





## ARTICLE

# Soil microbial influences over coexistence potential in multispecies plant communities in a subtropical forest

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## Abstract

Soil microbes have long been recognized to substantially affect the coexistence of pairwise plant species across terrestrial ecosystems. However, projecting their impacts on the coexistence of multispecies plant systems remains a pressing challenge. To address this challenge, we conducted a greenhouse experiment with 540 seedlings of five tree species in a subtropical forest in China and evaluated microbial effects on multispecies coexistence using the structural method, which quantifies how the structure of species interactions influences the likelihood for multiple species to persist. Specifically, we grew seedlings alone or with competitors in different microbial contexts and fitted individual biomass to a population dynamic model to calculate intra- and interspecific interaction strength with and without soil microbes. We then used these interaction structures to calculate two metrics of multispecies coexistence, structural niche differences (which promote coexistence) and structural fitness differences (which drive exclusion), for all possible communities comprising two to five plant species. We found that soil microbes generally increased both the structural niche and fitness differences across all communities, with a much stronger effect on structural fitness differences. A further examination of functional traits between plant species pairs found that trait differences are stronger predictors of structural niche differences than of structural fitness differences, and that soil microbes have the potential to change trait-mediated plant interactions. Our findings underscore that soil microbes strongly influence the coexistence of multispecies plant systems, and also add to the experimental evidence that the influence is more on fitness differences rather than on niche differences.

## KEYWORDS

Bayesian modeling, community persistence, feasibility domain, functional traits, plant–soil interactions, population growth rate, species coexistence, structural stability

Weitao Wang and Hangyu Wu contributed equally.

## INTRODUCTION

A fundamental issue in ecology is how biotic interactions within and across trophic levels influence species coexistence (Adler et al., 2007; Chesson, 2000, 2013; Levine et al., 2017; Tilman, 1982). In particular, plant–soil microbe interactions have been increasingly recognized as a critical driver of plant coexistence and community structure across ecosystems (Bever, 2003; Bever et al., 1997; van der Putten et al., 2013). Host-specific soil microbes can predominantly reduce the performance of plants due to high pathogen prevalence, while beneficial soil microbes such as mycorrhizal fungi can play a remarkably positive role in fitness (Liu & He, 2021, 2022; Lundell et al., 2022). While many studies have highlighted the influence of soil microbes on individual plant performance and on pairwise plant species coexistence (Chung et al., 2019, 2023; Ke et al., 2021), the impact of soil microbes on the coexistence dynamics among more diverse multispecies communities remains relatively underexplored. As a result, we lack a full understanding of how soil microbes shape natural plant community structure and function.

The role of soil microbes in mediating species coexistence can be evaluated in the context of at least three conceptual frameworks: plant–soil feedback (PSF) (Bever et al., 1997), modern coexistence theory (MCT) (Kandlikar et al., 2019; Ke & Wan, 2020), and the structural approach for multispecies coexistence (Saavedra et al., 2017; Song et al., 2018). The key insight from PSF theory is that negative pairwise feedbacks, which arise when plants grow better in heterospecific-conditioned soil communities than in conspecific soil, can stabilize species coexistence by generating conspecific negative density dependence. Empirical support for negative PSF comes from various studies (Bagchi et al., 2014; Bever, 2003; Bever et al., 1997, 2015; Crawford et al., 2019; Liu & He, 2021, 2022; van der Putten et al., 2013; Xi et al., 2021). However, recent theoretical advances have shown that the coexistence of more than two species is virtually impossible in multispecies extensions of the classic PSF model (Bever et al., 1997, but see Eppinga et al., 2018), which indicates that its application in diverse natural systems requires considering other ecological processes (Miller et al., 2022).

Soil microbial effects on plant coexistence can also be evaluated under the framework of MCT, which was originally developed to unravel the ecological drivers underlying species coexistence in competitive communities. In this framework, species differences are partitioned into niche differences and average fitness differences (Adler et al., 2010; Chesson, 2013, 2018; Chu & Adler, 2015). By applying this intuition to the

classic PSF models, Kandlikar et al. (2019) derived new metrics for quantifying the degree of microbially mediated stabilization and fitness differences, which can be used to infer pairwise coexistence in the Bever et al. (1997) model. Empirical evidence suggests that microbes generally generate stronger fitness differences than stabilization, and as a result are often expected to drive species exclusion (Kandlikar et al., 2021; Yan et al., 2022). While the classic PSF model (Bever et al., 1997) explores microbial effects on coexistence between plants that are otherwise equivalent, MCT can also be used to quantify microbial effects on coexistence between plants that also interact via other processes like resource competition (Kandlikar et al., 2019; Ke & Wan, 2020). Intuitively, through comparing niche and fitness differences when plants are grown with or without soil microbes, one can isolate the influence of soil microbes on the outcome of competition (Ke & Wan, 2020). However, a key limitation of this approach is that the niche and fitness difference metrics can break down in the face of positive interactions between plants (i.e., when the presence of neighbors increases rather than decreases plant growth; but see Spaak & De Laender, 2020), which occur frequently in natural communities (Bimler et al., 2018; Hart, 2023; Ke & Wan, 2022). Moreover, existing measures of pairwise niche and fitness differences cannot be readily extended to generate insights about microbial effects on multispecies assemblages (Barabás et al., 2016; Song et al., 2019), making it difficult to know how inferences from pairwise analyses scale up to species-rich communities.

Different from the dichotomous grouping of competitive outcomes into coexistence and exclusion, evaluating species interactions through a structural approach yields a probabilistic interpretation of coexistence from species pairs to multispecies systems (Rohr et al., 2014; Saavedra et al., 2017; Song et al., 2018). Structural approach posits that the structure of species interactions constrains the likelihood for multiple species to persist (i.e., achieving positive abundances at equilibrium) under changing environments (Saavedra et al., 2017). A key concept in the structural method is the feasibility domain, which represents the region of the parameter space that is compatible with multiple species simultaneously persisting in a community (García-Callejas et al., 2023; Saavedra et al., 2017; Song et al., 2018). The larger the likelihood (the size of the feasibility domain), the greater the range of environmental conditions that the community can withstand without species loss. Therefore, changes in the feasibility domain across different environmental contexts (e.g., in sterile soils vs. in soils with microbes present) can reflect the consequence

