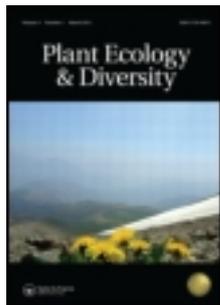


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### Plant-microbe interactions at multiple scales across a high-elevation landscape

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## Plant–microbe interactions at multiple scales across a high-elevation landscape

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Here we review the numerous studies of plant–microbe interactions conducted at the Niwot Ridge LTER site in Colorado, USA. By synthesising work at scales ranging from the rhizosphere to the landscape, we offer a mechanistic view of how these interactions are essential to understanding the spatial and temporal structuring of plant and microbial communities across this diverse and changing landscape. These new insights are also important for making predictions about how both plant and microbial communities and populations will respond to future changes in this environment, especially with regard to the potential uphill movement of plants and microbes in response to climate change and nitrogen deposition. We predict that the uphill movement of plants and microbes will be especially apparent, and have the most impact, in areas of the alpine that are now mostly plant free. These areas are currently undergoing a shift from a microbe-dominated ecosystem to one where microbe–plant interactions will play a critical role in reducing nutrient losses to downstream ecosystems.

**Keywords:** community assembly; endophytes; mycorrhizae; soil phenolics; spatial statistics

### Introduction

Here we review our growing understanding of the dynamics and importance of plant–microbe interactions across the elevational gradient that comprises the Niwot Ridge LTER site. The studies considered here started in the 1990s with work that was aimed at understanding plant community-level patterns in nitrogen (N) cycling by microbes and plants (e.g. Bowman et al. 1993; Jaeger et al. 1999) and trace gas fluxes (e.g. West et al. 1999) across the alpine landscape. Much of the work from the 1990s was summarised in the book edited by Bowman and Seastedt (2001).

In the present paper we build on those early studies to present our current, more mechanistic, understanding of microbial–plant processes across the alpine landscape. These more recent studies have expanded on our early focus on plant community-level interactions to both broader studies of landscape patterns (e.g. King et al. 2010) as well as more focused studies of plant–plant interactions mediated through microbes (e.g. Schmidt et al. 2000; Meier and Bowman 2008a; Suding et al. 2008). This review begins by describing the broadest-scale patterns of plant microbe associations across the alpine landscape and then narrows in scope to address interactions at the level of the rhizosphere.

### Landscape patterns of microbe–plant interactions

The research sites discussed in this review span an elevational gradient that crosses several ecosystem types and

their corresponding ecotones (Figure 1). Matching the decreasing levels of aboveground plant biomass across this gradient, soil microbial biomass levels show a marked decline with elevation, and plant communities shift, with a mean microbial biomass level of 2230  $\mu\text{g C g}^{-1}$  in soils of spruce-fir forests near the treeline, to 1270  $\mu\text{g C g}^{-1}$  in dry meadow tundra soils at mid-elevations, to 80  $\mu\text{g C g}^{-1}$  in the subnival zone above the tundra zone (King et al. 2008). These levels of microbial biomass C were directly proportional to the level of soil organic matter across this landscape, with organic matter levels of 49% (SD = 20%,  $N = 36$ ), 32% (13%) and 1.3% (0.4%) for forest, tundra and talus, respectively (A.F. Meyer and A.J. King unpublished). At a finer landscape scale, microbial biomass levels are intimately linked to the spatial distribution of vegetation, soil pH and seasonal snow depth (King et al. 2010).

The influence of plants on microbial abundance is especially evident in the subnival and nival zones, that is, areas where elevation (>3500 m a.s.l.) and late-season snow packs limit the abundance of plants (Figure 2). It is apparent that some of the hotspots in microbial biomass in this mostly plant-free zone coincide with areas of higher plant density (see Figure 2). Not surprisingly, these hotspots of microbial biomass are also hotspots of soil enzyme activity and other biogeochemical processes. For example, the best predictor of soil phosphatase and cellulase activity was microbial biomass C at these sites (King et al. 2008). Work in other ecosystems on Niwot Ridge, as

