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RESEARCH ARTICLE

Soil mycobiome dissimilarity, independent of fungal guild, is associated with increased probability of plant coexistence

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Abstract

1. Major theories regarding microbe-mediated plant community dynamics assume that plant species cultivate distinct microbial communities. However, few studies empirically assess the role of species-associated microbial community dissimilarity in plant competitive dynamics.
2. In this study, we paired a competition experiment between eight annual forbs with characterisation of species-associated fungal communities to assess whether mycobiome dissimilarity is associated with pairwise competitive dynamics.
3. Using a quantitative approach informed by modern coexistence theory, we found that fungal dissimilarity was correlated with both increased stabilising niche differences and fitness inequalities. Additionally, we found that the probability of coexistence increased with mycobiome dissimilarity.
4. When subsetting the community into different fungal functional groups (pathotrophs, saprotrophs, symbiotrophs), overall relationships between dissimilarity and competitive dynamics were independent of these functional groups.
5. *Synthesis*. These results suggest that fungal community divergence may play an important role in mediating plant competitive dynamics. Although fungal community dissimilarity is associated with both niche and fitness differences, complex biotic and/or abiotic interactions below-ground may result in an observed correlation between fungal community dissimilarity and plant coexistence. Ultimately, this study suggests a novel approach to better understanding how microbiome dissimilarity may impact host community dynamics.

KEYWORDS
coexistence theory, fitness inequalities, niche differences, plant-fungal interactions, plant-microbiomes

1 | INTRODUCTION

Interactions between plants and microbes have been central to many key hypotheses in plant community ecology (Bever et al., 1997; Keane & Crawley, 2002; Terborgh, 2020). Although definitive tests of whether microbes structure plant communities remain challenging (Harris, 2009), there is growing evidence that feedbacks link the structure of plant communities to that of soil microbial communities (Bauer et al., 2017; Fahey et al., 2020). Theory has shown how plant-microbe interactions may mediate plant community dynamics (Ke & Wan, 2020; Schroeder et al., 2020), and emerging sequencing technologies have expanded our understanding of interactions

between plants and their microbial communities (Liu et al., 2012; Rallo et al., 2023; Wilschut et al., 2019). Still, the discrepancy between the pace of theoretical and empirical research leaves many unexplored opportunities for the integration of theory and molecular characterisation of microbial communities.

Theories explaining how plant-microbe interactions scale up to influence plant community dynamics commonly assume that different plant species cultivate unique microbial communities. While there is growing empirical support that plant species are important indicators for soil microbial communities (Burns et al., 2015; Dagher et al., 2019; Fox et al., 2020), it remains unclear why plant species microbiomes differ. For example, the relationship between plant phylogeny and plant-microbe interaction similarity has received mixed support (Mehrabi & Tuck, 2015; Sweet & Burns, 2017), suggesting that phylogenetic relatedness per se may not be able to explain the role of species-specific microbial communities in mediating plant community dynamics. Thus, understanding exactly how dissimilarity of plant-associated microbial communities mediates plant–plant interactions remains necessary for describing how microbes may structure plant communities.

The ability of species to coexist in communities is generally related to trait differences among the species, as formalised by advances in quantitative ecology now referred to as modern coexistence theory (Chesson, 2000). Modern coexistence theory explores the mechanisms that maintain species coexistence by partitioning species differences into niche differences and fitness inequalities. While fitness inequalities describe intrinsic differences between species in their performance in a given context, niche differences are species differences that stabilise competitive dynamics by causing species to limit themselves more so than they limit their competitors (Adler et al., 2007). Whether two species are able to coexist depends on whether their niche differences are sufficiently large as to overcome their fitness inequalities (Blackford et al., 2020; Godoy & Levine, 2014; Kraft et al., 2015). Importantly, any trait difference that influences species interactions, by definition, alters both niche and fitness differences (Song et al., 2017), so quantifying the degree to which a given trait influences niche and fitness difference respectively is an important yet still understudied goal for community ecologists. Here, we contribute to this objective by treating dissimilarity between species' microbiomes as a trait difference (corresponding to ideas about microbiomes as extended phenotypes (de la Fuente Cantó et al., 2020)). Thus, the degree of dissimilarity in species' microbiomes may either stabilise coexistence (by increasing niche differences) or destabilise coexistence by increasing fitness advantages of one species over another. In fact, the importance of microbe-mediated fitness differences in plant–soil feedbacks has gained recent support (Yan et al., 2022).

The mechanisms by which plant microbiome dissimilarity may impact plant competition are related to the diverse array of functionally distinct microbial taxa. The hypotheses proposed for how particular functional groups of microbes may impact plant communities often depend on the degree of species-specificity of the microbial taxa (Bever et al., 2010; Semchenko et al., 2022). For example, species-specific plant-pathogens are hypothesised to induce negative intra-specific density-dependent feedbacks that contribute to niche differences and promote coexistence, but shared generalist pathogens may also affect inter-specific interactions and affect both niche and fitness differences (Mordecai, 2013). Conversely, plant mutualists may induce positive feedbacks, increasing fitness differences between species, if their benefit to the host plant differs across plant species (Zhang et al., 2010). However, species-specific mutualists and saprotrophs may also stabilise competitive interactions if they mediate resource partitioning among competitors (Barry et al., 2019). The role of these different functional groups in mediating plant interactions requires further empirical study.

To elucidate the role of microbiome divergence in plant community dynamics, we paired a common garden competition experiment with molecular characterisation of plant species' mycobiomes (fungal component of the microbiome). We hypothesised that mycobiome dissimilarity would be associated with both increased niche and fitness differences. However, because recent research has identified a larger role of plant-associated microbes in mediating fitness inequalities (Kandlikar et al., 2021), we hypothesised that mycobiome divergence would promote exclusion by increasing fitness inequalities more so than niche differences. Finally, we hypothesised that the relationship between mycobiome dissimilarity and competitive dynamics would differ across the functional groups of plant-associated fungi.

