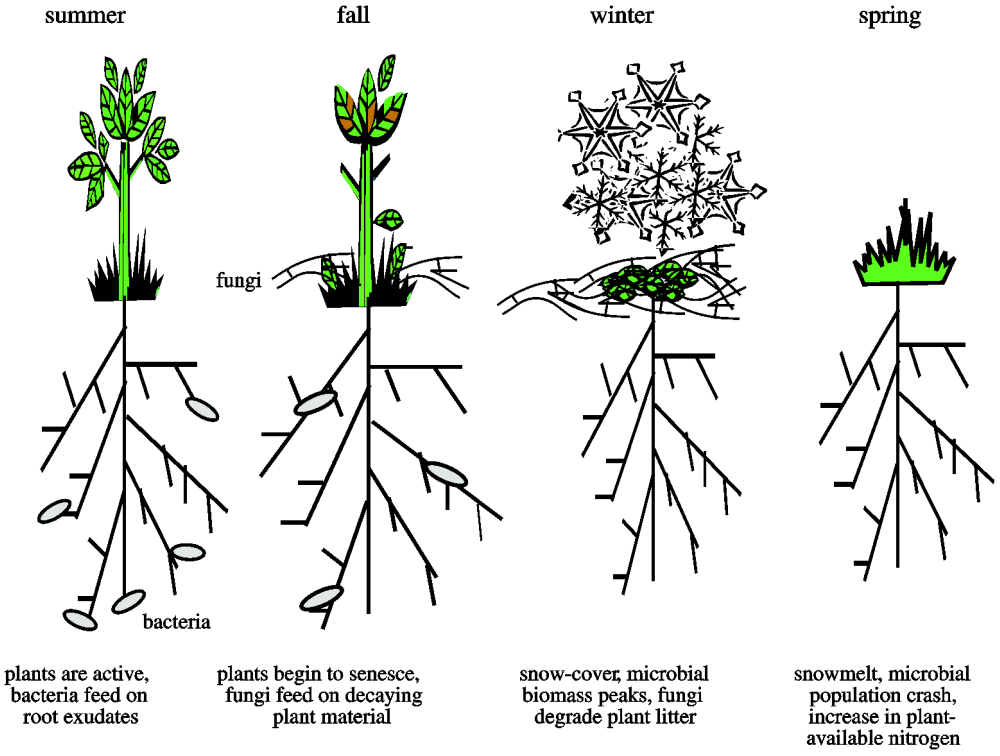

Fig. 2. Conceptual model of seasonal patterns in plant and microbial nutrient dynamics in the tundra systems of Niwot Ridge.

