

## ARTICLE

## Climate Ecology

# Warming benefits to sheep fescue are negated by nearby plants and moss–lichen layers facilitate mycorrhizae in a tundra

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**Abstract**

In systems where low temperatures limit plant productivity, facilitative effects of surrounding vegetation on juvenile plants may outweigh effects of competition for resources. This facilitation could occur through temperature buffering but also via increased availability of root mutualists such as mycorrhizal fungi. Climate warming could cause this balance between facilitation and competition to shift. We investigated how first-year plant performance, biomass allocation, and mycorrhizal colonization were affected by neighboring vegetation, both under ambient temperatures and under experimental warming. We planted juveniles of the grass species *Festuca ovina* L. (Poaceae) into an alpine tundra ecosystem in central Norway, into one of four microsite types: a moss and lichen layer, other graminoids, both groups, or neither (bare soil). Half of the microsites experienced ambient conditions and half were located within open-top warming chambers. Warming increased shoot biomass of *F. ovina*, but only when neighbors were not present (i.e., when planted in bare soil). Our results suggest that when abiotic stress was reduced by warming, the importance of competition among *F. ovina* juveniles and neighboring vegetation increased, in line with the stress gradient hypothesis. These results indicate that climate warming may shift the balance from facilitation to competition among plants in cold ecosystems, although the resource(s) competed for is (are) yet to be identified. We also found that when moss and lichen were present, planted *F. ovina* were more likely to form mycorrhizae, yet had a significantly lower root biomass, both absolute and relative to their total biomass. Thus, at the juvenile stage, belowground competition and/or increased mycorrhization may decrease plant root production yet without detectable benefits to aboveground growth.

**KEYWORDS**

alpine tundra, bryophyte, competition, experimental warming, facilitation, mycorrhizae, plant–fungal interactions, plant–microbial, tundra

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## INTRODUCTION

In all ecosystems, climate and neighboring vegetation both influence plant performance (Anthelme et al., 2014; Blonder et al., 2018) such as plant growth rate, fecundity, biomass production, and tissue nutrient content. Neighboring vegetation can compete with plants for nutrients, water, and light. On the other hand, neighboring vegetation can facilitate (*sensu* Bertness & Callaway, 1994) nearby plants. Facilitation can be defined as an increase in the biomass of a plant when neighboring vegetation is present or abundant relative to when it is not present and/or abundant. Facilitation can occur through mechanisms such as extreme temperature and wind buffering, decreasing microenvironment variability, and amelioration of other abiotic stressors (Brooker et al., 2008; Callaway et al., 2002; Havrilla et al., 2020; Sánchez-Martín et al., 2024). The stress gradient hypothesis (*sensu* Bertness & Callaway, 1994) predicts that facilitative interactions should be more common in unproductive, abiotically stressful ecosystems, while competitive interactions should dominate in productive environments not limited by abiotic factors (Doxford et al., 2013; Kjaer et al., 2018). Facilitative effects are provided not only by higher plants but also by mosses and lichens, which can lower daily maximum and mean temperatures (Mallen-Cooper et al., 2021; van Zuijlen et al., 2020; Nystuen et al., 2019) and increase soil moisture (Nystuen et al., 2019, but see Mallen-Cooper et al., 2021). Cushion plants (Angélica Casanova-Katny et al., 2011; Kjaer et al., 2018), lichens (Hagen et al., 2014; Nystuen et al., 2019), and bryophytes (Gavini et al., 2019) can promote growth and survival of surrounding plants in harsh environments. Neighboring plants can also alter biomass allocation, such as when increased competition for below-ground resources is associated with higher root mass ratios in competing plants, suggesting that plants are increasing absorptive surfaces belowground in service of capturing limiting resources (Bloom et al., 1985; Brouwer, 1962; Kobe et al., 2010; Robinson et al., 2010; but see Janeček et al., 2014).

In systems where low temperatures limit plant productivity, climate warming could cause the effects of neighboring species to shift from facilitation to competition, or vice versa. Studies examining these hypotheses have shown mixed, species-specific results and therefore these questions merit additional experimentation, especially in field settings (Anthelme et al., 2014; Cavieres et al., 2024; Pugnaire et al., 2020; Wang et al., 2023). Firstly, warming itself may have variable effects on plants. In habitats where cold is a major stress, warming could buffer low temperatures, thereby alleviating cold

stress in plants (Anthelme et al., 2014). Alternatively, warming could exacerbate plant stress. Warming may increase (Pastore et al., 2023) or decrease (Ho & Gough, 2006; Tang et al., 2022) the frequency of freeze–thaw events, and recovery from freeze–thaw events is costly to plants. When warming melts snow layers, this can increase plant stress because snow layers protect plants from frost damage (Pastore et al., 2023). Lastly, in exposed areas, warming could exacerbate heat stress during dry periods with intense solar irradiation (Ma et al., 2021). If warming increases plant stress, the benefits of microsite amelioration from neighboring plant cover may outweigh the costs of resource competition under warming, resulting in a net effect of facilitation of surrounding vegetation on plants. Conversely, if warming reduces plant stress, the impacts of resource competition may increase, and thus negative interactions between plants may become more frequent. Some support for this latter dynamic occurs in alpine communities (Klanderud & Totland, 2007; Li et al., 2018; Olsen & Klanderud, 2014).

