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REPORT

Fungal community dissimilarity predicts plant–soil feedback strength in a lowland tropical forest

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Abstract

Soil microbes impact plant community structure and diversity through plant–soil feedbacks. However, linking the relative abundance of plant pathogens and mutualists to differential plant recruitment remains challenging. Here, we tested for microbial mediation of pairwise feedback using a reciprocal transplant experiment in a lowland tropical forest in Panama paired with amplicon sequencing of soil and roots. We found evidence that plant species identity alters the microbial community, and these changes in microbial composition alter subsequent growth and survival of conspecific plants. We also found that greater community dissimilarity between species in their arbuscular mycorrhizal and nonpathogenic fungi predicted increased positive feedback. Finally, we identified specific microbial taxa across our target functional groups that differentially accumulated under conspecific settings. Collectively, these findings clarify how soil pathogens and mutualists mediate net feedback effects on plant recruitment, with implications for management and restoration.

Camille S. Delavaux and Janika K. Angst share first authorship. Edward A. Herre, James D. Bever, and Thomas W. Crowther share last authorship.

KEYWORDS
amplicon sequencing, arbuscular mycorrhizal fungi, density dependence, fungal pathogens, Janzen–Connell hypothesis, plant–soil feedback

INTRODUCTION

Accumulating evidence supports the contribution of belowground plant-associated microbes in maintaining plant diversity (Bever et al., 2012, 2015; Johnson et al., 2012; Mangan, Schnitzer, et al., 2010; Mordecai, 2011; van der Heijden et al., 2008; van der Putten et al., 2013). Perhaps the most referenced hypothesis invoking these belowground microbes, the Janzen–Connell (J–C) hypothesis, posits that the accumulation of species-specific plant enemies reduces conspecific fitness, allowing competing plant species to coexist (Connell, 1971; Janzen, 1970). The J–C hypothesis initially invoked herbivores and seed predators as natural enemies in generating feedback, but evidence suggests that soil microbes can be the most important mediators (Bagchi et al., 2014; Mangan, Schnitzer, et al., 2010).

Since the J–C hypothesis was first proposed, theoretical and empirical studies have demonstrated the importance of soil-borne pathogens in plant coexistence (Bever et al., 2015; Eppinga et al., 2018; Terborgh, 2012). Observational studies and greenhouse experiments have shown that soil-borne pathogens influence patterns of seedling growth and survival (Harms et al., 2000). Studies using fungicides have shown that removing the belowground microbiome removes density-dependent survival (Bell et al., 2006) and reduces overall diversity (Bagchi et al., 2014). Other observational and experimental studies have demonstrated the pervasive negative effect of local soil on conspecific seedlings and improved growth farther from the conspecific adult tree, likely mediated through pathogens (Augspurger, 1984; Comita et al., 2010; Mangan, Schnitzer, et al., 2010).

Although there is an appreciation for the role soil-borne plant pathogens can play in the maintenance of forest diversity via feedbacks, most work has neglected the other major component of the plant microbiome that is known to directly influence both plant growth and community composition (Bever et al., 1997; Mangan, Schnitzer, et al., 2010; van der Heijden et al., 1998): mutualistic fungi. Through their effects on nutrient uptake and induced resistance to pathogens (Delavaux et al., 2017), root-associated arbuscular mycorrhizal fungi (AMF) contribute to the growth and survival of most vascular plant species (Brundrett, 2009), and are ubiquitous in highly diverse tropical forests (Smith & Read, 2008; Steidinger et al., 2019). A local build-up of AMF, or other mutualistic fungi, exhibiting high plant species affinity can generate positive feedback by increasing the establishment and survival of conspecifics, thus potentially counteracting negative pathogen effects (Jiang, Zhu, et al., 2020; Liang et al., 2015; Schroeder et al., 2020). Conversely, AMF have also been shown to generate negative feedback through differential fitness effects on hosts (Bever, 2002b). Ultimately, identifying the relative impacts of pathogens and mutualists will be necessary for an integrated understanding of microbially mediated feedback that may underpin larger scale patterns of plant diversity.