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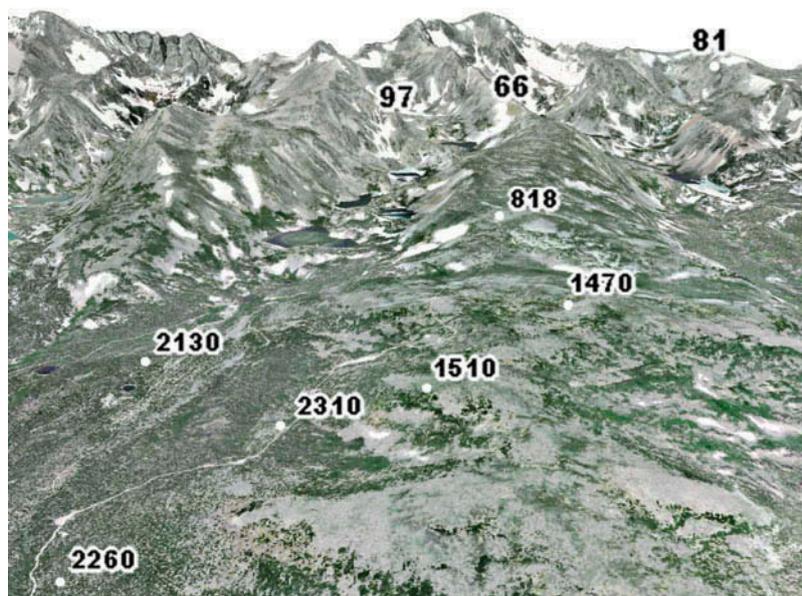


Figure 1. Landscape pattern in soil microbial biomass carbon (MBC) levels in ecosystems ranging from spruce-fir forests just below treeline at ca. 3400 m to mostly barren soils at the horizon (Continental Divide), Niwot Ridge LTER. Each point represents the mean of 30 soil samples collected in a nested sampling scheme at scales of 0.01, 0.1, 1, 10 and 100 m apart. The points are ca. 1000 m apart within each ecosystem type. The highest biomass levels were in soils of spruce-fir forests and the lowest were in mostly unvegetated talus field soils. Data for the highest elevation soils were previously analysed by King et al. (2008).

well as globally, has shown that hotspots in microbial abundance are important for net ecosystem nutrient cycling (Fisk et al. 1998; van den Heuvel et al. 2009; Darrouzet-Nardi and Bowman 2011). These plant-microbe hotspots in the subnival zone are influenced both by water and growing season length, such that areas of intermediate snow accumulations are the most productive and have the highest plant densities (King et al. 2010). Thus, these areas of higher productivity may shift in location in response to future changes in the timing of snow melt (Clow 2010) and the shrinkage of late-season snow beds (Naff et al. 2013).

Recent molecular studies in the subnival zone on Niwot Ridge have also offered new insights into landscape patterns of plant-microbe interactions. In areas of the subnival zone where plants are present in higher densities, a third of all bacterial 16S rRNA gene sequences are significantly correlated with individual plant species abundances, indicating that plant species are important in structuring high-elevation microbial communities (King et al. 2010, 2012). Interestingly, these plant-bacterial associations are stronger, but occur less frequently in the highest, most environmentally harsh reaches of the alpine landscape. This pattern of association strength and frequency suggests that some plants may be highly dependent on microbes in order to colonise extreme sites, but other plants may be able to colonise without the need for specific microbial associates, and also that the associations develop over time following plant colonisation (i.e., specialised microbes follow the plant species uphill). The most abundant bacterial clades in these extreme sites included those containing organisms with the ability to

promote plant growth, e.g. the Rhizobiales, Rhodospirillales, and Burkholderiales (King et al. 2010, 2012).

In areas of the subnival zone where plants have been established for longer periods of time (compared with the mostly plant-free areas discussed above), there is a greater diversity of bacterial clades associated with each plant species, and the most abundant plant species (*Geum rossii* (R.Br.) Ser. and *Deschampsia caespitosa* (L.) P.Beauv.) have the greatest diversity of associated microbes (King et al. 2012). However, these two plant species do not share any strongly associated bacterial clades (King et al. 2012), suggesting that the spatial pattern of plant species across the landscape may help explain the surprisingly small home ranges (high levels of community autocorrelation) in microbial community diversity we have observed in the subnival zone (Figure 2 and King et al. 2010; Robeson et al. 2011). Thus, the spatial heterogeneity in microbial biomass and plant abundance (Figure 2) in combination with the increased diversity of plant-microbial interactions in plant-dominated areas supports the idea that the strength and frequency of plant-microbial interactions changes with altitude within the subnival zone at Niwot Ridge. This is similar to recent observations from the Alps, where the diversity of cushion plant-associated microbes is more different from bulk soil microbial diversity in higher elevation locations (Roy et al. 2013). Because annual net nutrient cycling rates are tied to plant and microbial active periods, understanding the role of subnival plant-microbial interactions in alpine biogeochemical cycles and their seasonality is an important and active area of research.

