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Patterns of root colonization by arbuscular mycorrhizal fungi and dark septate endophytes across a mostly-unvegetated, high-elevation landscape

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ABSTRACT

Arbuscular mycorrhizal fungi (AMF) and dark septate endophytes (DSE) are two fungal groups that colonize plant roots and can benefit plant growth, but little is known about their landscape distributions. We performed sequencing and microscopy on a variety of plants across a high-elevation landscape featuring plant density, snowpack, and nutrient gradients. Percent colonization by both AMF and DSE varied significantly among plant species, and DSE colonized forbs and grasses more than sedges. AMF were more abundant in roots at lower elevation areas with lower snowpack and lower phosphorus and nitrogen content, suggesting increased hyphal recruitment by plants to aid in nutrient uptake. DSE colonization was highest in areas with less snowpack and higher inorganic nitrogen levels, suggesting an important role for these fungi in mineralizing organic nitrogen. Both of these groups of fungi are likely to be important for plant fitness and establishment in areas limited by phosphorus and nitrogen.

1. Introduction

Arbuscular mycorrhizal fungi (AMF) and dark septate endophytes (DSE) are two fungal groups that can directly influence plant success in a given environment, but little is known about how their abundances vary over local environmental and plant density gradients. AMF are obligate symbionts of living plant roots (Smith and Read, 2008) that form a monophyletic group in the subphylum Glomeromycotina (Spatafora et al., 2016) (formerly classified as the phylum Glomeromycota; Schüßler et al., 2001) and are characterized by the formation of arbuscules for nutrient exchange (Smith and Read, 2008). AMF protect plants from pathogens (Sikes et al., 2009), help plants cope with drought stress (Augé, 2001), and aid plants in the uptake of phosphorus (P) and nitrogen (N) (Johnson et al., 2010). DSE are facultative fungal symbionts that can live on organic debris and in biological soil crusts in addition to plant roots (Menkis et al., 2004; Green et al., 2008; Day and Currah, 2011), and several studies have reported enzymatic activities by DSE capable of degrading organic matter (Mandyam and Jumpponen, 2005; Mandyam et al., 2010; Knapp and Kovács, 2016). They are a polyphyletic group with members typically found in the phylum Ascomycota and are characterized by their dark, melanized, septate hyphae (Jumpponen and Trappe, 1998). DSE are relatively less studied than AMF, but have also been shown to have important beneficial impacts on plant growth (Mandyam

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and Jumpponen, 2005; Newsham, 2011), perhaps due to N mineralization (Newsham, 2011), protection from pathogens (Mandyam and Jumpponen, 2005), or uptake of N during snowmelt (Mullen et al., 1998).

Cold environments at high latitudes and high elevations that are experiencing rapid climate change provide an interesting context in which to study these two fungal groups. Recent work has argued that biotic factors need to be considered to accurately predict the effects of climate change on species distributions (van der Putten et al., 2010). For example, plant-pollinator interactions, plant-herbivore interactions, and plant-plant interactions have all been suggested to mediate distributional responses to climate change (Leathwick et al., 1996; van der Putten et al., 2010; Hillerislambers et al., 2013). While less studied, plant-microbe interactions are a very important type of interaction that can affect plant distributions as well (Pellissier et al., 2013; Bueno de Mesquita et al., 2015). AMF and DSE both appear to perform important functions for plant growth in cold environments, as they have both been found in abundance in arctic and alpine systems (e.g. Väre et al., 1992; Schmidt et al., 2008). In particular, the high melanin concentrations in DSE have been cited as an adaptation to cold temperatures, and AMF are capable of producing cold-active enzymes (Robinson, 2001). Nutrient cycling is typically slow in cold environments, so plants may rely on symbiotic fungi to acquire adequate nitrogen and phosphorus. Studying the landscape distribution of fungi in cold environments, including over plant density and snowpack gradients which are changing with climate warming, can help us understand the potential effects of climate change on plant-fungal interactions. Interestingly, Kytöviita and Ruotsalainen (2007) found that the benefits of an arbuscular mycorrhizal fungus increased at warmer temperatures, suggesting that some arctic or alpine fungi can have positive responses to warming.

While both AMF and DSE can be important determinants of a plant's ability to colonize and persist in cold environments, little is known about how these plant-microbial interactions vary across the landscape (Ranelli et al., 2015). While there have been global studies of the distributions of AMF (Davison et al., 2015), we lack information on their distributions in extreme environments. For DSE, there is substantial information on their occurrence in extreme environments, but no global studies. Here we focus on high-elevation alpine environments because alpine plants are vulnerable to climate change due to an often greater magnitude of change (Pepin and Lundquist, 2008) and susceptibility to habitat loss (Engler et al., 2011; Elsen and Tingley, 2015) compared to lower-elevation plants. Previous work suggests that AMF colonization increases at lower elevations (Schmidt et al., 2008; Kotilínek et al., 2017) as well as lower P, N (Johnson et al., 2015), and moisture levels (Augé, 2004; Smith and Read, 2008; Camenzind et al., 2014). Mechanisms discussed in this literature to explain these trends include both the temperature and moisture optima of the fungus, the amount of fungal spores, and the amount of photosynthate the plant devotes to the fungus. On the other hand, studies have found greater levels of DSE colonization at higher elevations, high nitrogen, and low moisture levels, and no relationship with phosphorus levels (Newsham, 2011; Kivlin et al., 2013; Ranelli et al., 2015). In addition to these landscape level patterns for each fungal group, AMF and DSE may interact with each other. In one of the few studies to assess such interactions, Ranelli et al. (2015) hypothesized that AMF and DSE would be negatively correlated due to competition for similar host tissue, but instead found positive correlations between AMF and DSE.

In this study, we build on this prior work by examining colonization across a wide range of different alpine plant species (forbs, grasses, sedges, rushes, N-fixers), including some not previously studied for fungal infection. We also add snowpack and plant density into models that typically include elevation, soil moisture, and soil nutrients. In many alpine environments, snowpack governs both growing season length and soil moisture (Williams et al., 2009) and provides insulation during winter; we know less about how these factors may translate to plant-fungal interactions. Alpine environments can also vary drastically in plant density and diversity. At our field site in the Colorado Rocky Mountains, which is located at the upper edge of the elevational range of vascular plants, plant density varies from intact tundra meadows to sparsely-vegetated talus slopes. These gradients may influence fungal colonization of plants because intact meadows should have higher levels of fungal inoculum in the soil (Cázares et al., 2005). We also tested for effects of plant functional group and plant phylogenetic relatedness on root colonization levels. These variables take into account the broader plant functional traits and evolutionary histories, which can play a role in determining plant-associated microbial communities (Scheublin et al., 2004). These variables have been studied in the context of broader microbial community composition in soils (e.g. Leff et al., 2018) but are rarely included in models of root colonization (but see Ranelli et al., 2015).

