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HIGHLIGHTED STUDENT RESEARCH

Soil microbes that may accompany climate warming increase alpine plant production

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Abstract

Climate change is causing species with non-overlapping ranges to come in contact, and a key challenge is to predict the consequences of such species re-shuffling. Experiments on plants have focused largely on novel competitive interactions; other species interactions, such as plant–microbe symbioses, while less studied, may also influence plant responses to climate change. In this greenhouse study, we evaluated interactions between soil microbes and alpine-restricted plant species, simulating a warming scenario in which low-elevation microbes migrate upslope into the distribution of alpine plants. We examined three alpine grasses from the Rocky Mountains, CO, USA (*Poa alpina*, *Festuca brachyphylla*, and *Elymus scribneri*). We used soil inocula from within (resident) or below (novel) the plants' current elevation range and examined responses in plant biomass, plant traits, and fungal colonization of roots. Resident soil inocula from the species' home range decreased biomass to a greater extent than novel soil inocula. The depressed growth in resident soils suggested that these soils harbor more carbon-demanding microbes, as plant biomass generally declined with greater fungal colonization of roots, especially in resident soil inocula. Although plant traits did not respond to the provenance of soil inocula, specific leaf area declined and root:shoot ratio increased when soil inocula were sterilized, indicating microbial mediation of plant trait expression. Contrary to current predictions, our findings suggest that if upwardly migrating microbes were to displace current soil microbes, alpine plants may benefit from this warming-induced microbial re-shuffling.

Keywords Bacteria · Fungi · Plant microbiome · Plant traits · Rhizosphere

Introduction

Species are shifting their ranges with climate change (Walther et al. 2002; Thomas et al. 2004; Lenoir et al. 2008), and these shifts in geographic ranges may cause novel interactions among species that had previously not interacted (reviewed by Van der Putten 2012). Experiments that create such novel interactions could improve understanding of the ecological consequences of climate change, particularly the indirect effects of climate on species interactions (Tylianakis et al. 2008; Alexander et al. 2016). For example, as climate warms, the upward migration of plant species into high-elevation communities may competitively exclude resident alpine plants (Alexander et al. 2015). For interactions involving plants, experiments on biotic interactions other than competition, such as plant–microbe interactions, are currently rare. However, recent studies suggest that even bacteria, with their fast generation times, have not equilibrated to ongoing climate change (Ladau et al. 2018),

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As climate change reshuffles biotic communities with species range shifts, there is a growing need to understand the consequences of novel biotic interactions for populations and communities. Experiments that attempt to reshuffle communities based on climate projections are rare, especially for plant–microbe interactions. Here, we introduced microbes into alpine-restricted plant species to simulate microbial migration up-mountain slopes under climate warming. Contrary to current ecological theory, our greenhouse experiment showed that if microbial communities colonize up-mountain with climate change, some plant species will benefit.

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portending high potential for novel plant–microbe interactions in the future.

The abundance and composition of plant-associated microbes can vary along elevation gradients (Ranelli et al. 2015; Kivlin et al. 2017a), often covariant with abiotic factors, like temperature, that suggest their ranges could shift upslope with climate warming. Recent meta-analysis found that both the abundance and species richness of arbuscular mycorrhizal fungi (AMF) tended to decrease with elevation (Kivlin et al. 2017a), although patterns were highly plant species-specific (see also Ranelli et al. 2015). However, such patterns in microbial diversity are not universal. For instance, soil bacteria diversity did not change systematically with elevation in a Peruvian mountain transect (Fierer et al. 2011). Macroecological analyses of how soil bacteria and fungi respond to abiotic drivers (temperature and pH) typically associated with elevation gradients present a full range of patterns (Hendershot et al. 2017). Given that microbial diversity and abundance tend to vary over elevation gradients and with abiotic factors that change with elevation, such as temperature and growing season length (Siles and Margesin 2016; Kivlin et al. 2017b), climate change could drive shifts in microbial distributions (reviewed by Classen et al. 2015). In addition, microbes have the capacity to evolve rapidly (terHorst and Zee 2016) given their short generation times, and climate change is likely to drive evolutionary change (reviewed by Classen et al. 2015), possibly towards functions similar to communities found in warmer current climates. How these range-shifting microbes will interact with resident plants is unknown.

Colonization by novel microbes may hinder plant tolerance of climate change-associated stress. Plant-associated microbes can ameliorate (or exacerbate) the stress induced by climate change (Kivlin et al. 2013), and microbial abundance and composition are often altered by in situ climate manipulations (Compant et al. 2010; Zhou et al. 2018). For example, experimental warming can increase microbial abundance, but decrease diversity in normal precipitation years, and warming may exacerbate declines in microbial abundance under drought conditions (Sheik et al. 2011). In addition, under 20 years of experimental warming, AMF colonization increased in two of six plant species examined, and plot-level root colonization by non-AM fungi increased, coincident with changes in plant composition (Rudgers et al. 2014). Other than the direct effects of climate change on microbes, climate-altered associations between plants and microbes may be a signal of increased reliance of plants on their symbionts. For instance, meta-analysis showed that plant-associated microbes generally bolstered plant production in response to global change factors (Kivlin et al. 2013). Examples include improved drought tolerance via plant growth-promoting bacteria (Yang et al. 2009) and enhanced plant performance when plants were paired with soil microbes from a similar soil moisture regime (Lau and Lennon 2012; Allsup and Lankau 2019). If climate change causes range shifts in microbes, there is potential for microbial colonizers to disrupt such benefits afforded to resident plants (Revillini et al. 2016).