2 | MATERIALS AND METHODS

2.1 | Competition experiment

In November 2021, in partnership with the Friends of Buford Park Native Plant Nursery, in Lane County Oregon, we set up a common garden competition experiment with the goal of measuring intraspecific and interspecific competitive effects across all pairwise combinations of eight species: *Acmispon americanus* (Nutt.) Rydb., *Calandrinia ciliata* (Ruiz & Pav.) DC., *Clarkia amoena* (Lehm.) A. Nelson and J.F. Macbr., *Clarkia purpurea* (W. Curtis) A. Nelson and J.F. Macbr., *Collomia grandiflora* Douglas ex Lindl., *Navarretia intertexta* (Benth.) Hook., *Plagiobothrys nothofulvus* (A. Gray) A. Gray and *Plectritis congesta* (Lindl.) DC. All species are native annual plants that occur in upland prairies throughout the Willamette Valley, Oregon. This ecosystem has a cool, wet winter and warm, dry summer, so species are adapted to germinate in the fall and winter after the first significant rains, and persist through the following summer. Additionally, all species were actively being grown for seed production in nearby monoculture plots at the nursery.

For each species, we established a background competitor plot in which a single background species was sown. Each plot was subdivided into three 0.8×1.0 m subplots that varied in the density of the background competitor. Background plots were separated by about 0.5 m of weed cloth. We sowed different numbers of seeds of each species (measured out by weight) in order to achieve the desired

density gradient. All analyses of density are based on counted numbers of adult plants in each competitive neighbourhood, not the density of seeds sown. In addition to the background species, seeds of each of the eight species were sown into each subplot and later thinned such that each subplot contained two focal individuals of every species. Thus, for each species, two focal individuals experienced competition at low, medium and high density from each of the other seven species as well as from its own species. Additionally, two 'alone plots' were established, in which two individuals of each of the eight species grew in the absence of a background competitor, to help estimate the performance of each species in the absence of competition (λ, below).

In April 2022, the number of competitors growing within a circle with a 19 cm radius around each focal individual was recorded. In the summer of 2022, we harvested focal individuals at the end of the season, after the last spring rains, defined as the apparent cessation of growth and new reproduction. To estimate fitness (seed output) for each focal individual, we counted the number of flowers or inflorescences on each focal plant and combined this with estimates of seeds per flower or inflorescence, similar to Wainwright et al. (2019) and Bimler et al. (2018). For those species that produce inflorescences, we counted the number of flowers per inflorescence for a random sample of at least 500 inflorescences and used those averages to estimate the number of flowers for the rest of the individuals. For species that produce multiple seeds per fruit, we similarly counted the number of seeds per fruit for a random sample of at least 80 fruits and used those averages to estimate the number of seeds for the remaining individuals of that species.

2.2 | Soil sequencing

In July 2022, we collected five 1 × 10 cm soil cores from monoculture plots where each species had been growing alone for 2 or 3 years. These monoculture plots were established by the nursery and offer a unique field-based analog to the 'culturing' phase of many plant–soil feedback experiments, for quantifying each species' microbial signature. In addition, we collected soil cores from the competition experiment directly after harvesting the focal species. Cores were collected directly under focal plants from the experimental con-specific competition plots (2 plants × 3 con-specific competition plots = 6 soil cores) and the competition-free control plots ($n = 4$), for a total of 15 soil cores per species. Soils were transported to the University of Oregon and stored at −20°C for no more than 9 months.

Individual soil cores were homogenised, and genomic DNA was extracted from 0.25 g of soil using DNEasy PowerSoil kits (Qiagen). The fungal ITS1 region was targeted using primers ITS1F (Gardes & Bruns, 1993) and ITS2 (White et al., 1990). Primers, barcodes and Illumina adapters were annealed through a two-step PCR. The first PCR was a 20 uL reaction with Promega GoTaq Green (10 uL), nuclease-free H_2O (7.9 μL), 0.5 μL of each primer with TruSeq stubs incorporated, bovine serum albumin (BSA; 0.1 μL) and 1 μL of genomic DNA template. The thermocycler was run for one cycle at 94°C for 3 min, 30 cycles of 94°C for 45 s, 54°C for 1 min, 72°C for 1.5 min and one cycle at 72°C for 10 min. The second PCR annealed Illumina-specific adaptors and multiplexed samples using the iTag protocol developed by the California Institute for Quantitative Biosciences at UC Berkeley. Samples were run in the thermocycler for one cycle of 94°C for 3 min, 12 cycles of 94°C for 45 s, 52°C for 1 min, and 72°C for 1.5 min, followed by one cycle at 72°C for 10 mins. Following each PCR, the PCR products were visualised on a 1% agarose gel. Samples were pooled in equimolar concentrations (~1.5 ng DNA per sample). Pools were then purified using Omega Mag-Bind TotalPure NGS Beads at 0.8x uL concentration of beads per pool. Sequencing was performed on a shared Illumina MiSeq lane using the v3 mode, which synthesises paired-end reads up to 300 bp in length. This run configuration produces up to 25 million reads per lane, making the target sequencing depth 30 k reads per sample for these samples.