To date, few empirical studies have explicitly considered the roles of both soil-borne pathogens and mutualistic fungi in mediating observed feedback in situ (Liang et al., 2021), with most work theoretical in nature (Jiang, Abbott, et al., 2020; Schroeder et al., 2020). Even though plant–soil feedbacks represent the net effect of these two major components of the microbiome (Bever et al., 2012; van der Putten et al., 2013, 2016), identifying the relative contributions of these different groups has remained a challenge. Importantly, the central prediction of the J–C hypothesis as it applies to the plant microbiome—that differential accumulation of microbial taxa beneath different plant species drives the differential survival and growth of recruits—remains untested in field conditions. Therefore, we build upon this work and address this remaining gap by characterizing the microbial communities of both pathogens and mutualists beneath trees in the field, and studying their subsequent influence on growth and survival of seedlings. To this end, we reciprocally planted seeds under four adult species to generate conspecific and heterospecific conditions. We continuously monitored the growth and survival of the seedlings, and characterized communities of pathogens and mutualists in the soil and roots via amplicon sequencing. With this experiment, we investigated whether the differential accumulation of mutualists and pathogens beneath tree species predicted pairwise plant–soil feedbacks. Specifically, we aimed to (1) determine drivers of the seedling soil and root microbiome, (2) quantify plant–soil feedback in the field, and (3) test the degree to which both the pathogen and mutualist components of the plant microbiome predict plant–soil feedback strength. Through this work, we link the microbiome and differential abundance of functional groups of microbes to pairwise feedback in field conditions, providing valuable information for conservation, restoration and land management efforts.

MATERIALS AND METHODS

Site description

Our field experiment was established at a 38.4-ha plot located on the Gigante Peninsula in Panama (Gigante) within the Barro Colorado Nature Monument managed by the Smithsonian Tropical Research Institute (Figure 1A; Appendix S1: Section S1). The forest within the site is a 60-year-old seasonally moist semideciduous lowland tropical forest (Schnitzer & Carson, 2010). The bulk of the 2600 mm of yearly rainfall occurs between May and November, with a 4-month dry season from December to April (Álvarez-Cansino et al., 2015; Schnitzer & Carson, 2010).