Microsite amelioration from neighboring plants could also improve conditions for plant mutualists, such as mycorrhizal fungi. Mycorrhizal colonization is impaired at soil temperatures below 15°C (Carvalho et al., 2015; Gavito & Azcón-Aguilar, 2012; Kilpeläinen et al., 2020), suggesting that temperature buffering from neighboring vegetation may also benefit the growth of mycorrhizae by reducing cold stress. Facilitation from neighboring plants by providing a source of microbial mutualists has been shown (Angélica Casanova-Katny et al., 2011; Rodríguez-Echeverría et al., 2016; Van Der Putten, 2009). Plant species that associate with arbuscular mycorrhizal fungi (hereafter AMF) can give neighboring plants access to established mycorrhizal networks and thus improve plant nutrient uptake (Muneer et al., 2020; Van Der Heijden, 2004). Despite these potential benefits, neighboring plants compete for resources, so their net effect on other plants could be negative regardless of the presence of mycorrhizae (Eissenstat & Newman, 1990). Whether climate warming in harsh environments will increase plant facilitation by stimulating mycorrhizal fungi associated with neighboring plants or whether it will increase competition by making the environment less stressful, as predicted by the stress gradient hypothesis, remains an open question.

Plant community assembly is driven by which plant species establish or fail to establish within a given site. Strong selective pressures occur during the juvenile phase of plant growth, so performance during this stage can indicate which individuals will establish into adulthood and reproduce (Kim & Donohue, 2012; Marcante et al., 2012). This is especially true in harsh environments where juvenile mortality can be substantial. Factors influencing juvenile performance have strong implications for plant

population growth (Berio Fortini et al., 2022; Cook, 1979; Kim & Donohue, 2012) and thus ecosystem functioning. Investigating how biotic and abiotic factors interactively affect juvenile plant performance is critical to predict how ecosystems will respond to environmental change.

Given our limited understanding of the role of warming in shaping competition and facilitation outcomes in cold ecosystems, we investigated how root and shoot biomass, biomass allocation to roots versus shoots, and mycorrhizal colonization of juveniles of the grass species *Festuca ovina* were affected by different types of neighboring vegetation (other graminoids, moss–lichen layers, or both) under ambient temperatures and under experimental warming, in an alpine tundra ecosystem.

We hypothesized that:

**H1.** Facilitative effects of neighbors will be reduced or even become net competitive under warming.

**H2.** Warming will increase juvenile performance in the absence of competing neighboring vegetation.

**H3.** Mosses and lichens increase juvenile *F. ovina* performance, given their reported buffering effect on microclimate, while neighboring graminoids will decrease juvenile *F. ovina* performance.

**H4.** Neighboring graminoids and moss–lichen mats will increase root mass ratios in juvenile *F. ovina*.

**H5.** Warming will support mycorrhizal colonization of experimental plants.

**H6.** Mycorrhization will increase in juveniles planted next to naturally occurring graminoids, which may offset potential competitive effects to some extent.

## METHODS

### Study site

The study site is located at 62.30553°N, 9.65095°E, at 1352 m above sea level (asl) on a west-facing slope in the Dovrefjell mountains of Norway. Annual average July and January temperatures (2014–2021) at the nearest meteorological station (Snoheim, 15.7 km W of the site, 1475 asl) are 7.4 and  $-8.6^{\circ}\text{C}$ , respectively (Norwegian

Center for Climate Services, 2023). Annual precipitation is 365–671 mm (2011–2022 data, Hjerkin II station, at 11 km from the study site; Norwegian Center for Climate Services, 2023). The habitat is an alpine tundra at the ecotone from shrub heathland with lichen-dominated groundcover into alpine meadow. Soil physiochemistry can be highly variable in alpine habitats, and thus access to nutrients may be low in some areas. Alpine meadow communities are limited in P at higher elevations even relative to adjacent heath communities (Sundqvist, 2011). Many co-dominant species occur, including the lichens *Cladonia stellaris* (43.4% cover), *Alectoria ochroleuca* (9.25%), and *Flavocetraria nivalis* (6.0%), the sedges *Carex bigelowii* (12.8%) and *Carex vaginata* (6.5%), the deciduous shrubs *Betula nana* (21.9%), *Salix herbacea* (8.5%), and *Salix lanata* (6.5%), and the ericaceous shrubs *Empetrum nigrum* (11.5%), *Pyllodoce caerulea* (8.3%), and *Kalmia procumbens* (8.0%). The community at this site is very diverse, with other common species such as *Cladonia stygia*, *Stereocaulon* spp., and *Flavocetraria cucullata* (lichens), species within the genus *Sphagnum* (moss), *Vaccinium uliginosum* (shrub), *Juncus trifidus*, *Festuca ovina*, *Bistorta vivipara*, and (grasses, sedges, and rushes), *Dryas octopetala*, *Silene acaulis*, *Sibbaldia procumbens*, and *Campanula rotundifolia* (forbs). Bedrock consists of Precambrian metamorphic rock such as garnet-mica-schist and green schist (Geological Survey of Norway, 2024). Alpine regions in northern Europe are predicted to experience daily maximum temperatures increases during the growing season of  $2.6^{\circ}\text{C}$  before 2100 under the  $2^{\circ}\text{C}$  SSP5–8.5 high emissions scenario (Gutiérrez et al., 2021). Annual extreme highs (i.e., the maximum of the maximum daily temperatures) are anticipated to increase by  $2.7^{\circ}\text{C}$  (Gutiérrez et al., 2021).

