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Wealth breeds independence: Alpine plants lose mycorrhizal dependence as community productivity increases

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Abstract

Mycorrhizal fungi can improve plant nutrition and protect roots from pathogens, but the importance of these benefits may vary among alpine communities. We tested whether fungal suppression reduces forb biomass in low-productivity vegetation while favouring grasses in more productive communities. We conducted a four-year field experiment (2014–2017) in four alpine communities in the northwestern Caucasus, Russia. In each community, 20 plots were randomly assigned to benomyl or nitrogen-matched tryptophan treatments. We counted shoots annually and measured species biomass and root colonisation in 2017. Benomyl reduced root colonisation in several species, but biomass responses differed among communities. In low-productivity alpine lichen heath, forb biomass was about 60% lower than in controls. In contrast, grass biomass was about 60% higher in the more productive *Festuca varia* grassland. However, a comparable grass response was not detected in productive *Geranium-Hedysarum* meadow. In snowbed communities, several species had lower biomass, although total biomass showed no clear treatment response. Changes in shoot abundance did not always match these biomass responses. These results partly support our productivity hypothesis. Reduced nutrient uptake may explain losses in lichen heath, while reduced pathogen pressure may favour grasses in productive grassland. Because benomyl affects both mycorrhizal fungi and other fungi, these proposed mechanisms require direct tests.

1. Introduction

Soil microbes, including mycorrhizal fungi, can shape plant communities (Bever et al. 2010). Belowground symbionts significantly influence plant species composition, nutrient capture, and aboveground biomass production (van der Heijden et al. 1998). Mycorrhizal status is associated with plant life-history traits and habitat conditions (Hempel et al. 2013). In a study of Caucasian alpine plants, highly colonised forbs grew more slowly under combined nutrient and mycorrhizal limitation, while grasses showed no comparable pattern (Elumeeva et al. 2018). .

Arbuscular mycorrhizal fungi (AMF) can help plants acquire nutrients, including phosphorus, which can limit growth in nutrient-poor soils (Lambers et al. 2008). AMF also protected the grass *Vulpia ciliata* from a root pathogen without increasing plant phosphorus concentrations (Newsham et al. 1995a). In maize, the abundance of soil fungal pathogens was the strongest predictor of growth responses to AMF inoculation (Lutz et al. 2023). Maintaining the association can also increase belowground carbon costs, as shown in perennial ryegrass (Grimoldi et al. 2006). The net effect on plant growth may therefore depend on the balance between these benefits and costs.

Evidence from high-mountain ecosystems demonstrates that alpine mycorrhizal interactions are highly complex and context-dependent. First, the composition of arbuscular mycorrhizal fungal communities can vary among closely related host species. For example, these communities differed between co-occurring *Gentiana verna* and *G. acaulis* in Swiss upper montane meadows (Sýkorová et al. 2007). Furthermore, fungal activity and plant growth are often decoupled in time. In the alpine plant *Ranunculus*

adoneus, phosphorus accumulated late in the season, when arbuscules were present and most vegetative growth had already occurred (Mullen and Schmidt 1993). Finally, suppressing these fungi does not automatically cause nutrient starvation: an earlier benomyl-exclusion experiment in alpine grasslands showed that reduced root colonization did not necessarily decrease leaf phosphorus concentrations (Fitter 1986). Together, these findings suggest that the role of alpine mycorrhizas cannot be inferred simply from colonization rates. Instead, their net impact must be evaluated experimentally across different community contexts and productivity gradients.

To explain how these roles shift, we propose a "productivity hypothesis." Alpine landscapes provide an excellent testing ground because contrasting plant communities occur over short distances under the same regional climate (Onipchenko 1994; Onipchenko et al. 2012). We hypothesize that in low-productivity, forb-dominated communities with poor soils, the primary role of mycorrhiza is mineral nutrition. In contrast, in highly productive, grass-dominated communities, the primary role of mycorrhiza shifts to pathogen protection.

To test this hypothesis, we conducted a four-year fungicide (benomyl) experiment across four contrasting alpine communities in the northwestern Caucasus: alpine lichen heath (ALH), *Festuca varia* grassland (FVG), *Geranium-Hedysarum* meadow (GHM), and snowbed communities (SBC). By recording annual shoot censuses, measuring final aboveground biomass, and assessing root colonisation, we evaluated how the suppression of soil fungi affects plant performance.

2. Materials and Methods

2.1. Study Area

The study was conducted in the alpine belt of the Teberda National Park, located in the north-western Caucasus, Russia (43°27' N, 41°43' E). The area has a temperate montane climate, with a mean annual air temperature of about − 1.2°C and mean annual precipitation of about 1 400 mm (Onipchenko 2004).

Topography and prevailing winds create strong local variation in winter snow accumulation (Rabotnov 1987; Onipchenko et al. 2009a). Differences in snow depth and melt timing shape a mosaic of plant communities, from wind-exposed lichen heaths on ridges to late-melting snowbeds in depressions (Onipchenko 2004).

2.2. Plant Communities

The experiment was established in four alpine plant communities that differ in snow cover, growing-season length and aboveground productivity (Onipchenko 2004; Onipchenko et al. 2009a). Earlier surveys using Selivanov’s method recorded high mycorrhizal infection intensities in many plant species from all four community types (Onipchenko 2004).

Alpine lichen heaths (ALH) occupy wind-exposed ridges and upper slopes with very shallow or absent winter snow cover. The growing season is relatively long, and the shallow, stony soils have low nutrient

content and dry quickly. These low-productivity communities are dominated by lichens, with scattered dwarf shrubs, grasses and forbs (Onipchenko 2004; Onipchenko et al. 2009a).