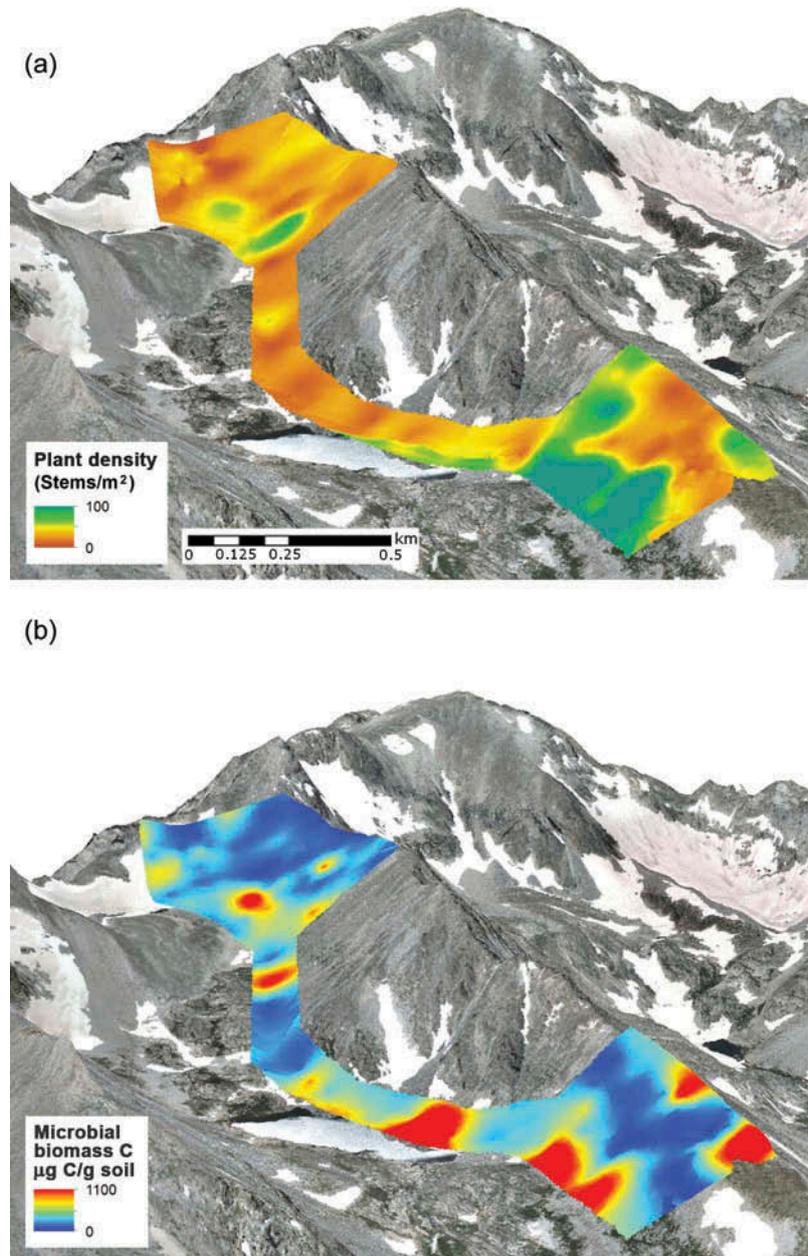


Figure 2. Plant density (plants  $m^{-2}$ ) across the subnival zone of Green Lakes Valley, Niwot Ridge LTER (a). Microbial biomass C levels ( $\mu\text{g C g}^{-1}$  of soil) across the same landscape. Data was originally used in the analysis of King et al. (2010, 2012) (b).

#### Seasonality of plant–microbe relationships

The landscape patterns in microbial taxa and biomass discussed above were measured during the late summer or autumn, and therefore may not represent the maximum microbial biomass levels or plant–microbe associations on a year-round basis. For example, numerous studies in all of the alpine and subalpine ecosystem types of Niwot Ridge have shown marked seasonal dynamics in soil microbial biomass levels. Weintraub et al. (2007) showed that microbial biomass levels reached peak values of over  $6000 \mu\text{g C g}^{-1}$  under late spring snowpack in spruce–fir forests (compared with  $\sim 2000 \mu\text{g C g}^{-1}$  for the rest of the year). Studies of dry meadow tundra and high-elevation plant-free sites have similarly shown that microbial

biomass peaked under the spring snowpack (Schadt et al. 2003; Ley et al. 2004; Lipson and Schmidt 2004). Peaks in microbial biomass levels beneath the snow were partially explained in all of these ecosystems by water limitation of microbial activity in the summer months (Fisk et al. 1998; King et al. 2008); the highest sustained soil moisture levels are reached in these seasonally dry ecosystems under the late winter and early spring snowpack (Freeman et al. 2009a; Ley et al. 2004; Monson et al. 2006). Furthermore, plant litter produced during the previous growing season is an active source of total organic carbon (TOC) and dissolved organic carbon (DOC) under the snowpack during this time period (Lipson et al. 2002; Meier et al. 2008).