### Study species

*Festuca ovina* (sheep fescue) is an important pasture grass (Koucheki & Read, 1976) that has been investigated for effectiveness in alpine tundra restoration (Hagen et al., 2014). Across its entire distribution, it is most common in well-drained lowlands (Tansley, 1939) but also occurs in meadow communities in high alpine zones (Torbjörn et al., 2021). *F. ovina* associates primarily with AMF (Makarov et al., 2014; Molina et al., 1978), though it can be colonized by other mutualistic soil fungi, including dark septate endophyte fungi (Boldt-Burisch & Anne, 2019) and the ectomycorrhizal fungi *Tuber melanosporum* (Mamoun & Oliver, 1997), and has shown altered nutrient uptake in the presence of ericoid mycorrhizae (Stribley & Read, 1980). Previous work has shown increases in first-year *F. ovina* growth in plants infected

by AMF relative to noninfected individuals when phosphorus is limiting (Koucheiki & Read, 1976). When grown with other grassland species, mycorrhizae strongly decreased the growth of the dominant *F. ovina* and congener *F. rubra* yet tended to stimulate the growth of subordinate co-occurring plant species (Grime et al., 1987). Similarly, Scheublin et al. (2007) found that mycorrhizal inoculation benefited *F. ovina* when grown alone, but its biomass was reduced at the expense of the highly mycorrhizae-dependent legume *Lotus corniculatus* when both inoculated species were grown together. *F. ovina* can respond strongly to mycorrhizal colonization with over 300% increases in *F. ovina* carbon allocation to roots when inoculated (Graves et al., 1997).

## Experimental setup

**Timeline summary:** We germinated seeds of our experimental plant species in late spring, grew them in the glasshouse for approximately 1 month, then transplanted them into the field for approximately 3 months before they were harvested for analysis.

### Plant material

On 29 May 2023, *F. ovina* seeds collected from the study region were seeded into germination flats with all-purpose potting soil (P-Jord, Hasselfors Garden, Örebro, Sweden) in a greenhouse at the Norwegian University of Science and Technology (NTNU, Trondheim, Norway). Plants were watered every other day. Plants were also water on each day that greenhouse temperature exceeded 30°C. On 16 and 20 June, individual plants were transplanted into 96-cell germination trays (VEFI, Norway) (cell dimensions 42 × 42 × 62 mm [0.109 L]) filled with the same soil. Juveniles were gradually acclimated to ambient temperatures by placing trays in an adjacent location outside the greenhouse for increasing 2-h intervals from 2 to 12 h within a 7-day period.

### Warming treatments

Experimental plots were warmed using open-top chambers (OTCs), consisting of six trapezoid-shaped polycarbonate panes arranged to form a hexagonal chamber with a 1 m<sup>2</sup> top opening, a 2 m<sup>2</sup> footprint, a height of 36 cm, and sides angled at 60° to the ground. On average, at our site during the dates of our experiment, these OTCs increased daily soil surface temperature maximums and ranges by 3.3°C and increased average temperatures by 1.01°C (daily max temp in OTC 24.2 ± 1.05°C, in ambient

20.9 ± 1.02°C, daily temp range in OTC 20.7 ± 1.18°C, in ambient 17.4 ± 1.14°C, daily temp average in OTC 10.98 ± 0.36°C, in ambient 9.97 ± 0.36°C; mean ± SE, based on 23 loggers at the site). OTCs of a similar design have increased summer monthly soil surface temperatures in other systems with no canopy cover (tundra and arid) by 1–4°C relative to ambient conditions (Bokhorst et al., 2011; Maphangwa et al., 2012). One of four 50 cm × 50 cm quadrants within (warming treatment) and a 50 cm × 50 cm area adjacent to (ambient/control treatment) each OTC was randomly chosen to be planting areas. In total, three plots were used in a paired split-plot design with each plot containing one warmed and one ambient area (Figure 1). A temperature logger was placed at the center of each of the three warming chambers. An additional temperature logger was placed in an area outside of each warming chamber and at a similar distance (<2 m) from each chamber. These adjacent areas had no experimental manipulations, and therefore the loggers serve as our controls in ambient temperatures. All loggers were placed at the soil surface.

### Warming treatments and microsites

Within each plot, for each warming treatment level (warmed or ambient), 16 circular areas with an 8 cm diameter were prepared (Figure 1). Of these 16 areas, four were assigned according to each combination of two

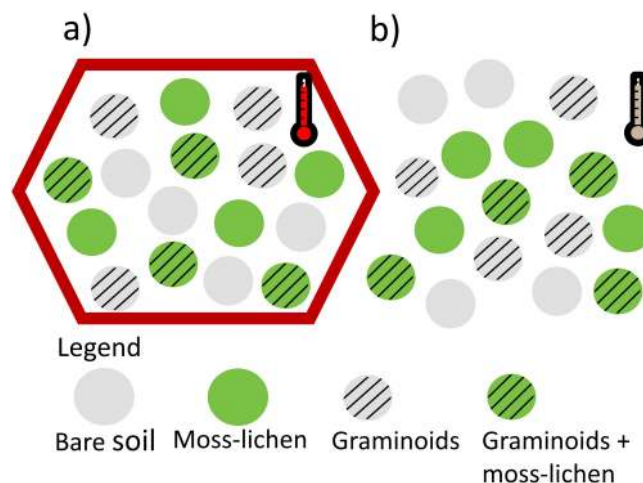


**FIGURE 1** Idealized depiction of four microsite combinations: within an 8-cm-diameter circle centered around it, each of four juvenile *Festuca ovina* plants (each symbol represents one plant) was planted into either bare soil, graminoids only, moss-lichen only, or both moss-lichen and graminoids. Thermometers depict the split-plot design wherein these four treatments are fully replicated under (a) experimental warming with open-top chambers and (b) in ambient conditions. This entire design was replicated three times, for a total  $n = 96$  plants.