Microbes associated with resource-acquisitive plant trait strategies (i.e., taller, thinner leaves) may benefit plants if climate warming increases the importance of plant competition (Fridley et al. 2016). Evidence for microbially driven intraspecific variation in plant traits is mixed (reviewed by Friesen et al. 2011). Lau and Lennon (2011) found that plants grown in simplified microbial communities that developed under low soil moisture had less conservative specific leaf area (higher SLA) than plants grown with microbes from well-watered soils. SLA correlates positively with plant growth and photosynthetic rate (Perez-Harguindeguy et al. 2013) and thus could improve plant competitive ability (Kraft et al. 2014). Similarly, different bacteria strains altered plant investment in leaves versus roots (Henning et al. 2016), suggesting that bacteria can alter plants' resource investment strategies. Improved understanding of how plant traits are influenced by novel interactions with microbes may aid in predicting species responses to a changing environment.

In this study, we created novel plant–microbe associations that may be expected if climate warming caused microbes to move upslope in mountain ecosystems. We tested the effects of soil provenance by comparing novel (low elevation) versus resident (high elevation) soil inocula on the growth, traits, and fungal root colonization of alpine-restricted grass species from the Colorado Rocky Mountains. Mountain ecosystems are advantageous for evaluating novel plant–microbe interactions, because abiotic conditions associated with microbial community turnover (Kivlin et al. 2017a) vary with elevation (Körner 2007). Thus, the potential exists for climate change to cause novel plant–microbe associations in mountain ecosystems. Specifically, we asked (1) do novel soil inocula reduce plant biomass more than resident soil inocula? (2) are plant traits more resource acquisitive with novel microbes than resident microbes? (3) do novel soil inocula increase colonization of roots by fungi relative to resident fungi? Finally, we combined plant traits and root colonization with plant growth responses to ask: (4) do relationships between plant biomass and plant traits or mycorrhizal colonization weaken in novel inocula relative to resident soils?

Materials and methods

Greenhouse experimental design

The experiment used a $2 \times 2 \times 3 \times 3$ factorial design, including an inoculum sterilization treatment (sterile vs.

live soil inocula), soil provenance (inocula collected from resident, high elevation vs. novel, low elevation), three independent mountains to replicate elevation geographically, and three grass species. This design resulted in 36 treatment combinations with 10 replicates per treatment ($N = 360$ pots). Plants were grown in ~ 150 mL plastic root trainer pots (Stuewe and Sons, Inc., Tangent, Oregon, USA). Each pot was filled with 80% of sterilized sand (80 mL, QUIKRETE Play Sand, Atlanta, Georgia, USA) topped with 10% of treatment inoculum (10 mL), and then topped with 10% of sterilized sand (10 mL) to reduce splash contamination. Sand was autoclave-sterilized for three cycles (each cycle: 1 h at 121C and 20 psi) separated by a 24-h cooling and rest period. Sand enabled easy cleaning of roots. Each pot was initially sown with 10 seeds of one focal species, to ensure at least one germinant. On 11-Oct and 30-Nov-2017, pots were thinned to one individual. All tools used for thinning were sterilized with 8.5% sodium hypochlorite bleach between pots. There were no treatment effects on rate of germination (93% of pots had germination, electronic supplementary material Table S4) or final plant survival (all pots with germination survived to harvest). Seedling survival was not monitored prior to thinning. Samples were fully randomized across eight blocks (trays) of pots. Plants were watered four times daily for 5 min using an automatic overhead spraying system (~ 50 mm per pot). The experiment began 15-Sep-2017. On 22-Nov and 21-Dec-2017, each pot was fertilized with FloraGro 2:1:6% N:P:K solution (General Hydroponics, Sebastopol, CA, USA) to reduce possible nutrient stress during long-term growth.

Study area

We collected soil inocula and seed from the Colorado Rocky Mountains within the Upper Gunnison Basin, Colorado, USA. The Colorado Rockies are expected to experience more pronounced warming trends over the coming decades compared to lower lying regions (McGuire et al. 2012; Rangwala and Miller 2012). All plant material and soil inocula were collected from three independent mountain peaks and associated valleys (Avery, Cinnamon, and Treasury), with a high (resident) and low (novel) site on each gradient (site coordinates in electronic supplementary material, Table S1), all within the Gunnison National Forest, CO, USA. The two elevation sites per mountain were selected approximately 430 m apart in elevation (range ~ 3200–3600 m a.s.l.) to represent ~ 3 °C difference in mean annual temperature (Pepin and Losleben 2002). The low sites were selected to be lower than the low-elevation range boundaries of the three focal plant species.

Soil inoculum

At each of the six sites, live soil was collected to serve as inoculum in our greenhouse experiment. Within a site, soil was collected at three points along a 40 m-long transect (0, 20, and 40 m). We collected approximately 1 L of soil at each collection point using an 8.5% sodium hypochlorite bleach-sterilized trowel, resulting in 3 L of soil per site. All soils were collected 14–25 Aug-2017. Soils were immediately stored at 4 °C after collection until used for inoculation 15-Sep-2017. In preparation for the experiment, soils were sieved through an ethanol-sterilized 2 mm grade sieve. Soil from each site was divided in half, with one half used for the live inoculum treatment and the other sterilized to better isolate the influence of living microbes from other edaphic factors. Sterilized soils were autoclave-sterilized for three cycles (each cycle: 1 h at 121 °C and 20 psi) separated by a 24-h cooling and rest period. Bulking soil may not accurately represent the spatial scale at which plants and microbes interact in the field (Rinella and Reinhart 2018). Our soils were combined over a 40-m area which may inflate the soil microbial diversity experienced by an individual plant as well as spread pathogens or mutualists among microsites; however, these potential effects may be consistent across all inocula. We focused replication at a larger spatial scale (six independent soil communities) rather than individual microsites, so that we could replicate high- and low-elevation sites on multiple mountains to more accurately capture elevation relative to comparing one low/high pair.

