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Microbes in the Middle: Elevation Gradients Reveal Drivers of
Belowground Ecosystem Processes with Climate Change

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Elevation gradients are an excellent tool that allow scientists to investigate the impacts of temperature change within a single system. While the effects of elevation on aboveground plant communities have been well studied, the effects on microbially-mediated ecosystem function remain unclear. Here, we review how belowground ecosystem processes are affected both directly by temperature variation and indirectly through plant functional trait differences across elevation. A better understanding of the mechanisms that drive belowground ecosystem function will enable more accurate predictions of how ecosystems as a whole will respond to climate change.



Introduction

As climate change accelerates, predictions of abiotic changes include warmer temperatures, drier climate, and elevated CO₂ levels (Stocker et al., 2013). While the aboveground responses of plant and herbivore communities to these changes have been well studied (Cleland et al., 2007; Ahuja et al., 2010; Chen et al., 2011; Sundqvist et al., 2013; Read et al., 2013), it is unclear what the ramifications of a changing climate will be for belowground soil communities. Because temperature and often precipitation co-vary with elevation, elevation gradients provide a tool with which to assess the ecosystem level effects of such changes. Abiotic factors have a largely direct impact on microbial communities while biotic interactions within plant communities and processes have significant direct and indirect effects belowground (Bardgett et al., 2008). It is increasingly apparent that biotic influences, in addition to traditional abiotic stress gradients, will drive belowground community dynamics in a way not currently accounted for in predictions for ecosystem response to climate change.

The mechanisms by which microbial communities act as drivers of ecosystem processes, especially with regards to carbon cycling, is becoming especially relevant in discussions of future climate change. As climate changes, the role of belowground communities in mediating carbon cycling becomes more important. Nitrogen fixing bacteria and mycorrhizal fungi contribute up to 50% of plant productivity to ecosystem carbon cycling (Heijden et al., 2008). Belowground communities have been shown to play a vital role in mediating ecosystem response to elevated CO₂ both by sequestering carbon and making soil nutrients available for plants to sequester carbon in the soil (Zak et al., 2000). For other factors including temperature, elevation gradients comprise a powerful tool for understanding what factors drive belowground communities and for making predictions about how these changes will affect ecosystem function. In this review we seek to synthesize known information about how microbially-mediated ecosystem processes are affected by climate change. We utilize studies that estimate a number of abiotic and biotic factors across elevations to understand complex above- and belowground interactions. We first summarize how abiotic factors vary with elevation and influence belowground communities directly and then explore the indirect relationships between the above- and belowground biotic spheres. By understanding the direct and indirect linkages between elevation and microbial communities, we can better estimate how climate change may influence microbially-mediated ecosystem processes.

Climatic conditions vary with elevation

Several climatic factors, such as temperature and snowfall dynamics, change predictably across elevation gradients, allowing these gradients to be used as natural treatments where the impacts of microclimate changes on many different ecosystem processes can be evaluated (Figure 1). It is estimated that air temperature declines with elevation by 5.5 to 6.5 °C per 1,000 m increase (Barry, 1992; Beychok, 2011). Since soil systems are buffered to these temperature changes given the insulating nature of the soil solid and fluid components, this pattern of temperature decline is less clear and the magnitude of the belowground temperature lapse rate varies among systems. In a study conducted in Swedish peat lands, an increase in ambient temperature of 2.0 °C triggered a 0.5 °C increase in soil temperatures (Dorrepaal et al., 2009). For example, Clinton (2003) showed that soil temperatures in the Southern Appalachian Mountains are not driven predominantly by elevation in the winter and fall. Additionally, extensive snow cover in high-elevation systems can insulate the belowground system, decoupling soil and air temperatures during times of heightened snow depth (Karrasch, 1973).