Here, we asked: (1) How does colonization by AMF and DSE vary among plant host species, functional group, and phylogenetic distance? (2) Do plant host and environment jointly predict fungal colonization? (3) What is the relationship between AMF and DSE colonization levels? and (4) Do plant hosts and environment influence the community composition of AMF and DSE taxa? We hypothesized that (H1) both AMF and DSE show patterns of differential colonization among plant hosts and functional groups, with higher AMF colonization in forbs due to their thicker root architecture in contrast to graminoids with higher DSE colonization (Ranelli et al., 2015); (H2) AMF and DSE colonization levels are influenced by both host plant and the environment, but host plant plays a more important role in AMF colonization due to their obligate status (Ranelli et al., 2015). Specifically, we predict that both fungal types show greater colonization as environmental harshness increases (higher elevation, more snow, fewer plants and less nutrients), except at the highest elevations with low plant densities, where AMF will decline (Kotilínek et al., 2017) (Fig. 1), while DSE will remain abundant (Schmidt et al., 2008, Fig. 1); (H3) AMF and DSE colonization is negatively correlated due to different responses to the environmental and plant gradients, and potential competition for host plant tissue (Fig. 1); and (H4) AMF and DSE community composition varies among plant hosts and environmental gradients in a similar manner to which the percent colonization does (i.e. different taxa at the harsh end of the environmental gradient).

2. Materials and methods

2.1. Study site

Our study was conducted along a 2 km portion of a south facing slope (King et al., 2010) at the Niwot Ridge Long Term Ecological Research (LTER) site, in the Front Range of the Rocky Mountains, Colorado, USA (40° 3′ 20′ N, 105° 35′ 22′ W, Fig. 2). Average precipitation from 1952 to 2012 in the alpine region at our site was $1090 \pm 230\ mm\ yr^{-1}$, with a $60\ mm\ yr^{-1}$ increase over that time period, driven mostly by increases in winter precipitation (Kittel et al., 2015). Recent (2011–2014) mean annual temperatures at the nearby D1 Meteorological station range from −4 °C to −7 °C, while mean summer (July–August) temperatures range from 4 °C to 10 °C (Losleben, 2017). Overall temperatures have been increasing over the past several decades (McGuire et al., 2012). This has led to increased positive degree days and earlier snow meltout times (Caine, 2010; McGuire et al., 2012; Preston et al., 2016). The

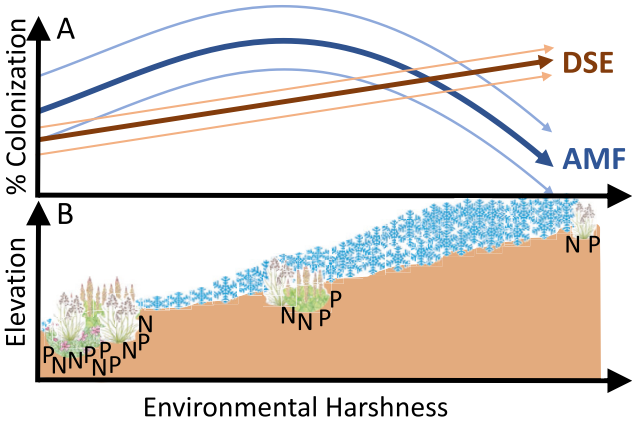

Fig. 1. Conceptual diagram of how arbuscular mycorrhizal fungi (AMF) and dark septate endophyte (DSE) root colonization levels are predicted to change over environmental and plant gradients. (A) We predict that AMF colonization will increase as environmental harshness increases, but then decline as plant density declines. We predict that DSE colonization will increase steadily with environmental harshness. The emboldened line for AMF and DSE show average colonization levels over all host plants across the environmental gradients; the two thinner lines around the bold line represent the variation in colonization among different host plant species. The spacing of the small lines reflects the expectation of a greater influence of the host plant on AMF colonization levels. (B) Environmental harshness increases moving up in elevation as nitrogen (N) and phosphorus (P) become more limiting, snowpack increases, and plant density decreases. We expect AMF to be driven primarily by phosphorus and plant density, and DSE by nitrogen. We also expect the community composition of AMF and DSE taxa to shift across the gradient.

plot locations range from continuous tundra meadows to sparsely vegetated talus (plant density gradient of 243 to 3 stems m^{-2}) near the continental divide, across an elevation gradient of 3636–3933 m a.s.l. The landscape 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 plant species in this landscape are *Festuca brachyphylla* (Poaceae), *Trisetum spicatum* (Poaceae), *Carex pyrenaica* (Cyperaceae), *Geum rossii* (Rosaceae), *Oxyria digyna* (Polygonaceae), *Senecio fremontii* (Asteraceae), and *Deschampsia cespitosa* (Poaceae) (Porazinska et al., 2018). Soils are shallow and show limited development, with mean sand contents of 71% (King et al., 2010). Circular plots (n = 160) with a radius of 1 m were established in 2007 in a spatially explicit sampling grid (plots were spaced 50 m apart, with 3 focal clusters with plots spaces 5 m apart) (King et al., 2010). In this study, we sampled plants and measured botanical and environmental variables (see below) from 74 of these plots (Fig. 2).

2.2. Variables

Elevation of each plot was obtained from a 2 m resolution LIDAR-based digital elevation model. Mean May snowpack depth was calculated for each plot based on krigged snow depth data for the study site from 1997 to 2015. Kriging was done each year on point depth data from annual snow surveys, in which snow depth was measured manually at an average of 483 random locations ~50 m apart across the study site during approximate peak snowpack in May.

In August and September of 2015, we conducted vegetation surveys and collected soils for nitrogen analysis. We identified all plants at the species level and conducted exhaustive stem counts of each species at each plot. At each plot, plant density was calculated as the number of stems per square meter. We collected three soil cores of 3 cm diameter and 4 cm depth, composited them into a plastic bag, gently homogenized them, and transported them on ice to the lab by the end of the day. Soil total inorganic nitrogen (TIN) was measured via soil extractions with 0.5 M K_2SO_4 and analyzed on a Lachat QuikChem 85000 Flow Injection Analyzer (Lachat Instruments, Loveland, CO, USA) (Porazinska et al., 2018). Soil total dissolved inorganic phosphorus (DIP) data came from a 2007 survey of these same plots (King et al., 2008) and could have changed over time. However, the relative levels of DIP across the landscape (i.e. high DIP versus low DIP areas) is likely the same. DIP was