of environmental variations on the potential of coexistence. For instance, if multispecies assemblages have larger feasibility domains in the presence of soil microbes than in their absence, this would indicate that microbes increase the opportunities for coexistence. Adopting this approach for evaluating microbial effects on plant coexistence has at least three key advantages. First, the structural approach is well-suited to projecting how positive interactions between species shape community dynamics, enhancing its applicability in diverse contexts, in studies of microbial effects on plant performance, where positive neighbor effects are common due to the importance of soil mutualisms (Peay, 2016). This is in contrast to MCT framework, which is designed to explain species coexistence when species interactions are primarily competitive. This limitation has led previous studies to impose constraints on the permissible range of interaction values (i.e., positive interactions were not allowed during coefficient estimation, or species pairs with positive interactions were dropped from analyses) (Bowler et al., 2022; Van Dyke et al., 2022), a practice that may not be appropriate when positive interactions genuinely exist in natural communities. A second benefit of the structural approach is that it can be readily extended to evaluating coexistence dynamics in multispecies communities—a critical knowledge gap in the field (Allen-Perkins et al., 2023; Song et al., 2021). Lastly, existing research has highlighted the significance of indirect interactions in facilitating the coexistence of multiple species (Aschehoug & Callaway, 2015; Levine et al., 2017). The application of the structural approach can incorporate the effects of interaction chains on multispecies' coexistence, which emerge predominantly in diverse systems (Saavedra et al., 2017).

Unraveling the trait basis of plant–microbe interactions also promises to help advance our understanding of how soil microbes shape species' coexistence in diverse plant communities. It has been long understood that functional traits, which to a large extent represent various life-history strategies between plants, could play an important role in maintaining species diversity. Many studies have tested the relationships of traits with drivers underlying coexistence (Funk & Wolf, 2016; Gross et al., 2015; Kraft et al., 2015; Kunstler et al., 2012; Xi et al., 2021). For instance, Kraft et al. (2015) found for several key traits, species dissimilarity between species was highly correlated with average fitness differences for annual plants, indicating that these traits drive competitive dominance. Xi et al. (2021) proposed a conceptual model to link PSFs and functional traits in the context of species coexistence, and demonstrated that PSF may reinforce the effect of trait dissimilarities on coexistence. Using the structural method, Saavedra et al. (2017) developed

structural counterparts analogous to niche differences and average fitness differences in MCT for both species pairs and multispecies communities, which provided the opportunity for exploring the linkage of functional traits with these coexistence metrics. For instance, if there is a positive correlation between trait differences in a pair of species and their size of feasibility domain, it suggests that larger trait disparities might enhance their chances of coexistence. However, in the MCT framework, the correlation of trait differences with niche or fitness differences by itself does not directly predict the consequences of species interactions. Developing a trait-based understanding of whether and how soil microbes influence multispecies coexistence dynamics is a key step for predicting plant community persistence, especially in light of the frequently documented consequences of environmental changes on the structure and composition of soil microbes (Jansson & Hofmockel, 2020; Yuan et al., 2021).

Here, we applied the structural approach to evaluate how soil microbes mediate multispecies coexistence for five tree species that co-occur in a subtropical forest at the Heishiding Natural Reserve in south China. We conducted a greenhouse experiment to estimate the strength of biotic interactions (intra- and interspecific interaction parameters) and intrinsic growth rates in sterilized and inoculated soils. In addition, we measured eight seedling functional traits and explored whether interspecific trait differences help explain pairwise coexistence. Our analyses aim to address the following questions: (1) How do soil microbes influence coexistence in multispecies communities? (2) Do soil microbes primarily alter multispecies coexistence by changing structural niche or fitness differences? (3) To what extent are microbial controls over plant coexistence explained by plant functional traits?

## MATERIALS AND METHODS

### Study site and species selection

We conducted the experiment in a greenhouse located at the Heishiding Natural Reserve (111°53' E, 23°27' N, 150–927 m elevation), Guangdong Province, south China. In this region, the mean annual temperature is 19.6°C and the mean annual precipitation is about 1744 mm. A 50-ha permanent forest plot including more than 200 plant species was established in the Reserve in 2011. Our experiment included five species that vary in their relative abundance in the reserve and in mycorrhizal types: *Artocarpus styracifolius* (ASTY), *Cryptocarya concinna* (CCON), *Cyclobalanopsis hui* (CHUI), *Castanopsis hystrix* (CHYS),

and *Cyclobalanopsis pachyloma* (CPAC) (Appendix S1: Table S1). Briefly, ASTY and CCON form root associations with arbuscular mycorrhizal (AM) fungi, and the others associate with ectomycorrhizal fungi.

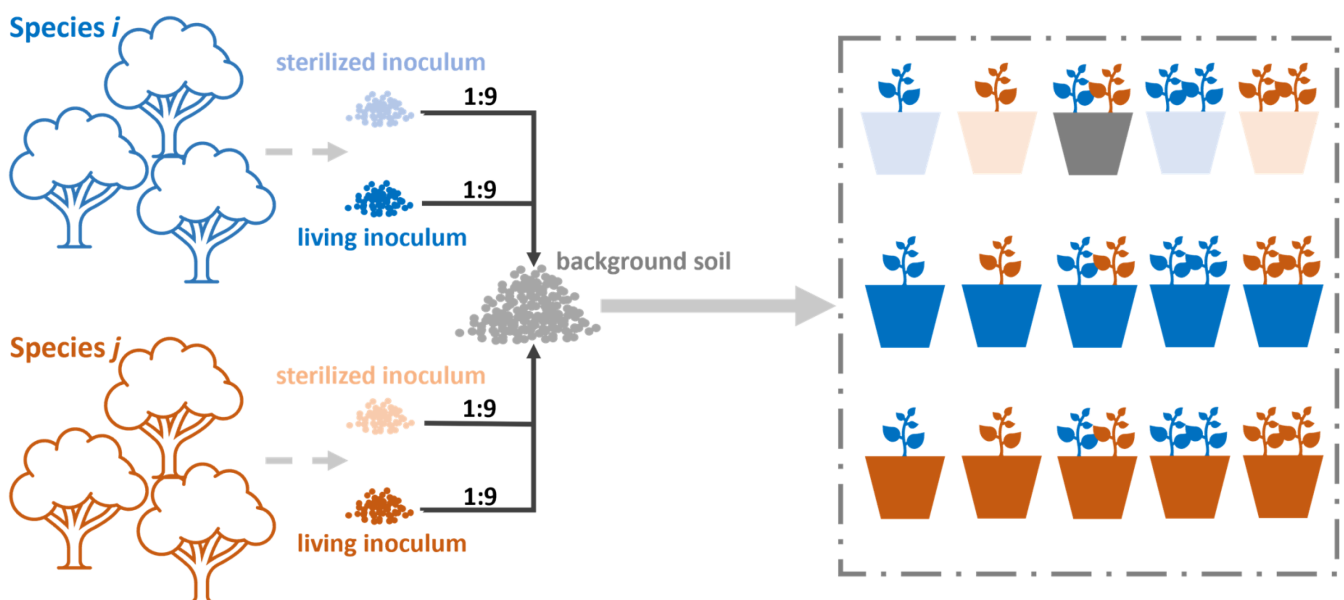
## Experimental setup and data collection