Focal plant species

We used three alpine-restricted grass species to test how soil communities affect plant growth and traits (all in family Poaceae, subfamily Pooideae; *Poa alpina*- tribe: Poeae, subtribe: Poinae; *Festuca brachyphylla*- tribe: Poeae, subtribe: Loliinae; *Elymus scribneri*- tribe: Triticeae). The focal species occupy the highest elevations within the region (~ 4000 m a.s.l.); locally, they are rarely observed below ~ 3500 m a.s.l. (Lynn et al. 2019). In the region, grasses have become more abundant in upland meadows and have often shifted their mean range to higher elevations (Zorio et al. 2016). Seeds for the focal plant species were collected in 2015 and 2016 from the same three high-elevation sites from which we collected resident soil inocula (Table S1). Seeds were bulked across years. Seeds were only grown in inocula from the same mountain gradient. We did not sterilize seeds. Therefore, microbes present in seeds occurred evenly across treatments and we only test the effects of novel soil microbes interacting with current seed microbes.

Response variables

Plant biomass harvest

We harvested plants on 16–18 Jan-2018. We washed roots through a 1 mm sieve. All biomass was dried at 60 °C for 48 h and then weighed to the nearest 0.001 g. Prior to drying roots, we placed ~0.2 g of wet root tissue in a plastic tissue cassette (Slimsette, Simport, Beloeil, QC, Canada) in preparation for microscopy. Root dry mass was corrected for removal of this sample by weighing the remaining roots both wet and dry. Cassettes were stored in 70% ethanol until processing for fungal colonization.

Plant traits

We measured the height of each individual in cm prior to harvest. We measured specific leaf area (SLA) on 3–5 fully expanded healthy leaves per plant. We scanned each leaf with a CanoScan LiDE 210 (Canon USA, Inc., Melville, NY, USA) flatbed scanner and measured area (in cm^2) using ImageJ software (Schneider et al. 2012). Each leaf was weighed on a mass balance to the nearest 0.0001 g. SLA was calculated as cm^2/g and individual leaves were averaged to obtain a single SLA value per plant. Root-to-shoot biomass ratio (hereafter root:shoot) is the biomass of roots divided shoot biomass.

Fungal colonization

Roots were soaked in 10% KOH, rinsed in water, soaked in 0.1 N HCl, and then soaked in preheated 5% Parker blue ink (Parker Pen Company, New Haven, East Sussex, UK) and vinegar stain, and rinsed in water again (Vierheilig et al. 1998). We scored root colonization via light microscopy with the magnified intersection method at 200× magnification (McGonigle et al. 1990) with 100 views per sample. Aseptate and septate hyphae were counted separately as indicators of AM fungi and non-AM fungi, respectively. Septate fungi were relatively rare (only ~34% of samples) and lacked sufficient data for analysis. A few individuals of each species lacked sufficient root material to assess colonization (7 of 333).

Data analysis

For questions 1–3, we expected novel, live soil inocula to reduce plant responses more than resident, live soil inocula (microbially driven provenance effects), but that soil provenance would not affect plant responses when inocula were sterilized (physiochemical-driven provenance effects), indicated by statistical interaction between soil provenance X sterilization. We used linear mixed-effects models with model selection procedures to evaluate the treatment effects on plant shoot, root, and total biomass, SLA, plant height, root:shoot, and fungal root colonization. Each model was fit separately for each grass species, and all models contained the random intercept effects of block (representing a tray of pots in a specific location in the greenhouse) and mountain identity (Avery, Cinnamon, or Treasury). We performed model selection procedures (Anderson 2008) for each dependent variable by comparing five models: (1) a null model (random effects only); (2) a model including the main and interactive effects of sterilization and inocula provenance (our hypothesized effects); (3) an additive model with sterilization and inocula provenance; (4) a model including the main effect of sterilization only; and (5) a model including the main effect of inocula provenance only. This model selection procedure addressed questions 1–3 by evaluating whether the influence of soil inocula provenance depended on soil sterilization (provenance X sterilization treatment interaction) by comparing model fit against a model that lacked the interaction.

All dependent variables were modeled using the "lmer" function in *lme4* (Bates et al. 2015). All models of biomass were natural log transformed to meet homogeneity of variance assumptions. Colonization data were proportions, necessitating a logit transformation prior to analysis (Warton and Hui 2011). We used Akaike's corrected information criterion (*AICc*) to select models based on within sample predictive ability given model complexity (lower *AICc* denotes a better fit of the model to the data). We calculated the *AICc* weights for each model, along with the marginal (based on fixed effects) and conditional (includes random effects) pseudo-R^2 for each model (Nakagawa and Schielzeth 2013). In addition, we performed Wald Chi-square tests on the full model (model 2 from above) and reported the results in electronic supplementary material Table S3. We found qualitatively similar results, suggesting that they were robust to analysis method. All models were fit in R (R Core Team 2018) using the *lme4* (Bates et al. 2015) and *MuMIn* (Bartoń 2018) packages.

For question 4, do relationships between plant biomass and plant traits or mycorrhizal colonization weaken in novel inocula relative to resident soils?, we used only the subset of live inocula treatments to construct linear models investigating how total plant biomass related to plant traits (or root colonization by fungi) as modified by inocula provenance. The interaction term fits a unique slope and intercept for the relationship between a trait and plant biomass for resident versus novel inocula. We compared these models against additive models in which intercepts were fit according to inocula provenance, but slopes were constrained to be the same for the two inocula (no interaction between trait X soil inoculum) using the model selection procedure described above. Analyses included only the individual plants for

which all variables were measured, enabling a comparison of among traits and colonization for their predictive ability of plant biomass.