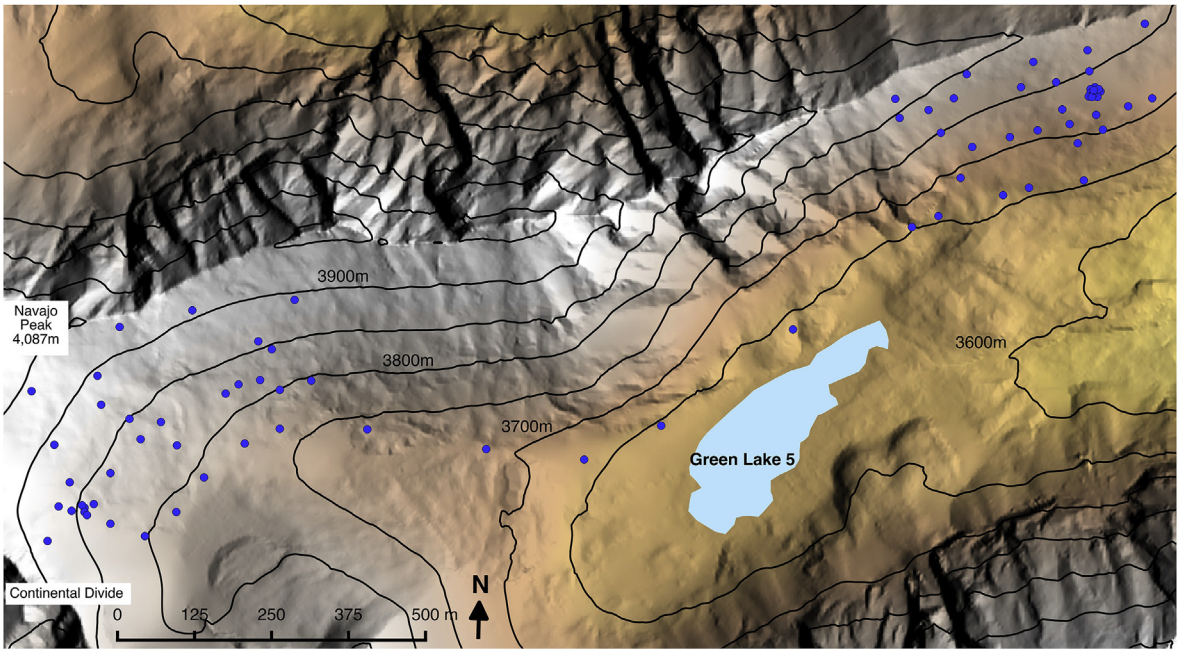

Fig. 2. Map of the seventy-four 1 m radius plot locations (blue circles) across the upper Green Lakes Valley in the Front Range of the Rocky Mountains, Colorado, USA. At each of these locations we measured soil nitrogen and phosphorus, counted the number of plant stems in a 1 m radius circle, conferred snow depth from annual snow surveys, and sampled 1–3 individual plants for fungal analyses (sequencing and microscopy).

determined by extracting the Olsen phosphorus with 0.5 M $NaHCO_3$ (Olsen, 1954) at pH 8.5 (pH was adjusted using 1 M NaOH). In 2016, we counted the number of arbuscular mycorrhizal fungal spores in 2.5 g of the 2015 soils (stored at −70 °C for ~11 months). Although this constitutes a smaller amount of what is usually used (25 g, Sieverding, 1991), to minimize plant and soil disturbance we used amounts of soil reflective of this landscape. We followed the differential water/sucrose centrifugation method to extract spores from the soil (Allen et al., 1979; Ianson and Allen, 1986; Sieverding, 1991) and then placed the suspended spores in a Petri dish to view under an inverted microscope at 100x.

From August 15–25, 2016, we harvested 177 individual plants from 74 plots from a total of 35 different species for microscopy and sequencing. We sampled one individual from the three most abundant species in each plot, but only if there were >5 individuals of that species, so as not to destroy locally rare populations. This resulted in sometimes sampling only the one or two most abundant plant species in a plot. Bulk soil was shaken off in the field, and plants and rhizosphere soil were placed in Ziploc bags and transported to the lab on ice, where samples were flash frozen in liquid nitrogen and then placed in a −70 °C freezer for later molecular processing. Within 1 month, roots were rinsed with DI water, surface sterilized with ethanol and bleach, and then a subset of roots was placed in FAA (63% ethanol, 30.15% water, 5% glacial acetic acid, 1.85% formaldehyde) and stored at 4 °C until staining and microscopy within 1 month. Another subset of roots was sequenced to identify the DSE and AMF taxa using the internal transcribed spacer (ITS) part of the genome (Schoch et al., 2012) (details below).

Staining and microscopy were performed following the procedures of Koske and Gemma (1989), Schmidt et al. (2008) and McGonigle et al. (1990). Roots were rinsed 3 times with DI water to remove FAA and then cleared with 10% KOH for 1 h in a 90 °C water bath. In some instances, if roots were still pigmented after this step, they were cleared with alkaline hydrogen peroxide for 10–45 min. Roots were rinsed 3 times with DI water to remove KOH and then soaked in 0.5% HCl at room temperature for 20 min. After another triple rinse with DI water, roots were soaked overnight in acidic glycerol with 0.05% trypan blue. In the morning, roots were destained with acidic glycerol and stored in acidic glycerol at 4 °C until microscopy was performed within 1 week. Several fine root segments and their branches (amounting to 20–30 cm of root length) were placed horizontally across slides, covered with a cover slip, and viewed at 200× magnification under a microscope with a crosshair on the ocular. Passes were made up and down the slide at random intervals and the presence of AMF or DSE structures at each of 100 intersections with the crosshair were recorded. Fine endophytes, now classified as in the Mucoromycotina (Orchard et al., 2017), were present and were included in counts for AMF. Percent colonization for each fungal group is the number of times out of the 100 intersections that a fungal structure was present. If no fungal structures were observed in the first 100 intersections, the entire slide was scanned for structures. Any fungi discovered in this case were given a score of 0.5%, to note their presence at a very low percentage which allows for more accurate assessment of the mycorrhizal status of the plants (Schmidt et al., 2008).

To identify AMF and DSE taxa, 0.1 g of wet roots from each of the 177 individual plant samples were frozen in liquid nitrogen and ground into a fine powder with a sterile mortar and pestle. Each individual plant was processed as a separate sample, although this included multiple roots from each individual. DNA was extracted from this powder using the DNeasy Plant Extraction Kit (QIAGEN; Hilden, Germany) and PCR was used to amplify the ITS1 region using the ITS1F forward primer and ITS2 reverse primer (White et al., 1990) 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 an ITS amplicon library and sequenced on one lane of an Illumina MiSeq 2000 (2 × 300 bp paired-end) 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 demultiplex and merge sequences, remove singletons, and then cluster sequences (including chimera filtering) into OTUs at 97% sequence identity and assign taxonomy using the UNITE database (Abarenkov et al., 2010). Sequences were rarefied at 5238 sequences per sample. AMF genera were identified as any genus in the subphylum Glomeromycotina (Spatafora et al., 2016). DSE genera were selected from reports of known DSE taxa (Jumpponen and Trappe, 1998; Jumpponen, 2001; Mandyam and Jumpponen, 2005; Newsham, 2011). Sequences for all of the OTUs are available on GenBank, accessible via the accession numbers SUB3901920: MH238510-MH240826.