During winter 2019, we collected seeds of the focal species in the Reserve, surface sterilized them (1 min 70% ethanol, 3 min 2.625% NaOCl, 1 min 70% ethanol, and 1 min distilled water), and stored at 4°C until March 2020. We then germinated the seeds in sand that was sterilized by autoclaving (three times within 24 h; for each time, lasting for 30 min under 121°C). In May 2020, we collected topsoil (0–15 cm) from three adult trees of each species within a 1 m radius surrounding each tree. Soil from three replicate individuals of the same species was then split into two equal parts. Both parts were thoroughly mixed and then sieved through a 10-mm mesh. One part was utilized to obtain living inoculum soil, while the other was sterilized by gamma radiation with a dose of 25 Gy to obtain sterilized inoculum soil. We additionally collected bulk soil in the reserve, which we homogenized, sieved (10-mm mesh) and sterilized by gamma radiation with a dose of 25 Gy to generate the background soil for experimental pots. Two soil treatment (inoculated or sterilized) groups were thus achieved by mixing 90% sterile background soil with either 10%

living inoculum soil or 10% sterilized inoculum soil (Figure 1). We then transplanted equally sized two-month-old seedlings into plastic pots (21 cm diameter × 17 cm height) filled with sterilized or inoculated soils.

Quantifying the effects of soil microbes on the structural stability of tree seedling communities requires the complete pairwise interaction matrices in sterile and inoculated soils, as well as vectors of each species' intrinsic growth rates. In our experiment, we grew either a single individual (to measure the intrinsic growth rate) or two conspecific individuals (to measure intraspecific interaction coefficients) of each species in pots inoculated with soil from conspecific adult trees, or in pots with only sterile soil (5 species × 2 soils × 2 density levels = 20 treatments; Figure 1). Additionally, we grew each pairwise combination of species (10 combinations) to obtain the interspecific interaction coefficients. To do so, we grew each pair of species ( $i/j$ ) in inoculated soil with species  $i$ 's soil microbes and separately with species  $j$ 's soil microbes (to quantify interaction coefficients in the presence of microbes), and in sterile soil (to quantify interaction coefficients in the absence of microbes), which led to a total of 30 treatments (10 species pairs × 3 soil microbial treatments = 30 treatments; Figure 1).

For each treatment, we established six replicate blocks. We shifted the position of every block in order and re-randomized pots monthly to minimize the effects of abiotic environmental factors. We replaced dead



**FIGURE 1** Schematic depiction of the experimental design with an example of a pair of species  $i$  and  $j$ . Soils were sterilized in the gray, light blue, and light orange pots. The soils were inoculated with species  $i$ 's and  $j$ 's microbes in the blue and orange pots. Intrinsic growth rates and intraspecific interaction coefficients were obtained by planting the same species (a single individual and two conspecific individuals). Planting species  $i$  and  $j$  together made it possible to obtain interspecific interaction coefficients.



seedlings within the first two weeks after initial planting. In sum, we planted 300 pots with 540 seedlings.

To generate allometric equations for estimating the initial biomass of experimental seedlings, we grew an additional 20 seedlings per species in the same greenhouse conditions in sterilized soils. In September 2020, we harvested these seedlings and measured each individual's height, basal diameter, leaf count, and total biomass. We performed linear regression models of the total biomass with these three predictors for each species (Appendix S1: Table S2). Using this linear regression, we estimated the initial biomass of seedlings based on height, basal diameter, and leaf count measurements from the beginning of the experiment.

In May 2021, after 12 months of growth, we harvested the total (above- and belowground) biomass for each seedling dried for 48 h at 60°C and weighed.

### Functional trait measurements

To investigate how functional traits relate to the microbially mediated plant coexistence metrics, we measured eight plant functional traits that are closely associated with plant life-history: Height (H, the shortest distance between the upper boundary of the main photosynthetic tissues on a plant and the ground level, in centimeters), specific leaf area (SLA, the one-sided area of a fresh leaf divided by its dry mass, in square centimeters per gram), total leaf area (TLA, one-sided or projected area of all leaf from the same plant, in square centimeters), root average diameter (RAD, averaged diameter of all roots, in millimeters), root length (RL, total length of all roots, in centimeters), root to shoot ratio (RS, the ratio of plant dry mass in root and shoot), root surface area (RSA, total surface area of all roots, in square centimeters), and specific root length (SRL, length per unit dry mass of roots, in centimeters per gram). Traits were measured using standardized protocols (Pérez-Harguindeguy et al., 2013). We separately measured these traits for seedlings growing in sterilized and inoculated soils. Leaf areas were scanned by the Canon lide 300, and images were processed in ImageJ (version 1.53, National Institutes of Health). Root traits were measured using WinRHIZO (Regent Instrument Inc).

### Quantifying demographic parameters

To estimate the interaction coefficients and intrinsic growth rates, we applied Bayesian modeling to fit plant biomass data using the canonical Ricker model

(Ricker, 1954). This model and its variants have been widely used to describe the growth ( $G$ ) of seedlings, with the assumption that biomass at the end of the experiment is proportional to population growth (Cardinaux et al., 2018; Hart et al., 2012; Hart & Marshall, 2013; Inouye, 2001; Van Nuland et al., 2022; Zhang & van Kleunen, 2019). In this model, the biomass ratio of the focal individual  $i$  at time  $t + 1$  relative to its biomass at time  $t$  is given by:

$$G_i = \frac{B_{i,t+1}}{B_{i,t}} = \lambda_i e^{\sum_{j=1}^n \alpha_{ij} N_{j,t}} \quad (1)$$

$B_{i,t+1}$  and  $B_{i,t}$  represent the biomass of species  $i$  at time  $t + 1$  and  $t$ , respectively.  $N_{j,t}$  denotes the abundance of species  $j$  at time  $t$  (here defined as the number of individuals),  $n$  is the number of species,  $\lambda_i$  is the intrinsic growth rate of species  $i$  in the absence of neighbors, and  $\alpha_{ij}$  is the interaction coefficient describing the per capita effect of species  $j$  on species  $i$  (considering intraspecific interaction when  $j = i$  and interspecific interaction when  $j \neq i$ ). Negative values of the per capita interaction parameters ( $\alpha_{ij}$ ) mean that performance of focal plants is reduced in the presence of neighbors (competition), while positive values imply facilitative effects of neighbors. This model was applied to fit the growth of seedlings growing in sterilized and inoculated soils separately. We then separately constructed the interaction coefficient matrices and intrinsic growth rate vectors for the sterilized treatment and the inoculated treatment.