### Seasonal trends in microbial groups

There are some consistent trends in the seasonal dynamics of major groups of microbes across the alpine landscape. In general, fungi are the dominant members of the microbial community in the colder months and bacteria become more important during the growing season of plants. For example, in dry meadow tundra dominated by the plant *Kobresia myosuroides* (Villars) Fiori, the active fungal to bacterial ratio (based on bio-volume conversions to biomass) was 15:1 in the winter versus 7:1 in the summer (Lipson and Schmidt 2004). Similarly, Ley et al. (2004) showed that fungi dominated the active microbial community during snowmelt, whereas bacteria were more important during the summer in mostly plant-free soils of the subnival zone. Surprisingly, the fungi that dominate the subnival zone (especially under long-lived snow packs) are mostly newly discovered clades of zoosporic fungi (chytrids) (Freeman et al. 2009b), some of which are ‘snow chytrids’, in that they live in the snow where they parasitise ‘snow algae’ or degrade aeolian-deposited pollen (Naff et al. 2013). In a similar vein, the dominant winter fungi in the spruce-fir zone are conspicuous mats of filamentous ‘snow moulds’ that develop under the melting snowpack where they decompose forest litter and DOC until the snow melts and soils dry out (see pictures in Schmidt et al. 2007, 2009). Overall, the seasonal dynamics of microbial communities across all of the alpine and subalpine ecosystems studied on Niwot Ridge are intimately linked to year-round changes in how nutrients are cycled, as discussed in the following section.

### Microbial activity and release of plant-available nutrients

One of the most important realisations that resulted from earlier work on Niwot Ridge (e.g. Brooks et al. 1998; Lipson and Schmidt et al. 1999) and work in other temperate environments (Grogan and Jonasson 2003; Edwards et al. 2006; Larsen et al. 2007) was that there are high levels of microbial activity during the snow-covered period. The build-up of microbial biomass under the snow results in the immobilisation of nutrients and the production of trace gases that contribute significantly to ecosystem-level budgets of nutrients and trace gases (Ley et al. 2004; Monson et al. 2006; Miller et al. 2009; Schmidt et al. 2009). It has emerged that the transition between the snow-covered and snow-free periods is critical in terms of ecosystem-level nutrient fluxes. Specifically, the die-off of the mostly psychrophilic under-snow community leads to release of plant-available nutrients into the soil (Lipson and Schmidt et al. 1999; Schmidt and Lipson 2004; Schmidt et al. 2007). A portion of these released nutrients are taken up by plants capable of early season activity (e.g. *Ranunculus adoneus* A. Gray and *Geum rossii*) and microbes (Mullen et al. 1998; Jaeger et al. 1999), but a significant fraction is lost in runoff to the aquatic environment (Brooks et al. 1998; Monson et al. 2006).

The transition from winter to summer microbial communities is driven not only by changes in temperature and moisture, but also by changes in the plant-derived carbon (C) substrates available to the microbial community. In the winter, polymeric C sources and DOC from litter predominate, resulting in a community that is well suited to degrade plant litter and dead roots (Lipson et al. 2002; Nemergut et al. 2005). This winter community is dominated by fungi as discussed above, and by bacteria in the polymer-decomposing Bacterioidetes group (Lipson and Schmidt 2004). In contrast, the summer microbial community feeds mostly on highly labile plant root exudates, and is dominated by bacteria and plant-root-inhabiting fungi (Lipson et al. 2002; Schmidt et al. 2007), including a ubiquitous, newly discovered group of root-inhabiting fungi that was originally described in association with *Kobresia myosuroides* on Niwot Ridge (Schadt et al. 2003; Rosling et al. 2011). Rhizosphere microbes can directly take up nutrients for plants (e.g. mycorrhizal fungi) or they can indirectly contribute to plant nutrition through the ‘soil microbial loop’, that is, via protozoal predation of rhizosphere bacteria (Moore et al. 2003). The rapid growth rate of warm-season alpine rhizosphere bacteria and their equally rapid turnover releases more than enough N to equal plant demand for N in the alpine environment (Fisk et al. 1998; Schmidt et al. 2007). Nitrogen tied up in microbial biomass turns over at least 10 times faster than plant N in alpine ecosystems (Fisk et al. 1998; Schmidt et al. 2007), and this rapid turnover and the less efficient metabolism of bacteria compared with fungi (Lipson et al. 2009) results in a flux of nutrients from rhizosphere microbes to mycorrhizae and plants during the growing season. A mechanical model depicting this relationship is shown in Figure 3.