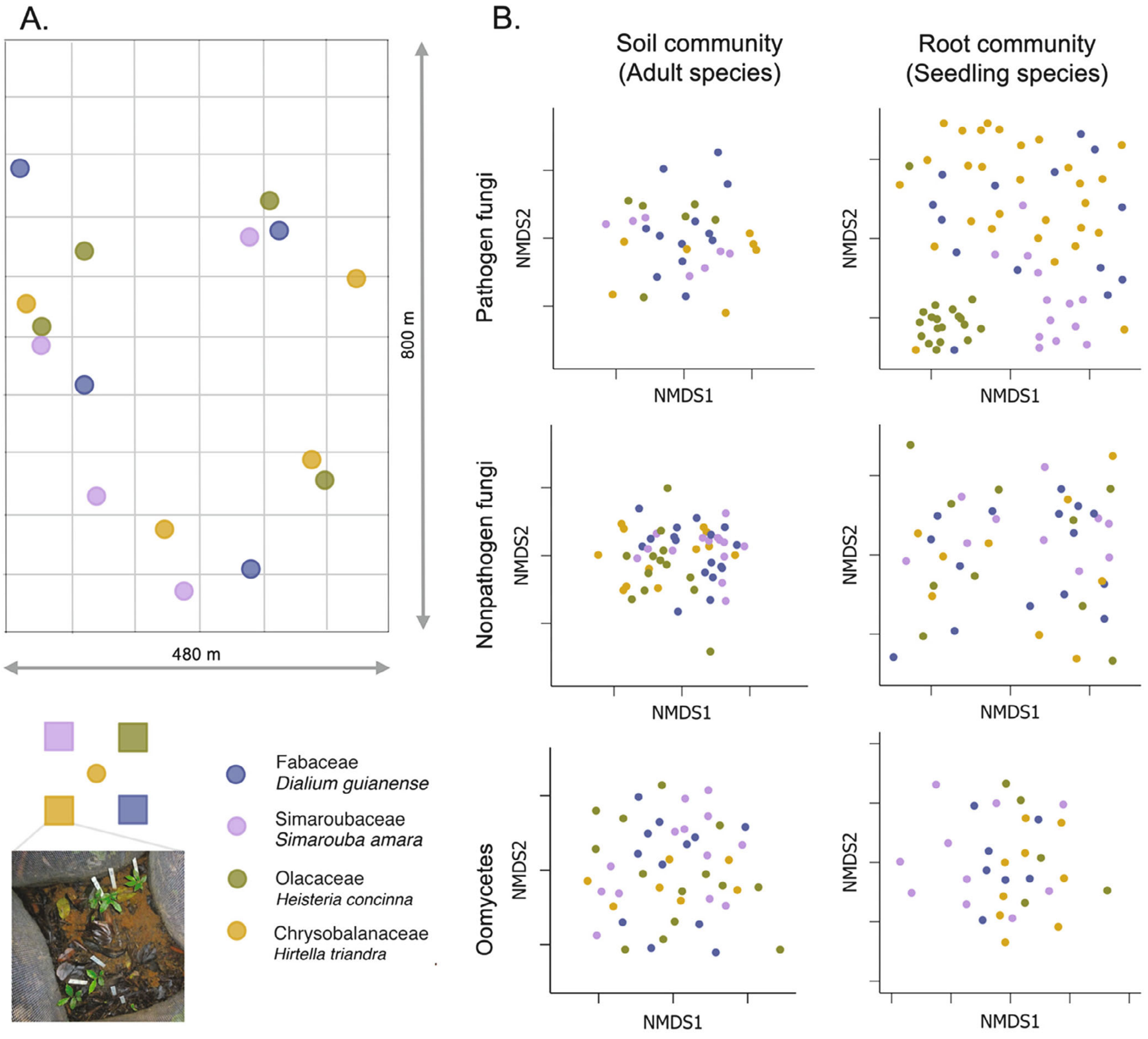

FIGURE 1 Experimental design and drivers of seedling microbiome by sample type. Across the field plot, four adult trees of each species were chosen to establish conspecific and heterospecific treatments by planting seeds of each focal species in a fully factorial design in exclosures beneath adults (A; PC: John W. Schroeder). Adult species was most important in driving soil microbial community composition, while seedling identity was most important for root microbial community composition (B). Adult species identity was a significant predictor for nonpathogen fungal, but not pathogen fungal soil community composition. Adult species identity was a marginally significant predictor of oomycete soil community composition. In contrast, seedling identity was most important for root fungal community composition for both nonpathogens and pathogens, but not oomycetes. For each plot, both *X* and *Y* axes are of equal length.

Experimental design and sample collection

We used four shade-tolerant, abundant tree species spanning four plant families, including *Heisteria concinna* (Olacaceae), *Dialium guianense* (Fabaceae), *Simarouba amara* (Simaroubaceae), and *Hirtella triandra* (Chrysobalanaceae). Seeds were collected from late 2018 to early 2019 using 4 m^2 elevated mesh seed traps across Gigante and nearby Barro Colorado Island. Seeds were cleaned and surface sterilized to remove as much of the surface microbiome as possible (Gallery et al., 2007). Experimental planting occurred in May 2019. For each of our study tree species, four naturally occurring adult individuals were identified, for a total of 16 adult trees (≥15 m from each other). Next, seedlings of each of the four species were planted under each adult tree, resulting in conspecific and heterospecific settings. Species were planted in exclosures beneath the adult crown to minimize the effects of herbivores. Throughout the experiment, each emerging seedling was periodically censused, with height, leaf count, and mortality documented. Each seedling observation in the census period was documented as a separate entry, resulting in a table with 222 seedlings and 4835 observations. For each species, 30 individuals from outside of the experiment were sampled to develop allometric biomass equations. Microbiome sampling for soils and roots was conducted once between 3 and 5 months after planting; soils were also sampled between 9 and 12 months after planting. This sampling included both planted seedlings within and naturally germinating seedlings adjacent to exclosures. Soil samples were simultaneously collected from each exclosure, with cores taken at a depth of ~20 cm in opposite corners and homogenized into one sample.