Festuca varia grasslands (FVG) occur on south-facing slopes with moderate winter snow accumulation and relatively long, warm growing seasons. Dense tussocks of *Festuca varia* dominate the vegetation. FVG is intermediate in productivity among the four communities (Onipchenko 2004; Onipchenko et al. 2009a).

Geranium–Hedysarum meadows (GHM) occupy lower alpine slopes with deep winter snow cover and relatively mild, moist conditions during the growing season. Tall forbs, especially *Geranium gymnocaulon* and *Hedysarum caucasicum*, dominate the canopy. GHM is the most productive of the four communities (Onipchenko 2004; Onipchenko et al. 2009a).

Snowbed communities (SBC) occupy depressions where snow accumulates to several metres and melts late in summer. They have moist soils, the shortest growing season of the four communities and low aboveground productivity. Low-growing forbs such as *Taraxacum stevenii* and *Sibbaldia procumbens* form a dense cover (Onipchenko 2004; Onipchenko et al. 2009a).

2.3. Experimental Design

2.3.1. Plot layout and treatments

In each of the four alpine plant communities (ALH, SBC, FVG, GHM), 20 permanent circular plots were established in 2014, giving a total of 80 plots (Fig. 1). Each plot had a diameter of 25 cm and was positioned within a visually homogeneous patch of the target community type, with a minimum distance of approximately 1 m between neighboring plots. On sloping terrain, plots were aligned along the slope contour to minimize downslope movement of water and solutes between treated and control plots.

Plots were randomly assigned to either a fungicide treatment or a control treatment, resulting in 10 fungicide and 10 control plots per community. The fungicide treatment consisted of applications of the benomyl-based product “Benorad” at a dose of 2.85 g of product per plot, corresponding to a circular area of 25 cm in diameter. Because benomyl decomposition in soil increases mineral nitrogen availability, control plots received 2.1 g of tryptophan per plot, which is not toxic to fungi but supplies an equivalent amount of organic nitrogen. Both substances were applied as aqueous suspensions: the weighed powder was dissolved in water and 600 mL of suspension was poured onto each plot per application.

To deliver the suspension directly into the rooting zone, five plastic laboratory funnels with long spouts were installed per plot, inserted into the soil to a depth of 2–3 cm near the plot edge and in the centre of the circle. The prepared suspension of Benorad or tryptophan was poured from bottles into these funnels, and any remaining suspension was distributed over the soil surface within the plot area. Fungicide and control suspensions were applied twice per growing season (shortly after snowmelt and in mid-summer) in 2014–2017, with application dates adjusted to snowmelt timing in each community.

2.3.2. Shoot counts

Aboveground plant abundance was monitored annually from 2014 to 2017 using a non-destructive census of shoots. Within each circular plot, a fixed 20 × 20 cm square was delimited in the same position each year, and all shoots of vascular plants rooted inside this square were counted. For each species, shoots were classified into three developmental categories: juvenile, vegetative, and generative. This provided a consistent time series of shoot density by species and life stage for all plots across the four years of the experiment.

2.3.3. Aboveground biomass

In the final year of the experiment (2017), aboveground biomass was harvested destructively after the last shoot census. All vascular plant material rooted within the 20 × 20 cm sampling square of each plot was clipped at ground level, sorted to species, and stored in paper bags. Samples were then dried at 80°C to constant mass and weighed to the nearest 0.001 g, yielding species-level dry biomass per plot. These data were later aggregated to the level of functional groups (e.g. grasses, sedges, forbs, legumes, shrubs) for statistical analysis.

2.3.4. Mycorrhizal infection

To quantify arbuscular mycorrhizal colonisation, root samples were collected from the experimental plots in the final year of the fungicide experiment (2017). We selected common species that occurred in both control and fungicide plots. The analysis included 126 root samples from 13 species: four in ALH, two in FVG, three in GHM and four in SBC. The number of samples per species and treatment ranged from one to six. Fine roots were excavated within each plot, targeting fresh, actively growing tips. In species with fibrous root systems, fine roots were collected from several locations to capture a range of mycorrhizal structures. In species with taproots, only fine lateral roots less than 1 mm in diameter were collected.

Immediately after collection, roots were gently shaken free of adhering soil and fixed in 4% formalin. In the laboratory, root samples were processed following the protocol described by Selivanov (1981). Roots were rinsed to remove formalin, macerated in 15% KOH until tissues became transparent, washed in water, stained for 8 h with aniline blue, and destained in 40% lactic acid before final rinsing in tap water.

For each sample, a total root length of 20 cm was analysed. The stained roots were cut into 1 cm fragments, and five microscope fields of view were examined on each fragment at 10×40 magnification. Each field of view was assigned an infection score from 0 to 5 following Selivanov's (1981) scale, based on the abundance of intraradical hyphae, vesicles, arbuscules and granular fungal structures. We calculated mycorrhizal colonisation intensity (M%) for each sample by applying the class weights of Trouvelot et al. (1986) to the field-of-view scores.

$$M\,(\%) = \frac{95n_5 + 70n_4 + 30n_3 + 5n_2 + n_1}{N}$$

Here, n_i is the number of fields with score *i*, and *N* is the total number of fields included for that sample, including fields scored 0. We included only fields with a recorded score and complete records for hyphae, vesicles and arbuscules. Samples were retained if at least 50 fields met these criteria. The analysed samples contained 91–99 such fields each. For each species within each community, we averaged the sample-level M% values separately for the control and fungicide treatments.