2.3. Statistical analysis

To test for differences in colonization levels among plant species (only for species with at least 3 samples) and functional groups (H1), we used the Kruskal-Wallis test (kruskal.test function in the R Package *stats*) followed by Nemenyi *post-hoc* tests (posthoc.kruskal.nemenyi.test function in the R Package *PMCMR*, Pohlert, 2014), because the data were not normally distributed (Shapiro-Wilk Test, $p < 0.05$) and the variance was not homogeneous among groups (Levene Test, $p < 0.05$). We defined functional groups as forbs, grasses, and sedges. Due to low sample sizes, N-fixers (1 species, 4 samples) and rushes (1 species, 2 samples) were removed from the functional group analysis. Because species differences and differences in species replication could mask differences among functional groups, analyses for functional groups were performed on species' means colonization percentages. We also tested for a phylogenetic signal in species' mean DSE and AMF colonization using the multiPhylosignal function (R Package *picante*, Kembel et al., 2010). The phylogenetic supertree of the plant species (identified to species and sampled at least 3 times) for this analysis was created using the software Phylomatic (Webb and Donoghue, 2005). Since we did not have a molecular phylogeny of our plant species, we subset the supertree down to our species. To test for spatial autocorrelation in DSE and AMF colonization, we calculated Moran's *I* (Moran.I function in the R package *ape*, Paradis et al., 2004). To test for relationships between spore counts and environmental variables and plant density, we ran univariate linear regressions (lm function in the R package *stats*, R Core Team, 2017). To find the best combination of variables that predicted AMF and DSE percent colonization (H2), we used an exhaustive all subsets method to select models based on the Akaike Information Criterion (AIC) (Akaike, 1974; function bestglm in the R package *bestglm*, Mcleod and Xu, 2017). Instead of using forward or backward selection to select variables, this function tests all possible combinations of predictor variables. Predictor variables were plant species, elevation, snowpack, plant density, TIN, and DIP. We did not include plant functional group in the analysis, because plant species had a much larger effect. These models did not take into account how plant species abundances vary over environmental gradients (i.e. species are not distributed evenly across the landscape; some species may be only present at low elevation areas with higher plant density). To improve the normality of the response variables and some predictor variables, colonization levels were logit transformed, and plant density, TIN, and DIP were log transformed. To test for associations between AMF and DSE colonization levels (H3) and richness of genera, we used the

Spearman rank correlation. Due to a possible exponential decay relationship after data visualization, we also evaluated an exponential decay model, which we fit using the nls function (R package *stats*). We ran this analysis on the full data set as well as on species' mean DSE and AMF levels, and on samples that contained both DSE and AMF. Lastly, to test for differences in AMF and DSE community composition among plant host species and functional groups (H4), we used permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001) on Bray-Curtis dissimilarities at the genus level, implemented with the adonis function in the R package *vegan* (Oehl et al., 2006). To test for environmental drivers of community composition we used the envfit function in *vegan*. We visualized compositional data using Principle coordinates analysis, calculated with the cmdscale function in R. All statistical analyses were performed using the statistical software R (version 3.4.0, R Core Team, 2017).

3. Results

The majority of the 177 plant individuals sampled, 86%, were colonized by either AMF or DSE, or both. A total of 43 individuals were colonized by AMF only, 36 individuals were colonized by DSE only, and 71 individuals contained both AMF and DSE. Percent of plant root length colonized ranged from 0 to 72% by AMF and 0–64% by DSE. We report colonization (or lack thereof) by AMF and DSE for nine plant species not previously characterized in the current literature as well as colonization of seven species that had previously been described as non-mycorrhizal (Table 1).

Neither of the fungal groups' colonization levels were spatially autocorrelated (Moran's $I = 0.01$, $p = 0.16$). The density of AMF spores increased significantly with plant density ($R^2 = 0.32$, $p < 0.001$), and was not significantly correlated with the other variables.

3.1. Plant species and functional group (H1)

There were significant differences in mean colonization among plant species for both AMF (Kruskal Wallis, $X_2 = 74.34$, $df = 20$, $p < 0.001$, Fig. 3A) and DSE (Kruskal Wallis, $X_2 = 54.65$, $df = 20$, $p < 0.001$, Fig. 3B). The highest levels of AMF and DSE colonization were found in *Besseya alpina* and *Silene acaulis*, respectively. While AMF colonization did not differ among functional groups (Fig. 4A), there were significant differences in mean DSE colonization among plant functional groups (Kruskal Wallis, $X_2 = 6.48$, $df = 2$, $p = 0.039$, Fig. 4B). Grass species had greater DSE colonization than sedge species (Nemenyi *post hoc* test, $p < 0.05$). There was no phylogenetic signal in mean AMF colonization ($K = 0.75$, $p = 0.42$) or DSE colonization ($K = 1.71$, $p = 0.16$).

3.2. Plant and environmental predictors of colonization (H2)

For AMF, plant species was the most important variable driving colonization extent and was a significant predictor in all of the top five models (Table 2). Plant species explained more variation in the data than environmental variables (Table 2). After plant species, several other variables were also important. The best model for AMF colonization included TIN, elevation, and snowpack, with percent colonization increasing at lower elevation areas with less snowpack and less nitrogen (Table 2). A slightly less parsimonious model that had similar support (AIC difference <1) also included DIP, with which there was a negative relationship (Table 2, Fig. 5A). For DSE colonization, the best model included snowpack and TIN, with the highest levels of colonization in areas with less snowpack (Fig. 5B) and higher soil nitrogen (Table 2). A less parsimonious model with similar support also demonstrated a positive relationship with plant density (Table 2).

3.3. AMF and DSE Co-occurrence (H3)

There was no significant correlation between AMF and DSE colonization across the whole dataset ($S = 883300$, $Rho = 0.04$, $p = 0.56$) or across species means ($S = 6742.1$, $Rho = 0.06$, $p = 0.75$). However, when looking only at roots that contained both DSE and AMF, the percent colonization of the fungal groups was significantly negatively correlated ($S = 75608$, $Rho = -0.27$, $p = 0.02$, Fig. 6). On the other hand, the genus richness of AMF and DSE was significantly positively correlated ($S = 20222$, $Rho = 0.34$, $p < 0.01$) for roots containing both fungal groups. There was no significant exponential decay of AMF colonization across DSE colonization levels for the whole dataset ($\lambda = 19.97$, $p > 0.05$), within species' means ($\lambda = 41.25$, $p > 0.05$), or across samples containing both fungal groups ($\lambda = 19.90$, $p > 0.05$, Fig. 6).

3.4. AMF and DSE community composition (H4)

The roots sampled contained a total of 29 genera of AMF and 14 genera of DSE. The most widespread AMF genera were *Acaulospora* and *Entrophospora*, found in 35 samples each. The genera *Archaeospora*, *Claroideoglomus*, and *Glomus* were also widespread, found in over 25 samples each. The most widespread DSE genus was *Phialophora* found in 125 samples, followed by *Capronia*, found in 43 samples. The genera *Leptosphaeria*, *Exophiala*, and *Cryptosporiopsis* were also widespread, each found in over 25 samples. AMF community composition did not differ significantly among plant species or functional group (PERMANOVA, $p > 0.05$). AMF community composition was driven by elevation, nitrogen, and plant density gradients (Fig. 7A). DSE community composition differed significantly among plant species and functional groups (PERMANOVA, $p < 0.05$), and was also driven by snowpack and nitrogen gradients (Fig. 7B).

