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Plant colonization of moss-dominated soils in the alpine: Microbial and biogeochemical implications

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ABSTRACT

A major impact of global climate change is the decline of mosses and lichens and their replacement by vascular plants. Although we assume this decline will greatly affect ecosystem functioning, particularly in alpine and arctic areas where cryptogams make a substantial amount of biomass, the effects of this change in vegetation on soil microbial communities remains unknown. We asked whether changes in bacterial community composition and enzyme ratios were consistent across two sites in moss versus vascular plant dominated areas. Using data from treeline and subnival ecosystems, we compared bacterial community composition, enzyme activity, and soil chemistry in moss dominated and vascular plant dominated plots of two unique alpine environments. Further, we used a time series to examine plots that actively transitioned from moss dominated to vascular plant dominated over a seven-year time period. Bacterial community composition in the soils under these two vegetation covers was significantly different in both environments and changed over time due to plant colonization. Microbial activity was limited by carbon and phosphorus in all plots and there were no differences in BG:AP enzyme ratios; however, there were significantly higher NAG:AP and BG:AP ratios in vascular plant plots at one site, suggesting the potential for shifts toward microbial N acquisition in vascular plant dominated areas in the alpine. As vascular plants replace mosses under warming conditions, bacterial community composition and nutrient availability shift in ways that may result in changes to biogeochemical cycling and biotic interactions in these vulnerable ecosystems.

1. Introduction

Vegetation patterns worldwide are changing due to global change factors such as climate change (Settele et al., 2014), rising CO_2 levels (Bazzaz, 1990), increased anthropogenic nitrogen (N) deposition (Vitousek et al., 1997), invasive species (Didham et al., 2005), and land use change (Houghton, 1994). One key change is a shift from moss-dominated communities to vascular plant-dominated communities, particularly in arctic and alpine ecosystems (Joly et al., 2007; Chapin et al., 1995; Walker et al., 2006; Epstein et al., 2004; Spasojevic et al., in review). Cryptogams (mosses and lichens) have declined in response to warming (Cornelissen et al., 2001; Molau and Alatalo, 1998; Walker et al., 2006; Wookey et al., 2009) and nitrogen deposition may accelerate this decline (Cornelissen et al., 2001; Molau and Alatalo, 1998; Wookey et al., 2009; Lang et al., 2009).

The shift from moss-dominated communities to vascular-plant dominated communities should impact many aspects of the soil environment and ecosystem functioning. Moss and vascular plants have different tissue chemistry (Lang et al., 2009) and the slower decomposition of moss tissue (Heal and French, 1974; Hobbie, 1996; Lang et al., 2009) can lead to the accumulation of organic matter and sequestration of carbon (C) (Gorham, 1991). Rates of decomposition and nutrient cycling are expected to increase as vascular plants colonize, which may lower the C stored in these systems (Lang et al., 2009). We build on the previous work on moss and plant decomposition by examining the response of microbial communities and their decomposition enzyme activities. As

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microbial community composition may help to mechanistically explain variation in C cycling (Cleveland et al., 2007, 2014) and enzymes can reveal nutrient controls on microbial mediated nutrient cycling (Sinsabaugh et al., 2008), such insights will help to delineate biogeochemical attributes associated with moss and vascular plant-dominated soils in the wake of immediate environmental change.

We investigate these effects at alpine tundra sites near treeline and near the limits of vascular plant life. The two sites represent different stages of soil development and carbon environments - a higher carbon alpine tundra landscape with more continuous plant cover (Yuan et al., 2016), and a sparsely vegetated talus-field system (King et al., 2010). These two sites represent some of the heterogeneity in alpine landscapes, and enable us to investigate potentially consistent responses across different alpine habitat types as well as differences that may relate to unique C environments, which are known to modulate microbial-mediated responses in biogeochemistry (Knelman et al., 2014).

In this study we explore the signature of moss and vascular plant dominated landscapes on bacterial composition, enzyme activity and soil biogeochemistry. Additionally, we look at plots in which this transition from moss to vascular plant communities, emblematic of climate change in the alpine, actively occurred between 2008 and 2015. While we do not attempt to separate the effects of all abiotic factors, such as snowfree period, on belowground processes, we do characterize the belowground environment associated with these moss and vascular plant dominated landscapes at a broad level. Vascular plant or moss cover may constitute proxies for a suite of environmental conditions related to timing of snowmelt, where moss dominated areas are located in the latest melting parts of the snowbed, for example. In total, this work seeks to understand belowground responses that are broadly associated with previously observed transitions from moss to vascular plant dominated landscapes in the alpine, which may encapsulate a variety of factors.