Microbiome sequencing and bioinformatics

To characterize root and soil microbiomes in our experiment, we used amplicon sequencing. As we were interested in pathogens and mutualists, we targeted three major groups: general fungi (putative pathogens and nonpathogens), oomycetes and AMF. Oomycetes generally act as plant pathogens (van West et al., 2003), while AMF represent the most common mycorrhizal mutualists in lowland tropical forests (Mangan, Herre, & Bever, 2010; Smith & Read, 2008).

Statistical analyses

We used different statistical approaches to answer each question in our study, all of which were conducted in R version 4.1.1 (R Core Team, 2022). First, to understand the relative importance of adult and seedling species identity as predictors of the soil and root community composition, we used permutational multivariate analyses of variance (PERMANOVAs). Next, to test for feedback between pairs of plant species (i.e., whether species grew significantly better or worse, or survived significantly more or less, when under their own species compared to the other species [Bever et al., 1997]), we used generalized linear mixed models (GLMMs) predicting fitness measures with adult species and seedling species as predictors, with random effects used to control for nonindependence due to spatial association and repeated measures. This was then followed by specific contrasts to test for pairwise feedback between species. We then tested for the ability of the microbiome to predict variation in feedback by relating microbiome dissimilarity (Bray–Curtis) to feedback strength. Finally, to test the differential abundance of specific microbial taxa and identify candidate taxa implicated in driving feedback, we used GLMMs for each taxon predicting relative abundance followed by contrasts. A detailed description of bioinformatics and statistical analyses can be found in Appendix S1: Sections S1 and S2. All results refer to timepoint one unless otherwise specified.

RESULTS

Drivers of microbial community composition

We found that adult plant species identity was the strongest predictor of soil microbial community composition, while seedling species identity influenced within-root microbial community composition the most (Figure 1B; Appendix S1: Table S1, Figure S1). Across the nonpathogens, adult plant species identity had a significant influence on the microbial community in bulk soil samples (time point one $p = 0.001$, $R^2 = 0.09$). This was consistent from samples collected at both time points (time point two $p = 0.001$, $R^2 = 0.09$) as well as for oomycetes (time point one, $p = 0.06$, $R^2 = 0.1$). In contrast, in root samples, we found an effect of seedling species identity on microbial community composition for both fungal pathogens and nonpathogens, although this was only marginally significant for pathogens (pathogens: $p = 0.07$, $R^2 = 0.08$, nonpathogen $p = 0.001$, $R^2 = 0.11$). However, there was still a significant influence of adult species identity on the nonpathogen root fungal microbiome (adult species $p = 0.01$, $R^2 = 0.03$). Adult species identity did not, however, have a significant influence on the fungal pathogen ($p = 0.15$, $R^2 = 0.07$) or oomycete root microbiomes ($p = 0.42$, $R^2 = 0.10$). No significant results were found when analyzing these patterns for AMF data.

Variation in pairwise feedback

We found substantial variation in feedback for biomass and survival (Figure 2A,B; Appendix S1: Table S2 and Figure S2). We found significantly positive pairwise feedback in plant biomass between *H. concinna* and *H. triandra* (total biomass $p = 0.03$, $t(60.60) = 2.24$, aboveground $p = 0.04$, $t(60.60) = 2.15$, belowground $p = 0.02$, $t(53.30) = 2.41$). Seedlings of both species showed increased total, aboveground and belowground biomass in conspecific compared to heterospecific settings. In contrast, we found one instance of marginally significant pairwise negative feedback in seedling survival, between *Dialium guianense* and *H. triandra* ($p = 0.10$, $z(\text{Inf}) = -1.65$; Appendix S1: Figure S2); each of these species showed reduced survival under conspecific compared to heterospecific adults.