Results

Plant biomass

We expected that novel live soils would reduce plant biomass relative to resident live soils due to mismatches between plants and microbial communities. Instead, for the three species, novel live soil often increased biomass relative to resident live soil (Fig. 1, electronic supplementary material Table S2). In addition, inocula sterilization increased biomass compared to live inocula for all species by an average of ~ 50% (Fig. 1, electronic supplementary material Table S2). The full model, including the interaction of soil provenance and sterilization, was most predictive of root (marginal $R^2 = 0.20$), shoot (marginal $R^2 = 0.32$), and total biomass (marginal $R^2 = 0.25$) for *P. alpina* (electronic supplementary material Table S2). *Poa alpina* plants had 47% greater root biomass, 30% greater shoot biomass, and 40% greater total biomass with live novel than with live resident soil inocula, while biomass differences in sterile controls from the different provenances were small (4% roots, 7% shoots, and 5% total greater in novel, Fig. 1a–c). The full interaction model was most predictive of *F. brachyphylla* shoot biomass (marginal $R^2 = 0.37$), while the models with only sterilization were most predictive for root (marginal $R^2 = 0.24$) and total biomass (marginal $R^2 = 0.31$, electronic supplementary material Table S2). *Festuca brachyphylla* shoots were 20% larger in novel live inocula compared to resident live inocula, while sterile novel inocula-treated plants were only 0.2% greater in shoot biomass over sterile-resident inocula (Fig. 1d). Root biomass was 103% and total biomass 76% greater in sterile over live inocula for *F. brachyphylla* (Fig. 1e, f). The additive model, with only the fixed effects of soil provenance and sterilization, was most predictive of root (marginal $R^2 = 0.11$), shoot (marginal $R^2 = 0.15$), and total biomass (marginal $R^2 = 0.13$) for *E. scribneri* (electronic supplementary material Table S2). *Elymus scribneri* plants had 26% greater root biomass, 21% greater shoot biomass, and 21% greater total biomass with novel

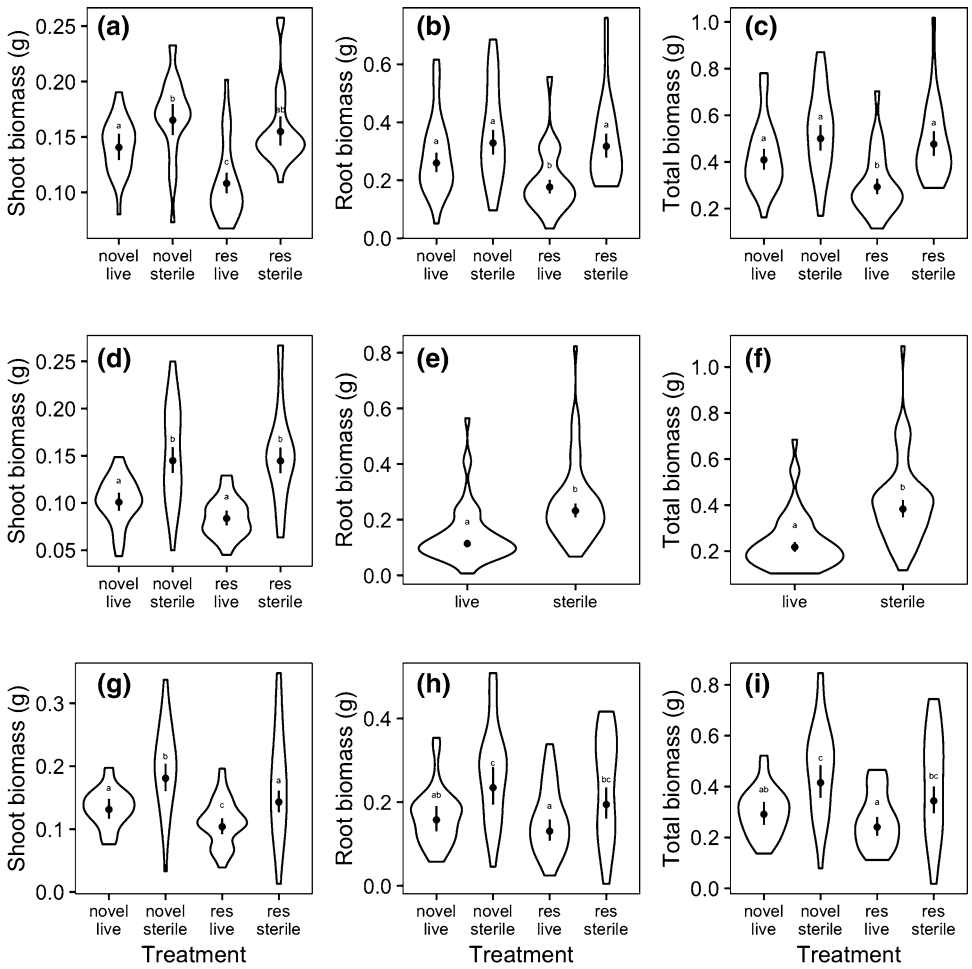


Fig. 1 Shoot, root, and total biomass was greater sterile inocula, and in live inocula from novel, low-elevation communities compared to live inocula from the plant species' resident ("res"), high-elevation community. Violin plots show the observed distribution of the data. The point and error bars are the predicted mean and standard error estimates from the models and account for the random group effects of mountain and greenhouse block. Results from the best models following model selection procedures are presented. Tukey's post hoc tests of significance differences are denoted by lowercase letters above model estimates at $P < 0.05$. **a–c** *Poa alpina*; **d–f** *Festuca brachyphylla*; **g–i** *Elymus scribneri*

over resident soil inocula, and sterilized inocula increased biomass by 38%, 49%, and 43% for roots, shoots, and total biomass, respectively (Fig. 1g–i).