We hypothesized that soils under vascular plants would have higher levels of nutrients due to more labile carbon inputs, and face unique nutrient constraints by nitrogen (N) and phosphorus (P) beyond C limitation that would prevail in moss dominated soils. We also hypothesized that aboveground driven differences in soil nutrient pools and edaphic properties would result in different bacterial community composition between the two vegetation types, with expected increases in root-associated bacteria and copiotrophic bacteria. Lastly, we hypothesized that bacterial community composition in the previously moss-dominated areas would change to become more similar to bacterial communities in existing vascular plant-dominated soils.

2. Materials and methods

2.1. Study site and sample collection

We collected data from two alpine areas at the Niwot Ridge Long Term Ecological Research Site (Fig. 1). Precipitation averages 930 mm/year, 80% of which falls as snow. Our lower elevation site, Soddie, is located just above treeline (3400 m.a.s.l.) in a snowbed community. We utilized the snowbed to sample from areas with just moss (n = 7) and areas with just vascular plants (n = 7) in a very small (~10 m) spatial scale (center to edge of one snowbed). The center of the snowbed with the deepest and latest melting snow is dominated by moss, while vascular plants, particularly *Ranunculus adoneus*, *Vaccinium myrtillus*, *Juncus drummondii*, *Antennaria alpina*, and *Carex rupestris* dominate parts of the snowbed with less snow. Soil samples were collected as a soil core of the top 5 cm of soil, and separate, paired samples were collected for the acetylene reduction assay in August, 2013. Soils were transported immediately to laboratories at the University of Colorado at Boulder. Acetylene reduction assay incubations were started immediately and soil samples for all other analyses were sieved to 2 mm mesh size. A subsample of soils was stored at 4 °C for pH and moisture analyses. A second subsample was stored at −70 °C for molecular work.

The higher elevation site, Arikaree (3650–3900 m.a.s.l.), is located at the west end of the Green Lakes Valley, on the south side of Niwot Ridge (Fig. 1). We collected data from points along a 2 km portion of the valley. The site is a matrix of block slope, late-melting snowbanks overlaying unvegetated gravel soils, fellfields, and small patches of vegetation (King et al., 2010). The most abundant plants in this landscape include *Festuca brachyphylla, Geum rossii, Trisetum spicatum, Oxyria digyna,* and *Erigeron simplex*. Soil texture is high in sand content (mean = 71%) and soil depth is shallow. Soils from this site were sampled in both 2007 and 2015 for time series analysis and sampling and processing were done following the same protocol. Soils were collected by homogenizing a ~50 cm^2 patch of soil *in situ* to a depth of 4 cm and then filling a 50 mL sterile conical tube or plastic bag. Samples were transported to the lab within 5 h of collection, and a subset was immediately taken and stored at −70 °C for DNA extraction. Soils from 2007 were stored at −70 °C for 8 years, and DNA was extracted with the same kit and sequenced in the same run (see below) as the 2015 soils. All remaining soil was held at 4 °C for up to a week while subsampling for soil biogeochemistry, enzyme, and moisture measurements. At each plot (1 m radius circles, n = 76), we conducted stem counts of vascular plants and clumps of moss in 2008 and 2015. From the original dataset (King et al., 2012), we selected 10 plots that were moss dominated (at least twice as many moss clumps as vascular plant stems) and 10 plots that were vascular plant dominated (no moss, > 50 plant stems). For the time series analysis, we used 4 plots that were moss dominated in 2008, but were vascular plant dominated in our resampling of the plots in 2015.