In the context of microbial-inoculated treatment group, considering species pair  $i/j$  as an example, when fitting the growth model for species  $i$ , it becomes imperative to account for potential differential impacts arising from microbes sourced from species  $i$  versus those sourced from species  $j$ . The same principle applies when fitting the growth model for species  $j$ . Consequently, we incorporate the microbial source as a random effect, resulting in a modified random-effect Bayesian model as follows:

$$G_i = \frac{B_{i,t+1}}{B_{i,t}} \Big|_{\text{inoculated}} = (\lambda_{i|\text{fixed}} + \lambda_{i|\text{random}}) e^{\sum_{j=1}^n (\alpha_{ij|\text{fixed}} + \alpha_{ij|\text{random}}) N_{j,t}} \quad (2)$$

Within the framework of our model, random effects are incorporated for both the intrinsic growth rate ( $\lambda$ ) and the interaction coefficients ( $\alpha_{i,j}$ ), derived from inoculation treatments that are specific to either species  $i$ 's soil (conspecific inoculation treatment) or species  $j$ 's soil (heterospecific inoculation treatment). Including random effects facilitates a more nuanced understanding

of the extent to which microbes influence tree species growth. To this end, we extracted fixed effects and incorporated corresponding random terms from heterospecific microbial inoculations for subsequent analyses.

For all model fitting, we utilized a Bayesian approach via the “rstan” package in R (Stan Development Team, 2020). In the Ricker model (Equations 1 and 2), observed growth rate ( $B_{t+1}/B_t$ ) was modeled as  $B_{t+1}/B_t \sim \text{lognormal}(\log(\hat{G}_i), \sigma)$ , where  $\sigma$  was given a cauchy prior as:  $\sigma \sim \text{cauchy}(0, 1)$ . We gave all interaction coefficients standard normal distribution priors:  $\alpha_{ij} \sim N(0, 1)$ . Intrinsic growth rates should be strictly positive, thus was given an uninformative gamma prior:  $\lambda_i \sim \text{gamma}(0.001, 0.001)$ . The models were run for a total of 20,000 iterations, with the first 10,000 iterations serving as a warm-up period. We initiated four independent chains for each model. Convergence was rigorously assessed by inspecting trace plots and using the Gelman–Rubin Rhat diagnostic. All parameter estimates were based on a combined total of 40,000 post-warm-up samples.

## Calculating the structural coexistence metrics

We used the resulting interaction matrices and intrinsic growth rates to calculate three metrics that capture the structural stability of multispecies coexistence (Saavedra et al., 2017; Song et al., 2018). At the community level, the structural analog of the niche differences is the size of the feasibility domain, which can be quantified by the solid angle of the cone generated by the interaction matrix. The feasibility domain of a  $n$ -species community is determined by its interaction matrix. The structural analog of the average fitness differences, denoted  $\theta$ , is quantified as the extent to which the vector of observed intrinsic growth rates ( $r$ ) deviates from the centroid of the feasibility domain. As the community-level structural niche differences are expected to decrease with an increase in community species richness (Song et al., 2018), we use the normalized version of the feasibility domain, which is quantified as the fraction of the volume of the feasibility domain in the unit sphere (Saavedra et al., 2017; Song et al., 2018). Mathematically, the upper limit of the normalized feasibility domain is 0.5. As the normalized feasibility domain approaches 0.5, the likelihood of a community being feasible for a given interaction matrix increases (Song et al., 2018). For consistency, we always refer to the normalized version of feasibility domain as  $\Omega$ , unless otherwise specified.

To evaluate microbial effects on species coexistence, we examined how the soil microbial context changes the

feasibility domain ( $\Omega$ ) and structural fitness differences ( $\theta$ ) in all pairwise interactions (10 combinations), as well as in communities assembled with all possible three, four, or five species combinations (10, 5, and 1 possible communities, respectively). Specifically, we quantified the relative magnitude of soil microbes on structural niche differences as  $(\Omega_{\text{inoculated}} - \Omega_{\text{sterilized}})/\Omega_{\text{sterilized}}$ , and microbial effects on structural fitness differences as  $(\theta_{\text{inoculated}} - \theta_{\text{sterilized}})/\theta_{\text{sterilized}}$ . We then used pairwise Wilcoxon tests to statistically compare the differences between treatments (sterilized vs. inoculated soils) for each assembled community. To account for multiple comparisons, we adjusted the  $p$ -values using Bonferroni correction. We also calculated shared  $\Omega$  normalized solid angles, which represent the intersection of feasibility domains in the presence and absence of microbes (Song et al., 2018). This intuitively indicates whether the microbes have altered the relative size of the feasibility domain. The result is presented in Appendix S1: Table S3.

In addition, Song et al. (2018) proposed a species-level metric, termed  $\omega$ , which quantifies the average probability that a randomly chosen species from a given community is feasible (i.e., has an equilibrium population size  $>0$ ). Unlike the community-level feasibility domain  $\Omega$ , the species-level  $\omega$  can be comparable among communities that vary in species richness. The species-level results ( $\omega$ ) are presented in Appendix S1: Figure S1.

## Evaluating trait correlates of coexistence metrics in two-species communities

To evaluate whether functional traits are related to coexistence metrics and explore the impact of soil microbes on coexistence metric–trait relationships, we tested for correlations between coexistence metrics ( $\Omega$  and  $\theta$ ) and trait dissimilarities for the 10 species pairs in sterilized and inoculated soils. Because here coexistence metrics ( $\Omega$  and  $\theta$ ) are inherently pairwise measures, we conducted Mantel tests (Spearmen method) to obtain correlations. For each species pair  $i/j$ , the trait dissimilarity could be different in sterilized and inoculated soils. Therefore, we calculated Euclidean distances between species pairs separately for different soil types. We did not test the trait correlates of multispecies structural niche differences as we did not plant seedlings in a multispecies combination in the greenhouse, and consequently had no corresponding functional trait values.