fully crossed categories: presence/absence of naturally occurring graminoids and presence/absence of naturally occurring lichens and/or mosses (hereafter moss–lichen). The presence of established graminoids was defined as graminoid stem density of  $>5$  stems/cm<sup>2</sup> occurring within 1 cm of the planted *F. ovina* juvenile. Graminoids, such as neighboring graminoids in this study, are generally classified as arbuscular mycorrhizal (Makarov et al., 2014), and moss tissues have been observed to be infected by both arbuscular and ericoid mycorrhizal fungi (Cairney & Meharg, 2003; Davey & Currah, 2006; Valdés et al., 2023; Zhang & Guo, 2007). At planting, established graminoids were primarily adults that were around two to four times as tall as experimental juveniles, and experimental juveniles were usually two to four times as tall as moss–lichen mats, except for two experimental juveniles which were planted in *Sphagnum* mats that were as tall as they were (GRG, personal observations). Because of the small size of *F. ovina* juveniles, it was feasible to plant each individual into its experimental area without disturbing graminoids  $>1$  cm distance from the plant. Experimental areas were selected such that juveniles were not planted directly among established graminoids, which could have both damaged the established graminoids and created difficulties in finding experimental juveniles at the end of the experiment. The presence of moss–lichen layers was defined as  $>75\%$  cover of  $>1$  cm tall lichen and/or moss within an 8-cm-diameter circle centered around the juvenile. The absence of either group occurred when no above-ground biomass of that group was visible within the treatment area. One individual *F. ovina* was planted within each circular area, for a total  $n$  of 96 *F. ovina* replicates: 3 plots  $\times$  2 warming treatments  $\times$  2 graminoid levels  $\times$  2 moss–lichen levels  $\times$  4 replicates. Each juvenile was planted at the center of its circular area (Figure 1). On 29 June and 9 July, three replicates were planted in each warming/graminoid/lichen/plot combination. On 9 July, one more replicate was planted in each warming/graminoid/lichen/plot combination.

## Harvest and processing of experimental plants

On 19 September, planted juveniles were harvested and placed in individual labeled plastic bags. Plants were processed and roots were stained between 21 and 25 September. Shoots were clipped, weighed (fresh mass), then dried at 65°C for at least 48 h and weighed again. Roots were washed thoroughly, weighed (fresh mass), then stained with 1.5 mL acid fuchsin solution according to the protocol of Baker and Gowen (1996). Roots were examined at 10 $\times$  and 40 $\times$  magnification for the presence of

mycorrhizal fungi (hyphae, vesicles, and/or arbuscules). On 4 July, 10 greenhouse-grown *F. ovina* were sampled at random to quantify pretreatment mycorrhizal presence. These *F. ovina* grew in the same trays as the experimental plants and received the same growing conditions described above but were not transferred to the field. No mycorrhizae were found, and thus a baseline of zero mycorrhizae was used to compare pre- and post-treatment presence. After inspecting the stained roots for AMF, these roots were dried and weighed as described above. The root mass ratio was calculated as the ratio of root dry mass to total dry biomass of the experimental *F. ovina* juvenile. Field sampling was conducted to investigate mycorrhizal presence in naturally occurring *Festuca ovina* in the field. On 19 September, nine individuals of established *F. ovina* were sampled in the field adjacent to the study site (also at the same elevation). Roots of these individuals were washed, stained, and examined as described above.

## Statistical analysis

Eighty-three *F. ovina* juveniles survived until harvest and were recovered. The remaining 13 were removed from the datasheet after they were lost due to ungulate trampling. All analyses were performed in R version 4.2.2 (R Core Team, 2022). Statistical analysis of graminoid and moss–lichen cover validated that our selected microsites differed as intended (Appendix S1: Table S1, Figure S1). Because percent cover of vegetation within vegetated microsites was at or near 100%, and because vegetation consisted primarily of moss–lichen and/or graminoids, the “moss–lichen and graminoids” microsites unavoidably had lower percent covers of both individual cover types as compared to the moss–lichen-only and graminoids-only microsites. However, this did not affect our results. We tested the effects of warming treatment, neighboring graminoids, moss–lichen layers, and all interactions (fixed effects) on root mass ratio and performance of the focal *F. ovina* juveniles using linear mixed models and on mycorrhiza presence using generalized linear mixed models with a binomial distribution and a logit link function. For this study, we define performance as dry biomass (above-ground/shoot, belowground/root, and total/root + shoot). Model residuals were checked for accordance with linear mixed-model assumptions using residuals versus fitted, normal Q-Q, scale-location, and residuals versus leverage plots. The plot and plot  $\times$  warming random effects were included in all models and removed only if their variance components were near-zero. We used the Kenward–Roger approximation of  $df$  for  $F$  tests and the `lmer()` and `glmer()` functions in the package `lme4` (Bates et al., 2015). Results were assessed using the `Anova()` function in the “car”

package (Fox & Weisberg, 2019). All models used type II sums of squares, and post hoc pairwise comparisons among selected microsites used false discovery rate  $p$  value adjustment (Benjamini & Hochberg, 1995) in the “emmeans” package (Lenth, 2023).

## RESULTS

No herbivore damage was found on recovered juveniles. Roots of 78% (7 of 9) of the pre-existing (field-collected) *F. ovina* were infected by AMF. Roots of 50% (40 of 80; three samples were lost in the staining process) of experimental plants were infected. These juveniles were 77% more likely to have mycorrhizae when a moss-lichen layer was present (probability  $35.0\% \pm 8.4\%$  when moss-lichen absent,  $61.9\% \pm 8.0\%$  when moss-lichen present; Figure 2, Table 1). Warming also increased AMF colonization (probability  $37.5\% \pm 9.0\%$  in ambient,  $59.4\% \pm 8\%$  in warming; mean  $\pm$  SE), though this trend was nonsignificant ( $p = 0.1$ , Table 1).