2.2. DNA extraction and 16S analysis

For the bacterial community assessment, DNA was extracted from 0.3 g (Arikaree) or 1 g (Soddie) of wet soil using a MO BIO PowerSoil DNA Isolation Kit according to the manufacturer's protocol (MO BIO Laboratories) and PCR was used to amplify the V4 hypervariable region of the bacterial 16S SSU ribosome gene using 515F and 806R primers following the methods of the Earth Microbiome Project (Amaral-Zettler et al., 2009; Caporaso et al., 2012; Smith and Peay, 2014). Amplified samples were purified and normalized with the SequalPrep Normalization Kit (Invitrogen Inc., CA), combined into a single pool of a 16S amplicon library (one pool for each site), and sequenced on one lane (separate runs for each site) of an Illumina MiSeq2000 (pair-end 2 × 300 bp) at the University of Colorado BioFrontiers Institute (Boulder, CO). Data were processed using a combination of UPARSE (Edgar, 2013) and QIIME (Caporaso et al., 2010) pipelines to pick OTUs at 97% sequence identity and assign taxonomy using the Greengenes database (DeSantis et al., 2006). Because we focused on major taxa at low taxonomic resolution and did not compare richness or diversity, rarefaction was not necessary. However, due to high variation, sequence reads from Soddie were rarified to 14,200 reads per sample before analyses. Arikaree site samples were not rarefied as the mean sequencing depth did not differ between years (*t*-test, p = 0.82) or between vegetation types (*t*-test, p = 0.63). The mean number of reads per sample was 35,669. Relative abundances were calculated by dividing the number of each operational taxonomic unit's (OTU) sequence reads by the total number of sequences in a sample.

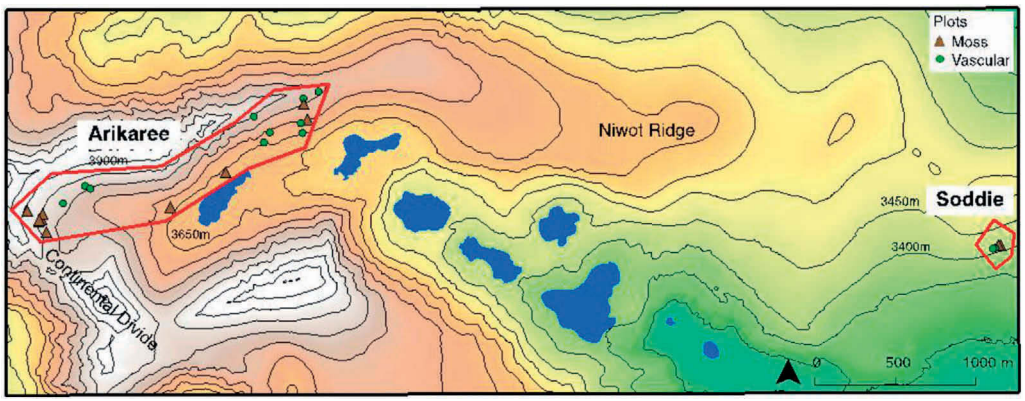

Fig. 1. Map of the study sites and plot locations at the Niwot Ridge Long Term Ecological Research Site in the Rocky Mountain Front Range, Colorado, USA.

2.3. Nitrogen fixation

Nitrogen fixation rates (at Soddie only), were assessed on field-wet soil (~5 g dry weight) using the acetylene reduction assay according to the specifications of Reed et al. (2010) and Knelman et al. (2012). Incubations were performed at 20 °C over 12 h within a day of collection. Sampled headspace was analyzed using a Shimadzu 14-A Gas Chromatograph (Shimadzu Corporations, Kyoto, Japan) equipped with a flame ionization detector and Poropak N column to measure ethylene concentrations. We used 10 and 100 ppm ethylene standards to construct a standard curve. N-fixation was calculated as ng N fixed cm^{-2} h^{-1}.

2.4. Enzyme activity

At both sites we measured β-1,4-glucosidase (BG), β −1,4-N-acetylglucosaminidase (NAG), and acid (alkaline) phosphatase (AP). Microbes use these enzymes to acquire carbon, nitrogen, and phosphorus, respectively. To compare across the two datasets, we evaluated the relative activity of carbon (BG), nitrogen (NAG), and phosphorus (AP) targeting enzymes by evaluating BG:NAG, NAG:AP, and BG:AP ratios. Because microbes devote more resources towards acquiring limiting nutrients, these ratios provide information about whether microbes are limited by C, N, or P (Sinsabaugh et al., 2008). Enzymes were measured using a fluorometric microplate method (Sinsabaugh et al., 2008; Weintraub et al., 2007). Briefly, the assay uses 1 g of soil in a 1 M sodium acetate buffer, 4-methylumbelliferone (MUB) standards, and MUB (fluorescently) labeled substrates. Activity on a nmol activity h^{-1} g $soil^{-1}$ basis was assessed by evaluating fluorescence on a microplate reader (Thermo Labsystems, Franklin, MA, USA).