2.4. Statistical analysis

All analyses were performed in R version 4.5.1 (R Core Team, 2025) using the packages *glmmTMB* 1.1.13 (Brooks et al., 2017), *DHARMa* 0.4.7 (Hartig 2024), *broom.mixed* 0.2.9.6 (Bolker and Robinson 2024), *ggplot2* 4.0.2 (Wickham 2016) and *car* 3.1.3 (Fox and Weisberg 2019) and RStudio IDE. Prior to modelling, we calculated summary statistics (means, standard errors, ranges) for each response variable and treatment combination, and visualised distributions using histograms and quantile–quantile plots. Homogeneity of variances and approximate normality of residuals were assessed using base R functions and the *car* package, while correlation structures and potential outliers were examined using scatterplots and boxplots. These preliminary checks guided the choice of error distributions and link functions in subsequent models.

2.4.1. Shoot counts

Shoot counts were analysed using negative binomial mixed models with a log link and an NB2 variance structure rather than conventional ANOVA. This approach accommodated overdispersion in the counts and allowed us to account for observations grouped within plots. Juvenile, vegetative and generative shoots were summed by species, plot and year. We report separate treatment contrasts for 2014 and 2017 in each community. Models that combined counts across species within a community included random intercepts for plot and species. For functional groups, counts were summed within plots before modelling. Functional-group and single-species models included a random intercept for plot only. Treatment effects were expressed as fungicide-to-control ratios of expected counts, with Wald 95% confidence intervals.

Species with $P < 0.15$ for the biomass treatment contrast were selected for exploratory shoot-count analyses. We examined treatment differences in 2017 and changes from 2014 to 2017 within each treatment. The temporal models included year as a fixed effect and plot as a random intercept.

For the models that combined species within communities, we used DHARMa to check simulated residuals for dispersion and excess zeros.

2.4.2. Aboveground biomass

We analysed aboveground dry biomass per plot in 2017 at the species, functional-group and community levels. When no shoots of a species were recorded in a plot, its biomass was set to zero. Functional-group biomass was calculated by summing the biomass of its constituent species within each plot.

Total living biomass was calculated by summing the biomass of all vascular plant species, excluding necromass.

For each community and response, we fitted a generalised linear model with a log link and treatment as a fixed effect. We used a Gamma distribution when all observations were positive and a Tweedie distribution when the data included zeros. Treatment effects were expressed as fungicide-to-control ratios of expected biomass, with Wald 95% confidence intervals.

2.4.3. Mycorrhizal colonization

For each species within each community, we calculated the mean of the sample-level M% values separately for control and fungicide plots. Differences in sample-level M% between control and fungicide plots were tested separately for each species and community using two-sided Wilcoxon rank-sum tests. We adjusted the resulting *P*-values across all 13 tests using the Benjamini–Hochberg procedure (Benjamini and Hochberg 1995).

These tests provided a formal check that the fungicide treatment effectively reduced mycorrhizal colonization in the target species, and allowed us to relate species-specific sensitivity of mycorrhiza to the observed shifts in shoot abundance and biomass across the productivity gradient.

2.5. Use of AI tools

Google Gemini 3 Pro, accessed through the Gemini web interface, OpenAI GPT-5 and GPT-5.5, accessed through the Codex client, were used to assist with developing and reviewing R scripts and checking consistency between the code, the described methods and the reported results. These tools also assisted with manuscript revision and proofreading. The authors reviewed the resulting code and text and take responsibility for the final analyses, interpretation and manuscript.

3. Results

3.1. Shoot abundance

Across the four alpine communities, the fungicide treatment did not produce a consistent pattern of shoot-abundance responses along the productivity gradient (Fig. 2). In the models fitted jointly across species, the only statistically significant treatment contrast was in GHM in 2017, when expected shoot counts were approximately 36% lower in fungicide plots than in controls (RR = 0.64, P = 0.030). In 2014, the GHM estimate was also below one, but the effect was not statistically significant (RR = 0.76, P = 0.079). Treatment effects in ALH, FVG and SBC were not statistically significant in either year. In ALH and SBC, estimates were slightly above one in 2014 and below one in 2017, but their confidence intervals included one.

When shoot abundance was partitioned among functional groups, responses were selective and varied among communities (Fig. 2). In ALH, forb shoot abundance was approximately 38% lower under

fungicide (RR = 0.62, P = 0.016), whereas sedge shoot abundance was approximately 71% higher (RR = 1.71, P = 0.048). In FVG, shrub shoot abundance, represented by *Vaccinium vitis-idaea*, was approximately six times higher under fungicide in 2017 (RR = 6.14, P = 0.028). Sedges also showed a positive treatment effect in FVG in 2014 (RR = 5.38, P = 0.028), but the 2017 estimate was imprecise and not statistically significant (RR = 5.26, P = 0.138). In GHM, forb shoot abundance was approximately 36% lower under fungicide in 2017 (RR = 0.64, P = 0.003). Grass and legume responses were not statistically significant. The estimate for sedges was above one, but its wide confidence interval did not support a clear treatment response (RR = 1.68, P = 0.584). No statistically significant functional-group responses were detected in SBC in either year.

3.2. Aboveground biomass

Overall, fungicide effects on aboveground biomass varied among communities, with opposite aggregate responses in ALH and FVG (Fig. 3). Total aboveground biomass was approximately 37% lower under fungicide in ALH and 67% higher in FVG. No statistically significant total-biomass response was detected in GHM or SBC. At the level of functional groups (Fig. 3), clear biomass responses were restricted to forbs in ALH and grasses and shrubs in FVG. In ALH, biomass of forbs was approximately 61% lower than in controls, whereas biomass of grasses, sedges, legumes and shrubs showed no statistically significant treatment differences. In FVG, shrub biomass, represented by *Vaccinium vitis-idaea*, was approximately four times higher under fungicide, while grass biomass was approximately 61% higher. In GHM and SBC, functional-group biomass responses were not statistically significant, and confidence intervals included one.