Plant traits

With few exceptions, the best models for plant traits included only the sterilization treatment, and effects of treatments on plant traits overall were weak with low marginal R^2 values (all < 0.06, Fig. 2, electronic supplementary material Table S2). SLA in every species was higher in live than sterile inocula, by 3%, 9%, and 5% for *P. alpina*, *F. brachyphylla*, and *E. scribneri*, respectively (Fig. 2a, d, g). Root:shoot had a similar but opposite response to sterilization alone; two species had higher root:shoot in sterilized than in live inocula (by 15% and 16% for *P. alpina* and *F. brachyphylla*, respectively, Fig. 2c, f). Root:shoot was higher (9%) in resident inocula for *E. scribneri* with no effect of sterilization (Fig. 2i). Plant height responses were idiosyncratic among grass species. *P. alpina* plants were 4% taller, and *E. scribneri* 3% shorter in live than sterile inocula (Fig. 2b, h). However, the best non-null model for height of *F. brachyphylla* included the interaction of inocula provenance and sterilization (electronic supplementary material Table S2). Plants in the resident live inocula were the tallest, growing 10% taller than an average *F. brachyphylla* in the novel live inocula (Fig. 2e). In the resident and novel sterile treatments, *F. brachyphylla* grew 1% and 6% taller than the novel live treatment, respectively.

Fungal root colonization

Sterilization successfully reduced fungi in plant roots. Averaged across species, live inocula had 12 times more aseptate fungal colonization (candidate AMF) than sterile inocula. Colonization of roots by aseptate hyphae was 10 and 12 times higher in live than sterilized soil for *P. alpina* and *F. brachyphylla* (Fig. 3, electronic supplementary material Table S2), respectively, and inocula provenance was not in the best model for either species (marginal $R^2 = 0.57$ and 0.53, respectively). In contrast for *E. scribneri*, colonization was ten times higher for resident live inocula than for resident sterilized inocula, while novel live inocula increased aseptate colonization 18 times more than novel sterilized

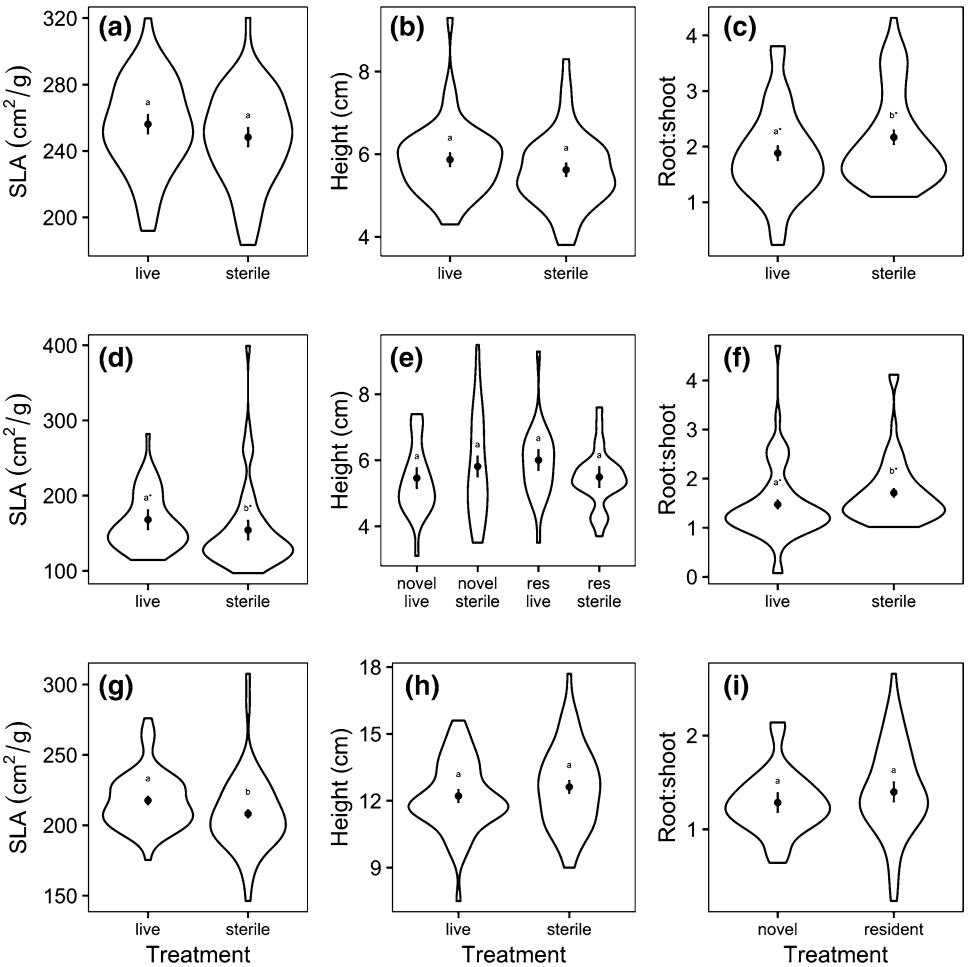


Fig. 2 Plant functional traits responded to the presence of live microbes and rarely to their inocula provenance (novel or resident "res"). Violin plots show the observed distribution of the data. The point and error bars are the predicted mean and standard error estimates from the models that account for the random group effects of mountain and greenhouse block. Results from the best models following model selection procedures are presented, unless best models were the null. Tukey's post hoc tests of significance differences are denoted by lowercase letters above model estimates at $P < 0.05$ and *indicates significance at $0.1 > P > 0.05$. **a–c** *Poa alpina*; **d–f** *Festuca brachyphylla*; **g–i** *Elymus scribneri*