Warming increased *F. ovina* shoot biomass by 54.4%, but only if planted in bare soil (biomass in bare soil  $0.0377 \pm 0.007$  g in ambient,  $0.0582 \pm 0.006$  g in warming). Relative to *F. ovina* in bare soil, shoot biomass was reduced by 38.1%–39.5% when moss-lichen and/or other graminoids were present, but this reduction was only significant under warming (in warming, biomass in bare soil  $0.0582 \pm 0.006$  g, in moss-lichen  $0.0352 \pm 0.006$  g, in graminoids  $0.0360 \pm 0.007$  g, in both  $0.0357 \pm 0.006$  g; Table 1, Figure 3a). These patterns were also

present, though marginally significant, for total biomass (in warming, total biomass reduced by 26.4%–46.2% in moss-lichen and/or graminoids relative to bare soil,  $p = 0.087$ ; Table 1, Figure 3b). Across temperature treatments, when moss-lichen layers were present, *F. ovina* had 29.1% lower total biomass, 32.1% lower root biomass, and a 7.9% lower root mass ratio, signifying that juveniles growing among moss-lichen grew less and invested proportionally less in roots than those growing without moss-lichen nearby (Figure 3b–d). *F. ovina* growing among graminoids had less shoot biomass than when it was absent (Table 1, Figure 3; Appendix S1: Figure S2). Although there was a significant three-way interaction among graminoid presence, moss-lichen presence, and warming in their effect on shoot biomass, none of the pairwise differences were significant after FDR correction (Appendix S1: Table S2). In the warming treatment, the reduction in shoot biomass by moss-lichen layers, other graminoids, or both compared to bare soil was near-identical (Figure 3c).

## DISCUSSION

### Warming increased competition among vegetation

Warming increased the importance of competition in the net outcome of interactions between juvenile *F. ovina* and surrounding moss-lichen assemblages or adult graminoids. Under warming, our experimental plants had smaller shoot biomass in the presence of neighboring

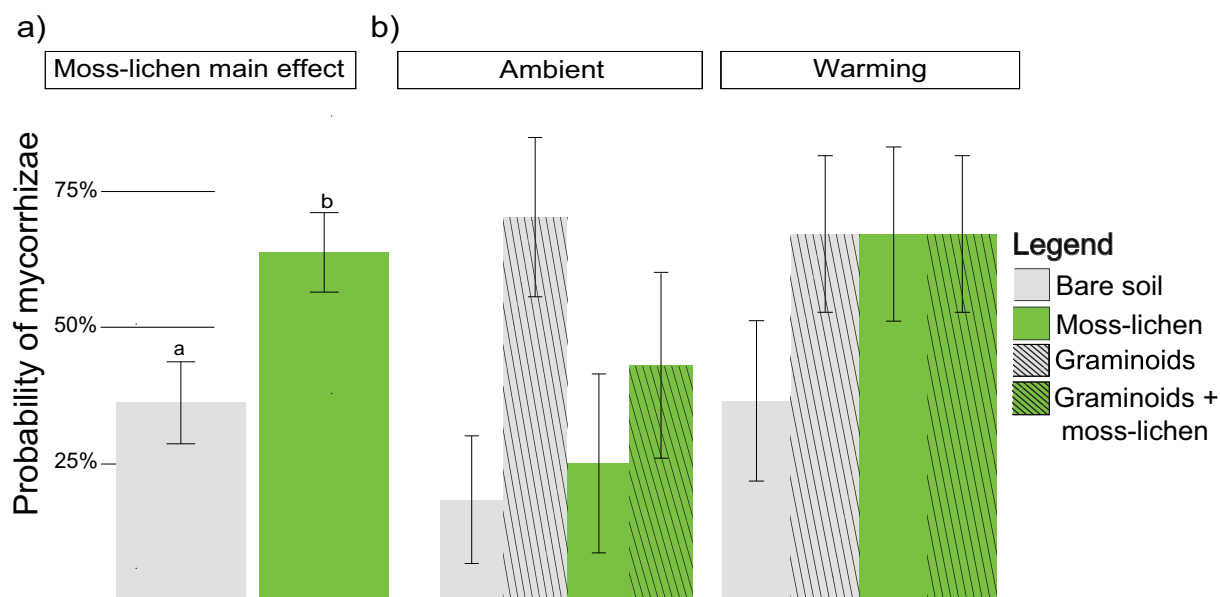


**FIGURE 2** Probability of mycorrhization as a function of selected microsites and warming treatments (mean  $\pm$  SE). (a) Main effect of lichen (Table 1), (b) interactive effects within each warming treatment. Significant differences are denoted with different letters above bars.