Species-level analyses (Fig. 4) revealed that statistically significant responses occurred in a subset of the analysed species. In ALH, biomass was lower under fungicide for the grass *Festuca ovina* and the forbs *Alchemilla caucasica*, *Pedicularis comosa*, *Campanula collina* and *Euphrasia ossica*. In FVG, biomass of both *Nardus stricta* and *Vaccinium vitis-idaea* was higher under fungicide. In GHM, the only statistically significant species-level response was lower biomass of *Carum meifolium*. The estimate for *Festuca brunnescens* was positive but uncertain (RR = 3.77, 95% CI = 0.74–19.13, P = 0.110). In SBC, several snowbed forbs (*Taraxacum stevenii*, *Corydalis conorhiza*, *Carum caucasicum*) had markedly lower biomass under fungicide, while the remaining species-level contrasts were not statistically significant. These species-level declines were not accompanied by statistically significant changes in total or functional-group biomass.

To compare biomass and shoot-count responses, we conducted exploratory shoot-count analyses for species selected using a biomass threshold of P < 0.15. We distinguished treatment contrasts in 2017 from temporal changes within each treatment (Table S1). In ALH, estimated biomass of *Euphrasia ossica* and *Campanula collina* was approximately 95% and 86% lower than in controls, respectively. *C. collina* also had approximately 52% fewer shoots in 2017 (RR = 0.48, P = 0.011). The shoot-count estimate for *E. ossica* was also lower, but uncertain (RR = 0.25, P = 0.123). In SBC, *Taraxacum stevenii* had approximately 73% lower biomass and 75% fewer shoots under fungicide. By contrast, *Carum caucasicum* had

approximately 90% lower biomass without a statistically significant shoot-count difference in 2017 (RR = 0.90, P = 0.923).

In FVG, *Nardus stricta* biomass approximately doubled under fungicide (RR = 2.05, P = 0.014), but no statistically significant shoot-count difference was detected in 2017 (RR = 0.90, P = 0.908). Its shoot abundance increased between 2014 and 2017 within fungicide plots (RR = 1.41, P = 0.017), which represents a temporal change rather than a between-treatment contrast. *Vaccinium vitis-idaea* had both higher biomass and more shoots under fungicide in 2017 (biomass RR = 4.12; shoot-count RR = 6.14). In GHM, *Carum meifolium* had both lower biomass and fewer shoots under fungicide (biomass RR = 0.24; shoot-count RR = 0.44). Overall, these patterns indicate that agreement between biomass and shoot-count responses varied among species. They do not establish that fungicide primarily affected per-shoot size or resource uptake.

3.3. Mycorrhizal colonisation

Mean mycorrhizal colonisation intensity (M%) was lower under fungicide in 12 of the 13 sampled species, with statistically significant reductions in 10 species after correction for multiple testing (Fig. 5). In ALH, mean infection intensity M% declined from about 17% in control plots to 2% in fungicide plots in *Anemone speciosa*, and from 3% to 0.6% in *Festuca ovina*. In FVG, *Nardus stricta* and *Festuca varia* showed reductions from approximately 34% to 8% and from 33% to 10%, respectively. In GHM, mean M% declined from approximately 38% to 8% in *Geranium gymnocaulon*, from 23% to 14% in *Hedysarum caucasicum*, and from 15% to 5% in *Phleum alpinum*. In SBC, mean (M%) decreased by approximately 10 percentage points in *Taraxacum confusum* and 20 percentage points in *Sibbaldia procumbens* under fungicide.

Because the number of species with root colonisation data per community was limited, we do not generalise these patterns to whole communities. Instead, we interpret them as direct evidence that our fungicide treatment effectively suppressed arbuscular mycorrhizal colonisation in most of the focal species used to assess treatment efficacy.

4. Discussion

Our four-year field experiment combined root-colonisation measurements, biomass and shoot counts across four contrasting alpine communities within one landscape. Microscopy confirmed that the fungicide effectively reduced mycorrhizal colonisation in most of the sampled focal species. Total biomass decreased in ALH and increased in FVG, while total shoot abundance declined in GHM. In SBC, several species lost biomass without a significant aggregate response. Earlier surveys reported high mycorrhizal infection intensities in species from all four communities (Onipchenko 2004). Their contrasting responses to fungal suppression suggest that high colonisation may reflect different balances of nutritional benefits, pathogen protection and carbon costs among communities. Together, these findings provide a comparative field test of the productivity hypothesis in natural alpine vegetation.

4.1. Biomass and shoot abundance as complementary measures

Biomass and shoot abundance provided complementary evidence of treatment responses. *Nardus stricta* had higher biomass without a significant shoot-count difference, while *Vaccinium vitis-idaea* and *Carum meifolium* showed matching responses in 2017. In prairie forbs, mycorrhizal suppression increased ramet density, while biomass per ramet decreased, increased or remained unchanged among species (Wilson et al. 2001).

Many alpine plants are long-lived perennials with persistent root systems (Dietz and Fattorini 2002; Chondol et al. 2023). This may limit short-term changes in shoot abundance, although GHM showed a significant decline within four years.