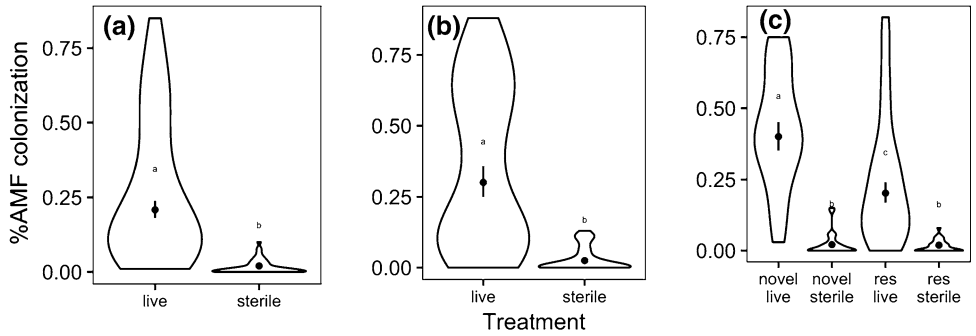


Fig. 3 Sterilized inocula reduced root colonization by aseptate fungi (AMF), and effects of inocula provenance (novel or resident "res") were plant species-specific. Best models for *P. alpina* and *F. brachyphylla* only included inocula sterilization, while *E. scribneri* models included the interaction of inocula provenance and sterilization. Violin plots show the observed distribution of the data (percentage views with fungi). The point and error bars are the predicted mean and standard error estimates from the models and account for the random group effects of mountain and greenhouse block. Tukey's post hoc tests of significance differences are denoted by lowercase letters above model estimates at $P < 0.05$. **a** *Poa alpina*; **b** *Festuca brachyphylla*; **c** *Elymus scribneri*

inocula. In addition, for *E. scribneri*, aseptate fungi were two times greater in novel live inocula than in resident live inocula (marginal $R^2 = 0.70$, Fig. 3c).

Soil inocula rarely influenced relationships among plants traits, fungal colonization, and plant biomass

There was some evidence (2/9 investigated relationships) that inocula provenance modulated the relationship between traits or fungal colonization and plant biomass. In *P. alpina*, plants with higher SLA had greater total biomass when grown in resident inocula, but when plants were grown in novel inocula, plants with lower SLA grew larger (interaction model (*), marginal $R^2 = 0.23$, Fig. 4a, electronic supplementary material Table S2). Taller *P. alpina* plants grew larger, but inocula provenance did not affect this relationship (additive model (+), marginal $R^2 = 0.17$, Fig. 4b, electronic supplementary material Table S2). In addition, greater aseptate fungal colonization (candidate AMF) was associated with lower total plant biomass regardless of inocula provenance, though the plants in novel inocula were larger than those grown in resident inocula (additive model best, marginal $R^2 = 0.18$, Fig. 4c, electronic supplementary material Table S2). Interestingly, aseptate fungal colonization was more predictive of *P. alpina* biomass than SLA or height; however, *AICc* differences were < 2 for the best models (electronic supplementary material Table S2).

For *F. brachyphylla,* SLA and height were poor correlates of biomass (additive model best (+)—though null better than both, marginal $R^2 = 0.08$ for both, electronic supplementary material Table S2), especially compared to fungal colonization (interaction model best (*), marginal $R^2 = 0.16$, electronic supplementary material Table S2). Though neither trait model garnered much support, taller *F. brachyphylla* plants grew larger, but SLA was a poor predictor of biomass (flat slope), and in both models, plants in novel inocula were larger than those in resident inocula (Fig. 4d, e). Surprisingly, in novel inocula, greater aseptate root colonization correlated with larger biomass of *F. brachyphylla*, while in resident inocula, greater colonization by aseptate fungi correlated with smaller biomass (Fig. 4f).

For *E. scribneri*, plants with higher SLA had lower biomass, and plants in novel inocula were larger than those in resident inocula, regardless of SLA (additive model best (+), marginal $R^2 = 0.12$, Fig. 4g, electronic supplementary material Table S2). Height had little effect on biomass (flat slope, null is better model), and plants grew larger in novel than in resident inocula (marginal $R^2 = 0.05$, Fig. 4g). *Elymus scribneri* plants in resident and novel inocula had smaller biomass with greater aseptate fungi colonization and novel inocula plants were larger (marginal $R^2 = 0.09$; Fig. 4i). Unlike *P. alpina* and *F. brachyphylla*, *E. scribneri* was best predicted by SLA, rather than aseptate fungal root colonization (electronic supplementary material Table S2).

Discussion

We expected that alpine grass biomass would be depressed by novel, low-elevation soil inocula relative to resident inocula, given the hypothesis that antagonists like pathogens proliferate in the warm, productive environments at low elevations relative to the cold, resource-poor environments at high elevations (Dobzhansky 1950; Givnish 1999; Reynolds et al. 2003). The overall effect of live soil inocula was suppression of plant biomass (Crawford et al. 2019), but in contrast to our hypothesis, this suppression was greater with resident, high-elevation live soils than with novel, low-elevation soils. We suggest three plausible explanations for this result.