2.5. Soil properties

At the Arikaree site, soil dissolved organic carbon (DOC), soil total dissolved nitrogen (TDN), and soil total dissolved phosphorus (TDP) were measured. DOC and TDN were measured via soil extractions with 0.5 M K_2SO_4. Chemical analysis on extracts were performed on a Shimadzu TOC-V CSN Total Organic Carbon Analyzer (Chimadzu TOCvcpn, Kyoto, Japan) and Lachat QuikChem 85000 Flow Injection Analyzer (Lachat Instruments, Loveland, CO, USA). TDP was determined by extracting the Olsen phosphorus with $NaCO_3$ (Olsen, 1954) at pH 8.5 (pH was adjusted using 1 M NaOH). At both sites pH and soil moisture were measured. Soil pH was measured at Arikaree after the addition of 2 ml ultrapure water to 2 g soil and shaking for 1 h, while the more organic Soddie soils were assessed using a 1:2 soil to ultrapure water ratio. Soil moisture at both sites were measured gravimetrically after oven drying 5 g of soil for 48 h at 95 °C (Soddie) or 60 °C (Arikaree).

Within each site, soil properties, enzyme activities, and individual bacterial taxa relative abundances (at phylum, class and order level) were analyzed with t-tests or the nonparametric Wilcoxon sum ranked test if the assumption of normality was violated. We used the Holm-Bonferroni correction procedure to control for multiple comparisons when comparing bacterial taxa relative abundances. Entire microbial community composition at the order level was analyzed with a Bray-Curtis dissimilarity matrix and PERMANOVA analysis utilizing the vegan package in R (Anderson, 2001; Oksanen et al., 2014; R Core Team., 2015 version 3.2.2). Community data was visualized with Principle Coordinates Analysis (PCoA) plots based upon these Bray-Curtis dissimilarity matrices.

3. Results

3.1. Bacterial community

Soil bacterial community composition was significantly different between moss dominated and vascular plant dominated plots at both Arikaree and Soddie at the phylum, class, and order levels (PERMANOVA, $p < 0.05$, Fig. 2). This was driven by increases or decreases in specific major taxa, but these taxa typically did not show consistent trends across the two sites (Fig. 3, Supplementary Table 1). At Soddie, taxa in the Actinobacteria and Proteobacteria phyla had higher relative abundances in vascular plots while taxa in the Actinobacteria and Chloroflexi phyla had lower relative abundances. At Arikaree, taxa in the Acidobacteria and Verrucomicrobia phyla had higher relative abundances in vascular plots. In plots that were moss dominated in both years, there were no significant differences in bacterial community composition (PERMANOVA, $p > 0.05$). In contrast, as vegetation changed from moss dominated to vascular plant dominated, bacterial composition shifted significantly over time, becoming more similar to communities in vascular plant dominated plots (PERMANOVA, $p < 0.05$, Fig. 2). There were proportionally more Verrucomicrobia in 2015 than 2007, which is consistent with greater Verrucomicrobia relative abundances in vascular plots compared to moss plots (Fig. 3, Supplementary Table 1).