4.2. Possible nutritional effects of fungal suppression in ALH

Earlier records from alpine lichen heath showed high mycorrhizal colonisation in *Anemone speciosa* (71%) and *Campanula tridentata* (80%; Onipchenko, 2004). In our experiment, fungicide markedly reduced colonisation in *A. speciosa* (Fig. 4), but we detected no clear biomass response. The biomass estimate for *C. tridentata* was lower under fungicide, but uncertain, and we did not measure its root colonisation. These observations suggest that high root colonisation alone is a limited guide to biomass responses to fungal suppression.

The hemiparasites *Euphrasia ossica* and *Pedicularis comosa* also had lower biomass. Some *Pedicularis* species form arbuscular mycorrhiza (Li and Guan 2008). In *P. rex* and *P. tricolor*, the fungal pathway supplied less than 1% of total plant P, while AM inoculation reduced P uptake from host plants (Li et al. 2013). The ALH declines could reflect changes in host performance or, if these hemiparasites form functional mycorrhizas locally, loss of their own fungal partners. Their local mycorrhizal status and the importance of these pathways need further research.

4.3. Positive biomass responses in FVG and contrasting responses in GHM

In the moderately productive FVG, fungicide increased total and grass biomass, with *Nardus stricta* biomass approximately doubling. This contrast with forb losses in ALH supports our productivity hypothesis. In a steppe field experiment, benomyl increased total aboveground biomass at high phosphorus addition rates, while C_3 grass biomass tended to increase (Yang et al. 2014).

In GHM, the analysis across species indicated lower shoot abundance under fungicide in 2017, as did the separate analysis of forbs. *Festuca brunnescens* had a positive but uncertain biomass response (RR = 3.77, 95% CI = 0.74–19.13, P = 0.110). Its direction matched the *Nardus stricta* response in FVG,

although there was no clear treatment effect on grass biomass in GHM. This mixed response limits a simple explanation based on community productivity.

Benomyl can reduce AM root colonisation and affect root pathogens (Fitter 1986; Newsham et al. 1995b). In *Vulpia ciliata*, AMF protected plants from root pathogens without increasing plant P concentrations (Newsham et al. 1995a).

Insect herbivory may also be relevant in FVG. A soil-fauna survey at the study site recorded weevils there, including *Otiorhynchus circassicus* (Onipchenko and Zhakova 1997). Benomyl inhibited the growth of a fungal pathogen of the related weevil *O. sulcatus* in vitro (Moorhouse et al. 1992), suggesting a possible indirect effect on herbivory. We did not measure weevil abundance or feeding damage, so whether changes in herbivory contributed to the biomass response remains unknown.

Vaccinium vitis-idaea also had approximately four times the control biomass and six times the control shoot abundance under fungicide in FVG. This extends the positive response beyond grasses to an ericoid shrub. Ericoid colonisation was not assessed, and the roles of fungal partners and competition could be examined in a separate study.

4.4. Growth season limitation as the primary ecological filter in SBC

In SBC, biomass estimates were lower under fungicide for *Taraxacum stevenii*, *Corydalis conorhiza* and *Carum caucasicum*, but total and functional-group biomass showed no significant response. Unlike ALH, significant biomass responses were therefore detected only at the species level. A five-year prairie experiment similarly found changes in species abundances without a change in estimated total biomass (Hartnett and Wilson 1999).

The short growing season provides a possible ecological context for this difference between SBC and ALH. In the north-western Caucasus, SBC have the shortest growing season of the four communities studied, lasting about 2–2.5 months (Onipchenko et al. 2009a). Snowmelt experiments showed that species responded differently to a longer growing season, with responses related to the timing of leaf growth (Galen and Stanton 1995).

The timing of nutrient uptake may also matter. In the snowbed herb *Ranunculus adoneus*, nitrogen uptake occurred during snowmelt, before active AM structures developed (Mullen et al. 1998). Phosphorus accumulated later, when arbuscules were present, and was stored for use the following spring (Mullen and Schmidt 1993). In Caucasian snowbeds, *Corydalis conorhiza* can acquire nitrogen directly from the snowpack through specialised roots (Onipchenko et al. 2009b). If some species in our snowbeds rely on AM fungi for late-season phosphorus uptake, fungal suppression could affect their biomass even where the snow-free period is short. We did not measure seasonal nutrient uptake, so this mechanism remains untested.

A short growing season still allows substantial biomass responses at the community level. NP fertilisation increased snowbed biomass by 110% after four to five growing seasons in the same region (Onipchenko et al. 2012).

5. Conclusion

Our four-year field manipulation compared the effects of fungal suppression across four contrasting alpine communities within one landscape. Root microscopy confirmed reduced arbuscular mycorrhizal colonisation in most focal species, while biomass and shoot abundance provided complementary evidence of vegetation responses. Fungicide reduced forb biomass by approximately 61% in ALH but increased grass biomass by approximately 61% in FVG. *Vaccinium vitis-idaea* also had higher biomass and more shoots, showing that the positive FVG response was not confined to grasses.

GHM and SBC extended this contrast. In GHM, total and forb shoot abundance declined, *Carum meifolium* had lower biomass, and the positive estimate for *Festuca brunnescens* remained uncertain. In SBC, several forbs lost biomass without significant changes in total or functional-group biomass. These mixed responses show that productivity is a useful but incomplete framework for interpreting responses to fungal suppression. Species identity and the level of analysis are also important.

By combining focal-species root measurements, annual shoot counts and final-year biomass across four community types, this study provides a comparative field test of the productivity hypothesis in natural alpine vegetation. The results support the predicted ALH–FVG contrast and suggest that nutritional benefits, pathogen pressure and carbon costs may contribute differently to plant performance among communities. These mechanisms, together with possible growing-season constraints in SBC, provide clear targets for future field experiments.