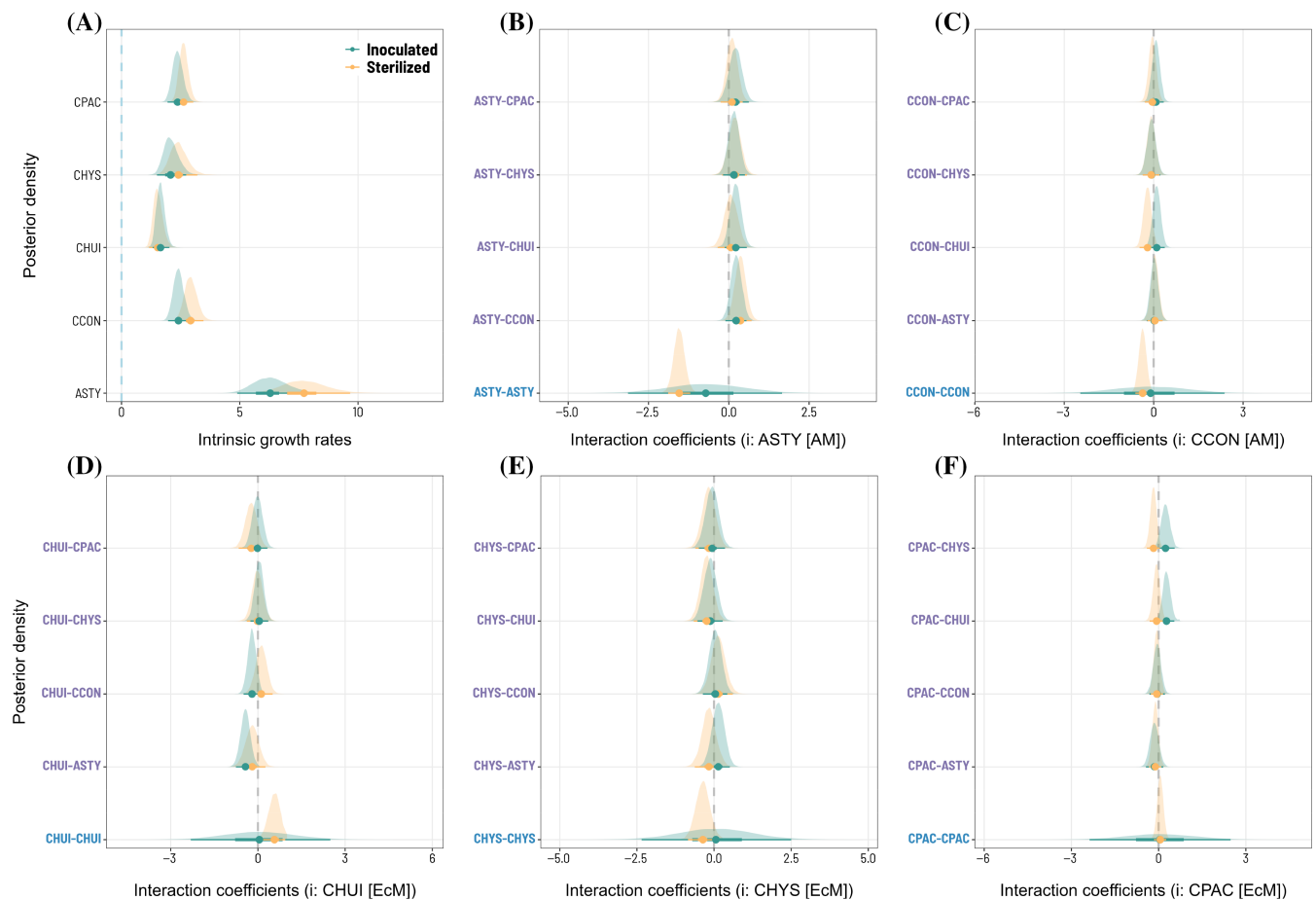
The code for implementing the structural method was used from Song et al. (2018). All analyses were implemented in R 4.1.1 (R Development Core Team, 2021).

## RESULTS

### Effects of soil microbes on intrinsic growth rates and pairwise interaction coefficients

Our Bayesian modeling approach yielded a satisfactory fit to the data. To provide a more comprehensive understanding of the coefficient's variability and to contextualize its potential effects, we visualized the models' posterior distributions (Figure 2; Appendix S1: Table S4). By inspecting the posterior summaries, we found that soil microbes decreased the mean intrinsic growth rates in four out of five species (all except CHUI, Figure 2; Appendix S1: Table S4). For the two species that associate with AM fungi, intraspecific interactions tended to be competitive, and the mean

competition strength was weaker in inoculated soils than in sterilized soils ( $\alpha_{ASTY-ASTY}$ ,  $-0.717$  vs.  $-1.543$ ;  $\alpha_{CCON-CCON}$ ,  $-0.097$  vs.  $-0.371$ , Figure 2; Appendix S1: Table S4). On the other hand, the three species that associate with ectomycorrhizal (EcM) fungi tended to be positive (facilitative) (except for CHYS with sterilized treatment), though such facilitation was relatively weak. Specifically, the presence of a live microbial community weakened intraspecific facilitation for CHUI ( $0.558-0.056$ ). For CPAC, intraspecific facilitation between the two treatments was nearly identical ( $0.057$  with microbes present and  $0.047$  without microbes). Meanwhile, for CHYS, the sign of intraspecific interactions shifted from negative ( $-0.36$ , competitive) to weakly positive ( $0.054$ , facilitative) in the presence of microbes.



**FIGURE 2** Posterior distributions of intrinsic growth rate ( $\lambda$ ) and interaction coefficients estimated using Bayesian modeling. The 50% and 95% credible intervals for each coefficient are shown as the colored lines at the bottom of the distribution, with points representing the mean values. “i” in the x-axis label means the focal species. The y-axis tick labeled “ASTY-ASTY”—displayed in blue—indicates the intraspecific interaction of species ASTY, and the same applies to other species. The y-axis tick labeled “ASTY-CCON”—displayed in purple—indicates the effect of species CCON on species ASTY, and vice versa. Positive interaction coefficients signify facilitation, while negative ones indicate competition. AM species: ASTY and CCON. EcM species: CHUI, CHYS, and CPAC. AM, arbuscular mycorrhizal; ASTY, *Artocarpus styracifolius*; CCON, *Cryptocarya concinna*; CHUI, *Cyclobalanopsis hui*; CHYS, *Castanopsis hystrix*; CPAC, *Cyclobalanopsis pachyloma*; EcM, ectomycorrhizal.

