ARTICLE



Plant interaction traits determine the biomass of arbuscular mycorrhizal fungi and bacteria in soil

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Funding information Marsden Fund, Grant/Award Number: 15-VUW-069; Victoria University of Wellington

Handling Editor: Kerri M. Crawford

Abstract

Plant-arbuscular mycorrhizal fungal (AMF) mutualisms are crucial to ecosystem biodiversity and productivity. Yet, our understanding of the functional roles of plants as AMF generalists or specialists, and the consequences of these plant interaction traits for soil ecosystems are virtually unknown. We grew eight pasture plant species under two experimental conditions, sequencing their root AMF communities to assess interaction traits using a range of numeric and phylogenetic diversity metrics, thereby characterizing each plant species' interaction generalism with AMF. We used lipid analysis of rhizosphere soils and Bayesian modeling to explore how host interaction traits affected carbon allocation to AMF and bacteria. We found that plant interaction traits for AMF remained stable despite large variation in soil conditions and AMF pools. Host interaction generalism was linked to contrasting patterns in bacterial and AMF biomass: Phylogenetic diversity in plant interactions was positively associated with AMF biomass, while numeric diversity was negatively associated with bacterial biomass in rhizosphere soils. Explicit consideration of plant interaction niches may enhance understanding of how changes in biodiversity affect ecosystem carbon cycling.

KEYWORDS

arbuscular mycorrhizal fungi, bacteria, community assembly, interaction generalist, next-generation sequencing, pasture plants, PLFA, soil microbial biomass

INTRODUCTION

Species interactions are important for maintaining biodiversity, productivity, and resilience of ecosystems (McCann, 2000; Ratzke et al., 2020; Tylianakis et al., 2010). Many species depend on mutualistic relationships for crucial processes such as pollination, dispersal, resource acquisition, or stress alleviation (Allesina & Tang, 2012; Bascompte et al., 2006), such that these interactions comprise a key component of a species' niche (Carscadden et al., 2020). A species' interaction niche, the degree to which it interacts with members of another trophic guild, such as its mutualistic partners, is often described as a continuum between specialism and generalism and has important ecological implications for both guilds (Poisot et al., 2015). For example, generalist

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pollinators tend to positively affect plant production (Maldonado et al., 2013), while specialists can enhance coexistence by reducing competition (Bastolla et al., 2009). In nature, the presence of a range of interaction niches contributes to biodiversity and community stability (Dehling et al., 2021; Poisot et al., 2015).

Despite this importance, the definition of a specialist and generalist is not always straightforward (Poisot et al., 2012; Rohr et al., 2014). For example, the term specialist is often applied to members of one guild that interact with few partners but also to those selectively interacting with phylogenetically related partners (Bascompte, 2009; Montesinos-Navarro et al., 2015). By contrast, a generalist is commonly defined either as a species with many or diverse interactions. These differences in the definitions of specialism and generalism are problematic because they lead to the pooling of species interaction traits that may vary in their effects on the community. Additionally, mutualistic interactions can be predicted through phylogenetic relationships (Rezende et al., 2007) or by species traits (Eklöf et al., 2013; Vázquez et al., 2009) and generality can be conserved across a species' range (Emer et al., 2016), yet interactions (particularly those of generalists) can be determined by random encounter probability (related to species' abundances; Vázquez et al., 2009) and shaped by the local environment (Tylianakis et al., 2008). Thus, it remains unclear to what extent the local environment shapes species interaction generalism. Resolving the various facets of interaction traits of mutualistic species would improve understanding of the assembly and maintenance of ecological communities.

Possibly the oldest mutualism among eukaryotes is that between plants and arbuscular mycorrhizal fungi (AMF), which occurs in more than three-quarters of vascular plant species and most terrestrial ecosystems (Brundrett & Tedersoo, 2018). Arbuscular mycorrhizal (AM) plants allocate on average 6% of photosynthetic carbon (C) to obligately biotrophic soil fungi of the subphylum Glomeromycotina (Hawkins et al., 2023). In exchange, plants receive multiple benefits from AMF, including improved water and nutrient acquisition (Vogelsang et al., 2006) and pathogen and stress resistance (Begum et al., 2019; Lutz et al., 2023). Consequently, AM plants are significant sinks for atmospheric carbon dioxide (Parihar et al., 2020). While AMF abundance is highly correlated to soil C sequestration in field studies (Wilson et al., 2009), it is less clear how AMF diversity, largely mediated by plant hosts, influences C allocation to the soil microbial community. Enhanced understanding of plant interaction traits for AMF may provide insight into how host species affect the diversity and production of soil ecosystems (Bennett & Groten, 2022).