4. Discussion

The majority of plant individuals and species sampled contained AMF, DSE, or both, highlighting the importance of these fungi in alpine ecosystems (Haselwandter and Read, 1980). Our work provides insights into several questions that we posed based on previous work (Ranelli et al., 2015), including decreases in colonization with higher elevations, increased AMF colonization at both lower nitrogen and phosphorus levels, increased DSE with higher nitrogen levels, and a negative relationship between AMF and DSE fungi.

4.1. Plant species and functional group (H1)

The high amount of variation in colonization among different plant species is not surprising and has been reported elsewhere (Ruotsalainen et al., 2004; Ranelli et al., 2015). However, a lack of differences among species has also been reported, possibly due to a low number of species sampled (Casanova-Katny et al., 2011). Our study confirms differences in colonization among plant hosts across a wide variety of species ($n = 35$). Our hypothesis that forbs would have greater colonization than other groups was not supported by the results. While forbs may generally have thicker roots than grasses, a trait which can be positively correlated with AMF infection (Maherali, 2014), we did not measure this trait and the lack of difference in colonization between the two groups could have been masked by high inter- and intra-specific variation in root architecture within the groups. Furthermore, variability in other traits, such as cool- or warm-season grasses, photosynthetic pathway, or clonal mobility, all of which can impact mycorrhizal

Table 1
Plant taxonomy, sample size, ranges of arbuscular mycorrhizal fungi (AMF) and dark septate endophyte (DSE) colonization, mycorrhizal status, ranges of number of genera in the root (from ITS sequences), and references where plants have been previously studied for AMF or DSE colonization. Abbreviations in the Other Reference column (AM = arbuscular mycorrhizae, DS = dark septate endophytes, EM = ectomycorrhizae, NM = non-mycorrhizal) note which fungi, if any, had been found in previous samples of the species. Obligate, facultative, or non-mycorrhizal status was assigned based on if a species always, sometimes, or never has DSE or AMF based on our findings and the literature. Codes marked with a cross (†) were previously thought to be non-mycorrhizal until our study.

Family	Species	Code	n	AMF			DSE			Other References
				%	Status	# Gen.	%	Status	#Gen.	
Apiaceae	*Angelica grayi*	AngGra	3	0–52	Facultative	0–7	0–4	Facultative	0–4	First report
	Oreoxis alpina	OreAlp	2	0–4	Facultative	0–5	0–4	Facultative	2–3	First report
Asteraceae	*Antennaria media*	AntMed	4	5–45	Obligate	0	0–1	Facultative	0–1	First report
	Cirsium scopulorum	CirSco	4	0–70	Facultative	1–8	0	Non-DS	1–2	First report
	Erigeron simplex	EriSim	3	6–15	Obligate	6	0–27	Facultative	2	AM/DS[a,b]
	Senecio fremontii	SenFre	9	0–32	Facultative	0–11	0–3	Facultative	1–4	NM/AM/EM[a,c]
Boraginaceae	*Mertensia lanceolata*	MerLan	1	2	Obligate	NA	62	Obligate	NA	NM/AM[d]
Caryophyllaceae	*Cerastium arvense*	CerArv	1	0.5	Obligate	1	0	Non-DS	0	NM/AM/DS[d,e,f]
	Minuartia obtusiloba	MinObt	3	0–0.5	Facultative	0–2	0–1	Facultative	2–3	NM[a]
	Silene acaulis	SilAca	6	0–28	Facultative	2–12	0–64	Facultative	1–2	NM/AM[a,b,g,h,i,j,k,l,m,n]
	Stellaria umbellata	SteUmb	5	0–0.5	Facultative	0–1	0–1	Facultative	2–5	First report
Cyperaceae	*Carex albonigra*	CarAlb†	5	3–20	Obligate	0–9	0–2	Facultative	1–3	NM[o]
	Carex heteroneura	CarHet	2	3–4	Obligate	0	0–1	Facultative	1	First report
	Carex perglobosa	CarPer	1	5–45	Obligate	1	0	Non-DS	4	First report
	Carex phaeocephala	CarPha†	3	12–40	Obligate	2–8	0–1	Facultative	1–4	NM[p]
	Carex pyrenaica	CarPyr†	11	0–12	Facultative	0–3	0–1	Facultative	1–3	NM[q]
	Carex rupestris	CarRup	1	0	Non-AM	7	0	Non-DS	3	NM[n,o]
	Carex scopulorum	CarSco	2	0–1	Facultative	5	3–8	Obligate	1	NM/DS[c]
	Carex species	CarSpp	1	0	Non-AM	4	0	Non-DS	3	NA
	Kobresia myosuroides	KobMyo	5	0–3	Facultative	0–6	0–4	Facultative	1–3	EM/DS[i,q]
Fabaceae	*Trifolium dasyphyllum*	TriDas†	4	0	Non-AM	0–6	0–13	Facultative	0–3	NM[r]
Juncaceae	*Luzula spicata*	LuzSpi†	2	0–27	Facultative	0–11	0–1	Facultative	2–4	NM[j,q]
Liliaceae	*Lloydia serotina*	LloSer	1	10	Obligate	NA	12	Obligate	NA	AM/DS[b]
Poaceae	*Agrostis variabilis*	AgrVar	1	0	Non-AM	1	4	Obligate	2	NM[c]
	Deschampsia cespitosa	DesCes	8	3–21	Obligate	0–17	0–5	Facultative	1–5	AM/DS[c,s]
	Elymus scribneri	ElyScr	6	0–3	Facultative	1–5	0–20	Facultative	0–3	AM/DS[t]
	Festuca brachyphylla	FesBra	35	0–12	Facultative	0–5	0–40	Facultative	0–5	AM/DS[b,t,u]
	Poa species	PoaSpp	3	1–2	Obligate	0–3	0–1	Facultative	0–1	AM/DS[a,h,j,t,v,aa]
	Trisetum spicatum	TriSpi	19	0–14	Facultative	0–7	0–55	Facultative	0–4	NM/AM/DS[t,w,x]
Polygonaceae	*Oxyria digyna*	OxyDig	9	0–28	Facultative	0–1	0–9	Facultative	0–4	NM/AM[a,g,l,n]
Ranunculaceae	*Aquilegia coerulea*	AquCor	1	15	Obligate	3	2	Obligate	1	First report
Rosaceae	*Geum rossii*	GeuRos	10	0–30	Facultative	0–6	0–34	Facultative	0–3	AM[a,b,y]
	Sibbaldia procumbens	SibPro	1	6–15	Obligate	NA	7	Obligate	NA	NM/AM[a,m,q,z]
Scrophulariaceae	*Besseya alpina*	BesAlp	4	29–72	Obligate	0–6	0.5–3	Obligate	0–4	First report
Unknown	Opposite Leaf Forb	UnkOpp	1	9	Obligate	0	0.5	Obligate	2	NA