**TABLE 1** Model output for treatment effects on performance metrics and probability of arbuscular mycorrhizae presence.

| Trait                    | Predictor                         | F     | df       | p            |
|--------------------------|-----------------------------------|-------|----------|--------------|
| Mycorrhizae presence     | Moss–lichen presence              | 5.07  | 1, 77    | <b>0.027</b> |
|                          | Graminoid presence                | 0.10  | 1, 77    | 0.75         |
|                          | Warming                           | 2.71  | 1, 77    | 0.10         |
|                          | Moss–lichen × graminoid           | 1.77  | 1, 77    | 0.19         |
|                          | Moss–lichen × warming             | 0.86  | 1, 77    | 0.36         |
|                          | Graminoid × warming               | 0.93  | 1, 77    | 0.34         |
|                          | Moss–lichen × graminoid × warming | 0.02  | 1, 77    | 0.89         |
| Total biomass            | Moss–lichen presence              | 10.18 | 1, 75    | <b>0.002</b> |
|                          | Graminoid presence                | 3.81  | 1, 75    | <b>0.055</b> |
|                          | Warming                           | 0.20  | 1, 75    | 0.66         |
|                          | Moss–lichen × graminoid           | 0.29  | 1, 75    | 0.59         |
|                          | Moss–lichen × warming             | 1.36  | 1, 75    | 0.25         |
|                          | Graminoid × warming               | 0.46  | 1, 75    | 0.50         |
|                          | Moss–lichen × graminoid × warming | 3.01  | 1, 75    | <b>0.087</b> |
| Shoot biomass            | Moss–lichen presence              | 2.15  | 1, 68.43 | 0.15         |
|                          | Graminoid presence                | 4.22  | 1, 68.79 | <b>0.044</b> |
|                          | Warming                           | 0.92  | 1, 69.60 | 0.34         |
|                          | Moss–lichen × graminoid           | 0.65  | 1, 68.13 | 0.42         |
|                          | Moss–lichen × warming             | 2.16  | 1, 68.05 | 0.15         |
|                          | Graminoid × warming               | 0.09  | 1, 69.44 | 0.76         |
|                          | Moss–lichen × graminoid × warming | 4.21  | 1, 68.18 | <b>0.044</b> |
| Root biomass             | Moss–lichen presence              | 10.55 | 1, 79    | <b>0.002</b> |
|                          | Graminoid presence                | 2.79  | 1, 79    | <b>0.099</b> |
|                          | Warming                           | 0.27  | 1, 79    | 0.61         |
|                          | Moss–lichen × graminoid           | 0.01  | 1, 79    | 0.94         |
|                          | Moss–lichen × warming             | 0.99  | 1, 79    | 0.32         |
|                          | Graminoid × warming               | 0.98  | 1, 79    | 0.33         |
|                          | Moss–lichen × graminoid × warming | 2.63  | 1, 79    | 0.11         |
| Root:total biomass ratio | Moss–lichen presence              | 9.08  | 1, 76    | <b>0.004</b> |
|                          | Graminoid presence                | 0.82  | 1, 76    | 0.37         |
|                          | Warming                           | 0.16  | 1, 76    | 0.69         |
|                          | Moss–lichen × graminoid           | 0.04  | 1, 76    | 0.84         |
|                          | Moss–lichen × warming             | 0.05  | 1, 76    | 0.82         |
|                          | Graminoid × warming               | 3.05  | 1, 76    | <b>0.085</b> |
|                          | Moss–lichen × graminoid × warming | 0.07  | 1, 76    | 0.79         |

Note: Non-integer degrees of freedom are Kenwood–Roger estimates for models with random effects included. The *p* values in boldface italics are significant (below 0.05). The *p* values that appear in boldface but not italicized are marginally significant (0.05–0.099).

vegetation, whereas under ambient conditions, experimental plants were of comparable size regardless of neighboring plant presence. This suggests that competition was less important under ambient conditions. These results support our hypotheses that the facilitative effects of neighbors will be reduced or even become net

competitive under warming (H1) and that warming will increase juvenile performance in the absence of competing neighboring vegetation (H2). Our results also align with previous work testing the stress gradient hypothesis in alpine systems (Callaway et al., 2002). Our experiment did not investigate the mechanisms of increased