Compared with other mutualisms, plant-AMF interactions are not well understood, partly due to the many stochastic, abiotic, and biotic filters that affect community assembly (HilleRisLambers et al., 2012; Vályi et al., 2016). For example, root AMF communities vary based on the available AMF pool (Šmilauer et al., 2020), which is context-dependent (Šmilauer et al., 2021; Tylianakis et al., 2008) and influenced by soil properties (Gerz et al., 2016). Locally, host-specific AMF assemblages suggest that host identity plays a key role in determining AMF composition and biomass (Leff et al., 2018; Veresoglou & Rillig, 2014). Increasing evidence points to the role of host traits in plant-AMF niche partitioning. AMF colonization rates correlate with AM plant root traits (Bergmann et al., 2020), shaping plant interaction niches for AMF. For instance, grasses tend to host more AMF taxa than forbs in grasslands and may also differ in AMF colonization rates and composition (Sepp et al., 2019; Šmilauer et al., 2020). AM hosts may adopt various strategies in selecting the number and taxonomic composition of their mutualists because AMF vary in root colonization patterns and nutrient transfer abilities (Horsch et al., 2023; Lendenmann et al., 2011). Generalist hosts may benefit from the complementary effects of multiple AMF (Jansa et al., 2008; Koide, 2000), but these benefits come with trade-offs, such as higher carbon costs, especially when cheaters are present (Bever et al., 2009; Kiers & Denison, 2008). In some environments, forming specialized interactions with a few beneficial AMF may be advantageous (Werner & Kiers, 2015).

Distinct plant interaction niches for AMF can influence ecosystem C cycling both directly by altering AMF communities and indirectly through AMF-mediated effects on soil bacterial communities. Up to 40% of photosynthetic C is lost from plant roots as fatty acids (FAs), carbohydrates, and other metabolites, fueling the growth of the AMF mycelium and a complex, yet specific, community of rhizosphere bacteria (Jiang et al., 2017; Marschner & Baumann, 2003). Arbuscular mycorrhizal fungi also produce metabolites that alter the bacterial composition of their hyphospheres (Huang et al., 2023) and nutrient availability in soil (Zhang et al., 2020). Together, these processes create plant-soil feedback that shapes future plant community assembly (Crawford et al., 2019), ultimately influencing ecosystem carbon cycling on larger spatial and temporal scales. While plant interaction niches play a crucial role in structuring soil communities, detailed knowledge of their effects on C allocation to AMF and bacterial communities remains sparse.

Here, we characterized plant interaction niches with AMF, which we define using a range of diversity metrics to encompass the various facets of specialism/generalism. We sought to understand how these interaction traits affect AMF and bacterial biomass in rhizosphere soil. Firstly, we generated different biotic and abiotic filters on AMF community assembly by growing eight plant species under two experimental conditions. We test the hypothesis (Hyp_1) that plant species' interaction roles as AMF generalists or specialists are stable to these changes, comparing the multidimensional plant interaction niches under different experimental conditions by Procrustes analyses. Secondly, we sought to learn how plant interaction niches affect AMF biomass in rhizosphere soil. We expected interaction generalist hosts to be capable of greater C allocation to AMF due to their enhanced nutrient supply resulting from complementarity effects of their AMF communities (Jansa et al., 2008; Koide, 2000). In turn, we expected that higher rhizosphere AMF biomass would lead to a greater root-encounter probability and a greater proportion of the root system being colonized, increasing interaction generalism. We therefore test the hypothesis (Hyp₂) that host interaction generalism is positively associated with AMF biomass in rhizosphere soils. We quantified the abundance of the neutral lipid fatty acid (NLFA) 16:1w5 as a proxy for AMF biomass and modeled its response to plant interaction generalism, while accounting for plant phylogeny, root, and shoot biomass in a Bayesian framework. Finally, we explore the effect of host interaction generalism with AMF on bacterial biomass in the rhizosphere. While plant and AMF species may have differential effects on bacterial communities (Scheublin et al., 2010; Söderberg et al., 2002), we expected a positive relationship between soil bacterial biomass and plant interaction generalism due to complementary effects of many AMF on bacterial species. We therefore test the hypothesis (Hyp₃) that soil bacterial biomass would increase in response to plants' interaction traits associated with host generalism for AMF. We estimate bacterial biomass using phospholipid fatty acid (PLFA) analysis of bacterial biomarkers and model the effect of plant interaction traits, accounting for plant phylogeny, root, and shoot biomass in a Bayesian framework. Our study reveals how plant interaction traits affect the productivity of soil ecosystems, contributing to the understanding of how changes in biodiversity affect ecosystem C cycling.

