



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.

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1. Introduction

Vegetation patterns worldwide are changing due to global change factors such as climate change (Settele et al., 2014), rising CO₂ 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 below-ground 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 cm² 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 rarefied 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.

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