Impact of the microbial community dissimilarity on pairwise feedback

Consistent with the hypothesis that local soil microbiome development drives plant–soil feedbacks, we found that specific components of the soil microbial community dissimilarity predicted observed feedback strength (Figure 2C; Appendix S1: Table S3). Across biomass, we found a positive correlation between microbial community dissimilarity and feedback for nonpathogens (total biomass $p = 0.04$, $t(19) = 2.231$; aboveground biomass $p = 0.03$, $t(19) = 2.324$). We further found a marginally significant positive correlation for AMF (total biomass $p = 0.08$, $t(19) = 1.784$; aboveground biomass $p = 0.06$, $t(19) = 1.932$). No relationships were detected in survival.

Differential abundance of microbial taxa

We found many microbial taxa whose differential abundance qualitatively matched the pairwise feedback patterns observed in the plant census data (Appendix S1: Figure S3; GitHub repository; see *Data availability statement*). These are cases where there is first a detected differential abundance between two seedling species, and second, the microbial taxon is only overrepresented in the conspecific setting of one member of the plant species pair. We would expect this pattern for both positive and negative feedback, as differential accumulation under conspecifics could lead to either positive or negative feedbacks. We detected significant differential abundance ($p < 0.05$, exact value can be found in the GitHub repository) in 865 taxa in soil (817 nonpathogens, 27 AMF, 21 oomycetes) and 876 taxa in roots (79 pathogens, 796 nonpathogens, one oomycete). Of these, 21 taxa in soil (16 nonpathogens, two AMF, three oomycetes) and seven taxa in roots (all nonpathogens) were overrepresented beneath conspecific trees for *H. concinna* and *H. triandra* seedlings and 22 taxa in soil (19 nonpathogens, three oomycetes) and 23 taxa in roots (six pathogens, 17 nonpathogens) were all overrepresented beneath conspecific adult trees for *Dialium guianense* and *H. triandra* seedlings. We do not report differential abundance detected in other species pairs here as they are not associated with detected significant feedback in biomass and survival; however, these taxa may be implicated in feedback that we were unable to detect or occur at later stages in seedling growth.

DISCUSSION

Our findings highlight the different roles of pathogenic and mutualistic components of the soil microbiome in mediating variation in pairwise plant–soil feedback in the field. First, we found that the microbial community differentiated from bulk soil to seedling roots; adult species identity was more important in determining bulk soil community composition, whereas seedling species identity was more important in determining within-root community composition. Next, we found evidence for variation in pairwise feedback across pairs of tree species in our experiment. Importantly, our results showed that soil microbial community dissimilarity predicts the observed variation in feedback strength. In particular, greater dissimilarity of nonpathogen and AMF communities predicted stronger positive feedback in biomass, consistent with localized concentrations of host-specific mutualists. We also demonstrated differential accumulation of specific microbial taxa qualitatively consistent with observed feedback. Together, this work demonstrates the direct influence of different functional groups in mediating feedback that affect the differential growth and survival of different host species in the field.

We found evidence that the seedling microbiome is diverging from the bulk soil microbiome, and that different seedling species accumulate specific microbial taxa. Our results showed that adult tree species identity exerts a significant effect on the pool of available microbes in the bulk soil, but that seedling species identity is more important in determining the composition of the microbial community directly interacting with tree