METHODS

Glasshouse experiments

We conducted two glasshouse experiments, differing only in soil substrate and abiotic conditions, to characterize plant interaction niches for AMF and test hypothesis 1, enabling us to assess whether interaction niches are sensitive to soil and environmental conditions. Experiment

2 was used to determine whether interaction traits affect AMF and bacterial biomass in rhizosphere soil. We selected eight co-occurring plant species from the pasture site where field soil was collected. In each experiment, five replicates per plant species were grown in mesocosms, with each mesocosm consisting of a single plant seedling in a potting mix containing field-collected soil as the AMF inoculum source. Three plant-free mesocosms were used as controls. To create different filters on AMF community assembly, we collected field soil in different seasons and altered the potting mix composition for experiments 1 and 2. All mesocosms were maintained in a glasshouse for 16 weeks. At harvest, we collected the aboveground plant biomass and roots to determine dry weight. We sampled rhizosphere soil and randomly subsampled from the roots for later lipid extraction from both substrates and collected a small random subsample from the roots for later DNA extraction. For experiment 1, only root samples for DNA analysis were collected as described. Details on the study site, glasshouse experiment, and harvest can be found in Appendix S1: Section S1.

Characterizing the AMF community

To identify AMF in plant root samples, we extracted DNA and amplified the internal transcribed spacer 2 (ITS2) region of the eukaryotic ribosomal DNA by polymerase chain reaction (PCR) using primers ITS3 and ITS4 (Tedersoo et al., 2014). The PCR products were sequenced on the Illumina MiSeq platform. The resulting amplicon sequence variants (ASVs) were assigned a fungal taxonomy using the UNITE 8.2 (2020) database (Nilsson et al., 2019). We filtered the data to contain only sequences assigned to the subphylum Glomeromycotina, analyzing each ASV as a proxy for AMF species (Fu et al., 2022). To test whether the soil AMF community significantly differed between the soils collected in different seasons, we applied a permutational analysis of variance (PERMANOVA). See Appendix S1: Section S2 for details of molecular, bioinformatics, and sampling completeness steps.

Defining the plant-AMF interaction niche

Interaction partner diversity has multiple components, and each can be measured in different ways (Morris et al., 2014). To comprehensively describe plant interaction niches for AMF, we calculated eight diversity metrics based on AMF sequences from plant roots, encompassing different numeric and phylogenetic components of of α -, β -, and γ -diversity. These included mean AMF richness and Shannon's diversity index per plant species (numeric

α-diversities), along with the average mean phylogenetic distance (MPD) for all replicates per species (phylogenetic α-diversity). We also calculated the proportion of core AMF species (those present in ≥60% of replicates) per species (β[core]) and the number of compositional units of AMF per species (β[CU]) to represent numeric β-diversity. The mean UniFrac distance per species was used as a measure of phylogenetic β-diversity. Finally, by pooling replicates per species, we calculated the total number of unique AMF (numeric γ-diversity) and total MPD (phylogenetic γ-diversity). Details of interaction niche metrics are in Appendix S1: Section S3.

Stability of plant interaction niche for AMF

To examine if plant interaction niches for AMF were stable under different environmental conditions, we compared plant–AMF interaction niches in experiments 1 and 2. For each plant species, we created a table of the absolute values of the diversity metrics in each experiment and applied symmetric Procrustes analysis (Peres-Neto & Jackson, 2001) in *vegan* (Oksanen et al., 2022) to test the correlation of the plants' interaction niches in the two experiments. A permutational test using the maximal number of permutations and the function *protest* was used to assess the statistical significance of each correlation. To visualize plant–interaction niches for AMF in the two experiments, diversity metrics were scaled to vary between 0 and 1, from most specialist to most generalist plant species and plotted as stacked radar plots.