3.2. Microbial activity

Microbial activity was limited by carbon and phosphorus, as

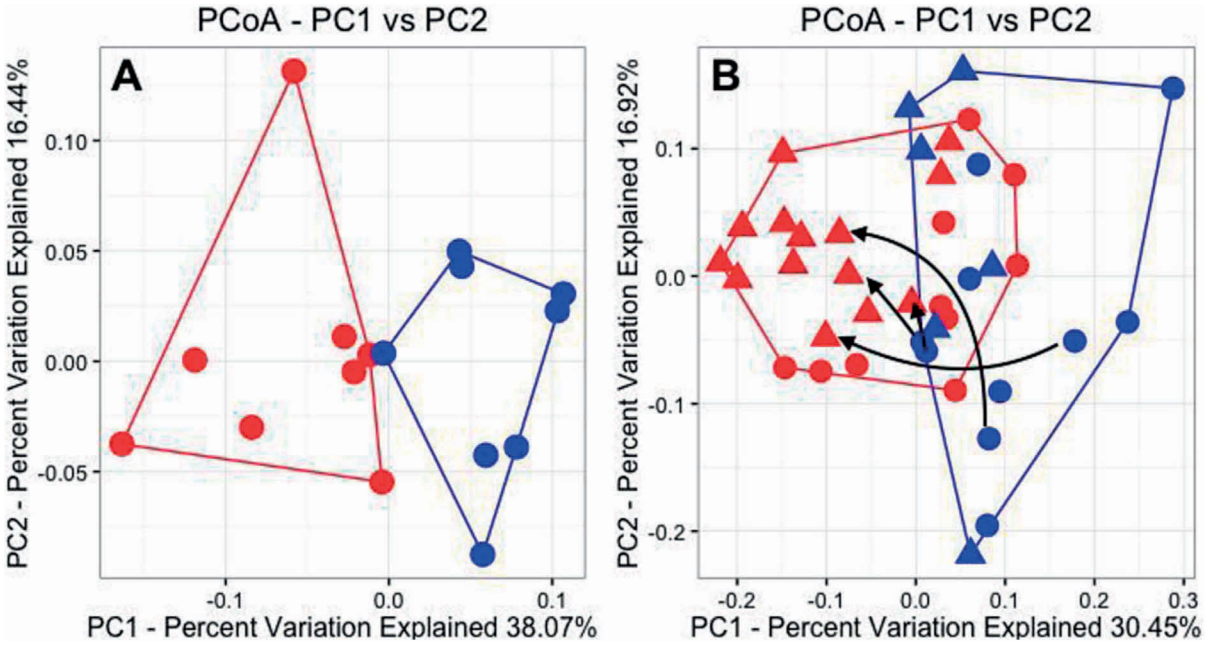

Fig. 2. Principle Coordinates Analysis (PCoA) ordinations of bacterial community dissimilarity (Bray-Curtis) at the order level in moss (blue) vs. vascular plant (red) dominated plots at A) Soddie and B) Arikaree. In panel B, circles are from 2007 and triangles are from 2015; the four arrows track the four plots that transitioned from moss to vascular plant dominated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

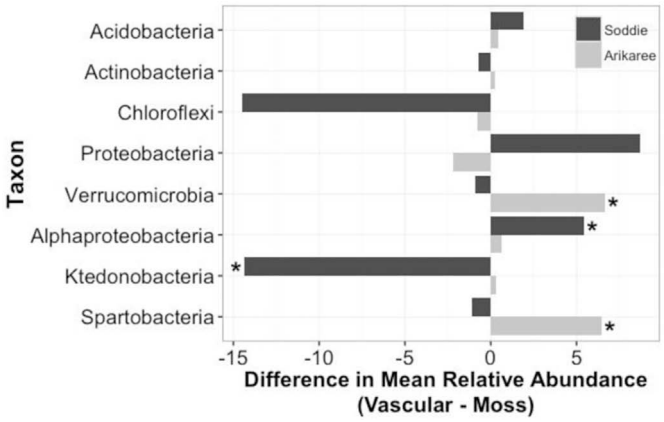

Fig. 3. Change in mean relative abundances for 8 major taxa that were shared between the two sites. Asterisks note that within a site, the difference in mean relative abundances between vascular plant and moss dominated plots was significant ($p < 0.05$). For means and standard deviations of the relative abundances of these taxa, refer to Supplementary Table 1.

shown by investment into BG and AP enzymes relative to the NAG enzyme (Fig. 4, Table 1). Across all data, investment is skewed toward C and P acquisition over N acquisition (Fig. 4). BG:NAG ratios were not significantly different in moss and vascular-dominated plots at either site (*t*-test, Wilcoxon test, $p > 0.05$, Table 1). NAG:AP and BG:AP ratios in moss and vascular-dominated plots at Arikaree were not significantly different from each other, but at Soddie the both ratios were significantly higher in vascular-dominated plots (*t*-test, $p = 0.001$, Table 1). There was no significant change in any ratio over time (*t*-test, $p > 0.05$). There was no significant difference microbial biomass C at the Arikaree site (t.test, $p > 0.05$, Table 1). N-fixation was not measured at Arikaree but was significantly higher in vascular-dominated plots at Soddie (Wilcoxon test, $p < 0.05$, Table 1).

3.3. Soil chemistry

Soil chemistry and moisture data indicate higher resource levels in vascular plant-dominated plots (Table 1). Soil dissolved organic carbon, nitrogen, and phosphorus levels were significantly higher in vascular-dominated plots than moss-dominated plots at Arikaree (*t*-test and Wilcoxon test, $p < 0.05$). Similarly, soil pH was significantly higher in vascular plots at Arikaree (*t*-test, $p = 0.005$), but there was no significant difference at Soddie (Wilcoxon test, $p = 0.32$). Soil moisture was significantly higher in vascular plots at Soddie (*t*-test, $p < 0.001$), but not at Arikaree.