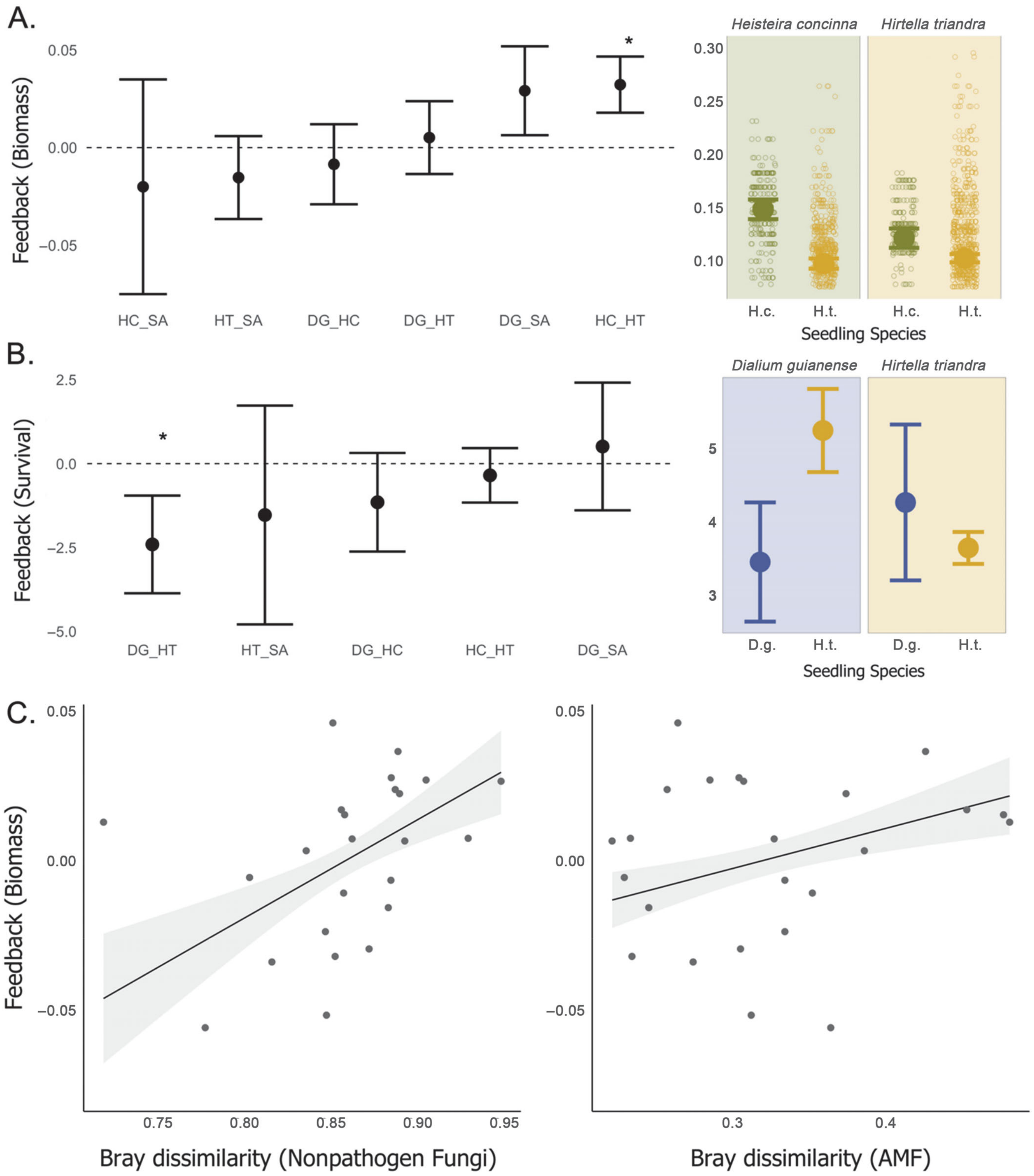

FIGURE 2 Variation in pairwise feedback across focal species is predicted by microbial dissimilarity. Variation in feedback in biomass (A) and survival (B), with pairs of plant species with significant positive and negative feedback in biomass and survival. Within both nonpathogen fungi and arbuscular mycorrhizal fungi (AMF), increasing dissimilarity in microbial communities is related to an increase in biomass-derived feedback (C). Large points represent means estimated from models, while small points represent raw data; error bars and bands represent standard errors. DT, *Dialium guianense*; HC, *Heisteria concinna*; HT, *Hirtella triandra*; SA, *Simarouba amara*.

seedlings' roots. This seedling species influence on the root microbiome is consistent with previous work that found seed species influence on the seed microbiome (Sarmiento et al., 2017). Further, we identified many microbial taxa that exhibited differential accumulation in paired species depending on conspecific versus heterospecific placement. Although we could not meaningfully test whether these taxa were implicated in driving observed feedback with our data, these patterns qualitatively match the differential accumulation required to drive pairwise feedback (Abbott et al., 2021; Bever et al., 1997). Therefore, these should be viewed as candidate taxa that may be important in driving feedback. Overall, both observed community and taxon level differentiation in the seedling fungal communities have the potential to drive plant–soil feedback.