Quantifying microbial biomass

To test whether the widths of plant interaction niches ("specialism/generalism") affected C allocation to the soil microbial community, AMF and bacterial biomass were quantified using neutral lipid and phospholipid fatty acid (NLFA & PLFA) analysis. The NLFA 16:1w5 is strongly correlated with AMF structures in roots and soil (Sharma & Buyer, 2015) and serves as a reliable proxy for C allocation to AMF, as AMF cannot synthesize FAs and depend on the host for FA C14:0 (Luginbuehl et al., 2017). Soil bacterial biomass was estimated using 31 bacterial PLFA biomarkers (Appendix S1: Table S3). Lipids were extracted from lyophilised rhizosphere soil and root samples in experiment 2 following Lewe et al. (2021) with modifications described in Appendix S1: Section S4. Soil bacterial biomass and AMF biomass in soil and roots are reported as mean ± standard deviation. Significant differences among groups were assessed using ANOVA or, when assumptions were violated, a Kruskal-Wallis test.

Effect of host interaction niches on C allocation to AMF and bacteria

To test whether host interaction traits for AMF influenced C allocation to AMF and bacteria in soils, we used Bayesian linear mixed modeling. Since diversity metrics are somewhat interdependent, we applied principal components analysis (PCA) to extract uncorrelated linear recombinations of the eight diversity metrics used to characterize plant interaction niches, calculated per replicate. Principal components (PC) 1-3 collectively described 87.6% of the variation in plant niche space for AMF. We therefore modeled AMF and bacterial biomass in soils as a function of PC1, PC2, and PC3. To account for possible effects of plant biomass on C allocation to soil microbes, we included plant root and shoot biomass or their ratio (root: shoot) as covariates in the models. We also included total AMF biomass of the plant's root system as a covariate to account for possible differences in soil AMF biomass due to variation in root AMF biomass. Because plant species were unevenly distributed across three families, we accounted for phylogenetic nonindependence among samples by including a phylogenetic covariance matrix as a random effect. Plant species identity was also included as a random effect to account for plant functional traits not explained by phylogeny or root and shoot biomass. The best fit model was selected based on convergence and accuracy criteria, including using posterior predictive checks and leave-one-out cross-validation (LOO-CV) from all possible variable configurations (Vehtari et al., 2017). For the best fit model, we tested our hypotheses that plant interaction generalism with AMF increases soil AMF biomass (Hyp2) and soil bacterial biomass (Hyp3) by computing evidence ratios (i.e., the ratio of the posterior probability of each hypothesis against its alternative) for the model parameters associated with plant interaction generalism (PC1, PC2, PC2). Using the same approach, we also tested if specific diversity metrics were a better fit and selected the metric explaining the most variance along each PC axis. AMF and bacterial biomass were then modeled as functions of those diversities. All Bayesian models were fitted in brms (Bürkner, 2017). Details can be found in Appendix S1: Section S5.

RESULTS

Plant species have stable interaction niches for AMF

The eight plant species differed in their interaction niches with AMF, as evidenced by large differences in both absolute (Appendix S2: Tables S3–S6) and relative (Figure 1)



FIGURE 1 Radar plots comparing the relative interaction generalism of eight plant species as measured by eight interaction metrics (numeric and phylogenetic α -, β -, and γ -diversities) under different experimental conditions (experiments 1 and 2). We conceptualize the plant interaction niche for arbuscular mycorrhizal fungi (AMF) as the area of the radar plot occupied by each plant species in each experiment. Values for each metric are the means per plant species and were scaled between 0 and 1 for each experiment. CU, compositional units.

diversity metrics. Also remarkable was the similarity of plant interaction niches under both experimental conditions, despite the two soils having significantly different AMF pools at the start of the experiment (PERMANOVA $R^2 = 0.25, F = 2.02, p = 0.019$). Niches were similar even though the plants hosted very different taxa and AMF communities in the two experiments (Appendix S2: Figure S3), suggesting considerable stability of interaction niche for AMF in the plant species we studied (Figure 1; Table 1). For example, in both experiments, the grasses Holcus lanatus and Agrostis capillaris were interaction generalists for AMF, with high numeric α -diversity, while the Asteraceae members Achillea millefolium and Cichorium *intybus* were specialists relative to the other plant species tested. In contrast, Lolium arundinaceus was a phylogenetic generalist, characterized by high phylogenetic diversities, while Poa cita had intermediate diversity levels. Permutational Procrustes analysis of the absolute values of the eight numeric and phylogenetic diversities for plant species confirmed that plant interaction niches with AMF were significantly correlated across both experimental

conditions (Table 1), supporting hypothesis 1 and indicating niche stability.