4. Discussion

Our data show that moss dominated soil environments have different bacterial communities and lower levels of soil nutrients (Fig. 5). While our time series demonstrated the speed at which vascular plants can colonize moss-dominated areas as climate changes, and the impact of this vegetation change on bacterial communities, our results suggest that this may not necessarily result in a shift in enzyme activity on short timescales. Our results at the Soddie site, with more established plant communities, suggest that the strength of nutrient limitation may vary between vascular and moss dominated landscapes resulting in differences in soil extracellular enzyme potential.

4.1. Bacteria

It is not surprising that the bacterial communities under moss and vascular plants differed from one another. Moss and vascular plants have different tissue chemistry which should select for different microbes (Lang et al., 2009; Wardle et al., 2004). While the two different sites showed distinct bacterial communities at the order level (Supplementary Table 1), some commonalities were observed, highlighting the possibility that generalizable changes in bacterial communities may accompany shifts from moss to vascular

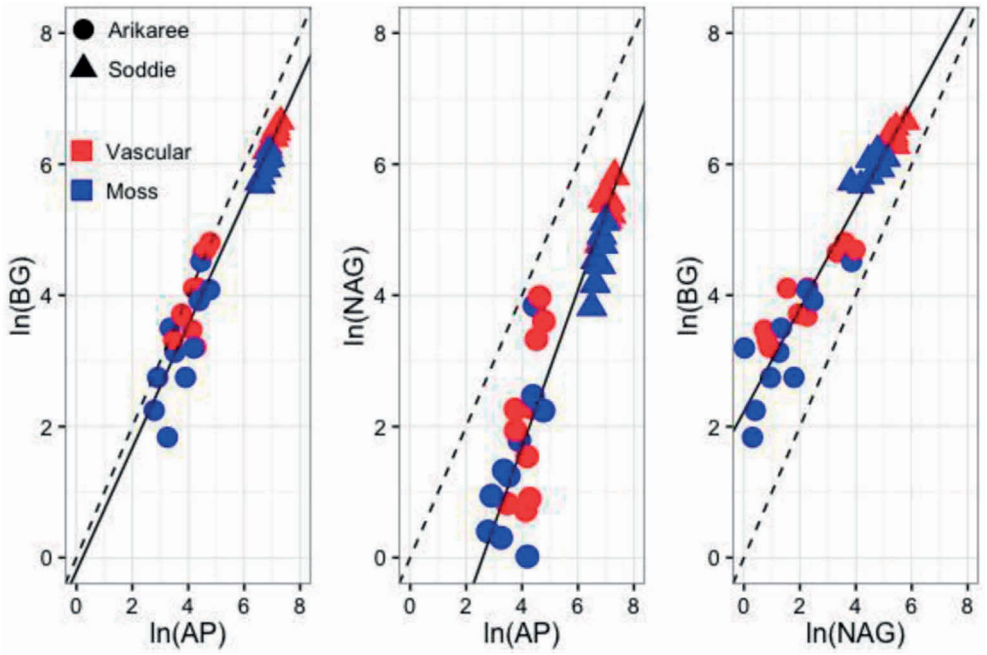

Fig. 4. Standard major axis regressions between log transformed BG vs. AP, NAG vs. AP, and BG vs. NAG. The solids line is the regression line and the dashed line is a reference line with slope = 1. All regression slopes were significant at $P < 0.05$. A regression line to the right of the 1:1 line suggests more resources devoted to the enzyme on the x-axis compared to the y-axis (e.g. AP compared to NAG). A regression line to the left of the 1:1 line suggests more resources devoted to the enzyme on the y-axis compared to the x-axis (e.g. NAG compared to BG).

Table 1
Microbial activity and soil properties and moss and vascular plant-dominated soils at the two alpine sites. The BG:NAG ratio represents the strength of C or N limitation to microbes, with a high BG:NAG ratio suggesting C limitation. The NAG:AP ratio represents the relative strength of N or P limitation in a system, with a high NAG:AP ratio suggesting N limitation. The BG:AP ratio represents the relative strength of C or P limitation, with a high BG:AP ratio suggesting C limitation. The mean (SE) is shown. Bolded numbers are significantly different within the site (*t*-test/Wilcoxon test $p < 0.05$). NM = not measured. Enzymes: nmol g dry soil^{-1} h^{-1}, Nutrients: ug g dry soil^{-1}, N-fixation: ng cm^{-2} h^{-1}, Moisture: % weight. Means and standard deviations of raw enzyme data are presented in Supplementary Table 2.