We found a large range of feedback strength in both biomass and survival across the four tree species included in our experiment, and that differences in the microbial community predicted this variation for biomass. We found that variation in feedback values could be explained by the dissimilarity of the microbial community, likely resulting from different growth rates of microbes driving divergence of this community (Abbott et al., 2021; Bever, 2002a). As the dissimilarity of nonpathogenic fungal and AMF communities between heterospecific trees increased, the growth of nearby conspecific seedlings *increased* relative to that of heterospecific seedlings. This likely reflects unidentified mutualists in the nonpathogen group, alongside AMF driving positive feedback, and is consistent with differential accumulation of host-specific mutualists contributing to positive feedback in seedling growth (Bever et al., 2013; Mangan, Herre, & Bever, 2010). Although we expected a negative relationship between microbial dissimilarity and feedback for survival in fungal pathogens and oomycetes, given the weak negative feedback observed, we only detected nonsignificant negative correlations. Weak negative feedback may be expected in these tree species as they represent common, abundant, species (Comita et al., 2014; LaManna et al., 2017). Together, these findings highlight the important role of differential accumulation of mutualists beneath different tree species within the microbiome mediating positive plant–soil feedbacks.

Although our focal tree species are known to associate with AMF, we only found relatively weak patterns consistent with AM taxa influencing feedback. This could be due to lower host specificity of AMF compared with pathogens (Bever et al., 2012; Crawford et al., 2019) or AMF impacts not being detectable on the timescale of our study. Although AMF are expected to exhibit lower host specificity, previous studies in similar forests have found evidence of AMF host affinity (Mangan, Herre, & Bever, 2010; Schroeder et al., 2019), suggesting that they should be involved in feedbacks. It is possible, however, that this is not as strong in our focal tree species. However, previous studies detecting feedback in the same forest controlled for abiotic soil properties (Mangan, Herre, & Bever, 2010; Mangan, Schnitzer, et al., 2010), which suggests this could explain the weak AMF feedback. Further, we had difficulties sequencing AMF from all acquired samples, which severely reduced our power relative to other fungal data. AMF may also grow more slowly and require longer initial plant investment relative to other fungi (Smith & Read, 2008), making it difficult for us to detect their impact when our samples were taken, 3–6 months after seed planting. Future studies should investigate the long-term impact of AMF on pairwise feedback, as most tropical plant species associate with AMF.

In summary, the work presented here represents an important step in clarifying the different roles of plant-associated microbes in plant–soil feedback, and ultimately plant community structure. We found evidence counter to the J–C hypothesis, where the accumulation of host-specific mutualistic fungi drives differences in plant recruitment. With our field experiment, we used (1) microbiome data to identify host-specific differential accumulation and composition of plant-associated microbes, (2) census data to detect evidence of plant pairwise feedback and (3) joint plant and microbial data to link changes in the microbiome to strength of pairwise feedbacks. By differentially impacting the growth and survival of conspecific seedlings, negative and positive plant–soil feedbacks may increase and decrease seedling diversity, respectively. As such, these opposing mechanisms are likely to interactively drive patterns of plant diversity and composition. Identifying how the relative importance of these opposing mechanisms varies across plant communities will provide key insight into the biogeography of plant diversity, facilitating management efforts to preserve and restore terrestrial plant biodiversity.

AUTHOR CONTRIBUTIONS

The study was conceived by John W. Schroeder, Edward A. Herre and Kirk Broders. The field experiment was carried out by John W. Schroeder, Daniel F. Petticord, Hilario Espinosa and Makenna Brown. Sequencing was led by Camille S. Delavaux. Analyses were led by Camille S. Delavaux and Janika K. Angst with input from James D. Bever, John W. Schroeder and Daniel F. Petticord. Manuscript writing was led my Camille S. Delavaux, with all other authors contributing substantially to revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data sets analyzed for this study and outputs for (1) guilds assigned to fungal taxa via FUNGuild and (2) model outputs for microbial differential abundance are available in Zenodo (https://doi.org/10.5281/zenodo.8407917). Raw sequence data (PRJNA838257) can be found at https://www.ncbi.nlm.nih.gov/bioproject/PRJNA838257.

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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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