Resulting sequencing depth averaged 27,947 ± 18,782 reads per sample. Meanwhile 3.15 million forward and reverse reads were demultiplexed, and primers were removed using cutadapt v. 4.4 (Martin, 2011). Raw reads were quality filtered using the DADA2 bioinformatics pipeline, adapted to account for interspecific variation in ITS1 region lengths in fungi (Callahan et al., 2016). Primers were trimmed with cutadapt v. 4.4 (Martin, 2011). Reads less than 50 bp were filtered out, and those with maximum expected errors greater than two for both forward and reverse reads were removed. Amplicon sequence variants (ASVs) were inferred using DADA2's core denoising algorithm, after which forward and reverse reads were merged. Chimeras were detected de novo using DADA2's isBimeraDenovo, which is more sensitive to nearby chimeras compared to other chimera detection algorithms, making it better suited for ASVs. Taxonomy was assigned to 5124 ASVs using the naïve Bayesian classifier method (Wang et al., 2007) with the UNITE fungal reference database (Nilsson et al., 2019). Samples were rarefied to 1953 reads. Low abundance ASVs (<5 reads/sample and occurrence in <5% samples) were removed per sample, leaving a total of 658 ASVs and a mean of 177.91 ASVs per sample. Ecological functions of ASVs were assigned using FUNGuilds (Nguyen et al., 2016), keeping only assignments labelled as probable or highly probable. Classifications were broadly defined as pathotroph, saprotroph and symbiotroph (including mutualists like mycorrhizal fungi as well as presumably commensalist endophytes). Because FUNGuild may classify taxa as any combination of these three guilds, we included any taxa that could be a given guild when subsetting the dataset by guild (e.g. a pathotroph/saprotroph taxon would be included in both the pathotroph and saprotroph datasets).

2.3 | Statistical methods

2.3.1 | Calculating coexistence

To estimate key demographic parameters involved in predicting competitive outcomes for each of the 28 species pairs, we fit

population models for each of the eight species. We fit three different population models that varied in how competition affects fecundity (Beverton-Holt, Lotka-Volterra, & Ricker), and ultimately used parameter estimates from the Beverton-Holt model (Hart et al., 2018) as it fit our data the best (description of model selection in Appendix S1). Competition coefficients were constrained to be competitive during parameter estimation (>0) because downstream analyses assume competitive interactions and because there was no apparent facilitation except for one interaction coefficient (Appendix S1). Thus, we fit population models with the following structure:

$$N_{i,t+1} = N_{i,t}\frac{\lambda_i}{1+\alpha_{ii}N_i+\alpha_{ij}N_j}, \quad (1)$$

which models next year's population size of species i $(N_{i,t+1})$ as the product of the current population size of species i and the per capita fecundity. Fecundity is defined as species i's growth rate in the absence of competition (λ_i) divided by the number of competitors and their associated per capita competition coefficients (α_{ij}).

From this model, we estimated λ for each species as well as all αs for all pairwise combinations of species to calculate niche and fitness differences. Following Godoy et al., 2014, we used these parameters to calculate niche overlap between each pair of species as:

$$\rho = \sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}} \quad (2)$$

and niche differences were calculated as $1-\rho$. We then calculated the fitness inequalities:

$$\frac{\kappa_j}{\kappa_i} = \frac{\lambda_j}{\lambda_i}\sqrt{\frac{\alpha_{ij}\alpha_{ii}}{\alpha_{ji}\alpha_{jj}}}, \quad (3)$$

where species j is the competitively superior species within the species pair. Note that unlike Godoy et al., 2014, we do not include germination or seed survival parameters (Dostál 2023). Thus, the fitness inequalities are equivalent assuming that germination and seed survival rates are 1 (though our results are rather insensitive to the assumed value; Appendix S1: Figure S1). We estimated these parameters using Bayesian hierarchical modelling in RStan (Stan Development Team, 2023) and used noninformative priors for all parameters. To propagate uncertainty in parameter estimates to inference about competition and coexistence, we retained 5000 samples from the distributions of both niche differences and fitness inequalities to use in subsequent analyses.

2.3.2 | Characterising fungal communities

Using the fungal community data, we first assessed whether plant species influenced microbial community structure using PERMANOVAs with Bray–Curtis dissimilarity which included plant species, sample type (monoculture or experimental) and an interaction between species and sample type. We paired these statistical tests with NMDS ordinations to visualise fungal community compositional differences. We repeated this procedure with pathotroph, saprotroph and symbiotroph subsets of the dataset.

To estimate the mean dissimilarity between plant species' associated fungal communities, we first computed a distance matrix between all samples using Bray–Curtis dissimilarities. We then estimated the mean dissimilarity within samples for each species as well as between species. We repeated this procedure for pathotroph, saproptroph and symbiotroph communities. Posterior distributions of these average dissimilarities were retained to use in subsequent analyses. We also assessed the degree to which mean fungal dissimilarity (total and guild specific) was predicted by plant phylogenetic dissimilarity by fitting linear models with phylogenetic distances retrieved from V.PhyloMaker (Jin & Qian, 2019). Residuals from this model were used to ensure subsequent analyses were not biased by any phylogenetic signature. Methods and results for these phylogenetic analyses can be found in Appendix S2.

2.3.3 | Assessing dissimilarity/competition relationship

To assess whether fungal community dissimilarity is associated with competition strength (α_{ij}), we fit linear models using random pulls from the posterior distribution of the α_{ij} parameter as a response variable and mean dissimilarity estimates as a predictor. To propagate the uncertainty in both population parameters and our estimated average fungal community dissimilarity, we repeated this process 5000 times, generating distributions that quantify the uncertainty in association between competition coefficients and microbial dissimilarity. Although excluded from subsequent models, these competition models include the mean dissimilarity within species (D_{ii}), representing the degree of variability within a species' associated soil microbiome. We repeated this process with all competition coefficients as well as either inter- or intraspecific competition coefficients.

To assess how niche and fitness inequalities are related to fungal dissimilarity, it is necessary to take into account that, according to theory, niche differences must range from negative infinity to one and fitness inequalities range from one to infinity. Therefore, instead of fitting linear models (which would make predictions outside of these ranges), we fit exponential models for niche and fitness differences that conformed to their natural asymptotes but were also free to vary in the direction and magnitude of their growth/decay rate (see Appendix S3 for further rationale and interpretation of results). Thus, the function for niche differences was:

$$1-\rho = 1 + a_{ND}\cdot e^{D_{ij}k_{ND}}, \quad (4)$$

where k_{ND} is the growth/decay rate at which niche differences changed with increasing dissimilarity, D_{ij}. We bound the intercept

parameter a_{ND} to be negative, which constrains this function to remain below the asymptote of one. Given this constraint, negative values of k_{ND} represent a positive relationship between dissimilarity and niche differences.