[a] Cázares et al., 2005
[b] Schmidt et al., 2008.
[c] Cázares et al., 2005.
[d] Kivlin et al., 2013
[e] Porazinska et al., 2018
[f] Casanova-Katny et al., 2011
[g] Newsham, 2011
[h] Sieverding, 1991
[i] Haselwandter and Read 1980.
[j] Read and Haselwandter 1981.
[k] Treu et al., 1996.
[l] Väre et al., 1992.
[m] Väre et al., 1997.
[n] Bueno de Mesquita et al., 2017
[o] Raab et al., 1999.
[p] Titus et al., 1998.
[q] Onipchenko and Zobel 2000.
[r] Day and Currah, 2011
[s] Leathwick et al., 1996
[t] Ranelli et al., 2015.
[u] Darcy et al., 2018
[v] King et al., 2012
[w] King et al., 2012
[x] Lugo et al., 2012.
[y] Leathwick et al., 1996
[z] Zubek et al., 2009
[aa] For *P. alpina, P. arctica, P. glauca.*

infection levels (Hetrick et al., 1991; Wilson and Hartnett, 1998; Onipchenko and Zobel, 2000; Lugo et al., 2012), may not have been captured by our functional groups. For DSE, forbs (all dicots except one individual) had similar levels of DSE colonization to graminoids and sedges (all monocots), contrary to previous results showing greater colonization in monocots (Weishampel and Bedford, 2006; Newsham, 2011). The low level of DSE colonization in the sedges we studied was surprising, as it was much lower than in other studies

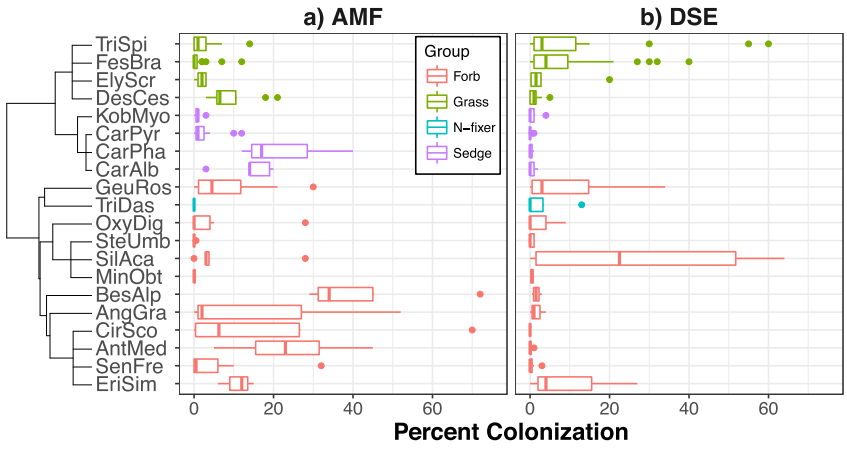

Fig. 3. Percent of root length colonized by (A) AMF (arbuscular mycorrhizal fungi) and (B) DSE (dark septate endophytes) across the 20 different plant species that were sampled at least 3 times. Plant host species had a greater influence on AMF than DSE. Plants are ordered phylogenetically. For plant family, genus, and species names, refer to Table 1. Boxplots show the median, 25–75th quantiles, 95% confidence intervals, and outliers.

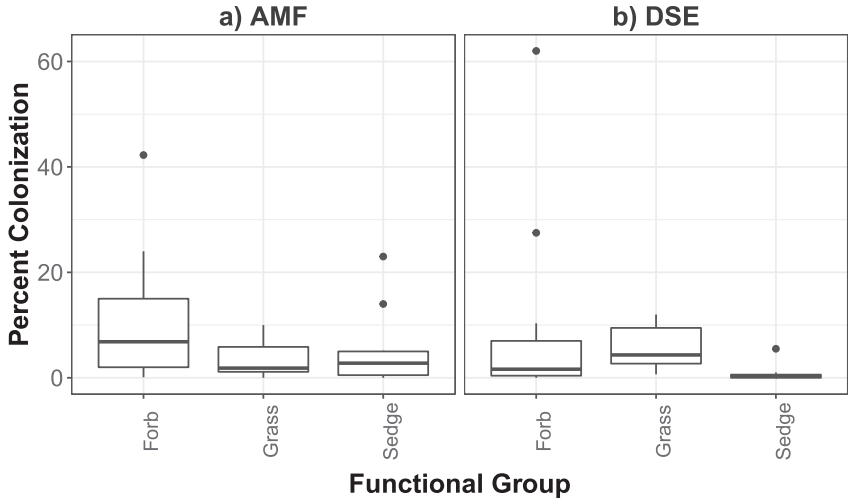

Fig. 4. Percent root colonization by (A) AMF (arbuscular mycorrhizal fungi) and (B) DSE (dark septate endophytes) across forb (n = 18 species means), grass (n = 6), and sedge (n = 9) functional groups. Different letters represent significant differences in colonization based on the Nemenyi *post hoc* test ($p < 0.05$). Boxplots show the median, 25–75th quantiles, 95% confidence intervals, and outliers of species' means.

Table 2
Results of all subset modeling of arbuscular mycorrhizal fungi (AMF) and dark septate endophyte (DSE) colonization. Shown are the included variables and their coefficients of the top 5 models for each fungal group, the AIC scores, and partial R^2 scores for plant and environmental variables. All models except for the 5th DSE colonization model were significant. The spatial distributions of a significant continuous predictor variable (DIP for AMF, Snowpack for DSE) are shown in Fig. 5. TIN = Total inorganic nitrogen. DIP = Total dissolved inorganic phosphorus.

Response Variable	Best Predictor Variables (coefficient sign)	AIC	Plant R^2	Env R^2
AMF Colonization	Species, TIN(−), Elevation (−), Snowpack (−),	357.23	56.06	8.57
	Species, TIN(−), Elevation (−), Snowpack (−), DIP(−)	357.53	56.30	9.71
	Species, TIN(−), Elevation (−)	357.64	56.60	4.15
	Species, TIN(−), Elevation (−), DIP(−)	357.76	56.93	5.58
	Species, TIN(−)	358.03	56.22	1.96
DSE Colonization	Snowpack (−), TIN(+)	382.34	NA	5.15
	Snowpack (−), TIN(+), Density (+)	382.87	NA	5.32
	Snowpack (−), Density (+)	383.03	NA	5.38
	Snowpack (−)	383.15	NA	4.90
	Snowpack (−), Elevation (+)	384.89	NA	3.98

(Read and Haselwandter, 1981), and DSE benefit sedge growth (Haselwandter and Read, 1982). However, many sedges can take up organic nitrogen without the help of mycorrhizas (Raab et al., 1999), and increasing rates of atmospheric deposition of inorganic nitrogen at our site (Burns, 2003) may negate the beneficial effects of DSE for some plant species.