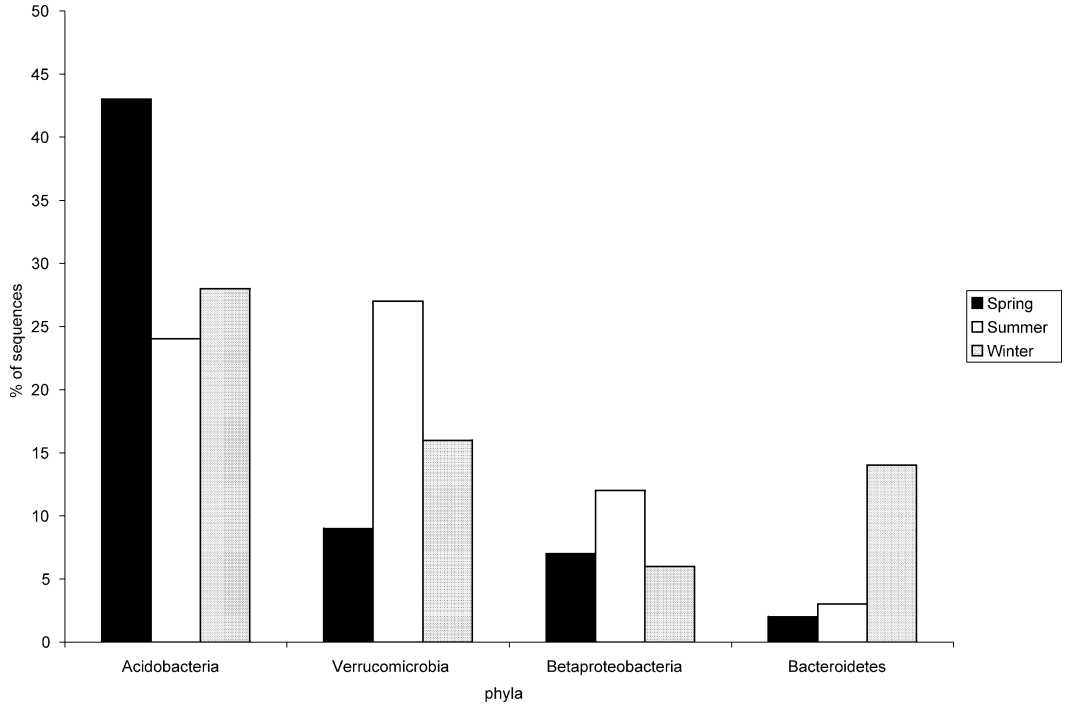

Fig. 3. Frequency of sequences related to major bacterial groups in 16S rRNA gene clone libraries from Niwot Ridge alpine tundra dry meadow soil during spring, summer and winter. Adapted from Lipson and Schmidt [28].

demonstrate considerable spatial variation, some of which is also controlled by snowpack. For example, in the alpine, deeper and earlier snowpack correlates with higher levels of under-snow microbial respiration and accelerated litter bag decomposition rates [62]. Rates of methane efflux are also higher under deeper snow, probably due to the increase in free water promoting the anoxic conditions necessary for increases in methanogenesis and decreases in biological methane oxidation [60]. Nitrogen cycling is also affected by snowpack in the alpine; snowfence manipulations, which increase the duration and size of the snowpack, can increase N_2O production by 3-fold [62].

The seasonal and spatial variability typical of microbial processes in alpine tundra systems is thought to be tightly linked to shifts in microbial community composition. For example, using inhibitors, Lipson et al. [26] showed that the fungal and bacterial communities were most active in the subnival and snow-free soils, respectively, in the dry meadow on Niwot Ridge (Fig. 2). Also, Schadt et al. [48] microscopically examined soil samples, confirming that the fungal to bacterial ratio was highest in the winter in dry meadow soils. Molecular techniques also support these shifts in community composition; Lipson et al. [26] showed that the total genomic DNA of the winter microbial community was different from the summer community on Niwot Ridge. In addition, Costello and Schmidt (in preparation) used 16S rRNA terminal restriction fragment length polymorphisms (tRFLPs) to show a shift in the bacterial community with depth in wet meadow tundra soils. More recently, these communities have been analyzed in detail, by amplifying and sequencing SSU rRNA genes from the microorganisms in these communities. Below, we discuss our current understanding of the bacterial, archaeal and eucaryal diversity in alpine soils from these sequence-based approaches.

2.2. Alpine tundra Bacteria

Lipson and Schmidt [28] looked at the diversity of bacterial 16S rRNA genes in Niwot Ridge dry meadow tundra soils collected in winter (under snow), spring (at snowmelt), and summer. Two candidate divisions (novel lineages with no cultured representatives) were discovered in the spring (SPAM) and summer (SAM) soils. These sequences form supported clades with other 16S rRNA genes from a variety of environments, including an arid Australian soil, the Changjiang River, and earthworm casts. The biogeochemical roles of these deeply divergent Bacteria found in such diverse environments are completely unknown.