Declarations

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary materials

Table S1. Statistical results for shoot abundance, aboveground biomass and mycorrhizal infection intensity in four alpine communities

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Author Contribution

Conceptualization: V.O., N.L.Methodology: N.L., V.O. Formal analysis: N.L. Investigation: N.L., K.M., N.F., V.O. Visualization: N.L.Writing – original draft: N.L. Writing – review & editing: V.O. Funding acquisition: V.O. Resources: V.O. Supervision: V.O.

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Data availability

The data and R scripts supporting the findings of this study are publicly available in Zenodo at https://doi.org/10.5281/zenodo.24164544.

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Figures



Figure 1

Experimental setup in the alpine lichen heath (ALH). Five funnels per plot were used to apply benomyl or tryptophan to the soil in fungicide plots and tryptophan in control plots

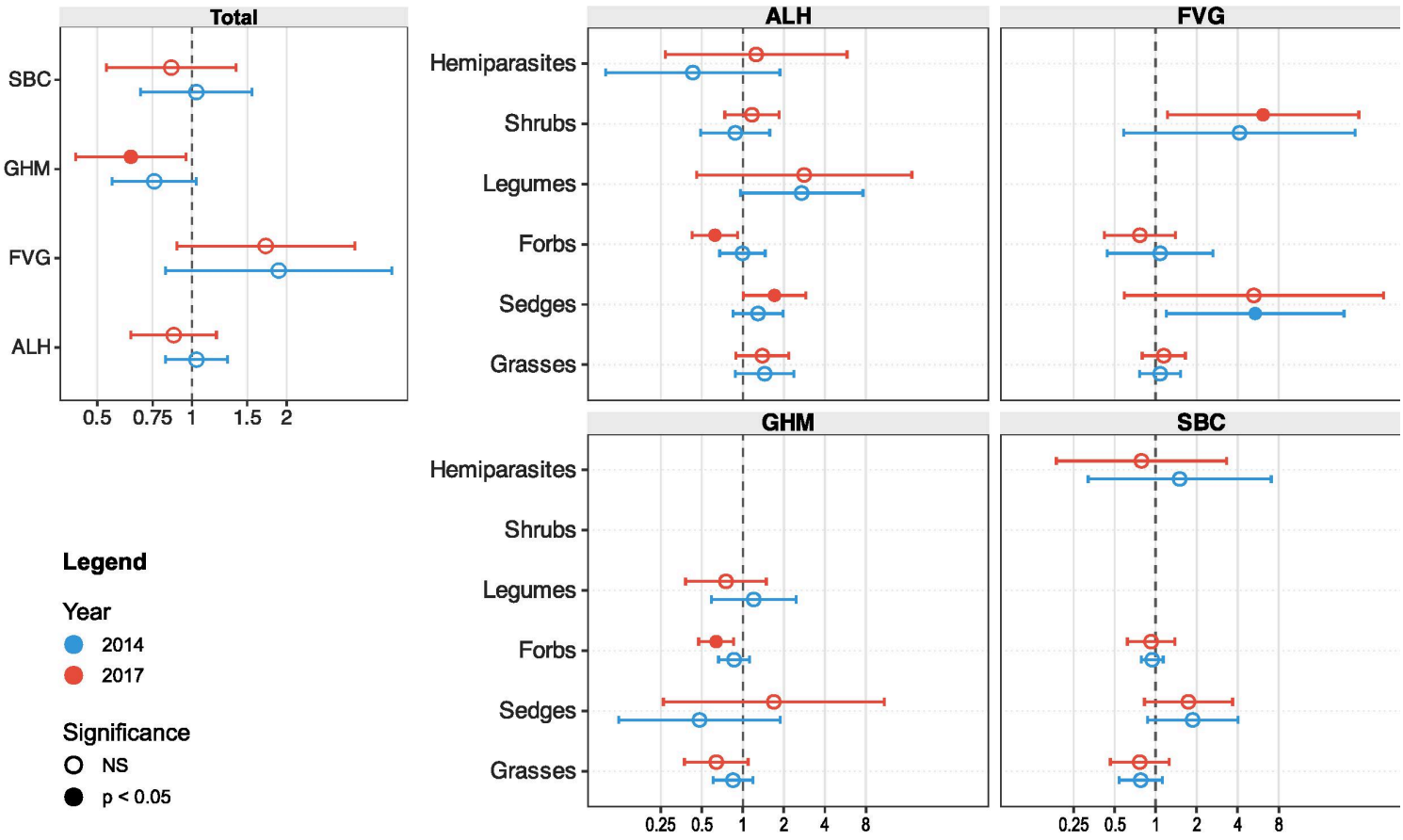

Figure 2

Fungicide effect on shoot total abundance and separated by functional groups within plant communities