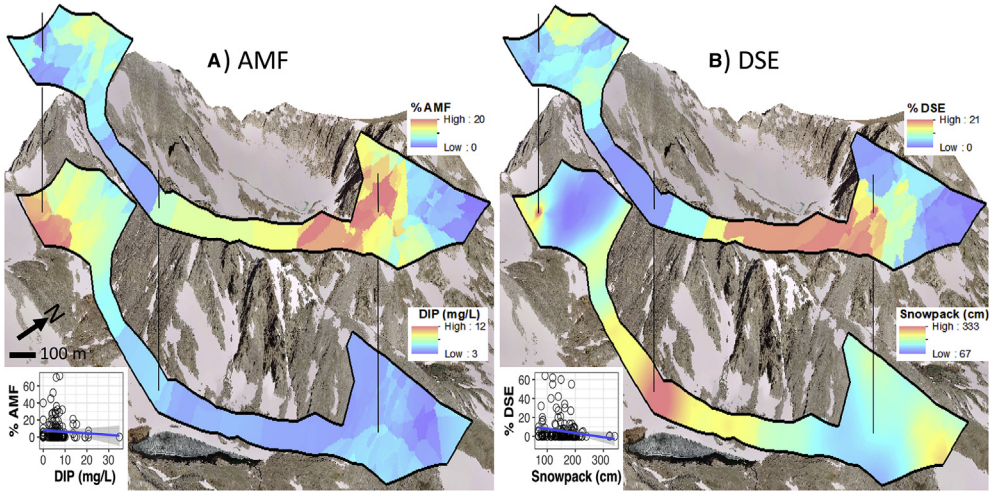

Fig. 5. (A) Kriging interpolation and scatterplot of total dissolved inorganic phosphorus (DIP) and the percent of arbuscular mycorrhizal fungi (AMF) root colonization. (B) Kriging interpolation and scatterplot of mean snowpack and the percent of dark septate endophyte (DSE) root colonization. DIP and snowpack were two of the significant predictors of AMF and DSE colonization, respectively.

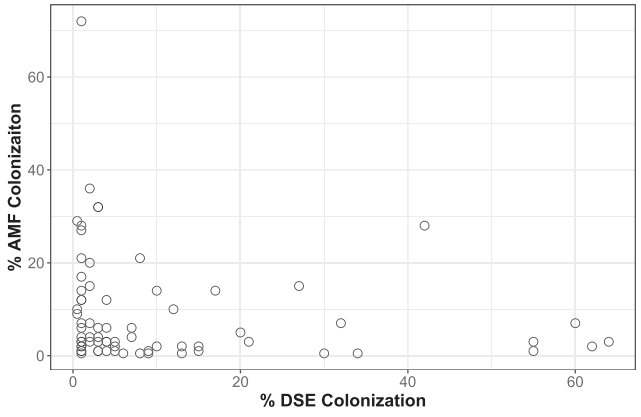

Fig. 6. Arbuscular mycorrhizal fungi (AMF) versus dark septate endophyte (DSE) root colonization for individuals that contained both fungi (n = 71). Root colonization levels of the two groups were significantly negatively correlated (S = 75608, Rho = −0.27, p = 0.02). An exponential decay function was not significant (λ = 19.90, p > 0.05).

4.2. Plant and environmental predictors of colonization (H2)

Plant species was important in all of the top five multivariate models for AMF percent root colonization, but not for DSE. Plant species also explained more of the variation in AMF colonization than environmental variables. This result supports the hypothesis that AMF are obligate symbionts and are expected to depend on plant hosts more than the environment, while DSE are facultative symbionts that may be structured more by environmental variables (Ranelli et al., 2015), although this remains to be tested in other systems.

Elevation, snowpack, plant density, phosphorus, and nitrogen were also important predictors of AMF and DSE colonization. AMF were more abundant at lower elevations, while DSE showed no significant relationship with elevation. Decreases in AMF root colonization with increasing elevation have been reported in most other mountain ranges (Haselwandter and Read, 1980; Väre et al., 1997; Ruotsalainen et al., 2004; Schmidt et al., 2008; Lugo et al.,

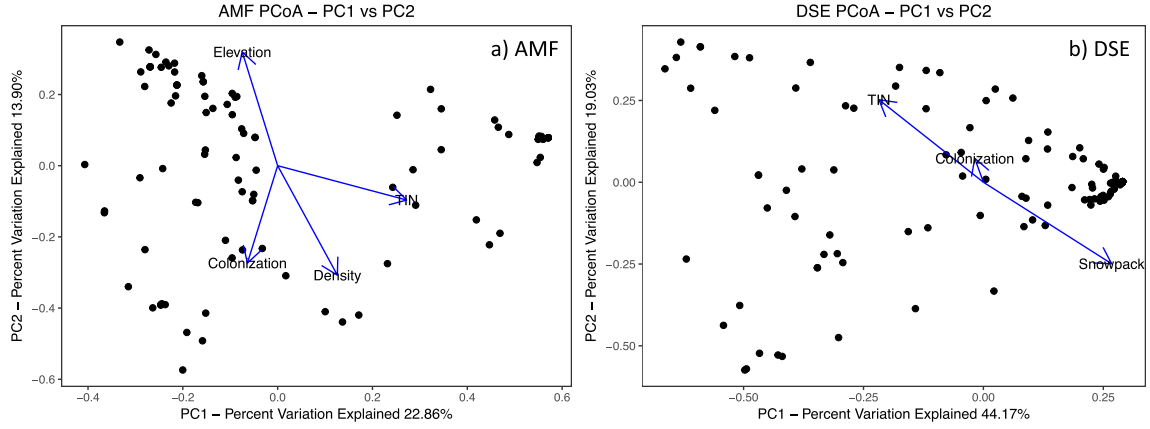

Fig. 7. Principle coordinates analysis of arbuscular mycorrhizal fungi (A) and dark septate endophyte (B) community composition at the genus level based on Bray-Curtis dissimilarity. Vectors show significant variables that drive community dissimilarity, as determined by the envfit function in the R package *vegan*. Also shown are vectors for percent colonization, to represent on the graphs areas where there was higher percent root colonization by each fungal group.

2012; Shi et al., 2014; Kotilínek et al., 2017). Samples from even lower elevation intact tundra meadows on Niwot Ridge (3500 m elevation) have shown over 80% colonization in some samples, which further supports this trend (Schmidt et al., 2008). This could be due to a lack of inoculum at high elevations (but see Marín et al., 2017 for increases with elevation), which could be a function of low plant density or a negative effect of cold temperature on AMF (Lugo et al., 2008; Yang et al., 2016). Since DSE are common in arctic and alpine environments, can tolerate cold temperatures (Mullen et al., 1998), and have been found in abundance at over 5250 m a.s.l. in the Andes (Schmidt et al., 2008), and at 6000 m in the Himalayas (Kotilínek et al., 2017), our finding of no relationship with elevation is consistent with other studies (Ruotsalainen et al., 2004; Schmidt et al., 2008; Zubek et al., 2009).

Both AMF and DSE showed greater colonization in areas with shallower snowpacks, which may be explained by more developed soils and plant communities and subsequently more fungal inoculum, in these areas. Another explanation for this relationship is that both AMF (Augé, 2001) and DSE (Barrow, 2003) can help plants cope with low soil moisture conditions where snow melts earlier (Williams et al., 2009). Snowpack is a variable expected to decline as climate warms. While our site shows increasing winter precipitation trends (Kittel et al., 2015), there are declining trends in snow meltout date and lake ice-off dates over the past few decades due to warming and less spring snow (Preston et al., 2016). Our results suggest that fungal inoculum could increase in these conditions and plants have the potential to become more colonized by fungi to cope with moisture limitations, but this remains to be tested.