The impacts of soil microbes on interspecific interactions were species-specific and idiosyncratic (Figure 2; Appendix S1: Table S4). In most cases, the interaction strength of species pairs grown in sterilized soils was higher than that of species pairs grown in inoculated soils. The presence of a live microbial community can also change the type of interspecific interactions. For instance, the mean estimate of CHUI's effect on CPAC shifted from competition ( $-0.068$ ) in the absence of microbes to facilitation ( $0.275$ ) in their presence.

## Influences of soil microbes on coexistence metrics $\Omega$ and $\theta$

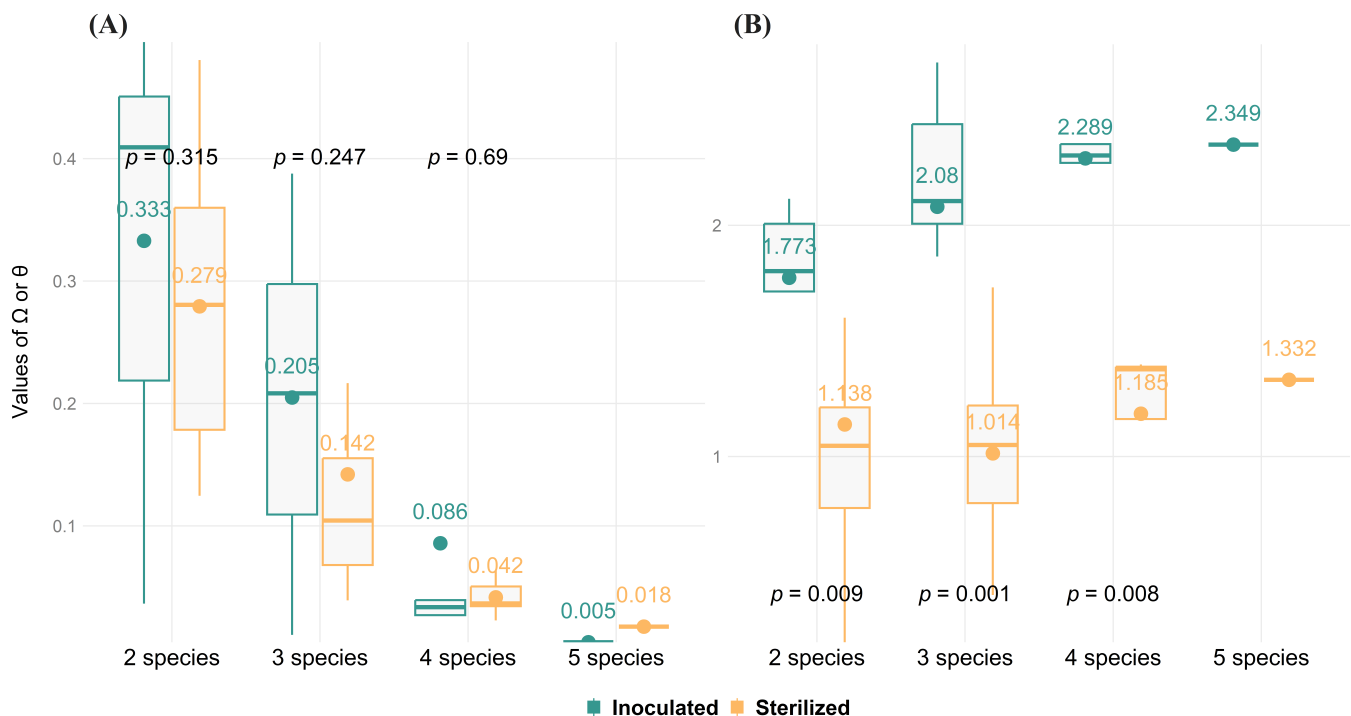
Soil microbes primarily affected multispecies communities by altering the strength of structural fitness differences ( $\theta$ ), with weaker effects on the structural niche difference ( $\Omega$ , Figure 3;  $\omega$ , Appendix S1: Figure S1). For assembled communities with varying species number, no significant differences were detected between sterilized and inoculated treatments ( $p > 0.05$ ) for  $\Omega$ . In contrast, for  $\theta$ , significant differences were observed for two-species communities ( $p = 0.009$ ), three-species communities ( $p = 0.001$ ), and four-species communities ( $p = 0.008$ ). Meanwhile, soil microbes increased

structural niche differences  $\Omega$  in assembled communities except with five species (Figure 3A), but consistently increased structural fitness differences  $\theta$  in all scenarios (Figure 3B). For instance, for 10 two-species communities, soil microbes increased two coexistence metrics, with  $\Omega$  by 19.4% and by 55.8% for  $\theta$ . For the community composed of five species, the existence of soil microbes reduced  $\Omega$  by 72.2%, but increased  $\theta$  by 76.4%.

Regarding the shared  $\Omega$  (Appendix S1: Table S3), when the community is composed of only two species, in most cases (7 out of 10 species pairs),  $\Omega_{\text{shared}} \approx \Omega_{\text{sterilized}} < \Omega_{\text{inoculated}}$ . When the number of species in the community exceeds 2, the majority of  $\Omega_{\text{shared}}$  values are nearly 0.