Others argue that mean annual temperature (MAT) is inherently influenced by other climatic and geographic parameters which are not reported, but which may be the main drivers

behind differences in ecosystem function. Körner (2007) states that MAT is confounded by distance from the sea and the length of the dormant season, and that the crucial factor that demonstrates the influence of temperature on ecosystem function is mean growing season temperature, standardized by climatic continentality. Because MAT is an average of air temperatures across the entire year, longer winter seasons or dormant periods will drive this mean temperature observation down despite the fact that growing season temperatures are much warmer and will result in higher levels of productivity than would be expected given the MAT. As temperatures cool with increasing elevation, growing season length, on average, declines by 3 to 4 days per 100 m increase in elevation (~ 7 days / $^{\circ}\text{C}$) (Moser et al., 2010).

Conversely, mean annual precipitation (MAP) and, consequently, soil moisture content, show no general pattern across global elevation gradients. Declining atmospheric temperature with increasing elevation affects the atmospheric moisture content by lowering the ability of atmospheric gases to hold water vapor. In some systems, higher elevations receive more precipitation than do lower elevations, as is the case in the Southern Appalachian Mountains (Clinton, 2003). In contrast, precipitation declines with elevation in the Andes Mountains, or even peaks at mid-elevations as on Mt. Kilimanjaro (Körner, 2007). However, soil moisture regimes are driven most strongly by elevation during wet periods characterized by significant downslope drainage, while soil moisture is seemingly unaffected by elevation during drier seasons or in semi-arid systems (Western et al., 1999). When montane hydrology is predominantly driven by nival (i.e., winter snow) contributions, soil moisture is driven most strongly by snow distribution, snow depth, topography, and soil texture (Williams et al., 2009). Patterns relating soil moisture and elevation are most clear during wet periods, and the patterns become less apparent as the watershed dries.

Snowfall characteristics such as snow depth and cover, as well as general wind exposure and topography, largely control vegetation distribution at high elevation sites (Billings and Mooney, 1968; Walker et al., 1993). Warmer, low elevation sites receive less snow and vegetation communities are therefore shaped by different combinations of factors. Since plant communities condition the surrounding soil system, we can conclude that the same snow characteristics that drive plant communities will also shape microbial communities in the belowground system. It should also be noted that high elevation systems are subject to different disturbance regimes than are low elevation sites. In cooler, high elevation locations, wind velocity, timing of snowmelt, and the duration and depth of snow cover serve as disturbances whose strength varies seasonally and annually (Komárková, 1993). These parameters also affect soil moisture content during the following growing season.