Despite a positive relationship between plant density and AMF spores, there was no relationship between AMF colonization and plant density. Interestingly, percent root colonization and spore density are not necessarily correlated (e.g. Aguilera et al., 2017). Since AMF are obligate symbionts, they are expected to be more abundant where there are more individual plants that associate with them (regardless of plant species richness). We originally thought DSE would be most important for plants in sparsely vegetated areas because we did not expect them to decline at low plant densities; however, DSE colonization did decline with decreasing plant density, even though they can survive without a plant host. Thus, AMF may be just as important as DSE for plant survival in sparsely vegetated and newly vegetated areas. As climate warms at our site, vascular plant density is increasing in the subnival zone (Bueno de Mesquita et al., 2017). Most of the stem counts from our 2015 survey were higher than those in a 2008 survey of the same plots (King et al., 2012). This increase in plant density may lead to both an increase in AMF inoculum levels and DSE colonization levels, which may in turn be important for alpine plants to cope with warmer maximum temperatures and lower soil moistures (Kivlin et al., 2013).

The negative relationship between phosphorus and AMF colonization supports our hypothesis and suggests that AMF help plants acquire phosphorus in high-alpine systems, as has been shown in other systems (e.g. Lingfei et al., 2005; Camenzind et al., 2014). Phosphorus is a limiting nutrient for plant growth at our site in both tundra meadows (Seastedt and Vaccaro, 2001) and in the subnival zone (King et al., 2008), as well as in the high alpine of Perú and Alaska (Darcy et al., 2018). P limitation at our site could be due to phosphorus-poor granite-gneiss parent material, or insufficient weathering (Bowman and Seastedt, 2001; King et al., 2008; Vitousek et al., 2010; Porder and Ramachandran, 2012). Consequently, plants may devote more photosynthate to AMF in low P areas to increase P uptake via the fungus (Johnson et al., 2010). Furthermore, previous work at our site demonstrated correlations between plant tissue P and the amount of arbuscules in the roots (Mullen and Schmidt, 1993), which is strong evidence of AMF-mediated P uptake in the field.

There was more AMF colonization where soil inorganic nitrogen was low, suggesting that AMF are also helping plants acquire N at our site, consistent with previous studies (Augé, 2004; Smith and Read, 2008; Camenzind et al., 2014). On the other hand, there was a positive relationship between DSE colonization and TIN, also consistent with our hypothesis and other studies (Newsham, 2011). This result, especially given the context of our alpine study site, where decomposition rates are slow and N can be stored in organic form for long periods of time (Bowman and Seastedt, 2001), supports the idea presented by Newsham (2011) that DSE break down organic N in the rhizosphere into more plant-available forms (Mandyam and Jumpponen, 2005). Together, these results are consistent with the idea that DSE help make inorganic N available, and AMF help plants take up the inorganic N, especially when it is more limiting (Smith and Read, 2008; Newsham, 2011).

4.3. DSE and AMF Co-occurrence (H3)

Our results contradict those of Ranelli et al. (2015), who found a positive relationship between AMF and DSE colonization. In our data, there appeared to be a trend of an exponential decay relationship, though this was likely confounded by many instances of low colonization of both DSE and AMF, and thus was not significant. In the 71 individuals colonized by both AMF and DSE, AM and DSE colonization levels were negatively correlated. This could be due to different responses to environmental and plant gradients or competition for host plant root tissue. Interestingly, there was no negative correlation in the number of DSE and AMF genera in the roots, suggesting that multiple taxa can share the same root, even if some taxa have low abundance. While many studies have examined both AMF and DSE colonization, few of them have explicitly analyzed correlations between the two (Ranelli et al., 2015; Kotilínek et al., 2017). Competition studies between AMF and DSE are necessary to tease apart these dynamics.

4.4. DSE and AMF community composition (H4)

The most abundant AMF genera identified in the roots show a cosmopolitan distribution, as was found in a global distribution study on the Glomeromycotina (Davison et al., 2015). *Acaulospora* has been reported in a wide variety of ecosystems and countries (Schenk and Smith, 1982; Oehl et al., 2004, 2006; Zhang et al., 2004; Andrade et al., 2009), and has been shown to increase plant foliar P concentrations (Klironomos, 2000). *Entrophospora* is similarly widespread (Palenzuela et al., 2010), but to date, no targeted inoculation studies have been conducted to determine its function. While the percent root colonization by AMF varied among plant species, community composition did not. These results show that different plant species may be more dependent on AMF than others, but they do not necessarily rely on only certain taxa. In other words, the plants in our study associate with a variety of AMF taxa, and AMF taxa colonize a wide variety of plant species. This is in contrast to other studies that have found differences in community composition among plant hosts (Vandenkoornhuyse et al., 2003; Hausmann and Hawkes, 2009; Martínez-Garcia et al., 2015), which may be explained by the number of plant species we sampled and the environmental gradients we encompassed compared to other studies, or differences in methodology. AMF composition is driven by the harshness gradient, with certain taxa more abundant in high-elevation, sparsely-vegetated areas, and others more abundant at high plant densities and N concentrations.

The abundant DSE genus *Phialophora* has been previously found in alpine forbs (Schadt et al., 2001) and conifer roots (Wang et al., 1985), as well as moss in Antarctica suggesting a global

distribution for the taxon (Yu et al., 2014). *Capronia* has been found in lichens in Bolivia (Etayo et al., 2013), Turkey and Spain (Halici et al., 2010), in oak forests (Friebes, 2011), and even in intertidal environments (Au et al., 1999). While *Capronia pilosella* is cited as being a dark septate fungus (Jumpponen and Trappe, 1998), most sequences in our study aligned more closely (95%) to *Capronia peltigerae*, which is a lichenicolous fungus (Untereiner et al., 2011). While the *Exophiala* genus also contains non-endophytic soil fungi, our sequences closely aligned (97%) with an endophyte isolated from fine pine roots in the mountains of Montenegro (Lazarević and Menkis, 2017). Unfortunately, there are no studies of how targeted inoculations with these taxa affect plant fitness, which is an avenue for future research. DSE community composition varied among plant species and functional groups, just as percent root colonization did. Similarly, nitrogen and snowpack gradients, the key drivers of percent root colonization, also drove community composition, with certain taxa associated with high N, low snow areas, and others in late-melting snowbed areas.

5. Conclusions

Our work builds on other surveys of AMF and DSE colonization and contributes to a growing body of knowledge on these two important fungal groups. Our data show that extent of colonization by both fungal groups varies significantly among different plant species. As plants shift their ranges in response to climate change and changes in snowpack, interactions with these two fungal groups will be important for some plant species and not others. Our work provides new insights into how colonization varies across the landscape and highlights the important role of AMF in plant acquisition of both nitrogen and phosphorus, and of DSE in nitrogen cycling in alpine ecosystems. Interactions with these two fungal groups will likely prove crucial for alpine plants responding to global change (Kivlin et al., 2013), which is an important avenue for future research. For example, plants moving uphill to track warming may have to colonize unvegetated areas, which could be limited by phosphorus or nitrogen, and fungi could help facilitate movement into these habitats.

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