Similarly, we fit an exponential model for fitness inequalities with the structure:

$$\frac{\kappa_j}{\kappa_i} - 1 = a_{FI} \cdot e^{D_{ij} k_{FI}}, \quad (5)$$

where we bound a_{FI} to be positive, constraining the predicted fitness inequalities to be greater than the asymptote zero. Thus, positive values of k_{FI} represent a positive relationship between dissimilarity and fitness inequalities. We fit similar models for the competitive ratio $\left(\sqrt{\frac{\alpha_{jj}\alpha_{ji}}{\alpha_{ii}\alpha_{ij}}}\right)$ and the demographic ratio $\left(\frac{\lambda_i}{\lambda_j}\right)$ to identify whether an association with increased competitive ability or demographic performance drove the potential trend in fitness inequalities. For each of these models, we again fit models using 5000 random pulls from the posterior distributions of niche and fitness differences and competitive and demographic ratios and mean fungal community dissimilarities to generate distributions of a and k. To assess whether niche differences or fitness inequalities changed more or less steeply with fungal community dissimilarity, we constructed a contrast distribution by subtracting the absolute values of k_{ND} and k_{FI}. Finally, to evaluate the effect of fungal dissimilarity on the probability of coexistence, we first calculated coexistence probability as the proportion of posterior samples from the demographic models that predicted coexistence given the following criterion for coexistence reported in Chesson & Kuang, 2008:

$$\rho < \frac{\kappa_j}{\kappa_i} < \frac{1}{\rho}. \quad (6)$$

We fit a quasi-binomial regression using random pulls from the posterior distribution of mean fungal community dissimilarities and the calculated coexistence probabilities (a fractional response variable including values of zero and one). For each draw from the posteriors, we fit a glm using the glm() function in R with a logit link function, yielding a distribution of the relationship between coexistence probability and microbiome dissimilarity that takes into account underlying uncertainties in the estimates of each variable. The coexistence criterion (Equation 6) was also used for determining the required niche differences for coexistence based on our predicted fitness inequalities (from the fitted asymptotic model of fitness inequalities as a function of mycobiome dissimilarity).

2.3.4 | Assessing transferability of models

It is not uncommon to find very little predicted coexistence for species pairs in competition experiments despite their known co-occurrence in the field (Kraft et al., 2015). This discrepancy may influence our confidence that any coexistence mechanisms identified within experiments translate well to field systems. Thus, we have conducted additional analyses to try to explain any discrepancies between the predictions from our population models and known co-occurrence patterns of our species pairs. Many mechanisms of coexistence in the field are, by design, absent from isolated experiments. However, we were able to investigate two other potential sources of this discrepancy: (1) poor model fit (Armitage, 2022) and (2) the omission of stabilising indirect species interactions (Saavedra et al., 2017). Our model selection procedure outlined above and in Appendix S1 serves as an attempt to limit the potential for poor model fit to influence our results, and we provide additional information regarding the posterior predictions of our population models within Appendix S1 to further contextualise our results.

To quantify the degree to which indirect interactions may lead to more or less coexistence than predicted by our pairwise approach, we have additionally implemented the structural approach for multispecies coexistence (Saavedra et al., 2017). Using this approach, we can assess which species might feasibly coexist as well as the degree to which indirect interactions underlie multispecies coexistence. To do this, we calculated the percent of species combinations across all possible n-species combinations that were predicted to feasibly coexist. We also calculated the community-pair differential, a metric that describes the degree to which n-species coexistence is more or less feasible than the coexistence of the component species pairs (Saavedra et al., 2017). For both the percent of feasible combinations and the community-pair differential, we repeated these calculations across all samples from our posterior distributions.

3 | RESULTS

3.1 | Species effect on fungal community composition

The composition of fungal communities in soil samples varied among both plant species and sample type (monoculture vs. experimental) (Figure 1). We found stronger evidence for an association between composition and sample type ($p < 0.001$; $F = 7.4655$; $R^2 = 0.0582$) than that of composition and species ($p = 0.002$; $F = 1.6102$; $R^2 = 0.0879$). Importantly, results from a PERMANOVA for the entire fungal community suggest an interaction effect between species and sample type ($p < 0.001$; $F = 1.7874$ $R^2 = 0.0976$). Because the effect of species depends on differences between the experimental and monoculture plots, we report analyses using both sample types aggregated into one dataset in the main text and include analyses using each sample type separately in Appendix S4. Further, a model with the z-scores of mean fungal dissimilarity and phylogenetic distance between species pairs showed a positive relationship between phylogenetic distance and fungal dissimilarity (Median Estimate = 0.57; 95% CI [0.21, 0.92]; R^2 = 0.31; Appendix S2: Figure S1). These results were similar when segregating the community into trophic mode, but the average distances between plant species's fungal communities varied across the trophic modes (Appendix S5: Figure S1).