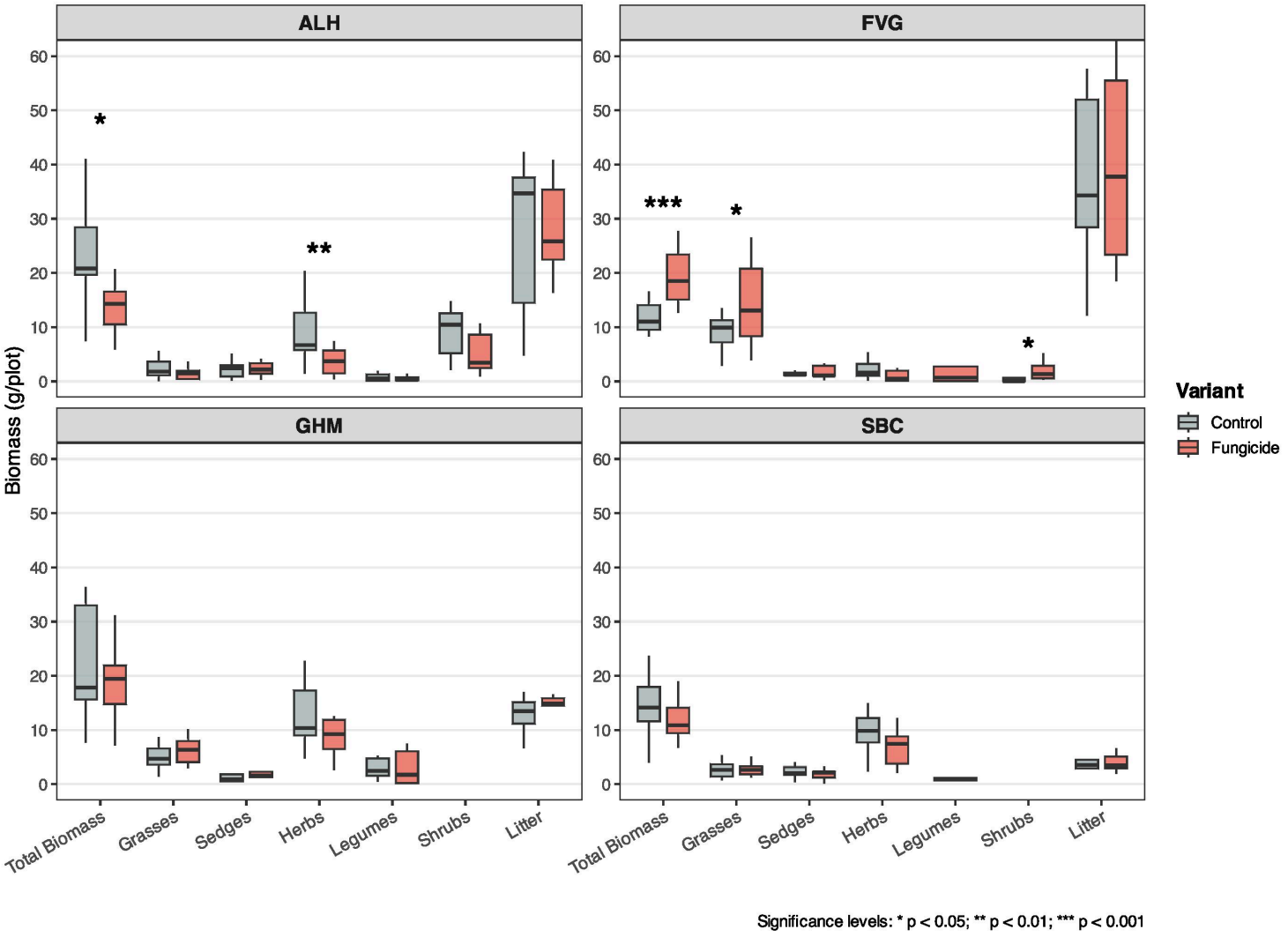

Figure 3

Fungicide effect on biomass by functional groups within plant communities

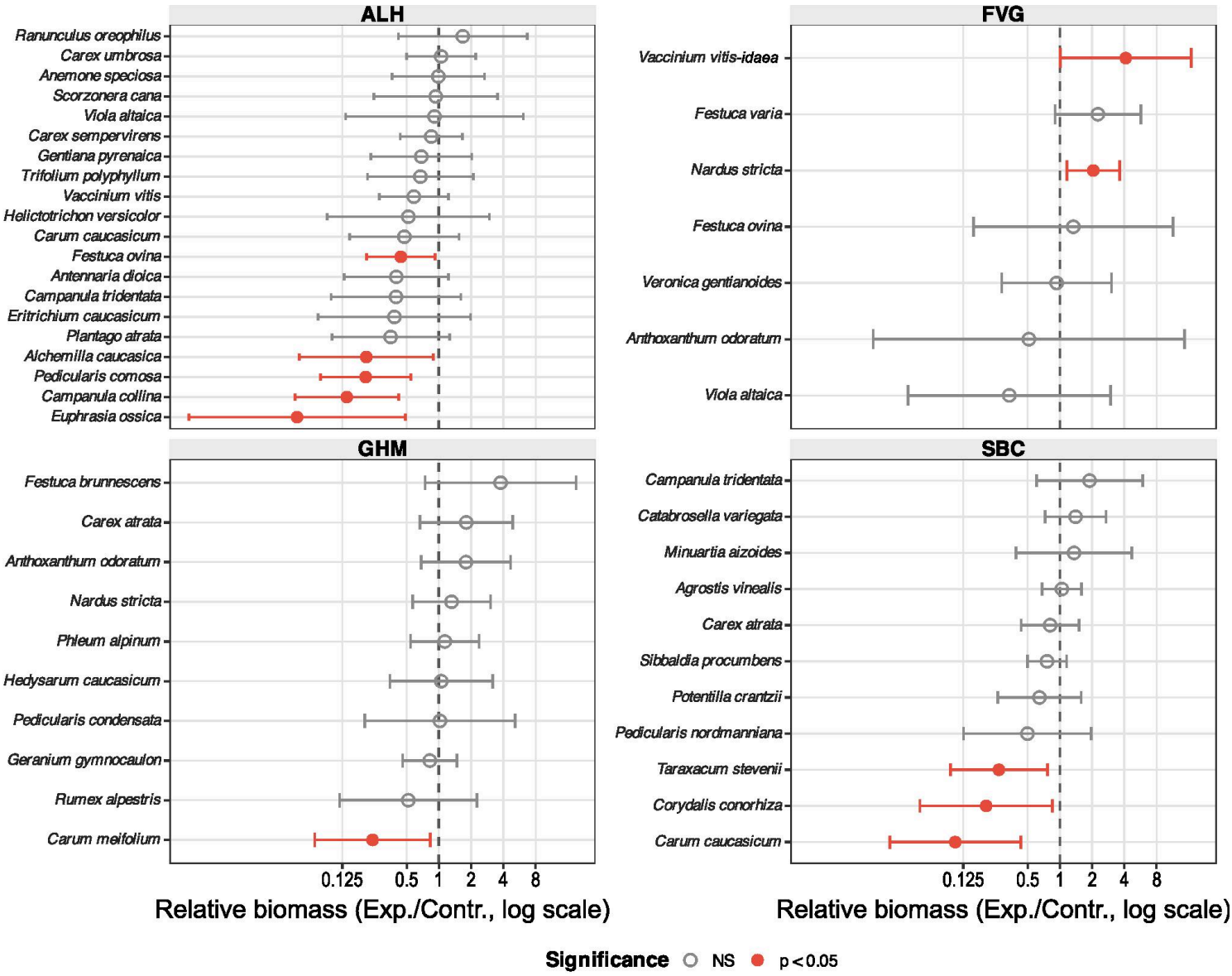

Figure 4

Fungicide effect on species biomass