Site	Dominant Cover	Microbial Activity				Soil Properties				
		BG:NAG	NAG:AP	BG:AP	N-fixation	Carbon	Nitrogen	Phosphorus	pH	Moisture
Arikaree	Moss	7.15 (1.4)	0.14 (0.03)	0.64 (0.07)	NM	**43.35 (2.72)**	**6.39 (0.65)**	**4.25 (0.42)**	**4.37 (0.04)**	6.73 (1.49)
	Vascular Plant	7.62 (1.1)	0.19 (0.03)	0.86 (0.06)	NM	**81.97 (14.33)**	**12.25 (1.85)**	**9.67 (1.46)**	**4.79 (0.08)**	6.71 (1.14)
Soddie	Moss	3.66 (0.49)	**0.11 (0.01)**	**0.39 (0.04)**	**0.14 (0.04)**	NM	NM	NM	4.6 (0.05)	**21.25 (0.01)**
	Vascular Plant	3.03 (0.16)	**0.18 (0.01)**	**0.53 (0.01)**	**0.40 (0.41)**	NM	NM	NM	4.69 (0.06)	**32.38 (0.01)**
Global Soil Mean[a]		1.93	0.32	0.62						
Tropical Soil Mean[b]		1.827	0.126	0.214						

[a] Sinsabaugh et al. (2008, 2009).
[b] Waring et al. (2014).

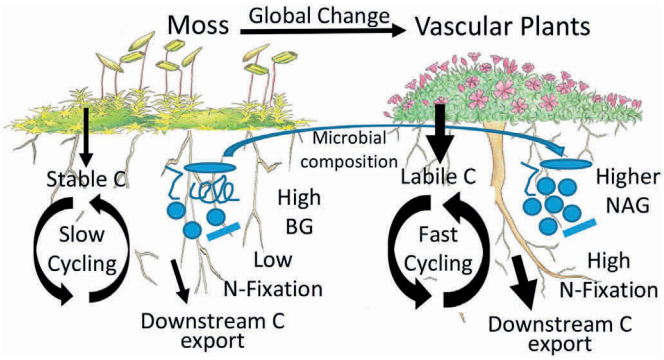

Fig. 5. Synthesis of the influence of vegetation type on belowground processes. Over time, as vascular plants introduce labile C into the soil, nutrient cycling rates and export may increase, along with shifts in microbial community composition and increased resources devoted to nitrogen acquisition. Wider arrows represent greater magnitudes of fluxes. BG = β-1,4-glucosidase enzyme for carbon acquisition; NAG = β −1,4-N-acetylglucosaminidase enzyme for nitrogen acquisition.

plant dominated soils with climate change. For example, in both the Soddie and Arikaree sites, vascular plant dominated soils contained higher acidobacterial taxa than moss dominated sites, although this trend was not significant at Soddie. This is surprising given that previous work found that Acidobacteria were more abundant in soils with lower resource availability (Fierer et al., 2007; Cleveland et al., 2007). The time series also confirmed that the replacement of mosses with vascular plants results in the enrichment of Verrucomicrobia, consistent with differences observed between more established moss and vascular plant communities at Arikaree.

While this study demonstrates differences in microbial community structure between moss and vascular plant dominated landscapes across sites and within actively transitioning plots, it also highlights that these differences may be context dependent upon the unique biota that are present at a particular site. Except at the phylum level, there were not many major taxa (>5% of the community) that were shared between the sites (Supplementary Table 1). The site-specific shifts in bacterial communities we

observed may indicate that both plants and environment play some role in driving change in belowground bacterial communities associated with moss and vascular plant soils (Fierer and Jackson, 2006). For example, Chloroflexi are known to respond strongly to moisture and plant species gradients in the alpine (Yuan et al., 2016), while Rhizobiales are more directly associated with colonization by vascular plants in early ecosystem succession (Knelman et al., 2012), and both these bacterial groups show changes between moss and vascular plant dominated soils at the Soddie site. The lack of consistent taxonomic trends between the sites is likely mostly due broader site differences in climate, snow cover, and plant abundance and composition.