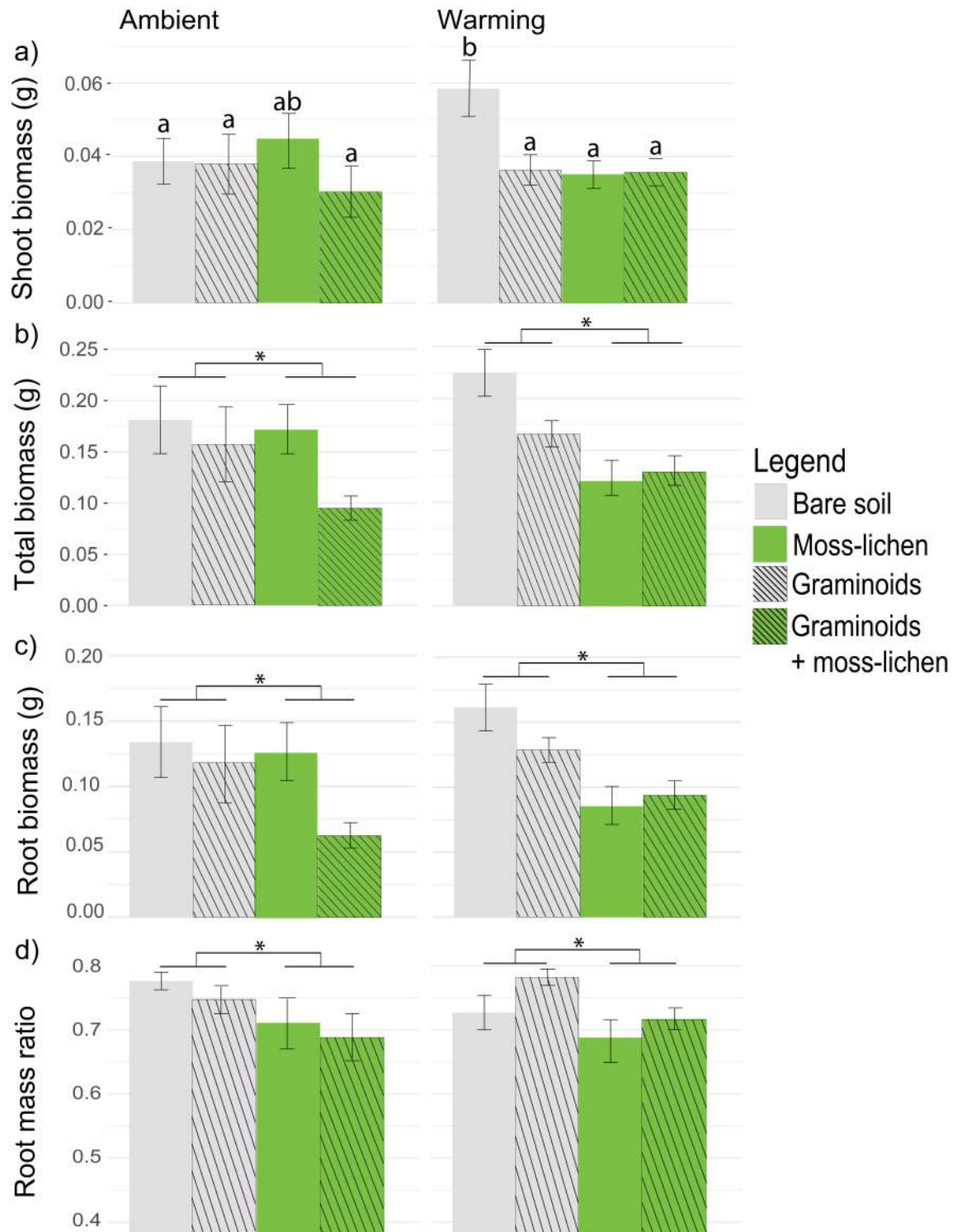


**FIGURE 3** Juvenile *Festuca ovina* (a–c) biomass and (d) biomass allocation response to selected microsites and warming treatments (mean  $\pm$  SE). Letters represent significant differences for pairwise comparisons between warming treatment/graminoid/moss-lichen combinations for each response at  $p < 0.05$  before FDR correction (for FDR-corrected  $p$  values, see Appendix S1: Table S2). The main effect of moss-lichen layers on total biomass, root biomass, and root mass ratio was significant across all levels of all other predictors (Table 1).

competition between warmed plants, such as which resources became scarcer for our experimental plants. Though competition could have also occurred at ambient

temperatures, potential positive effects of low-temperature buffering from competing vegetation may have mediated negative effects of competition, thus making the net

interactive effect neutral. The cumulative effect of warming throughout the growing season may have increased temperatures enough so that plants were released from some cold stress, thus reducing the importance of microsite amelioration by neighboring plants and increasing the relative importance of competition. In alpine tundra, even small increases in temperature experienced by plants could release plants from abiotic stress. During the 83 days of our experiment, the 3.3°C increase in daily maximum temperatures in warming chambers resulted in plants experiencing a heating of 273.9 (i.e.,  $83 \times 3.3$ ) degree days relative to plants in ambient conditions. In some alpine ecosystems, competition is the primary driver of alpine plant community structure, and warming may increase the extent of interspecific competition (Klanderud & Totland, 2007). Alternatively, because average and maximum summer temperatures are decreased by lichen (Mallen-Cooper et al., 2021), moss (Gornall et al., 2007; Startsev et al., 2007), and the shade from other graminoids (Shen et al., 2015), growth of warmed juveniles under moss–lichen mats or among other graminoids may have been slowed down relative to those in bare soil. Whether alleviation of cold stress increased the relative importance of resource competition from neighboring plants or shading from neighboring plants counteracted the benefits of warming for growth, the resulting pattern would be similar. Each of these two mechanisms could therefore be at play here, or both.

Mechanisms of interactions with neighboring plants may differ based on the functional traits of neighbors. Here, we found that, while both neighboring moss–lichen layers and graminoids reduced root and shoot biomass of the *F. ovina* juveniles to some extent, the main effect of neighboring graminoids was to reduce shoot biomass, whereas moss–lichen layers mainly reduced root biomass and proportional root investment. These results contrast our hypotheses that mosses and lichens would increase juvenile *F. ovina* performance and both neighboring graminoids and moss–lichen would increase root mass ratio, and they support our hypothesis that neighboring graminoids will decrease *F. ovina* performance (H3 and H4). Because our experimental plants were juvenile graminoids, neighboring graminoids were primarily mature individuals with taller shoots than juveniles. Thus, competition for light from these mature graminoids could have been the primary mechanism reducing shoot biomass in competing juveniles. In contrast, moss–lichen layers were shorter in stature than juveniles but with denser biomass at the ground surface. Thus, our result that root biomass of juveniles was altered by moss–lichen layers could be due to moss–lichen altering the soil microclimate in ways that are suboptimal for *F. ovina* root growth. For example, moss–lichen could have increased soil moisture and

decreased soil surface temperatures (Gornall et al., 2007; Nystuen et al., 2019; Startsev et al., 2007; van Zuijlen et al., 2020) and prevented root aeration.