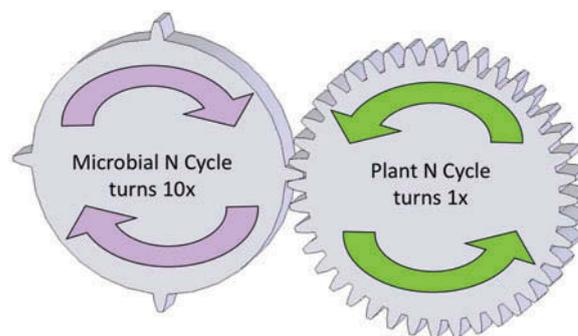


Figure 3. Conceptual/mechanical model of the summer nitrogen cycle for soils under *Kobresia myosuroides* dominated vegetation on Niwot Ridge. The gear ratio is 10:1, representing the fact that the microbial N pool turns over at least 10 times faster than the plant N pool (Schmidt et al. 2007). In fact the turnover rate of the microbial N pool may be over 100 times faster than the plant N pool, resulting in an almost continuous release of nutrients from microbial cells, providing more than enough N for plants in this system (Fisk et al. 1998).

### Plant–plant interactions mediated through soil microbes

Our knowledge of plant–plant competition mediated through soil microbes has increased markedly since the publication of the 2001 synthesis volume (Bowman and Seastedt 2001). The capacity of plants to compete for soil resources has traditionally focused on traits related to their uptake rates for nutrients and water. Alternatively, plants can limit neighbour acquisition of limiting nutrients through manipulation of the amount and activity of soil microorganisms (Schmidt 1990; Schimel et al. 1998). With the realisation that plant chemistry can profoundly affect the size and composition of the soil microbial community in alpine ecosystems (e.g. Schmidt et al. 2000; Bowman et al. 2004), it has become apparent that alpine plants can, to some degree, control the rate of microbial turnover and activity (Meier and Bowman 2008a, 2008b). In essence plants can change the rate at which the microbial N cycle turns (Figure 3), presumably making the soil nutrient milieu more favourable to themselves at the expense of other plant species. For example, in a study of two co-dominant alpine species (*Geum rossii* and *Deschampsia caespitosa*) it was shown by Bowman et al. (2004) that microbial immobilisation of N was higher in microcosms treated with *Geum* litter compared with those treated with *Deschampsia* litter, and microbial biomass N was higher in field soils under *Geum* canopies compared with *Deschampsia* canopies. *Geum* litter also significantly reduced the growth and N acquisition of *D. caespitosa* relative to the control and *D. caespitosa* litter treatments. These results (Bowman et al. 2004; Meier and Bowman 2008a) indicate that phenolics in *G. rossii* are an excellent C source for soil microorganisms and result in increased microbial activity and N immobilisation, thereby reducing N supply to neighbouring plants (Figure 4).

Subsequent work has shown that the majority of the labile C leached from leaf litter of *Geum* is consumed by microbes during the winter, and that the high soil DOC found in soils under *Geum* canopies during the growing season is

derived from root exudation (Meier et al. 2008). These root exudates have different phenolic chemistry compared with leaves (both litter and fresh), but their overall influence on microbial biomass and inhibition of neighbouring plant growth is similar (Meier et al. 2009). Most *Geum*-derived phenolic compounds enhance microbial respiration, but one fraction, the low molecular weight hydrophobic phenolics, added in isolation to soils failed to stimulate microbial respiration and actually killed *Deschampsia* plants (Meier and Bowman 2008a). The failure of bulk fractions to kill neighbouring plants may be associated with microbial consumption or detoxification of the low molecular weight hydrophobic phenolic fraction.

Investigation of soluble C compounds in tissues of other alpine species suggests that a similar potential exists for impacts on microbial activity and supply of nutrients to neighbours (Meier and Bowman 2010). *Artemisia scopulorum* A. Gray and *Potentilla* species exhibit a similar or even higher capacity to stimulate microbial activity relative to *Geum*. The potential for plant chemical mediation of plant–plant interactions via soil microbes appears greatest in moist meadow tundra, due to higher abundance of plant species with labile C, higher soil moisture, and a greater degree of nutrient limitation of growth relative to other alpine plant communities. Rates of microbial activity and soil organic matter decomposition are highly dependent on the chemical composition of litter inputs, are positively associated with the chemical diversity of the litter, and more poorly correlated with the diversity of plant species which may not adequately reflect the chemical diversity of the fresh soil organic matter (Meier and Bowman 2008b, 2010).