4.2. Enzymes and N-fixation

Enzyme ratios are used to understand microbial nutrient limitations, as microbes allocate resources toward the acquisition of limiting nutrients via the production of extracellular enzymes (Sinsabaugh et al., 2008). In this way, the BG:NAG ratio can be interpreted as representing the relative strength of C or N limitation to microbes, with a high BG:NAG ratio suggesting C limitation. Not surprisingly, the BG:NAG ratio at Arikaree was very high compared to the global mean (Sinsabaugh et al., 2008, 2009; Schmidt et al., in review). Greater carbon limitation may be expected in such soils as a high elevation subnival system that has low plant cover in general and is snow covered for 9–11 months out of the year. Relative to Arikaree, the Soddie site, a higher carbon environment with more developed and persistent plant communities, showed far lower BG:NAG ratios, though still much greater than the global average. Neither site showed differences in BG:NAG ratios between vascular and moss dominated soils, suggesting that moss versus vascular plants do not immediately change microbial demands for carbon versus nitrogen, which may be more associated with longer term soil organic matter buildup, as evidenced by the large differences in BG:NAG ratios between the higher-C Soddie site and low-C Arikaree site.

Phosphatase (AP) enzymes remove a phosphate group from its substrate by hydrolyzing phosphoric acid monoesters into a phosphate ion and a molecule with a free hydroxyl group. The NAG:AP and BG:AP ratios indicate the relative strength of N vs. P limitation and C vs. P limitation, respectively, in a system. The low NAG:AP ratios at both sites suggest phosphorus limitation similar to what is seen in tropical soils (Waring et al., 2014). At Arikaree, there was no difference in NAG:AP ratios between moss and vascular plots likely because even in the vascular plots, the microbes are fundamentally carbon limited. In total, our work suggests C and P and prevailing nutrient limitations in these environments. At Soddie, where C is less limiting, as reflected in lower BG:NAG ratios, the NAG:AP ratio was significantly higher in the vascular plots than moss plots, suggesting a shift towards investment in nitrogen acquisition. The BG:AP ratio was also significantly higher in vascular plots, confirming slight shifts in microbial nutrient demands despite overall C and P limitations observed. Furthermore, differences in N-fixation rates between moss and vascular communities at the Soddie site are consistent with the increased investment in extracellular enzymes toward N-acquisition. While abiotic and biotic controls may influence N-fixation, and increases in microbial biomass may also underlie these shifts, both the levels and relative change in N-fixation are consistent with similar undeveloped soils encountering vascular plant colonization in a glacial forefield in Alaska (Knelman et al., 2012), in which resulting shifts in bacterial community composition were connected with changes in N-fixation rates. Our work supports observations that the carbon environment may modulate responses in microbial extracellular enzyme activity to environmental change and shifting nutrient availabilities (Göransson et al., 2011; Knelman et al., 2014; Yoshitake et al., 2007). Indeed, microbial extracellular enzyme activity may prove most informative in revealing the nutrient constraints on biogeochemical rates in general than the rates themselves.

4.3. Implications

In total, our research lays the groundwork for better understanding emblematic shifts between moss and vascular plant dominated communities in alpine ecosystems that are vulnerable to climate change. This work demonstrates that such plant communities, as well as active and rapid transitions between these two aboveground community types, have corresponding differences in microbial community composition as well as biogeochemical function (Fig. 5). While we found some generalizable differences between these two landscape types in microbial community composition, we also highlight that patterns of change also depended on the biota unique to particular sites. Further, this work shows that at a biogeochemical level, such as in decomposition enzyme activity, responses to changes in moss vs. vascular plants may be muted, likely due to prevailing C limitation in these environments. Nonetheless, in higher C, tundra meadow environments such as the Soddie site, we observed a shift toward microbial N acquisition (NAG:AP ratios and N-fixation) with vascular plant communities. Furthermore, the higher C levels in vascular plant dominated areas at Arikaree suggest that increased plant colonization of high elevation catchments could lead to increased carbon export to alpine lakes and streams. Many of these aquatic systems are severely carbon limited, and even small increases in DOC levels can lead to drastic changes (Sommaruga et al., 1999; Parker et al., 2008), underscoring the need for further research on this topic. Our work highlights the need to build mechanistic understandings between environmental, microbial, and biogeochemical properties of such systems (Graham et al., 2016). As high elevation and high latitude ecosystems increasingly transition from moss to vascular plant dominated landscapes, better understandings of associated belowground biotic and abiotic factors will be key to understanding responses of these environments to the effects of global change.

Declaration

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2017.04.008.

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