### Moss–lichen complexes facilitate arbuscular mycorrhizae

The likelihood of mycorrhizal colonization was higher under warming than in ambient conditions, in support of our hypothesis that warming will support mycorrhizal colonization of our plants (H5), but this effect was non-significant. The presence of neighboring graminoids did not affect mycorrhization, so we did not find support for our hypothesis that mycorrhization will increase in juveniles planted next to naturally occurring graminoids and thus potentially offset competitive effects to some extent (H6). Moss–lichen presence did significantly affect mycorrhization, with juvenile *F. ovina* nearly twice as likely to develop mycorrhizae when planted among naturally occurring moss–lichen mats. At our site, the mats of lichen and moss consisted primarily of moss. Mycorrhizal fungi species such as *Acaulospora laevis*, *Rhizophagus (Glomus) fasciculatus*, *Rhizophagus tenuis*, *Glomus mosseae*, and *Gigaspora* sp. associate with both mosses (Zhang & Guo, 2007) and *Festuca* (Molina et al., 1978). Mycorrhizal fungi form spores inside and directly infect moss rhizoids, thalli, stems, and leaves (Davey & Currah, 2006; Valdés et al., 2023; Zhang & Guo, 2007), taking up nutrients released from decomposing tissues and transferring them to nearby vascular host plants (Davey & Currah, 2006; Kuyper & Jansa, 2023; Valdés et al., 2023). Mosses can buffer soil temperatures (Nystuen et al., 2019), stabilize soil, increase soil water content, and elevate extractable P, factors which benefit growth of some mycorrhizal fungi (Bi et al., 2021). Throughout the experiment, daily minimum temperatures ranged from  $-7.3$  to  $8.9^{\circ}\text{C}$  across the warming treatments. Root colonization of AMF is sensitive to temperatures below  $15^{\circ}\text{C}$ , so buffering of minimum temperatures by moss–lichen layers may have ameliorated cold stress and hence also stimulated AMF growth. Thus, in moss–lichen layers there may have been more abundant fungal hyphae relative to areas without moss or lichen, so the *F. ovina* juveniles growing near such moss–lichen layers could have been more likely to encounter and associate with AMF.

The higher frequency of mycorrhizal fungi on the roots of *F. ovina* grown in moss–lichen layers may have explained the low root–shoot ratios we observed in these plants. AMF provide water and nutrients to plants via hyphal networks, and mycorrhizal fungi hyphae may be able to access soil nutrients in forms and/or locations that are unavailable to plants (Kuyper & Jansa, 2023). If mycorrhizal fungi allow

plants to capture additional resources without investing in more root biomass, then plant root–shoot ratios of mycorrhizal plants may be lowered. If such additional belowground resource acquisition is to the benefit of plant growth, we would expect that changes in root–shoot ratio with mycorrhization would be due to an increase in shoot biomass while maintaining or decreasing root biomass. For example, mycorrhizae can improve plant shoot biomass under drought relative to non-inoculated plants, thereby decreasing root–shoot ratio (Tang et al., 2024). However, our plants in moss–lichen layers had decreased root biomass while maintaining a similar shoot biomass relative to plants grown without a moss–lichen layer. This suggests that the energy that was not used for additional root biomass could have been invested in other benefits to shoots, such as better chemical defenses and metabolic adaptations to cold. Similar to our results, in a 65-day experiment of wheat (*Triticum aestivum*) inoculated with the AMF *Rhizophagus irregularis*, inoculated plants had lower root biomass while maintaining similar shoot biomass as non-inoculated plants (Henkes et al., 2018). Our study spanned just one growing season, so potential long-term gains from mycorrhizal association may not have had sufficient time to develop (*F. ovina* is a long-lived perennial). The short timeline is a limitation of our manuscript because mycorrhizal relationships can shift over time. Future research that investigates these dynamics on longer timescales could accurately characterize how mycorrhizal fungi and warming interactively affect perennial host plants in alpine environments throughout the lifecycle of the plant.

Another possibility is that these moss–lichen complexes present inferior microsite conditions for *F. ovina*, resulting in lower root growth. For example, though *F. ovina* readily grows in alpine tundra, it is drought tolerant and most abundant in well-drained, lowland areas (Qiu et al., 2021; Samuel & Dines, 2023). Thus, the wet, cool soil environments created by lichen may not be ideal for root growth. Alternatively, the observation that *F. ovina* plants supported a similar shoot biomass with less root biomass when grown in moss–lichen layers points to increased resource use efficiency, which may be due to the increased frequency of mycorrhizae or increased soil resource availability in this microhabitat.

## CONCLUSION

Our results show that warming altered species interactions among a common alpine tundra grass and neighboring vegetation. These results were in support of the stress gradient hypothesis; when abiotic stress was reduced by warming, the strength of negative interactions between *F. ovina* and its neighbors increased. While

competition is a likely mechanism, temperature buffering due to shade from neighboring vegetation may also have counteracted the positive effects of our warming treatment on *F. ovina* growth. Our study thus demonstrates that climate warming could increase competitive intra- and interspecies interactions among dominant plants and cryptogams in ecosystems in which plant growth is limited by cold temperatures. In this alpine tundra, we also observed that neighboring moss–lichen assemblages can increase mycorrhization rates in *F. ovina*. Both observations warrant further research into the mechanisms underlying the effects of climate change on plants and their fungal associates. Both direct effects of climate change and those mediated by changes in the abundance of other above- and belowground organisms should be examined. Our work underlines how trajectories of alpine plant community composition and ecosystem processes under climate change may be controlled by a combination of warming and shifts in species interactions.

## AUTHOR CONTRIBUTIONS

Grace Rose Gutiérrez and Martijn L. Vandegehuchte conceived the ideas and designed the methodology with input from Sidonie Loïez; all authors collected the data; Grace Rose Gutiérrez and Martijn L. Vandegehuchte analyzed the data; Grace Rose Gutiérrez led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data and code (Gutierrez et al., 2025) are available from Dryad: <https://doi.org/10.5061/dryad.qbzhkh18tx>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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