### The importance of mutualisms in alpine and subalpine ecosystems

Studies of plant–fungal symbioses in alpine ecosystems have a long history (e.g. Haselwandter and Read 1980; Cripps and Eddington 2005 and references therein), but

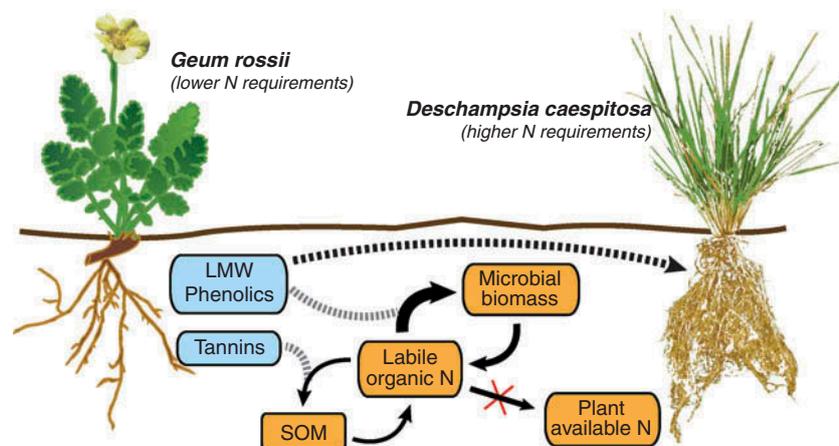


Figure 4. A conceptual model, with broad support from multiple experiments, illustrating how phenolic C (blue boxes, dashed grey lines) can influence key components of the N cycle (orange boxes), reduce plant-available N (red X), and reduce growth of a neighbour with higher N requirements. Low molecular weight (LMW) phenolics also directly inhibit neighbour growth, possibly via an allelopathic mechanism (dashed black arrow).

such research at Niwot Ridge only began in the 1990s with the pioneering work of Renee Mullen (Mullen and Schmidt 1993; Mullen et al. 1998). The most significant finding of those early studies was the demonstration (in the field) that arbuscular mycorrhizal fungi (AMF) were important in the uptake of phosphorous (P) by alpine plants, such as *Ranunculus adoneus* (Mullen and Schmidt 1993) and that ectomycorrhizal fungi (EMF) and dark septate endophytes (DSE) were involved in N uptake by alpine plants (Mullen et al. 1998; Schadt et al. 2001). DSE are common in seasonally cold ecosystems and are a phylogenetically diverse group of septate, melanised fungi that inhabit healthy roots (Laursen et al. 1997; Jumpponen and Trappe 1998; Schadt et al. 2001). EMF are also common in plants of the forests and tundra on Niwot Ridge (Schadt 2002), and the EMF associates of the tundra plant *Kobresia myosuroides* have been shown to take up (and transfer to the plant) many forms of N, including amino acids (Lipson and Schadt et al. 1999).

The spatial distribution of mycorrhizae and DSE may also provide glimpses of their functionality and importance in alpine ecosystems. Early workers hypothesised that mycorrhizae should be less common as elevation increased, because climate rather than nutrient supply should limit plant growth at higher elevations. This hypothesis was supported by some observational studies conducted in the Alps (Read and Haselwandter 1981). Along the Colorado Front Range and Niwot Ridge, AMF in plant roots decrease with elevation – being almost completely absent from the patchy plant communities found above 4000 m a.s.l. (Schmidt et al. 2008). By contrast, DSE do not decrease with elevation and are present in the roots of all plant species ( $N = 10$ ) growing at the highest elevation sampled (4300 m a.s.l.) by Schmidt et al. (2008). The reasons for these elevational patterns are not clear at present; however, the fact that AMF are mostly involved in P uptake and DSE are involved in N uptake may suggest that N is more limiting to plant growth at higher elevations and P is more important at lower elevations. It is also possible that DSE are better adapted for dispersal to, and survival in, extreme high-elevation soils than are AMF. AMF are mostly obligately biotrophic and therefore do not survive for long periods in the absence of plants (Miller et al. 1985), whereas many DSE fungi can grow in the absence of plants and therefore are more likely to be found in early successional, plant-free soils. Indeed, the dominant DSE fungus (DS16b, GenBank#AF168167) found in the roots of *Ranunculus adoneus* on Niwot Ridge is also common in clone libraries of unvegetated glacial forelands; sequences 99% similar to DS16b made up 6% of fungi in clone libraries from young unvegetated soils in the high Cascades (Jumpponen 2003). The presence of DSE in soils before plants invade would allow them to colonise early successional plants before slow-to-disperse and metabolically

challenged AMF fungi can. These ecological differences between DSE and AMF could have profound implications for which plants can move to higher elevations in the face of global warming and changing patterns in nutrient deposition; that is, we would expect plants that do not require AMF to be the first colonists of previously ice-covered habitats (Schmidt et al. 2008). In addition, it is likely that rhizosphere bacteria also play a role in the interaction between these fungal mutualists and the growth of their plant hosts, yet we know comparatively little about this. The elevational gradient at Niwot Ridge provides a perfect natural experiment to study the importance of symbioses in future plant adaptations to climate change.