AMF biomass in rhizosphere soil increases with phylogenetic plant interaction generalism

All plant species translocated substantial amounts of C into the AMF mycelium. The AMF biomarker NLFA 16:1 ω 5 was present in all root and rhizosphere soil samples, as well as in small amounts in plant-free control soils (0.32 ± 0.29 nmol g⁻¹ DW soil). Across rhizosphere soils, the AMF biomarker varied significantly from 5.71 ± 2.56 to 37.61 ± 13.07 nmol g⁻¹ DW soil (*H* = 15.8, df = 7, *p* = 0.027). However, similar amounts of the AMF biomarker in the roots of all species suggested comparable AMF colonization (Appendix S2: Table S7), with values varying from 1.45 ± 0.62 µmol g⁻¹ DW root in *C. intybus* to 4.81 ± 1.39 µmol g⁻¹ DW root in *Poa cita* (*F* [7, 28] = 2.35, *p* = 0.051).

The PCA of the diversity metrics revealed that numeric measures of α - and β -diversity (richness, Shannon's diversity, β [CU], and β [core]) were strongly associated with PC1, which explained 52.2% of the variation in the plant-AMF interaction niche space. PC2 explained 23.4% of the variation and corresponded to phylogenetic β -diversity (UniFrac), as well as numeric and phylogenetic γ -diversity. PC3, largely influenced by phylogenetic α -diversity (MPD),

TABLE 1 Permutational Procrustes analysis of plant interaction niches for AMF in experiments 1 and 2.

Plant species	m^2	Correlation coefficient p	p value
Agrostis capillaris	0.049	0.975	0.0002
Achillea millefolium	0.005	0.997	0.0001
Bromus willdenowii	0.003	0.999	0.0001
Cichorium intybus	0.011	0.994	0.0004
Holcus lanatus	0.066	0.966	0.0018
Poa cita	0.007	0.997	0.0002
Plantago lanceolata	0.012	0.994	0.0001
Lolium arundinaceus	0.005	0.997	0.0001

Note: Significant correlations are in bold.

Abbreviations: AMF, arbuscular mycorrhizal fungi; m^2 , Procrustes sum of squares.

accounted for an additional 12.0% of the variation (Appendix S2: Figure S4).

Our model for the AMF biomarker NL 16:1 ω 5 indicated strong evidence that PC3 and plant root biomass had significant positive effects on AMF biomass in rhizosphere soil (Figure 2; Appendix S2: Section S4). The final model explained 35% of the variation of the AMF biomass in rhizosphere soil (Bayes $R^2 = 35.4 \pm 10.5\%$). The retention of root biomass but not total root AMF biomass as a covariate in the final model suggests that C allocation to AMF is greatest for species with large root systems, regardless of AMF colonization levels. However, the effect of root biomass was more variable than that of PC3. These results provide partial support for hypothesis 2, indicating that while interaction generalist hosts allocate more C to soil AMF, this relationship is primarily driven by the phylogenetic α -diversity aspect of interaction generalism.

Bacterial biomass in rhizosphere soil decreases with numeric plant interaction generalism

Rhizosphere bacterial biomass varied significantly among plant species (H = 15.5, df = 7, p = 0.003) ranging from 14.66 ± 4.39 nmol g⁻¹ DW soil for *P. lanceolata* to



FIGURE 2 Predicted changes in arbuscular mycorrhizal fungi (AMF) biomass (NLFA 16:1 ω 5) in rhizosphere soil as a function of principal component 3 (PC3) and root biomass (n = 32). PC3 represents phylogenetic diversity, suggesting that these aspects of the plant interaction niche for AMF are associated with positive changes in AMF biomass in the rhizosphere. Root biomass was modeled as covariate, but is visualized here at three levels (mean root biomass \pm standard deviation, uncertainty interval = 0.5). Final model: AMF biomass ~ PC3 + root biomass.