Lipson and Schmidt [28] also found that alpine tundra bacterial communities differed significantly across seasons and that many changes in the population structure were consistent with previously described ecological patterns (Fig. 3). For example, in winter, proportions of genes related to the Bacteroidetes were higher than in the spring or summer. The Bacteroidetes include many cold-tolerant degraders of complex substrates, consistent with the hypothesis that under-snow communities are feeding on plant polymeric compounds. In addition, sequences related to the Acidobacteria were dominant at spring snowmelt. Isolates from this division are capable of anaerobic organotrophy, a good strategy when soils are wet and contain large amounts

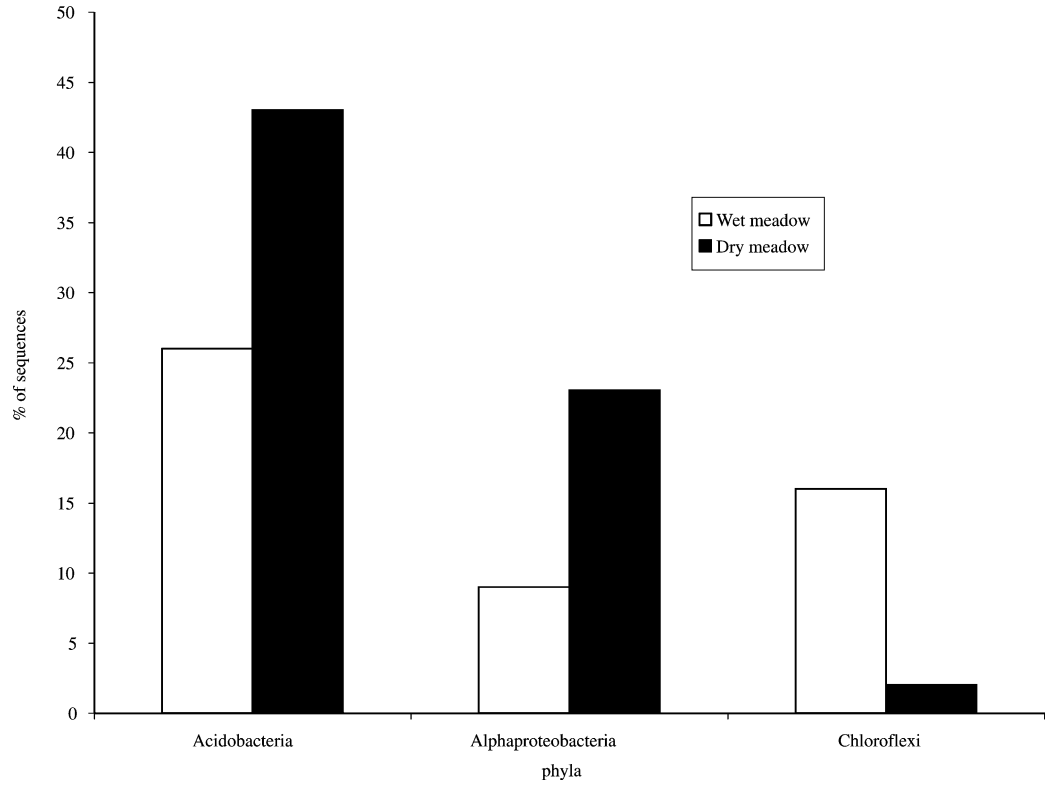

Fig. 4. Frequency of sequences related to major bacterial groups in 16S rRNA gene clone libraries from Niwot Ridge wet (Costello and Schmidt, in preparation) and dry [28] tundra soil collected during spring.

of organic material from lysed cells. Finally, sequences related to the Verrucomicrobia and Betaproteobacteria were in highest abundance during the summer. Cultured relatives within these divisions are plant-root fermenters, as well as oligotrophs that may thrive when substrate availability decreases in summer. Large numbers of betaproteobacterial sequences have also been sequenced from a Japanese alpine snowpack [54], where conditions are likely very oligotrophic.