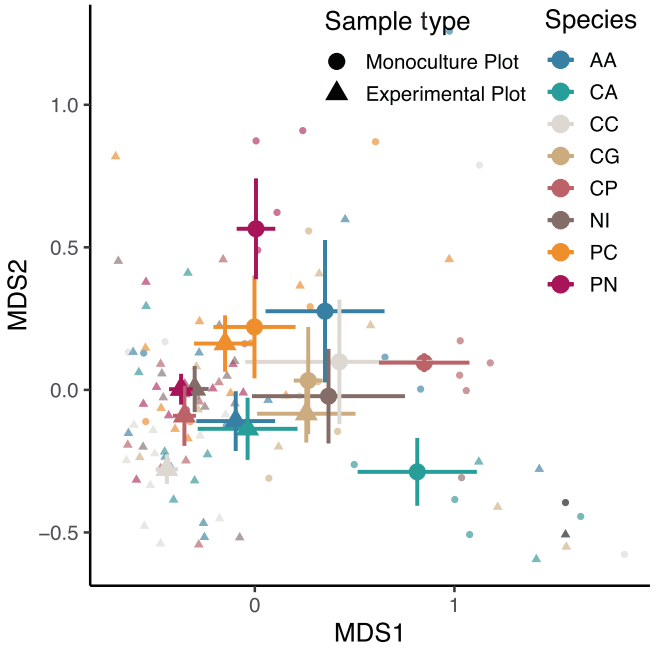

FIGURE 1 Non-metric multidimensional scaling using Bray–Curtis dissimilarities of total fungal community composition across all samples. Small transparent points represent sample scores; larger solid points represent the average scores with error bars equal to one standard error. Shape of points represents which plots samples came from, and colour represents which species samples are associated with.

3.2 | Plant population models and coexistence outcomes

Out of the four model structures we assessed, the Beverton-Holt model provided the best fit to the data (Appendix S1), so we used parameter estimates from this model for all downstream analyses. Median estimates of niche differences between the 28 species pairs were variable (Median = 0.41; Standard Deviation = 0.47). Although most species pairs had positive niche differences, four species pairs had negative niche differences, suggesting destabilised interactions. Median estimates of fitness inequalities also varied across species pairs (Median = 5.66; Standard Deviation = 33.60). Species pairs varied in their expected outcome of competition, and thus, varied in their probability of coexistence (Figure 2). Predictions made from the medians of parameters' posterior distributions suggest that competition between three species pairs result in coexistence, 25 species pairs result in exclusion, and no species pairs result in priority effects.

3.3 | Fungal dissimilarity and competitive dynamics

Overall, there was no relationship between fungal community dissimilarity and competition strength (Median = −0.61; 95% CI [−4.88, 3.43]). Similarly, when divided into intra- and inter-specific

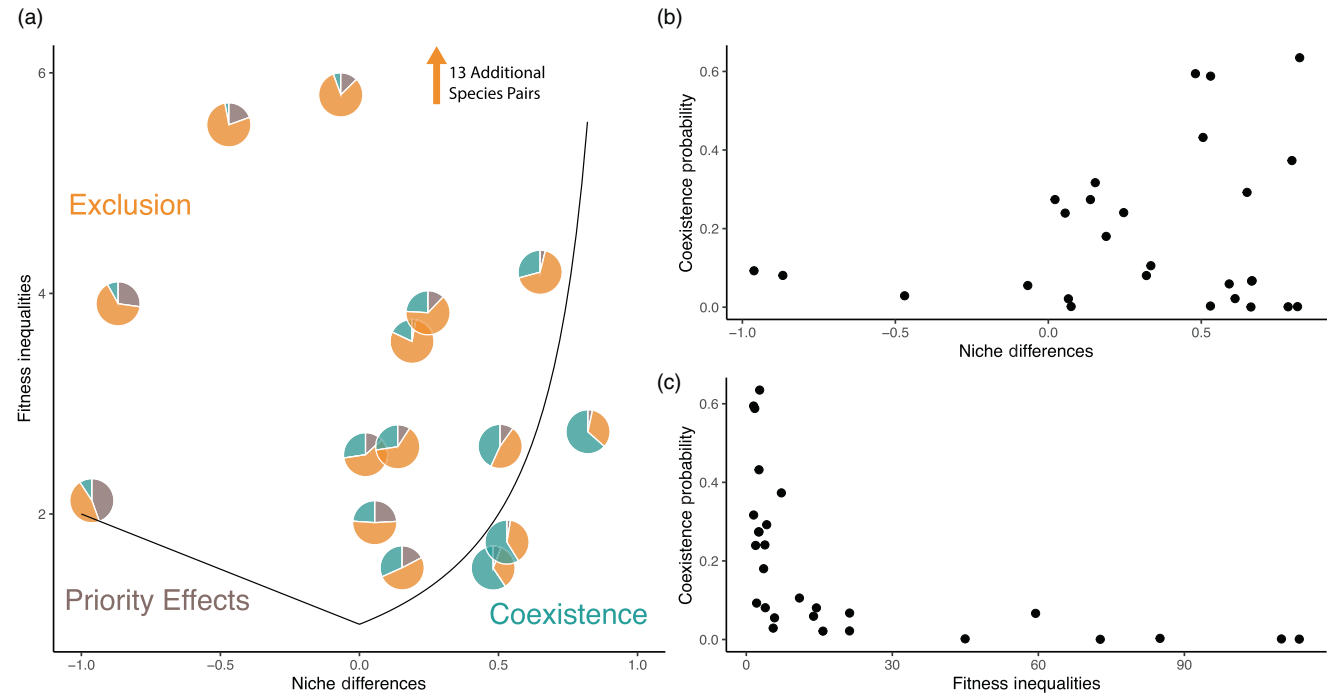

FIGURE 2 (a) Scatterpie plot of niche differences and fitness inequalities. Each point is a pie chart representing the probability of each competitive outcome (coexistence, exclusion or priority effects) for a given species pair. Probabilities were calculated as the proportion of posterior samples corresponding to each outcome. Position of the pie charts corresponds to the median of the distributions of niche difference and fitness inequality. Black lines represent the inequalities between niche and fitness differences that partition the outcomes (from Equation 6). Thirteen species pairs were excluded from this graph but had large fitness inequalities and high probabilities of exclusion. (b) Niche differences and (c) fitness inequalities plotted against the coexistence probability for all 28 species pairs.