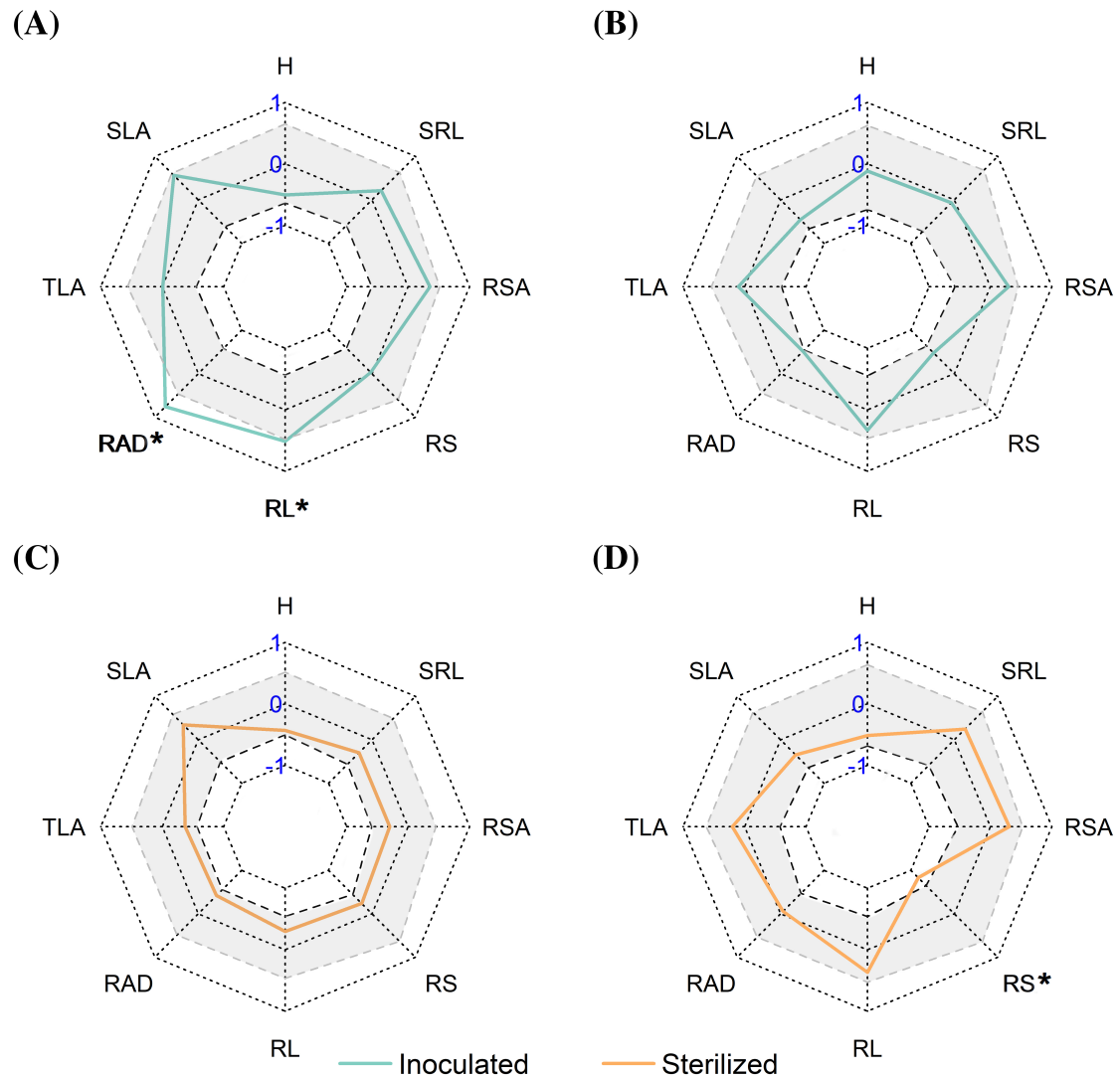
## Impacts of soil microbes on coexistence metric–trait relationships in two-species tree seedling communities

Trait relationships with pairwise structural niche and fitness differences were uncommon, and were often contingent on microbial contexts. In inoculated soils, structural niche difference ( $\Omega$ ) was positively correlated with the RAD difference (Mantel statistic 0.758,  $p = 0.008$ ; Figure 4A) and the RL difference (Mantel statistic 0.515,



**FIGURE 3** Boxplot of structural niche differences ( $\Omega$ , A) and fitness differences ( $\theta$ , B) for tree seedling communities composed of two, three, four and five species in sterilized and inoculated soils. The mean values are marked with dots in the graph and the specific values are shown above the dots. Pairwise Wilcoxon tests were used to compare the differences between sterilized and inoculated soils for each level of species richness except for the five-species group. The adjusted  $p$ -values using the Bonferroni correction are shown in black.





**FIGURE 4** Correlations of trait dissimilarities with structural niche difference ( $\Omega$ ) and fitness difference ( $\theta$ ) for two-species tree seedling communities. Correlations were calculated with Mantel tests. Significant correlations are marked in bold font at the level of 0.05. (A)  $\Omega$ —traits in inoculated soils. (B)  $\theta$ —traits in inoculated soils. (C)  $\Omega$ —traits in sterilized soils. (D)  $\theta$ —traits in sterilized soils. H, height; RAD, root average diameter; RL, root length; RS, root to shoot ratio; RSA, root surface area; SLA, specific leaf area; SRL, specific root length; TLA, total leaf area.

$p = 0.042$ ; Figure 4A), respectively. However, these relationships did not hold in sterilized soils (Figure 4C). For structural fitness difference ( $\theta$ ), no statistically significant correlations were observed between trait differences and  $\theta$  regardless of soils with or without microbes (Figure 4B,D).

## DISCUSSION

To the best of our knowledge, our study is the first attempt to experimentally explore the impact of soil microbes on multispecies coexistence using a structural approach. Our findings show that soil microbes exert

varying effects on growth rates and interaction coefficients, which consequently influence the opportunity of coexistence with a stronger modification on structural fitness differences than structural niche differences.

The presence of soil microbes decreased intrinsic growth rates of four in five target species (all except CHUI, Figure 2), which indicates a net pathogenic effect of soil microbes on these species. Interestingly, we found that AM tree seedling performance is generally hurt by the presence of conspecific neighbors (competitive intraspecific interactions), while EcM seedlings generally benefit from the presence of conspecific neighbors (facilitation). This outcome may be the result of less protection of roots of AM trees from soil pathogens due to the lack of mantle

formation, or because EcM trees are better able to mine nutrients from soil organic matter (Bennett et al., 2017; Chen et al., 2019; Liang et al., 2021; Zhong et al., 2021). However, a recent study also found evidence of negative conspecific density dependence in temperate ectomycorrhizal trees (Jevon et al., 2022). Compared with the relatively consistent effects of soil microbes on intrinsic growth rates and intraspecific interactions, the impacts of microbes on interspecific interactions were idiosyncratic, with microbes driving stronger competitive interactions in some cases and stronger facilitation in others (Figure 2). As a result, the community-level consequences of changes in both biotic interactions (i.e., framed into an interaction matrix) and intrinsic growth rates modified by soil microbes jointly influenced the structural niche differences ( $\Omega$ ) and fitness differences ( $\theta$ ), and consequently would determine the ultimate outcomes of interactions. For various scenarios with different species identities and the number of species, on the one hand, the existence of soil microbes increased the coexistence potential for two-, three- and four-species communities (i.e., increase in  $\Omega$ ), and drove species exclusion for five-species communities (i.e., decrease in  $\Omega$ ) (Figure 3A). On the other hand, soil microbes consistently increased the structural fitness differences  $\theta$ , that is, favoring species exclusion, but with a decreasing trend along the increase in species richness (Figure 3B). While the structural approach for evaluating coexistence is not a perfect predictor of coexistence in multispecies communities ( $\Omega$  and  $\theta$  are usually not comparable in communities with three or more species), our study presents a critical step to assess the potential role of soil microbes in shaping species coexistence in natural species-rich ecosystems.