In addition to season, topography also appears to structure bacterial communities on Niwot Ridge. In contrast to the windswept dry meadows of the alpine tundra, wet meadow soils form in landscape depressions and receive snowmelt throughout much of the growing season. As a consequence, these soils are more anoxic and have higher plant productivity, soil organic matter, microbial activity, and methane emissions than dry meadow soils [15,59]. Costello and Schmidt (in preparation) examined 16S rRNA gene diversity in a wet meadow tundra soil collected during spring snowmelt (Fig. 4). Some major differences were seen between the wet and dry meadow, which may be due to different sampling methods (wet meadow soils were sampled over greater depths), but may also reflect the biogeochemical differences in these systems. For example, in the wet meadow, although there were many genes related to both the Acidobacteria and the Alphaproteobacteria, these sequences were in lower abundance than in the dry meadow. In addition, wet meadow soils contained a high proportion of novel sequences distantly related to the Chloroflexi. While rare in the dry meadow, sequences related to the Chloroflexi were the third most abundant bacterial division in the wet meadow soil. Specific amplification and sequencing of these novel 16S rRNA genes revealed that they are present in dark, frozen soil under winter snowpack, and may be localized to mineral subsurface soil in the spring (Costello and Schmidt, in preparation). Their spatial distribution suggests that these organisms do not seem to require light and appear to favor anoxic conditions, implying that they may be functionally more similar to anaerobic heterotrophic Chloroflexi than the better-studied filamentous anoxygenic phototrophs. However, the ecological roles of these organisms are totally unknown.

2.3. Alpine tundra Eucarya

Microbial eucaryotes are also major participants in the alpine tundra soil community [26,48] and we have used molecular phylogenetic techniques to more specifically investigate the eucaryotes in these soils. In the dry meadow, Meyer [33] investigated subnival and summer eukaryotic communities and found sequences related to the fungi, cercozoans, alveolates and lobosea. Fungi dominated this soil, and three major fungal phyla (ascomycetes, basidiomycetes, zygomycetes) were present [33]. In a separate study, three new class-level lineages of the fungal phylum Ascomycota were discovered in the dry meadow [48]. As is the case

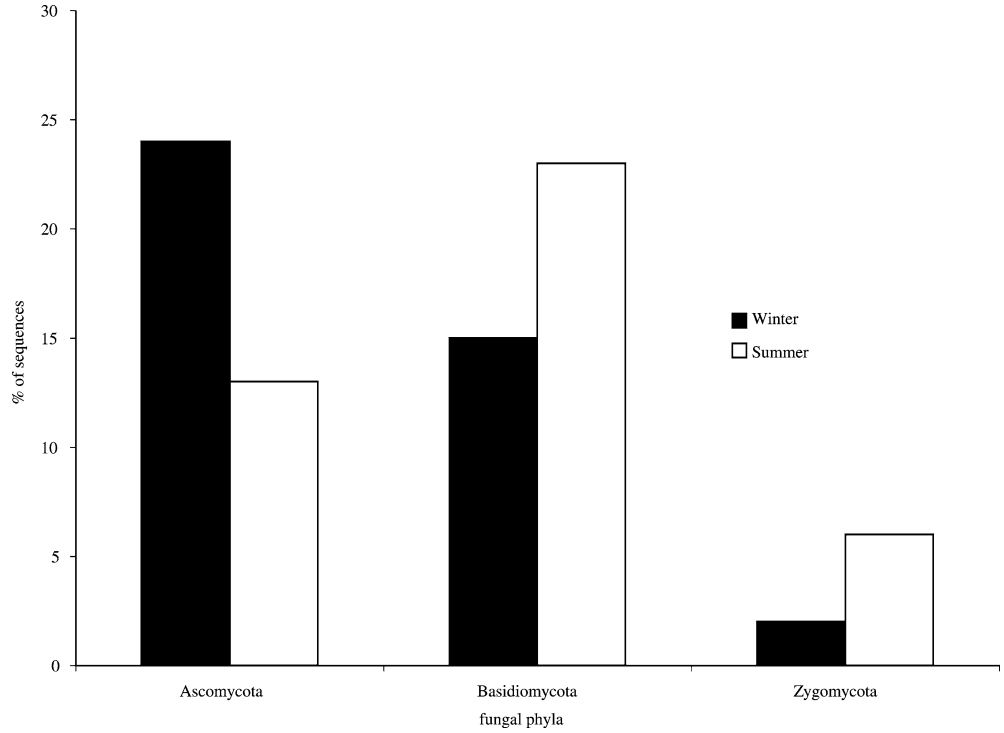

Fig. 5. Frequency of sequences related to three fungal phyla in 18S rRNA gene clone libraries from Niwot Ridge alpine tundra soil during winter and summer. Adapted from Meyer [33].