competition, fungal community dissimilarity was not associated with interspecific competition (Median = −0.38; 95% CI [−5.31, 4.59]) or intraspecific competition (Median = 5.17; 95% CI [−6.57, 17.70]). There was a positive association between fungal community dissimilarity and both niche differences and fitness inequalities (Figure 3a). From our distribution of 4287 niche difference *k* parameters, 86.49% of samples predict a positive association between dissimilarity and niche differences (Median = −6.16; 95% CI [−16.63, 4.50]). From the distribution of 1063 fitness inequality *k* parameters, 90.03% of the *k*s predict a positive association between dissimilarity and fitness inequalities (Median = 6.95; 95% CI [−3.38, 13.84]). There was no relationship between the competitive ratio and fungal community dissimilarity (Median = 0.58; 95% CI [−13.99, 11.78]). However, there was a positive relationship between fungal community dissimilarity and the log demographic ratio, with 88.40% of the 4959 samples predicting a positive association (Median = 3.39; 95% CI [−2.24, 10.16]). Finally, there was no difference between k_{ND} and k_{FI} (Median = −0.64; 95% CI [−12.68, 9.82]).

Interpreting these functions together, to evaluate how dissimilarity affects coexistence, the asymptotic niche difference function was consistently outside the area of coexistence calculated from the asymptotic fitness inequality function throughout the range of the observed fungal community dissimilarities. This suggests that these fungal dissimilarities, per se, cannot explain any observed coexistence (Figure 3a). However, the gap between the predicted niche differences and the minimum required niche differences for coexistence (a function of the predicted fitness inequalities) becomes more narrow as fungal community dissimilarity increases, suggesting an increased chance of coexistence. This is congruent with the results from the quasi-binomial regression which suggested that, although coexistence probabilities are consistently low within the range of fungal dissimilarity, there is a positive association between fungal dissimilarity and the probability of coexistence (Figure 3b; 96.36% >0, Median = 2.77, 95% CI [−0.25, 5.89]). These trends were similar across all guilds: pathotrophs, saprotrophs and symbiotrophs (Appendix S5: Table S3).

3.4 | Model transferability

Because the population models parameterised with the experiment overwhelmingly predicted exclusion, we explored possible reasons why the predictions of our population models do not correspond with known co-occurrence patterns. Although it is possible that such discrepancies could be related to poor model fit, we used model selection of three common annual plant population models (Appendix S1) and used parameter estimates from the best performing model. From a posterior predictive check from this model, 95.77% of our fitness data fell within the 95% credible intervals of our posterior predictive distributions.

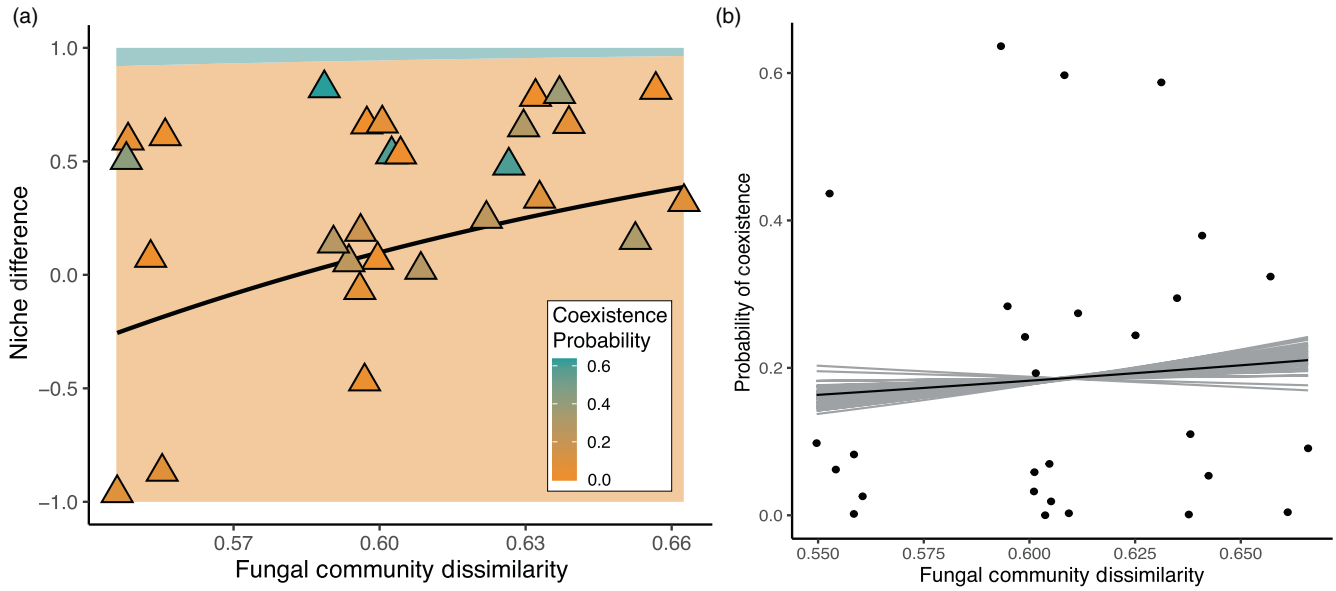

FIGURE 3 (a) Niche differences as a function of fungal community dissimilarity. All points represent the median of the distribution for their respective quantities, and their colour indicates that species pair's probability of coexistence. The black curve is the fit asymptotic equation relating niche differences to fungal community dissimilarity. The blue shaded area represents the coexistence domain when including the fit asymptotic function of fitness inequalities into the inequality statements derived from the criterion for coexistence (Equation 6). Similarly, the orange shaded area represents the area at which species pairs would not be expected to coexist based off of the estimated fitness inequalities as a function of fungal community dissimilarity. (b) Probability of coexistence as a function of fungal dissimilarity. Dissimilarity values correspond to the median posterior distributions for species pair dissimilarities. Probability of coexistence was calculated as the proportion of samples from the posterior distribution that were predicted to coexist. The black curve is the fractional logistic regression using the median slope and intercept parameters. Grey curves are 50 random draws from the distributions of slope and intercept parameters.