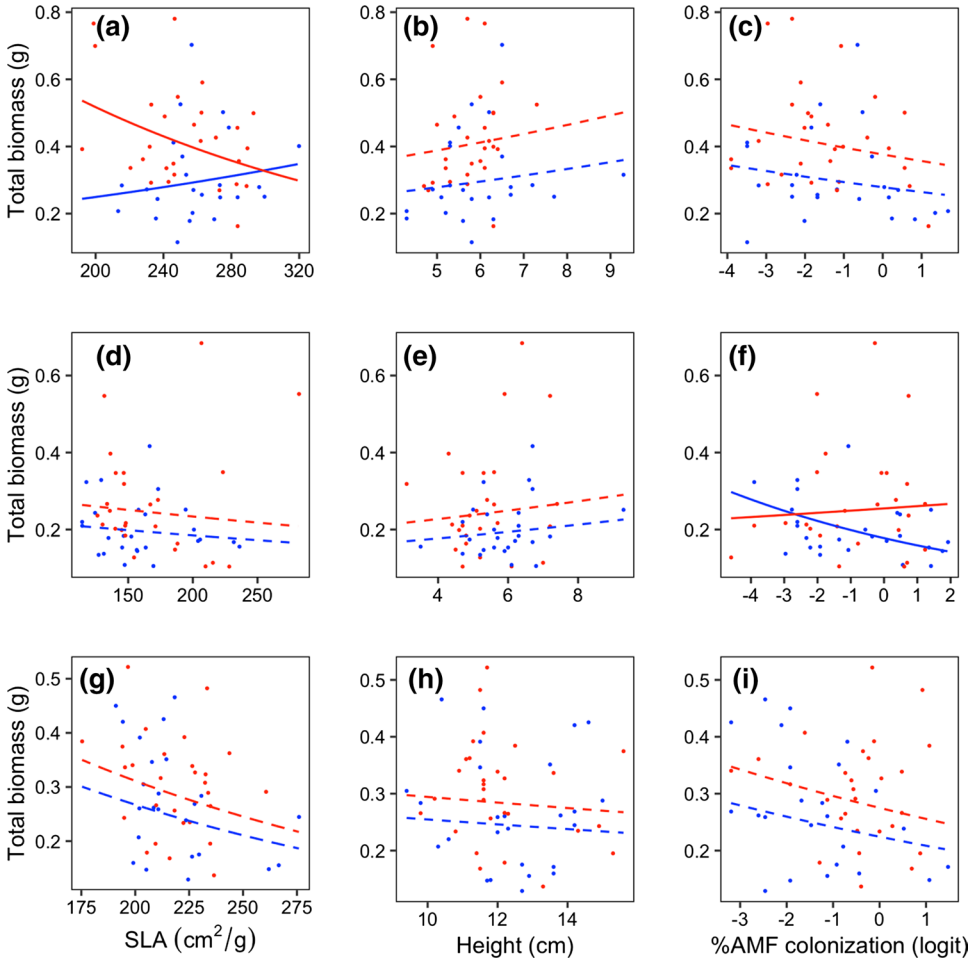


Fig. 4 Resident, high-elevation soil inocula decreased overall plant biomass, but had a little effect on trait relationships to biomass. Colonization of roots by aseptate fungi (AMF) was more negatively correlated with biomass in resident compared to novel inocula. Solid lines represent best models including the interaction of inocula provenance and trait/colonization (different slopes), while dashed lines denote cases for which the additive model was best (treatment have the same slope). Red (gray) points and lines represent plants grown in live-novel elevation inocula, and blue (black) points and lines represent plants grown in live-resident elevation inocula. Lines are the predicted relationship determined by the model, including random effects, while the points are the raw data. **a–c** *Poa alpina*; **d–f** *Festuca brachyphylla*; **g–i** *Elymus scribneri* (color figure online)

First, soil from the plants' home range may have a greater incidence of host-specific pathogens than low-elevation soils, where the focal plant species do not currently reside. Host-specific pathogen build-up is commonly observed in both natural and agricultural ecosystems (Klironomos 2002; Mangan et al. 2010; Chung and Rudgers 2016). For instance, rare plants growing in soil from beneath their own species had suppressed growth compared to plants growing in soil from underneath other plant species (Klironomos 2002). In addition, coexistence between two competing plant species was mediated by the superior competitor responding more negatively to its self-cultivated microbes than to those of its competitor (Chung and Rudgers 2016). Our results support a small but growing literature, suggesting that novel soil communities originating from beyond a species' range limits may be less costly to plant growth than resident microbes from the home range (Van der Putten et al. 2016). For instance, microbes from drier sites can promote the growth of tree seedlings compared to microbes from the seedlings' resident site (Allsup and Lankau 2019). However, the extensive literature on invasive species suggests that the responses of plants to novel microbes may be both plant species- and context-dependent (Reinhart and Callaway 2006; Van der Putten et al. 2016). In studies on invasive plants, which encounter novel microbes in their new range, these naturalized plants can respond to novel microbes positively or negatively. Studies report that invasive plants can benefit from novel soils, acquiring new mutualists or escaping native natural enemies, or have reduced performance in novel compared to resident soils, due to the lack of key soil mutualists in new habitats (reviewed by Reinhart and Callaway 2006).

Second, depressed plant growth in resident, home-range soils may reflect greater investment by young plants into the early development of arbuscular mycorrhizal networks, effectively resulting in AMF symbioses that are net pathogenic during early plant life history. In nature, plants can often tap into an established mycorrhizal network, supported by neighboring adult plants (Smith and Read 2010). In our greenhouse experiment, where plants were grown individually in pots, a newly establishing plant would provide all of the carbon for mycorrhizal development. For instance, Olsson et al. (2010) found decreased early plant growth when plants were grown with AMF inocula in sand compared to

sterile controls lacking fungi. It is not uncommon for fungal symbioses to suppress one aspect of a plant's life history while benefiting another (e.g., Rudgers et al. 2012). Our analyses for *F. brachyphylla* showed that higher root colonization correlated with reduced plant biomass in resident inocula, while higher colonization in novel inocula had small, positive or neutral relationships with plant biomass, lending support to the hypothesis that resident AMF may exact higher costs on plants than AMF in novel soils.