with the bacterial community, eucaryotic diversity in the dry meadow shifts seasonally; the fungal communities are particularly seasonally dynamic (Fig. 5). At snowmelt, eucaryotic SSU rRNA gene surveys suggest that the population of ascomycetes drops by about 50%, while the populations of zygomycetes and basidiomycetes increase in abundance. Another molecular study, using fungal-specific primers, discovered the appearance of one of the above mentioned, novel ascomycete clades in the summer, coupled with nonrandom shifts in fungal community composition across the seasons [48]. The biogeochemical roles of these highly divergent organisms, and the environmental shifts driving these changes in community structure are yet to be uncovered.

2.4. Alpine tundra Archaea

Compared to Eucarya and Bacteria, the diversity of terrestrial Archaea remains relatively unexplored. However, these organisms may be important in cold environments; indeed Crenarchaeota constitute 39% of the prokaryotic biomass in cold, deep oceanic waters [11]. In addition, they are consistently found in molecular surveys of soil microbial communities [41]. Very recently Oline et al. [43] examined the diversity of soil Crenarchaeota across an elevation gradient of ecosystem types, from foothills forest to the alpine tundra on Niwot Ridge. They identified two novel, tightly clustered groups of sequences—one closely related to SCA1145, an abundant globally distributed clade within the Terrestrial Group of Crenarchaeota, and another nested within the more basal FFSB group of sequences. Of course, the ecological roles of the organisms represented by these sequences remain unknown. However, some very preliminary results from stable isotope probing experiments (West and Schmidt, unpublished data) suggest that alpine Crenarchaeota may be involved in the oxidation of C1 compounds, including methanol.

2.5. Alpine talus soils

Much less is known about nutrient cycling in cold, unvegetated soils in the alpine, such as those found on talus slopes and in newly exposed glacial forelands where long, seasonal snow-cover prevents plant establishment. We have monitored the year-round physical environment of Niwot Ridge talus soils and have shown that the optimal time for microbial growth in the talus is the last two months before snow melt [24]. During this period, there is abundant available water and soil temperatures are slightly above freezing, allowing for the proliferation of cold-tolerant microbes. In contrast, the snow-free summer soils are much drier, and are subject to dramatic diurnal temperature fluctuations (sometimes 30 °C in one 24 h period) and high UV radiation [24].

Preliminary work suggests that microbial population shifts in talus soils may mirror those seen in the tundra, with fungi dominating subnival communities and bacteria dominating snow-free soils on Niwot Ridge [23]. However, there is some evidence that carbon cycling is markedly different in the talus than in tundra soils. For example, Ley et al. [22] found that, unlike most soils, organic matter content does not correlate with heterotrophic microbial biomass

in the barren talus soils on Niwot Ridge. This may be due to a large population of autotrophic organisms. Indeed, other, unpublished work from our laboratory suggests that microbial photosynthesis is important in these soils. For example, Pescador and Schmidt (unpublished data) documented light-dependent carbon dioxide influx in unvegetated soils.

Molecular phylogenetic work also supports the presence of autotrophic organisms in unvegetated soils. For example, we used molecular techniques to examine the microbial community from a recently deglaciated, barren soil in the Cordillera Vilcanota of Southeastern Peru and found that a significant portion of the bacterial community is related to the photosynthetic bacterial division Cyanobacteria [38]. The eucaryotic communities in unvegetated soils have also been investigated, and these talus soils harbor deeply diverging microorganisms. In the unvegetated talus soils on Niwot Ridge, Meyer [33] identified a eucaryotic lineage that cannot be ascribed to any known clade and may represent a novel group at the kingdom level. In addition, other deeply branching eucaryotic SSU rRNA genes were sequenced from these soils. For instance, new fungal groups were found within the chytrid and ascomycete lineages, as well as novel sequences within the metazoan, green algal, alveolate and the cercozoan kingdoms. The roles of the organisms represented by these genes remain unknown.