Our results suggest that soil microbes primarily affect pairwise and multispecies coexistence by affecting the structural fitness differences rather than changing opportunities for feasibility by altering the structural niche differences (Figure 3). While ours is the first study to quantify microbial effects on niche and fitness differences beyond pairwise interactions, our result is consistent with that of recent studies for species pairs. For example, soil microbes generated stronger fitness differences than stabilization among California annual plants (Kandlikar et al., 2021), and Yan et al. (2022) found that across 518 plant species pairs compiled from the literature, though soil microbes generated both stabilization or destabilization and fitness differences, the microbially mediated fitness differences were dominant. While results from assembled species-rich communities were qualitatively similar with those from species pairs, our findings demonstrated for the first time that soil microbes played a more important role through altering fitness differences than niche differences even in species-rich

natural systems with potential indirect interactions. Even in the community with five species, where soil microbes reduced the structural niche differences by 72.2% (unlike the increase observed in the two-, three-, and four-species communities), this reduction remains smaller than their 76.4% effect on structural fitness differences, which was an increase. For this scenario, the likelihood of feasibility of these five species was practically negligible ( $\Omega = 0.005$ ).

While there were no significant differences in the  $\Omega$  across various treatment groups, an examination of  $\Omega_{\text{shared}}$  (Appendix S1: Table S3) highlighted a clear influence by soil microbiome.  $\Omega_{\text{shared}}$  represented the intersection of the feasibility domain of communities with the same species composition when inoculated with microbes and when sterilized. For two-species communities, most  $\Omega_{\text{shared}}$  aligned closely with  $\Omega_{\text{sterilized}}$  and are lower than  $\Omega_{\text{inoculated}}$ , suggesting that microbial inoculation broadens communities' feasibility domain and the feasibility domain under sterilization was a subset of that under inoculation. As species richness in the community increases, most  $\Omega_{\text{shared}}$  became zero, indicating that microbes significantly altered the position or shape of the feasibility domain in multispecies communities. The presence or absence of microbes might not significantly alter the size of a community's feasibility domain, but it may shift the feasible parameter range. Moreover,  $\Omega_{\text{shared}}$  observed in our study revealed that multispecies coexistence dynamics are far more intricate than those of two-species communities.

Previous studies reported that trait dissimilarity usually was poorly correlated with coexistence metrics (Funk & Wolf, 2016; Gross et al., 2015; Kraft et al., 2015; Kunstler et al., 2012). However, Pérez-Ramos et al. (2019) found that traits and their plasticity promoted species coexistence by enhancing stabilizing niche differences. In our study, we found that most correlations were nonsignificant, and structural fitness differences ( $\theta$ ) did not correlate with any trait differences (Figure 4). Our results offer an intuitive connection of trait differences to species coexistence: the greater the differences in RAD and RL between two species, the larger the structural niche differences ( $\Omega$ ) become (Figure 4A), indicating a higher likelihood of coexistence between these species pairs. Specifically, larger differences in RAD represent a more divergent foraging strategy between species. Thin-rooted species are typically considered to be acquisitive in nutrient acquisition because of their lower RAD that can explore larger soil volumes efficiently. By comparison, thick-rooted species are typically considered to be conservative in nutrient acquisition because of their intrinsically poor capacities to acquire soil resources (Baylis, 1975). Such difference in diameter-mediated difference in nutrient acquisition efficiency between thin- and thick-rooted species

may generate a positive relationship with structural niche differences ( $\Omega$ -RAD) in inoculated soils as observed here (Figure 4A). However, it is important to note that when soil microbes are present, thick-rooted species may rely more on soil microbes for nutrient foraging (mycorrhizal fungi), thus leading to comparable competitiveness between thick- and thin-rooted species in a shared environment (Bergmann et al., 2020; Chen et al., 2016; Liu et al., 2015). Previous studies have already shown that soil microbes can alter root traits, thereby affecting plant performance (Lugtenberg & Kamilova, 2009; Newsham, 2011; Van Der Heijden et al., 2015). Our findings demonstrate that the presence/absence of soil microbes could influence the potential linkages between coexistence metrics and root functional traits, which would bring more uncertainties when inferring and predicting the tolerance of a community to the change in soil microbes caused by environmental variations through functional traits.

## CONCLUSIONS

In summary, our study demonstrates that soil microbes can have drastic effects on multispecies coexistence dynamics between plants, and that soil microbes could modify the coexistence metric–trait relationships in pairwise plant interactions. The structural approach applied here represents a natural extension from species pairs to multispecies systems, thus addressing a key gap in the field (Chung & Rudgers, 2016; Kandlikar et al., 2019; Miller et al., 2022; Siefert et al., 2019). Future studies equipped with density gradient designs (Ke & Wan, 2022) could comprehensively explore mechanisms of how microbes generated these observed patterns. In addition, though our work adds to the experimental evidence that soil microbes play a larger role in mediating fitness differences than niche differences (Kandlikar et al., 2019, 2021; Yan et al., 2022), its generality in natural species-rich communities needs more exploration.

## AUTHOR CONTRIBUTIONS

Chengjin Chu and Hangyu Wu designed the research. Hangyu Wu conducted the field work and collected the data. Weitao Wang, Tingting Wu, Hangyu Wu, Yuanzhi Li, Chengjin Chu, Chuliang Song, and Gaurav Kandlikar analyzed the data. Chengjin Chu, Weitao Wang, and Hangyu Wu wrote the first draft with substantial input from Gaurav Kandlikar. All authors contributed to the writing and editing of the work.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Wang et al., 2024) are available in Dryad at <https://doi.org/10.5061/dryad.vt4b8gtx9>.

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## SUPPORTING INFORMATION

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

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