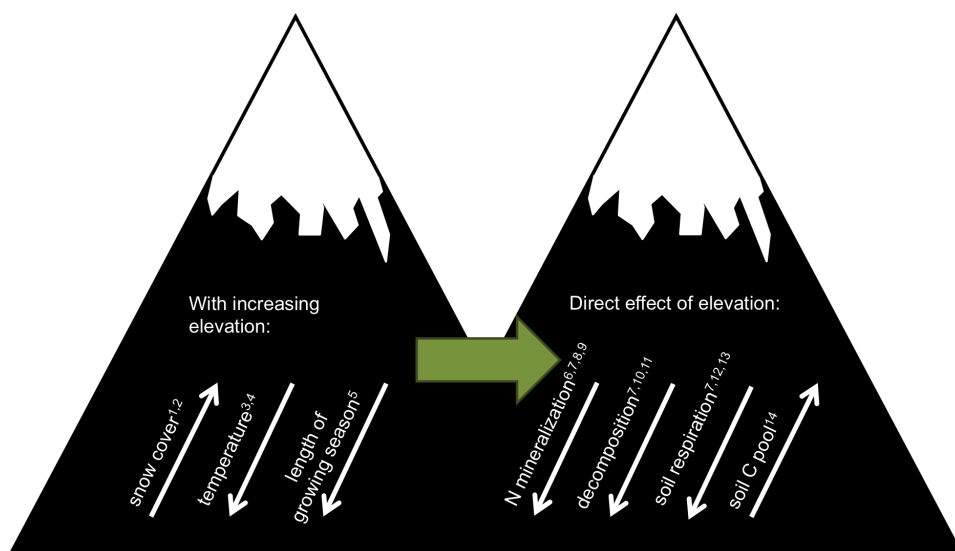


Figure 1: Climate variation along elevation directly influences ecosystem processes. Climatic conditions such as temperature and length of growing season decrease with elevation, while snow cover increases with elevation. Changes in these abiotic conditions directly influence rates of ecosystem processes, with rates of N mineralization, decomposition, and soil respiration declining with increasing elevation and cooler temperatures, resulting in a larger soil C pool at higher elevations. (Walker et al., 1993)¹, (Billings and Mooney, 1968)², (Barry, 1992)³, (Beychok, 2011)⁴, (Moser et al., 2010)⁵, (Matson and Vitousek, 1987)⁶, (Sveinbjörnsson et al., 1995)⁷, (Powers, 1990)⁸, (Bonan and Van Cleve, 1992)⁹, (Kitayama and Aiba, 2002)¹⁰, (Murphy et al., 1998)¹¹, (Rodeghiero and Cescatti, 2005)¹², (Li et al., 2008)¹³, (Fu et al., 2004)¹⁴.

While several aspects of the aboveground microclimate vary predictably with elevation, as described above, no such generalized trends are found in belowground physical properties. No patterns relating elevation and soil physical characteristics such as texture, soil depth, pH or parent material exist as generalized patterns seen globally (Kitayama and Aiba, 2002; Shen et al., 2013). Most soil properties are seen as the result of a region's dominant substrate or parent material (Kitayama and Aiba, 2002). This can perhaps be seen as an advantage to study designs that utilize elevation gradients; climatic parameters vary in a predictable manner while geologic belowground properties remain fairly stable across the elevation gradient, allowing scientists to isolate the influence of climate on ecosystem function.

Direct effects of climatic variation across elevation on ecosystem processes

Elevation drives changes in soil nutrient pools

As elevation increases and air temperature declines, soil organic matter and the size of soil stable carbon (C) pools also increase (Fu et al., 2004). The increase in the size of soil C pools is likely due to declining decomposition rates in the cooler microclimate of high elevation-systems. While temperature is one of the most important drivers of C cycling and the size of soil C pools, moisture limitation in some systems may overshadow this relationship (Kitayama and Aiba, 2002). This effect is apparent in tropical mountain systems in the South Pacific where organic C pools peak at mid elevations, the region that is most moisture-limited (Kitayama and Aiba, 2002). The size of soil N pools shows a more variable response to changes in temperature as elevation increases. A study by Kitayama and Aiba (2002) in the South Pacific showed that total nitrogen (N) pools peak at mid elevations, exhibiting a similar pattern to that of soil C

pools in the same region. In South-Central Alaska, organic soil ammonium concentrations are negatively correlated with elevation such that soil ammonium content was lowest in the colder, high-elevation sites (Sveinbjörnsson et al., 1995).

Abiotic factors directly influence rates of ecosystem processes

Temperature has long been acknowledged as the most important driver of microbial activity and microbially-mediated ecosystem processes, in the absence of moisture limitation (Davidson et al., 1998) (Box 1). In this way, temperature variation with elevation directly influences the rates of ecosystem processes. Soil respiration rates increase with temperature in the Italian Alps, South-Central Alaska, and in Chinese mountain systems, with highest soil respiration rates experienced at warmer, low elevation locations (Sveinbjörnsson et al., 1995; Rodeghiero and Cescatti, 2005; Li et al., 2008). Li and colleagues (2008) also note that though soil respiration rates do increase predictably with warmer temperatures, soil moisture may control the response of soil respiration to warming when soil moisture limits microbial activity. Similarly, decomposition rates increase with warmer temperatures, meaning that decomposition is negatively correlated with elevation (Sveinbjörnsson et al., 1995; Murphy et al., 1998; Kitayama and Aiba, 2002).