Additionally, indirect interactions that are not captured within our pairwise approach may cause such discrepancies between co-existence predictions and the co-occurrence patterns in the field. However, the multispecies analysis found minimal evidence for diversity-promoting intransitive competitive dynamics, with most credible intervals overlapping with 0 (Appendix S6). All median estimates of community-pair differentials for our species combinations were between −0.1 and 0.1 (Appendix S6: Figure S1), whereas for reference, other studies have calculated empirical community-pair differentials that spread across nearly the entire range of possible values from −1 to 1 (Granjel et al., 2023). Moreover, the percent of feasibly coexisting species combinations decreased with species richness and was highest for the two-species combinations (Appendix S6: Figure S2).

4 | DISCUSSION

Most of our understanding of how microbes influence plant community dynamics have come from theory (Bever et al., 1997; Kandlikar et al., 2019; Ke & Wan, 2020) and experimental tests of net microbial effects (Kulmatiski et al., 2008; Pernilla Brinkman et al., 2010), yet we still lack a robust (predictive) understanding of how differences in plant species-associated microbial communities contribute to observed plant community dynamics (Forero et al., 2019). To tackle this gap in our understanding of plant–soil feedbacks, we linked molecular characterisation of plant-associated fungal communities with a competition study and theoretical models of species coexistence. We found that the fungal community dissimilarity of all trophic groups of fungi (saptrophs, pathogens, mutualists/endophytes) was positively associated with both niche and fitness differences; however, fungal community dissimilarity alone was insufficient to promote coexistence. Nonetheless, a positive relationship between fungal community dissimilarity and coexistence probability suggests that the net effect of mycobiome differences contributes to competitive stabilisation and thus increases in the probability of plant coexistence. These results help elucidate how shared microbes may impact the competitive dynamics of host species, suggesting that dissimilarities between species' mycobiomes cause differences in competitive dynamics that may ultimately contribute to coexistence between competing species.

Theory suggests that contributions of fungal interactions to plant competition should depend on the trophic mode of the fungus as well as species-specificity of the plant-fungal interactions (Bever et al., 2010). Overall, we found little evidence suggesting that fungal community dissimilarity affects coexistence outcomes differently between fungal trophic modes. Notably, however, we found that interspecific competition was stronger among species with more similar symbiotroph communities, counter to all other trophic modes. Symbiotroph dissimilarity also had the weakest association, although still positive, with coexistence probability. These results offer an interesting counterpoint to the long-standing hypothesis that species-specific mutualists should destabilise coexistence (Johnson, 2021). The larger lack of evidence for trophic mode-specific effects on competitive dynamics may result from our incomplete understanding of fungal ecology at the species level. Although datasets such as FunGuild offer the best understanding of the ecological characteristics of different taxa, we lack resolute functional characterisation of most fungal species. Even within genera, fungi vary greatly in their ecology (Zanne et al., 2020), and particular species can exhibit a great degree of plasticity, interacting differently with host organisms depending on their abiotic or biotic context (Donald et al., 2021; Lee et al., 2013). These are general challenges to functional characterisation of microbes across host-microbe systems (Liu et al., 2022). Thus, continued research into the natural history and functional ecology of host-microbial interactions will allow deeper understanding of the role of particular functional groups of microbes in mediating host community dynamics.

The result that differences in mycobiome composition among plant species help stabilise coexistence is consistent with hypotheses implicating host species-specific microbial interactions (e.g. pathogenic interactions) in diversity maintenance (Bever et al., 2010). Congruent with other studies of plant-microbe mediated coexistence, there was a relationship between mycobiome dissimilarity and fitness inequalities between species pairs (Kandlikar et al., 2019; Yan et al., 2022). Unlike previous studies, however, we further dissected this relationship into the demographic and interaction components of the fitness inequalities. Interestingly, this increase in fitness inequalities was driven by a positive association between fungal community dissimilarity and differences in the demographic performance of species (measured as the demographic ratio). Thus, as opposed to exacerbating competitive asymmetries between species, distinct fungal associations may increase fitness inequalities by shifting species intrinsic growth rates, independent from competitive interactions.

Notably, our models predicted very little pairwise coexistence and that fungal community dissimilarity, *alone*, was insufficient to promote coexistence. Results from our model fit assessment suggest that poor model fit is an unlikely explanation for the discrepancy between our model predictions and known field dynamics. Additionally, the multispecies analyses suggest that indirect interactions among our species pairs are not likely to increase species coexistence. It is possible that interspecific variation in germination and survival rates (unmeasured in this study) might alter fitness differences, but we have no a priori reason to believe that this variation should consistently decrease fitness inequalities (increasing predicted coexistence). Thus, it is likely that this study (and similar competition experiments) underestimates the niche differences of the community (and the stabilisation offered by fungal community divergence) because both the experimental design and downstream calculations of niche and fitness differences are designed to quantify fluctuation-independent mechanisms of coexistence. Although these mechanisms may be crucial for species coexistence (Armitage & Jones, 2019; Zepeda & Martorell, 2019), environmental variation leads to a myriad of fluctuation-dependent mechanisms of coexistence (Chesson, 2000). It is likely that microbial communities could

also affect fluctuation-dependent stabilisation, whereby the effects of fungi on plant competition interact with environmental fluctuations, because many plant-microbe interactions are highly dependent on the environmental context (Hoeksema et al., 2010; Johnson & Pfleger, 1992). Specifically, Willamette Valley prairies host considerable heterogeneity in edaphic variables (Reed & Hallett, 2023), which was absent from our experiment, and may further mediate the stabilising potential of plant mycobiomes.