Another recent development in the field of plant–fungal interactions was the discovery at the Niwot Ridge LTER site of a previously unknown and extremely diverse new group of root-associated fungi (Schadt et al. 2003). After the initial discovery of this new group in eukaryotic clone libraries from dry meadow soils (Schadt et al. 2003), related sequences have subsequently been found in association with plant roots in almost all ecosystems globally (Lindahl et al. 2007; Rosling et al. 2011) and can be the dominant rhizosphere organisms in coniferous forests, including the heavily studied C1 site on Niwot Ridge (Porter et al. 2008). Originally called Soil Clone Group 1 (Schadt et al. 2003; Porter et al. 2008), they have only recently been officially named the Archaeorhizomycetes (Rosling et al. 2011). The function of the Archaeorhizomycetes in the rhizosphere is still unknown, but given the global distribution and abundance of this group, future intensive studies of their function in the rhizosphere are warranted.

### Impacts of nitrogen deposition on microbe–plant interactions

High-elevation mountain systems are particularly sensitive to human-induced impacts; deglaciation, increased positive degree-days, and changes in atmospheric N deposition (Caine 2010) are affecting plant (Pauli et al. 2012) and microbial (Nemergut et al. 2007; Nemergut et al. 2008) communities across the globe. At the Niwot Ridge LTER site there have now been two decades of work looking at the effects of increased N deposition on plant and microbial diversity and processes. Early work by Fisk and Schmidt (1996) showed that the microbial biomass of dry meadow showed increased immobilisation of N in fertilised soils, especially in the autumn after plants senesced, indicating a greater than expected microbial N sink for added N in the alpine. N fertilisation also greatly increased the flux of nitrous oxide and decreased the uptake of methane from these same soils (Neff et al. 1994). Long-term N addition of relatively high amounts of N in the dry meadow plant community resulted in significant loss of soil light fraction C, but increased stabilisation of C in

heavy fractions, with no change in total soil C stocks (Neff et al. 2002). More recent work in the alpine tundra of Niwot Ridge confirmed that the autumn and winter microbial community is more resilient to increased N loading than the summer microbial community (Schmidt et al. 2004), perhaps because they are already adapted to higher N levels (Jaeger et al. 1999). Long-term N fertilisation has also greatly impacted the overall diversity of soil microbes. Nemergut et al. (2008) used molecular phylogenetic approaches to show that chronic N additions reduced the relative abundance and diversity of Basidiomycete fungi and almost completely eliminated archaea related to known nitrifiers. These changes coincided with shifts in chemistry of soil C pools as well as changes in soil enzyme activity. Together, these results support a close coupling between plant/microbe community shifts and nutrient cycling in response to N deposition in this ecosystem.

While we know that increased N inputs often cause declines in both microbial and plant diversity in alpine tundra, it is less clear whether the decline in both groups is due to direct effects of N or whether the increased N changes plant-microbial interactions (decline in one group may be related to changes in the other group). Understanding these interactions is challenging, but we are beginning to amass experimental evidence that plant-microbe interactions are shifting on Niwot Ridge in response to elevated N, and this shift may affect the abundance of plant species. For example, root-associated fungal communities of two abundant plants in moist meadow tundra, *Geum rossi* (which strongly declines due to N deposition) and *Deschampsia caespitosa* (which increases in abundance in response to N) showed that the fungal community of *Deschampsia* was more responsive to N enrichment compared with that of *Geum*. In both *Deschampsia* and *Geum*, many of the fungal taxa that changed in abundance with N matched known saprotrophic fungi, ericoid mycorrhizal fungi, dark-septate fungi, and plant pathogens (Dean et al., 2014). In *Geum*, the fungal community was dominated by Helotiales (83% relative abundance) in control conditions, and 7 years of N addition caused Helotiales to decline by almost a third (Dean et al., in press). These results suggest that *Geum* may be losing mutualists at high N or that *Deschampsia* may benefit from a flexible fungal community. Nitrogen enrichment also altered root-associated bacterial communities, and more taxa from *Geum* roots responding to N compared with *Deschampsia* roots (S.L. Dean et al., unpublished data). A related  $^{13}\text{C}$  tracer experiment found that carbon allocation patterns in *Geum* changed more strongly in response to increased N, and gram-negative bacteria received twice as much carbon from *Geum* in N-enriched plots compared with control plots (Farrer et al. 2013). These findings bring into question the widespread assumption among plant ecologists that plant diversity decline is due to changes in plant

competitive interactions, and suggest that microbial community changes at high N inputs might strongly affect the plant community.