3. Arctic tundra

There are many similarities between arctic and alpine regions, as evidenced by the overlap in their plant communities. For example, 37% of the alpine plant species in Colorado also occur in the arctic [4]. In addition, some similar biogeochemical patterns are seen in the arctic, including high rates of subnival microbial respiration [12,16,65] and decomposition [17]. Also, it appears that depth of snowpack may structure microbial activity in the arctic as well; for example, higher rates of nitrogen mineralization [49] and respiration [58] are observed under deeper snowpack.

However, some environmental conditions are markedly different in the arctic and alpine, including precipitation, angle of solar insolation, atmospheric thickness, partial pressure of atmospheric gases, and the duration of the plant growing season [46]. Photoperiods are also dramatically different, resulting in greater diurnal oscillations in air temperature in alpine regions during the snow-free season [46]. Mid-latitude alpine regions also experience greater seasonal oscillations in soil temperatures than arctic regions, because the presence of permafrost in arctic soils tends to buffer soil temperatures [46].

Differences in permafrost cover also structure differences in water availability [4,46]. In arctic soils, permafrost isolates the active layer, preventing the deep drainage of water [4]. In addition, the release of water from thawing permafrost provides a water source in arctic tundra soils [4]. Alpine soils less frequently have continuous permafrost to trap soil moisture, and are often characterized by steep slopes that enhance runoff [46], which can further exacerbate moisture stress. Wet, cold conditions in arctic soils tend to inhibit decomposition, and as a result, organic matter often accumulates in arctic tundra soils, especially those occurring in flat, poorly drained areas [50]. These differences in arctic and alpine soils are likely to create important differences in nutrient cycling in arctic and alpine soils.

Indeed, biogeochemical cycling in arctic and alpine tundra systems differ in many ways, including the timing of plant nutrient uptake. For example, in a study where N was added to the spring snowpack, alpine plants acquired 100 times more of the added N than arctic plants [3]. Other work may explain these discrepancies: unlike alpine plants, arctic plant growth in the first half of the growing season often does not depend on nutrient uptake from the soil. Instead, early season growth relies on nutrients stored in plant tissues (reviewed in [57]). This adaptation is necessary for life in the arctic, since these soils typically remain frozen for several weeks after air temperatures are above freezing, limiting nutrient uptake.

Because of differences in the timing of nutrient uptake between arctic and alpine environments, there are probably differences in the timing of root growth, and therefore root C inputs to the soil. Furthermore, differences in soil moisture availability between arctic and alpine tundra environments result in alpine plants often having deeper penetrating roots than their arctic counterparts [4]. Thus, both the timing and distribution of root C inputs to the soil are likely to vary between the two regions, with root C inputs entering the soil earlier and deeper in alpine regions. Since root C inputs to the soil are one of the principal sources of labile C to soil microbes during the plant growing season, differences in root growth between these environments have the potential to result in significant differences in soil microbial dynamics between arctic and alpine regions across both time and space. However, unlike the alpine tundra, very little is known about the microbial diversity in arctic soils. Below, we summarize all published data from 16S rRNA gene clone libraries of arctic tundra soils.

3.1. Arctic tundra microbial diversity

16S rRNA gene clone library sequencing methods have also been applied to survey bacterial diversity from only two arctic tundra soils. Zhou et al. [64] sequenced 43 unique 16S rRNA genes from the melted active layer of a Siberian permafrost soil while Neufeld et al. [40] sequenced approximately 2500 short, variable 16S rRNA gene fragments from a pristine soil in the Canadian arctic. Nearly 24% of sequences from the Canadian site could not be phylogenetically resolved, and may represent novel, deeply branching organisms, or may be an artifact of sequencing only a relatively small, variable region within the 16S rRNA gene. Both arctic studies revealed the high diversity typical of soil microbial communities, including many sequences that were