A third hypothesis is that resident and novel inocula differed, because the warm conditions of the greenhouse environment better matched the warm native environment of the low elevation, novel inocula than the cooler environment of resident, high-elevation microbes. Our result of smaller biomass in live-resident than in live-novel inocula also aligns with past work, showing that the cool-adapted *Poa pratensis* had lower biomass when growing with AMF isolates from cool regions compared to isolates from warm regions (Antunes et al. 2011). In our case, greater colonization of roots by fungi in the novel inocula than resident inocula was associated with larger plant biomass in only one species (*F. brachyphylla*), suggesting that the more likely explanation for inocula provenance effects is a difference in pathogen (or parasitic AMF) presence or abundance (Beckstead and Parker 2003). Experiments that separate the effects of pathogenic versus mycorrhizal components of soil communities are required and could be achieved by selective filtration (Klironomos 2003).

A limitation of our study design lies in bulking soils, which has consequences for the biological interpretation of our results. There is a high degree of heterogeneity in microbial diversity over space (Wolfe et al. 2009), such that pooling samples across a transect will likely artificially inflate or deflate microbial diversity relative to that in a single patch. This can create treatments with no analogue to field conditions, where a plant would colonize a single patch (Reinhart and Rinella 2016; Rinella and Reinhart 2017, 2018). As such, our results should be interpreted cautiously. However, our results are bolstered by two elements. First, we drew soils from three independent mountain transects, which gives the study true replication of elevation—replication that is often missing from biogeographic studies (Kivlin et al. 2017a). Second, any effects of bulking soils may be consistent across the novel and resident treatments—in which case, combining soils across 40 m is not likely to be confounded with our soil treatment effects. However, if novel and resident sites fundamentally differed in the spatial patchiness of microbial distributions (which is not well resolved for most ecosystems, Wolfe et al. 2009), then bulking soils across microsites could have had divergent consequences for resident versus novel soils.

Our result suggests upslope migration of low-elevation microbes under warmer climates could have net positive effects on alpine plant residents. However, these microbes would have to overtake the existing microbes at high elevations. Further experiments that introduce novel microbes into live, resident soils could help test for the potential of such takeovers. In addition, our results may simply indicate lower abundance of host-specific pathogens at low elevation than at high elevation, and if low-elevation soils had alpine grass populations present over generations, these pathogens would increase in abundance and have stronger negative effects on plants. Finally, any benefit of upward-migrating microbes could be swamped out by upward migration of plant competitors from low elevations (Alexander et al. 2015), which are likely to colonize alpine zones with ongoing climate change (Zorio et al. 2016). Experiments that reassemble and compete microbial communities and plant communities that are expected to newly interact with future migration will be valuable for improving predictions on interaction outcomes under climate change.

There is mixed evidence that plant traits are microbially mediated (Friesen et al. 2011), and in our experiment, plant traits responded weakly (~ 10% change) to the presence/absence of microbes, but not much to inoculum provenance. We consistently found that the root:shoot ratio declined in live soil, suggesting that the amount of root required for foraging is reduced when fungi are present (Smith et al. 2009). Live microbes also increased specific leaf area (SLA): leaves were thinner and more resource acquisitive with live soil than sterile. Increased SLA with microbes has been a common result in prior studies (Wright et al. 1998). For example, the observation of higher SLA in mycorrhizal plants than non-mycorrhizal plants disappeared when non-structural carbohydrates were subtracted from leaf dry mass (Miller et al. 2002), suggesting that plants growing with mycorrhizal fungi transported more photosynthate away from leaves, potentially to their symbionts. Maximum plant height is another important trait related to the competitive ability of plants for light (Westoby 1998), but evidence for microbial mediation of this trait is limited (Friesen et al. 2011). One of the few examples comes from *Rhizobium* bacteria in roots driving height increases in rice (Perrine-Walker et al. 2007).

Despite the effect of live soil on plant traits in our study, soil provenance had little-to-no effect on intraspecific variation in plant traits. Inocula provenance had negligible effects on traits of *P. alpina* and *E. scribneri*. However, *F. brachyphylla* grew 10% taller in resident, home-range inocula compared to novel inocula, suggesting that association with low-elevation microbes could decrease its competitive ability for light. If taller, more competitive plants (Alexander et al. 2015) from low elevation also move up slope along with novel microbes, declines of *F. brachyphylla* populations could be accelerated.

As the climate warms, we expect that species with more resource-acquisitive trait strategies will benefit (Fridley et al.

2016). We augmented this hypothesis by investigating how soil inocula from different climatic/elevation conditions altered plant trait relationships with plant biomass. In general, plant biomass production increases with higher SLA (Bilton et al. 2010) and taller height (Conti and Díaz 2013), and we expected that microbes from resident sites would steepen the slope of the trait–biomass relationship (a positive effect), because resident microbes would match and then benefit from larger, more productive plants (Grigulis et al. 2013). This expectation held for only one of the relationships investigated (Fig. 4a). Results suggested that novel, low-elevation inocula reduced biomass with increasing SLA, while resident inocula increased biomass with higher SLA for *P. alpina*. In every other case, there was little evidence that inocula provenance altered the relationship between a plant trait and biomass (electronic supplementary material Table S2). Future experiments could investigate the coupled processes of plant and microbe migrations with climate change (i.e., transplant experiments along climatic gradients), to improve forecasts of community and ecosystem dynamics in a changing climate.

Conclusion

Our results demonstrated that novel soil inocula taken from beyond species' low-elevation range edges generally depressed the growth of alpine-restricted plants to a lesser extent than soil inocula from their home range. In addition, plants with greater root colonization in resident inocula were smaller than plants with the same level of colonization in novel soil inocula. The relative consistency of these results across three alpine grass species suggested that, under climate warming, an upslope migration of low-elevation soil communities into alpine environments may benefit plants, if those communities can overtake the residents at high elevations.

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Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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