FIGURE 3 Predicted changes in soil bacterial biomass as a function of principal component 1 (PC1) modeled for three levels of shoot and root biomass, uncertainty interval = 0.5 (n = 32). PC1 represents numeric α - and β -diversity (richness, Shannon's diversity, β [CU] and β [core]), suggesting that these aspects of the plant interaction niche for arbuscular mycorrhizal fungi are negatively associated with bacterial biomass in rhizosphere soils (Best model: Soil bacterial biomass ~ PC1 + root biomass + shoot biomass). Bacterial biomass was estimated using phospholipid fatty acid (PLFA) analysis.

31.00 \pm 6.30 nmol g⁻¹ DW soil for *Cichorium intybus* (control soil: 14.02 \pm 4.52 nmol g⁻¹ DW soil; Appendix S2: Table S7). The best model for bacterial biomass explained 49% of the variance (Bayes $R^2 = 49.2 \pm 9.0\%$) and, contrary to our third hypothesis, showed a strong negative effect of PC1 on bacterial biomass. Bacterial biomass in rhizosphere soils was affected by plant shoot and, to a lesser extent, root biomass (Figure 3, Appendix S2: Section S5).

DISCUSSION

We found that pasture plant species exhibit stable interaction niches for AMF, even under varying environmental conditions. Our comprehensive characterization of plant–AMF interaction niches provides novel insight into how plant niche partitioning for interaction partners affects C allocation to soil microbial communities. We show that C allocation to AMF and bacteria is associated with different aspects of the plant interaction niche. Further, we show that interaction generalism had opposite effects on AMF and bacterial biomass in soils. Below, we discuss these results in detail and explore how plant interaction niches for AMF may impact ecosystem C cycling.

We found remarkable similarity in plant species' interaction niches in experiments 1 and 2, supporting our

first hypothesis, despite that different edaphic conditions and AMF inoculum pools used in the two experiments generated substantial differences in the taxonomic composition of AMF communities of plant species. Although rhizosphere AMF communities respond to edaphic conditions (Davison et al., 2021) and available AMF pools (Van Geel et al., 2018), the stability of plant interaction niches suggests that plants exhibit fundamental interaction niches for AMF. This observation is consistent with findings from plant-pollinator networks, where species retain their interaction niches moving from their native to alien ranges (Emer et al., 2016). However, given that only eight plant species in two experiments were compared, further work is needed to confirm the general stability of plant interaction traits for AMF. Nonetheless, our findings suggest that plant interaction generalism for AMF could serve as a useful functional trait (Funk et al., 2017) for understanding how interactions with soil organisms drive ecosystem processes.

Our multidimensional approach to interaction generalism allowed us to resolve niche partitioning among generalist hosts for AMF partners. We found that generalists partitioned interaction trait space through variation in numeric and phylogenetic AMF diversity, which likely involves distinct trade-offs. Niche partitioning may occur as plants select the most beneficial AMF partners (Werner & Kiers, 2015) or interact with AMF exhibiting diverse nutrient acquisition strategies (Powell & Rillig, 2018). Thus, plant niche partitioning for AMF partners may significantly contribute to maintaining ecosystem functional diversity (Dehling et al., 2021), enhancing ecosystem resilience to environmental change (Turnbull et al., 2016).

We found some support for our second hypothesis that plant interaction generalism for AMF is positively related to AMF biomass in the rhizosphere. However, the increase in soil AMF biomass was driven by the phylogenetic α -diversity aspect of host interaction generalism. Phylogenetically diverse AMF communities are linked to higher variability in traits like hyphal growth (Hart & Reader, 2002) and nutrient acquisition (Horsch et al., 2023). This may suggest that complementarity among AMF taxa increased C allocation to the rhizosphere. Alternatively, interaction generalists hosting diverse AMF taxa may have been less able to downregulate C flow to less favorable mutualists (Grman, 2012) making them more susceptible to cheaters (Kiers & Denison, 2008). Indeed, the significant positive effect of $\beta(CU)$, which reflects heterogeneity of AMF among replicates of a host species, supports the idea that generalist hosts may have been less selective for beneficial AMF. Root biomass, rather than AMF biomass in roots, was an important covariate. While root traits (e.g., diameter, branching) influence plant interaction niches for AMF (Bergmann et al., 2020; Ramana et al., 2023), our results likely reflect that plants with higher root biomass provide more habitat for AMF (Sweeney et al., 2021). Greater habitat availability can reduce competition, favoring higher AMF diversity (Bergmann et al., 2020; Mony et al., 2021). Given the role of AMF in C sequestration into the soil organic C pool (Zhu & Miller, 2003), the relationship between soil AMF biomass and the phylogenetic diversity aspect of plant interaction generalism highlights the importance of generalist plants in regulating C flux between the atmosphere and biosphere.