It has been widely described that N mineralization rates increase with mean annual soil temperatures (Matson and Vitousek, 1987; Powers, 1990; Bonan and Van Cleve, 1992; Sveinbjörnsson et al., 1995). Nitrification potentials also decrease with increasing elevation (Matson and Vitousek, 1987). In many systems, the crucial driver of N mineralization rates, a process controlled by microbial activity, is not mean annual soil temperature in general, but specifically growing season temperatures, especially in high latitude or extremely high alpine environments (Sveinbjörnsson et al., 1995). In South-Central Alaska, Sveinbjörnsson and colleagues (1995) revealed that these temperature-dependent mineralization patterns exist in both the organic and mineral soil horizons. Increasing N mineralization rates with climate change, as temperatures climb, affect nutrient limitations to growth and productivity in ecosystems across the globe. These processes, when amplified or suppressed, affect rates of nutrient cycling as well. Bonan and Van Cleve (1992) found that in Canadian boreal forests warmer soil temperatures increased the decomposition rate of spruce litter while N mineralization rates simultaneously increased, allowing for greater nutrient availability. Increased N content in the soil stimulated tree growth that ultimately offset the added C from increased decomposition, maintaining the C sink status of these systems. The balance of C and other nutrient reservoirs has the potential to be altered depending upon the strength and connectedness of above- and belowground linkages as the mechanisms of nutrient cycling shift.

Indirect effects of elevation on ecosystem processes through plant functional traits

Variation in plant functional types and foliar traits

Due to these environmental selective pressures, plant community composition and plant functional traits are largely filtered through ecosystems with elevation. Because temperature varies predictably across elevation gradients, leaf traits also predictably vary with elevation (Figure 2). Broadly, vegetation changes in functional types from forest through treeline and into treeless high alpine systems occur in almost every ecosystem (Körner, 1998). Along with this change in vegetation type, functional groups and plant community composition vary across elevations (Sundqvist et al., 2013).

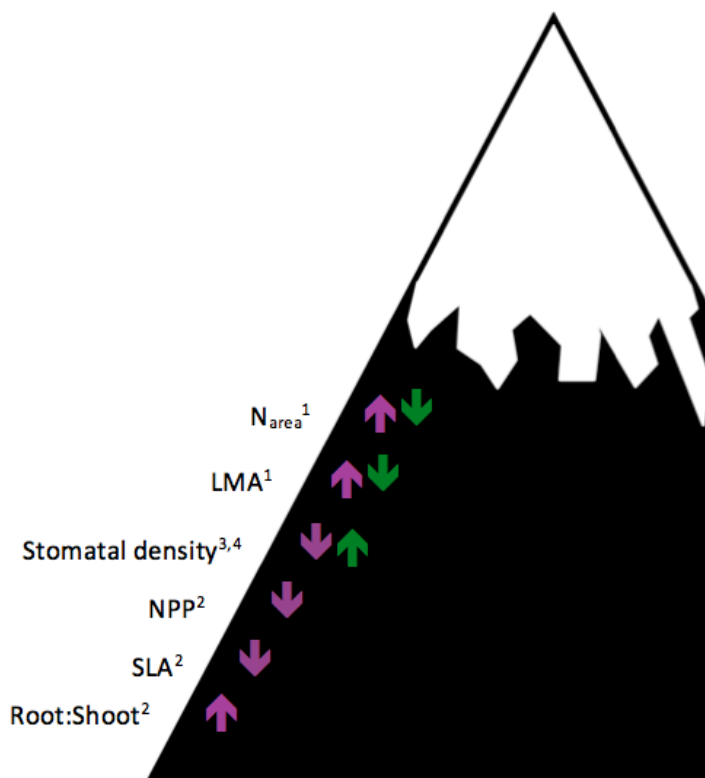


Figure 2. Plant traits vary predictably with elevation. Summary figure showing patterns of angiosperm (purple) and gymnosperm (green) plant traits with increasing elevation. These results stem from meta-analyses and elevational field experiments. Elevation has an indirect effect on microbially-mediated ecosystem processes through plant functional trait variation. In general, plants allocate more C belowground, have tougher leaves, and grow less at high elevations in comparison to low elevations. Abbreviations: LMA (leaf mass to area ratio), Narea (leaf N per unit area). (Read et al., 2013)¹, (Sundqvist et al., 2013)², (Kouwenberg et al., 2007)³, (Hultine et al., 2000)⁴.