Another aspect we are just beginning to explore is how anthropogenic inputs of N may be affecting the microbes (and eventually plants) in mostly plant-free (subnival zone) soils that abut the Continental Divide which delimits the western extent of the Niwot Ridge site. These sites have shown increased flux of nitrate in stream water over recent years (Williams et al. 2011; Mladenov et al. 2012). Microcosm experiments indicate that N additions do not stimulate heterotrophic microbial respiration because the system is C limited, at least for microbial heterotrophs (Figure 5). However, the presence of excess C, N (and P) cause significant increases in microbial respiration, indicating that the system could rapidly adapt to increased C inputs from invading plants (and immobilise more N). N additions also result in dramatic shifts in microbial community structure, including increases in the relative abundance of Gammaproteobacteria and decreases in the archaeal to bacterial ratio, both of which are indicative of a shift to a microbial community adapted to excessive N levels. These results support the idea that microbial communities adapt very rapidly to N additions (Schmidt et al. 2007), and suggest that future changes in deposition across the alpine landscape may lead to changes in microbial community structure and function in currently unvegetated regions.

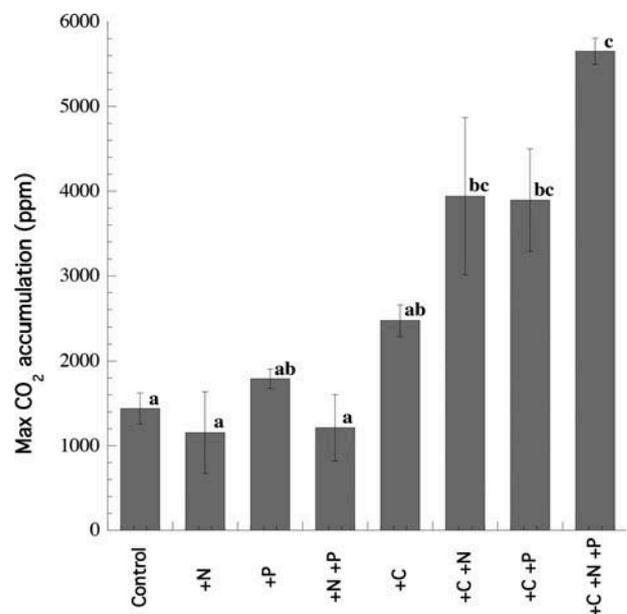


Figure 5. Effects of added C, N and P on heterotrophic microbial activity (total CO<sub>2</sub> respired) in microcosms of soil from the subnival zone of the Niwot Ridge LTER site. Only microcosms receiving C in combination with N and/or P had total levels of CO<sub>2</sub> accumulation that were significantly different from the control soils. Full respiration curves from the microcosms receiving C and P were previously published (King et al. 2008).

### Conclusions and future directions

One of the obvious future directions for research on Niwot Ridge are questions related to how microbes and plants will adapt (or ‘move uphill’) in response to a changing environment. At this and other high-elevation mountain sites, deglaciation, increased temperature, and changes in atmospheric deposition (Caine 2010) will likely allow plant species to move uphill and colonise previously barren soils (Pauli et al. 2012). As plants move uphill, we expect the plant–microbial associations we have discussed here – both the broad-scale patterns across the alpine landscape and as well interactions at the level of the rhizosphere – will exert strong effects on the resulting community assembly processes for microbes and plants. Our initial understanding of community assembly processes over these landscapes suggests several factors that might be important to understand how alpine vegetation will move uphill. Both microbial and plant communities are structured by edaphic factors (King et al. 2010), with soil moisture and snow depth being the controlling factors shared by both plants and microbes. In addition, heterotrophic microbes are limited by carbon (King et al. 2008) and therefore should respond positively to plant invasion. In turn, microbes can create niches for some plant species and restrict niche space for others, depending on the effects of pathogens, symbionts (e.g. mycorrhizal fungi), and microbially accumulated nutrients (e.g. N fixation, weathering of rock P). The chance successful establishment of C- and N-fixing microbes, such as cyanobacteria (Schmidt et al. 2009; Schmidt et al. 2011) and the concurrent weathering of parent material by organic acids, can set some sites on a trajectory towards high-nutrient status. Similarly, we expect that high variability in the distribution of microbes that are known symbionts with plant species, such as mycorrhizal fungi (Schmidt et al. 2008; King et al. 2012), will strongly influence which plants can invade particular sites.

Finally, as plant communities move uphill into sparsely vegetated regions, the functioning of these ecosystems will change. For instance, in plant-free areas, the microbial community is largely limited by carbon, with several groups (in particular zoosporic fungi) associated with increased amine-containing compounds and nitrification. As plants colonise barren soils, we expect plants to decrease the abundance of zoosporic fungi due to competitive exclusion (shading) of algae (their food source). As plants take up much of the available nitrate, they should therefore reduce nitrate export from the watershed. This and other hypotheses remain to be tested, and we hope the next 10 years of plant–microbe research will yield significant new insights into the functioning of the Niwot Ridge LTER site at multiple scales.

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