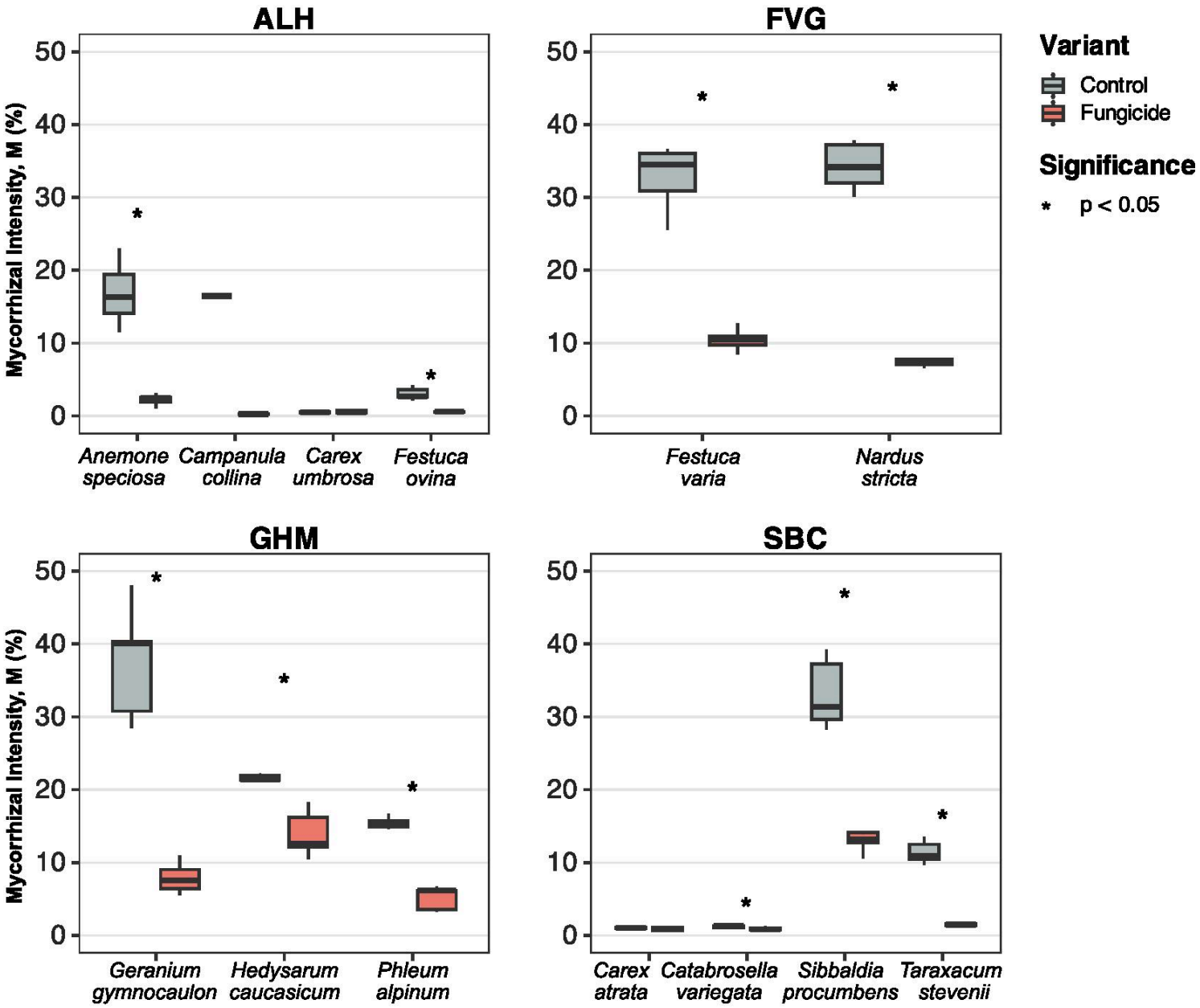

Figure 5

Fungicide effect on mycorrhizal intensity by plant species within communities

Supplementary Files

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