Plant functional traits such as biomass, aboveground net primary productivity (ANPP), leaf area index (LAI), and leaf physical and chemical properties are lower in more stressful environments, like high elevation systems (Sundqvist et al., 2013; Kitayama and Aiba, 2002). The range of intraspecific variation in foliar traits can be consistently greater within species, within clines, than across species across continents and biomes. Specifically, high elevation ecotypes exhibit high leaf mass to area ratios (LMA) and low leaf nutrient content (Hultine et al., 2000; Read et al., 2013). Positively correlated with ANPP, stomatal density and N per unit leaf area (Narea) decrease with elevation (Kouwenberg et al., 2007; Read et al., 2013). Interestingly, even population dynamics of plant species can change predictably across elevation, including an observed increase in male to female ratios of dioecious flowering plants (Field et al., 2013). These leaf trait schemes correspond with growth strategies along the leaf Worldwide Economic Spectrum that examines evolutionary tradeoffs of growth strategies in plants (Wright et al., 2004).

Differences in microbial community structure along elevation gradients

While plant functional differences vary predictably along elevation gradients, microbial communities do not follow the same patterns in diversity as aboveground communities. Plant

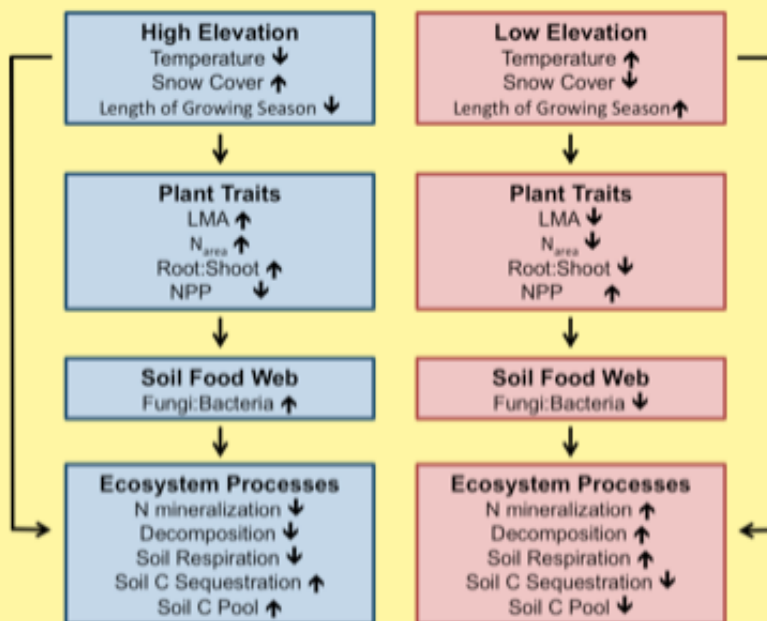
communities tend to be most diverse at intermediate elevations, but microbial communities decrease monotonically with elevation, most likely due to soil heterogeneity across landscapes and elevations (Decaëns et al., 2010). Furthermore, bacterial richness and phylogenetic diversity decrease linearly with elevation (Bryant et al., 2008). While plant phylogenetic relatedness decreases with elevation, bacterial communities exhibit phylogenetic clustering along elevation gradients, highlighting the differences between evolutionary structure of above and belowground systems.

Plant functional traits affect ecosystem processes through microbial communities

It has been shown that plant functional traits significantly affect C cycling rates (Box 1). These patterns emerge as a result of plant functional trait dynamics with microbial communities according to leaf economics and microbial processing of C from plant to soil.