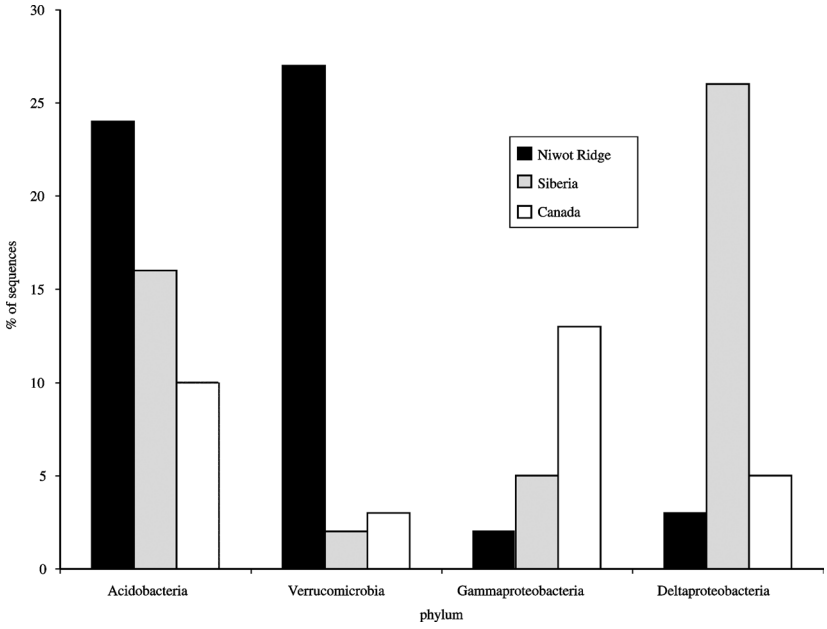

Fig. 6. Frequency of sequences related to major bacterial groups in 16S rRNA gene clone libraries from Niwot Ridge [28], Canadian [40], and Siberian [64] tundra soils.

related to the Proteobacteria, Acidobacteria, Actinobacteria and Bacteroidetes. A notable difference between the two sites was that the Canadian soil had a high proportion (13%) of sequences related to the Gammaproteobacteria while the Siberian soil harbored many (26%) sequences related to the Deltaproteobacteria (Fig. 6). A comparison of the arctic summer microbial communities with the alpine tundra summer communities shows that the alpine contains many more sequences related to the Verrucomicrobia (Fig. 6). As mentioned above, these organisms may be involved in fermenting plant-root compounds, and the lower abundance of sequences from this clade in the summer arctic soils may reflect differences in timing of root C inputs or rooting depth between arctic and alpine plants.

Kobabe et al. [21] used fluorescence in situ hybridization (FISH) to quantitatively examine the vertical distribution of specific bacterial groups in the active layer of Siberian tundra permafrost-affected soil. They found that the percentage of total cells detectable by both general and specific phylogenetic probes decreased with soil depths, perhaps suggesting that cells are less active at greater depths in these soils. Others have been able to cultivate and identify a number of different types of bacteria directly from permafrost ([55] and references therein). Whether these microbes are actually growing and active in permafrost remains unknown.

As is the case for many soil types that are biogeochemically relevant on a global scale, information about the microbial communities in arctic soils is grossly lacking. Indeed, approximately 0.2% of 16S rRNA genes from soil that are deposited in Genbank originate from the arctic tundra, yet this ecosystem occupies nearly 5% of land on Earth. In addition, although fungi are important players in nutrient cycling in the arctic tundra, very little information is available on the microbial eucaryotes in these soils. And, of course, the actual functional roles of the organisms represented by these SSU rRNA genes remain a mystery. A major challenge for microbial ecologists will be not only to describe microbial communities in these soils, but also to describe how these communities will be affected by climate change.

4. Conclusions and future directions

Cold ecosystems are already experiencing the effects of human-induced environmental change, and are likely to be heavily affected in the coming decades [5,53]. Both the alpine and arctic may experience more rapid warming than other systems [18], and high mountain areas may also be subjected to disproportionate amounts of N deposition [8,63]. How these changes will affect the microbial community, and therefore, nutrient cycling, is poorly understood. However, recent studies demonstrate that warming [35] and nutrient deposition [37,52] clearly affect the biogeochemistry of cold soils. A focus of future work will be to determine exactly how these projected effects will change microbial communities and, alter nutrient cycling patterns.

Acknowledgements

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