Contrary to our third hypothesis, we found that interaction generalist plants were associated with lower bacterial biomass in rhizosphere soils. The interactions between plants, AMF, and bacteria in the hyphosphere and rhizosphere are complex, with both plants and AMF releasing compounds that can affect bacterial taxa either positively or negatively (Bharadwaj et al., 2012; Changey et al., 2019). Furthermore, AMF and soil bacteria often compete for resources, and AMF can outcompete bacteria in the rhizosphere as AMF hyphae can significantly reduce bacterial access to nutrients (Bukovská et al., 2018). Indeed, the effect of AMF on bacteria strongly depends upon the nutrient status of the host plant and AMF (Huang et al., 2023; Lanfranco et al., 2018). The positive effect of nutrient limitation on plant C allocation to mycorrhizas is well known (Huang et al., 2023). Under nutrient-limited conditions, plants hosting large AMF communities may generate strong competitive effects on rhizosphere bacteria. In our study, nutrient limitation was likely, as mesocosms consisted primarily of sand with only small amounts of field soil as inoculum and no mineral nutrient supplementation. Despite ample light, the relatively small plant size at harvest suggests nutrient stress. Root and shoot biomass were significant covariates in our bacterial biomass model, indicating that larger plants were associated with larger bacterial communities. Together, these findings suggest that competition between AMF and bacteria for C limited bacterial biomass in our study.

We sought a better understanding of plant interaction niches for AMF and their effects on soil microbial biomass. We demonstrate that, despite variation in environmental conditions, plant interaction niches for AMF were stable relative to other plants in their community. This aligns with niche theory and other studies of plant functional traits (Funk et al., 2017) and interaction traits in other types of networks (Emer et al., 2016). However, under field conditions, we expect realized plant-AMF interaction niches to be shaped by various filters on community assembly including biotic and stochastic factors like priority effects and plant-soil feedbacks (HilleRisLambers al., 2012). et Under the nutrient-limited conditions of our experiments, we found that plants with high phylogenetic interaction generalism were associated with higher soil AMF biomass, while high numeric interaction generalism was linked to lower bacterial biomass, suggesting strong AMF-bacterial competition for C in the rhizosphere. These findings align with well-described patterns in community and ecosystem ecology, such as greater fungal-to-bacterial biomass (Wardle et al., 2004) and plant-mycorrhizal dependence (Huang et al., 2023) under nutrient limitation. Nonetheless, over 50% of the variance in AMF and bacterial biomass remains unexplained, suggesting that other factors may also play important roles. We propose that plant interaction niches for AMF are a promising new avenue to enhance understanding of how plant traits alter key ecosystem functions, such as C cycling.

ACKNOWLEDGMENTS

This research was supported by a Marsden Fast Start Fund (15-VUW-069) awarded to Julie R. Deslippe and Jason M. Tylianakis. Natascha Lewe was supported by a Victoria University of Wellington (VUW) Doctoral Scholarship. We appreciate Jan Vorster's assistance with GC-MS inquiries, the team from "Rāpoi," VUW's High Performance Computing system, and Dr. Lisa Woods for her valuable

feedback on Bayesian modeling. We thank Maedeh Jafari Rad and the Deslippe lab group for their help in setting up and harvesting glasshouse experiments. Open access publishing facilitated by Victoria University of Wellington, as part of the Wiley - Victoria University of Wellington agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The sequencing data are available in the National Center for Biotechnology Information (NCBI) under accession number PRJNA997080 at https://www.ncbi.nlm.nih.gov/ bioproject/PRJNA997080. Code (Lewe, 2024) is available in Zenodo at https://doi.org/10.5281/zenodo.14248920.

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SUPPORTING INFORMATION

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How to cite this article: Lewe, Natascha, Robert A. Keyzers, Jason M. Tylianakis, and Julie R. Deslippe. 2025. "Plant Interaction Traits Determine the Biomass of Arbuscular Mycorrhizal Fungi and Bacteria in Soil." *Ecology* 106(2): e70011. https://doi.org/10.1002/ecy.70011