The ratio of fungi to bacteria in soil reflects the types of relationships in which plants engage with microbes. Across elevations, fungal to bacterial ratios have been shown to decrease with elevation while total microbial biomass also decreased with elevation (Balser et al., 2005; Fierer et al., 2011). Fungal and bacterial dominance is largely determined by nutrient availability that suggests low nutrient environments favor fungal microbial communities while bacterially dominated ecosystems are found in high nutrient environments. Moreover, there is evidence that these relationships occur due to positive feedbacks governed by inherent differences in nutrient acquisition and transformation strategies of fungal and bacterial microbial communities (Wardle et al., 2004). These fertility scenarios can be represented in elevation gradients where low elevation soils are bacterially dominated and exhibit high enzyme activity (Margesin et al., 2009). Fungal-dominated ecosystems most often occur in low quality soil and litter ecosystems, in which low litter quality with high lignin and secondary compounds inhibits nutrient cycling, which prompts plants to require higher proportions of fungal symbionts to maintain slow rates of long-lived, recalcitrant tissues (Bardgett, 2005; Heijden et al., 2008; Deyn et al., 2008). These low-quality ecosystems tend to have high root to shoot ratios, presumably to maximize fungal symbioses by increasing the amount of surface area available for symbiotic colonization and increase nutrient foraging distance (Deyn et al., 2008; Moeller et al., 2014). In the opposite case of fast-growing, high-quality litter systems, root to shoot ratios are smaller and growth tends to be quick with short-lived leaves and labile leaf litter.

Box 1. Climatic variation along elevation directly and indirectly influences ecosystem processes.



Climatic variation along an elevation gradient can both directly and indirectly influence ecosystem processes. In this figure, arrows following response variables indicate a positive or negative correlation with increasing elevation. Lower temperatures (Barry, 1992; Beychok, 2011), increased snow cover (Walker et al., 1993; Billings and Mooney, 1968), and a shorter growing season (Moser et al., 2010) directly decrease the activity of microbes responsible for major nutrient-cycling ecosystem processes such as N mineralization (Matson and Vitousek, 1987; Powers, 1990; Bonan and Van Cleve, 1992; Sveinbjörnsson et al., 1995), leaf litter decomposition (Sveinbjörnsson et al., 1995; Kitayama and Aiba, 2002; Murphy et al., 1998), and soil respiration (Sveinbjörnsson et al., 1995; Rodeghiero and Cescatti, 2005; Li et al., 2008), causing a decline in the rate of C and N cycling. Colder temperatures also kinetically inhibit the rate of these chemical reactions, further slowing ecosystem processes in high elevation systems. As rates of decomposition and breakdown of soil organic matter decrease, the size of soil C pools inherently increases (Fu et al., 2004), leading to greater soil C sequestration (Sundqvist et al., 2013).

The response of plant functional traits to climatic conditions and the consequences of those traits for soil microbial communities indirectly compound the slowing of ecosystem processes at higher elevation, cold systems as described above. At these high elevations, plants exhibit functional traits typical of high-stress environments with thick leaves (i.e. high Leaf Mass to Area ratio—LMA) (Hultine et al., 2000; Read et al., 2013). Stressed for nutrients, plants shunt more C into belowground root systems (Sundqvist et al., 2013) and exhibit lower N per area (N_{area}) in leaf tissue (Read et al., 2013). In high elevation systems, plants exhibit lower net primary productivity (NPP) than at low elevations (Sundqvist et al., 2013). The suite of plant functional traits at high elevations is more stress-tolerant, and therefore recalcitrant. Because of these litter qualities, belowground microbial systems are fungal dominated at high elevations. In contrast, plant functional traits at low elevations make them labile and easily decomposed, favoring bacterial dominance belowground (Sundqvist et al., 2013). These shifts in soil food web dominance combined with slower decomposition caused by more recalcitrant leaf litter at high elevations and more labile litter inputs at lower elevations, rates of ecosystem processes are further driven toward faster rates of cycling in low elevation systems and slower, more conservative nutrient cycling rates at high elevations.

These fast-cycling, high-nutrient ecosystems are often light-limited (Deyn et al., 2008; Wardle et al., 2004). It has been suggested that microbes are most important for low-nutrient ecosystems in which plants must rely on the mineralization and fixation of nutrients by microbes for survival.