The functional traits relevant to plant-microbe interactions are likely related to the evolutionary history of plant species, suggesting an interdependence of phylogeny, traits and species interactions (Williams et al., 2022). We found support for a plant phylogenetic signature in the soil mycobiome data, but mycobiome dissimilarity explained competitive dynamics even after accounting for phylogenetic relatedness (Appendix S2). Although the effects of phylogenetic distance (Godoy et al., 2014) and plant trait dissimilarities (Kraft et al., 2015) on coexistence have been explored, this is the first attempt to quantify how dissimilarity in species interactions per se (here, associated mycobiomes) may mediate coexistence. This approach may help elucidate whether plant-microbe interactions are a key mechanism underlying the complex relationships between phylogenetic distance and plant competitive dynamics (Cadotte et al., 2017; Godoy et al., 2014). Future studies that also analyse plant genomes and soil metabolomics may further help identify which traits mediate the relationships between phylogeny and plant–soil feedbacks (Kardol et al., 2015; Leff et al., 2018).

We collected soil samples from the competition experiment as well as monoculture beds maintained by the plant nursery for multiple years. Although the effects of dissimilarity on niche and fitness differences were generally similar when analysing the whole dataset or samples from our experimental/monoculture plots (Appendix S4: Figure S2), the effects on competition strength and coexistence probability differed between the datasets. These differences are related to the interaction effect between plant species and sample type in mediating fungal community composition. Species mycobiomes might vary between the two sample types for two reasons. First, monoculuture beds were spatially separated from experimental plots and had a different management history than experimental plots (i.e. recent tilling in experimental plots). Although there were no observable differences between soils during collection, we did not measure soil abiotic or chemical properties, which could also vary across space. Plant-microbe interactions are highly idiosyncratic, and both spatial autocorrelation as well as management legacy effects may mediate plant–soil feedbacks (Crawford et al., 2019; Eppinga et al., 2022; Wubs & Bezemer, 2016). Another reason for this soil sample discrepancy is the difference in cultivation time between these plots. In a system dominated by linear dynamics, we might expect that the effect of species in our monoculture samples resembles that in our experimental sample, but each species average composition diverges due to the additional 2 years of cultivation of the mycobiome. However, nonlinear dynamics that may be common in microbial communities may explain why the relative difference between species' associated fungal communities could shift as cultivation time increases (Faust et al., 2015). If cultivation time does lead to nonlinear trends in community composition across time, this limits the insight we can possibly gain from the sorts of ecological snapshots that are commonplace in the plant-microbe literature (Ke et al., 2021), but promising research in time-series analysis may help overcome this challenge (Chang et al., 2021; Munch et al., 2023).

Our results, along with others showing that microbes can affect the fitness of plant species (Kandlikar et al., 2019; Yan et al., 2022), may also have implications for the eco-evolutionary dynamics of plant-microbe systems. In addition to the mycobiome composition varying among plant species, we found considerable sample-level variation in fungal community composition even within plant species, in accordance with other studies finding significant intraspecific variation in plant-associated microbial communities (Foster et al., 2022; Lankau, 2011; Lumibao et al., 2020). If this variation is heritable, and multiple mechanisms of hertitability have been proposed for microbiomes (Opstal & Bordenstein, 2015; Wagner, 2021), the association between microbial communities and host fitness suggest that microbiome composition may be subject to selection. Although evidence for intraspecific variation is ample and hypotheses for 'holobiont' evolution have received increased attention in the past decade (Guerrero et al., 2013; Roughgarden, 2023; Roughgarden et al., 2018), few models incorporate interspecific variation in shared microbial taxa between host species. Scaling up these models to a host community context may provide essential insight for understanding the mechanisms of microbiome evolution. A more refined understanding of how variation in microbial communities influences host species interactions is a key step in unravelling the eco-evolutionary dynamics of host-associated microbial communities.

5 | CONCLUSIONS

Using a novel approach to studying the role of microbial communities in mediating plant community dynamics, we have identified a strong association between fungal community dissimilarity and both niche and fitness differences. Although the data predicts low overall probabilities of coexistence in this system, fungal dissimilarity was positively related to the probability of coexistence. Further, fungal dissimilarity was related to the demographic ratio as opposed to the competitive ratio, suggesting the predicted rise in fitness inequalities is likely due to shifts in plant species' intrinsic demographic performance in response to distinct fungal associations. Overall, these results add support for the importance of microbes in mediating plant competition. Further, these results suggest that studying the cultivation of particular microbial communities may provide insights that traditional exploration of bulk microbial effects on plants (e.g. greenhouse plant–soil feedback experiments) may miss.

AUTHOR CONTRIBUTIONS

Jeremy A. Collings, Emily J. Cook and Jeff M. Diez contributed to the experimental design and data collection. Jeremy A. Collings and

Carolyn A. Delevich contributed to the molecular characterisation of fungal communities and Carolyn A. Delevich performed all bioinfomatics. Jeremy A. Collings developed the conceptual and statistical framework for the study, performed all statistical analyses and wrote the first draft of the manuscript. All authors contributed to subsequent revisions of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data required to generate the reported results are kept in Dryad at datadryad.org/stash/dataset/doi:10.5061/dryad.cfxpnvxfp (Collings et al., 2024). Sequences generated in this study are deposited in NCBI GenBank under the accession number: PRJNA1127829. All code needed to perform our analyses can be found on GitHub (https://github.com/jeremyacollings/CAMS) as well as on Zenodo (Collings & Delevich, 2024).

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SUPPORTING INFORMATION

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

Appendix S1: Demographic model selection and interaction coefficients.

Appendix S2: Phylogenetic analyses.

Appendix S3: Asymptotic functions.

Appendix S4: Results from experimental and monoculture samples.

Appendix S5: Results from different fungal guilds.

Appendix S6: Multispecies coexistence analyses.

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