In low-nutrient ecosystems for which microbes are a vital player in ecosystem processes, soil microbial diversity is the highest and it declines with available nutrients (Heijden et al., 2008). Trait-mediated relationships between plant-microbe interactions are context dependent, and their relationship changes over elevation and stress gradients. For plants growing along elevation gradients, stress context determines the direction of species interactions. At low elevations where stress is low, plants compete with one another both inter- and intra-specifically; however, at high elevation, high stress environments plants exhibit intraspecific facilitative behavior by which neighboring plants enhance the survival, growth, and fitness of one another (Callaway, 2002). Similarly, negative interactions between soil microbial communities such as competition and parasitism decrease with elevation (Defosse et al., 2011).

Variation in microbial communities drives variation in ecosystem functioning

Because of the specific roles microbes play in nutrient cycling, differences in microbial community structure affect ecosystem function (Box 1). In slow-growing, fungal-dominated communities, nutrients are repeatedly cycled between plants, litter, and fungi in a closed nutrient system. In bacterially dominated systems, nutrients can more easily be lost from the system through leaching and other processes (Wardle et al., 2004). As stress increases along elevation gradients and nutrients become more limiting, fungal dominance increases with elevation. In the same way, N and phosphorous use efficiency increase with elevation and nutrient limitation (Kitayama and Aiba, 2002).

Although the patterns of ecosystem processes across elevations including decomposition and respiration have been well studied, many studies overlook the mechanistic role of belowground communities in driving these patterns. In semi-arid systems such as Arizona, litter decomposition rates actually increased with elevation because higher elevations were characterized by higher soil moisture content (Murphy et al., 1998). Such results indicate that with global warming and climate change, increasing soil temperatures may not result in higher decomposition rates unless more precipitation is also received to lift water limitations in semi-arid systems. The interactive effects of temperature and moisture on decomposition rates clearly have significant implications for microbially-mediated C cycling with climate change.

Conclusions

Microbially-mediated ecosystem processes are driven both by abiotic and biotic components that vary along elevation gradients. Abiotic factors have largely direct effects on microbial communities through climatic parameters that control microbial activity. Microbial communities are also structured by biotic interactions with plants. Plant communities have direct effects on belowground communities through fungal associations, which are more abundant in high stress, high elevation ecosystems. Conversely, biotic interactions are largely indirect at low elevations where bacterial communities are structured by plant and litter functional traits. Through these indirect interactions, major microbial functions including decomposition and mineralization will be controlled by the quality and quantity of litter provided by plant communities. With low productivity, high elevation systems, low rates of decomposition and mineralization can be expected in fungal dominated systems where nutrients are cycled conservatively. Alternately, high productivity, low elevation systems show higher rates of these important nutrient cycling processes and are typically dominated by bacterial belowground

communities.

As the climate warms, elevation gradients allow scientists to determine how other abiotic and biotic factors influence microbial communities and their associated functions. Elevation gradients are unique in that climatic variation is typically the only abiotic variable while geological and historical factors remain consistent. Using these gradients, the influence of climate on community dynamics and ecosystem processes can be isolated to aid in predicting how climate change will affect systems in the future. However, while elevation gradients generally provide scientists with a natural temperature gradient within a single system, not all systems prescribe to these patterns. Other climatic variables such as soil weathering, hydrology, annual precipitation, and wind patterns can be confounding in some sites (Körner, 2007). In light of these variations, accounting for these variations allows elevation gradients become a unique way to predict how climate change may affect not only aboveground but also belowground systems. Climate may affect belowground communities not only directly through temperature, but also indirectly through plant-microbe interactions. While the aboveground response to climate change has been well-predicted using elevation gradients, the belowground response may be more complicated. Because soil systems have important consequences for ecosystem function and processes, understanding how both plant and microbial systems will react to climatic changes and potential range shifts will be an integral part of predicting whole ecosystem response. Placing belowground ecosystem processes in the greater context of their direct and indirect influences stemming from climatic variability will aid scientists in identifying systematic patterns that can be extrapolated to understand ecosystems in the future.

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