

ARTICLE

Linking genetic diversity and species diversity through plant–soil feedback

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Abstract

Genetic diversity and species diversity are typically studied in isolation despite theory showing they likely influence one another. Here, we used simplified communities of one or two populations of one or two species to test whether linkages between genetic and species diversity can be mediated by interactions between plants and their soil microbiota, or microbe-mediated plant–soil feedback (PSF). Interspecific PSF promotes the maintenance of species diversity when plants grow better with heterospecific soil microbes than with conspecific microbes. Similarly, intraspecific PSF promotes the maintenance of genetic diversity when plants grow better with heterogenotypic than with congenotypic microbes. In a two-phase greenhouse experiment, we conditioned the soil microbial community with pairs of plants that were either two individuals of the same species (lower species diversity) or one individual of each of two species (higher species diversity), and with pairs of plants that were either two individuals from the same population (lower genetic diversity) or one individual from each of two populations (higher genetic diversity). We then tested the effects of these microbial communities on plant growth in a second phase. We found that higher genetic diversity reduced the ability of interspecific PSF to promote plant species diversity, and for one of our two study species, higher species diversity reduced the ability of intraspecific PSF to promote plant genetic diversity. If these patterns occur in more diverse communities, then our results suggest that PSF may dampen the negative effects of diversity loss by promoting diversity at other levels of biological organization.

KEYWORDS

coexistence, genetic variation, negative feedback, soil microbes

INTRODUCTION

Genetic diversity and species diversity are ultimately controlled by similar processes, namely selection, drift, migration, and mutation/speciation (Vellend, 2010), yet they are typically studied in isolation. However, the possibility that genetic diversity and species diversity could influence one

another has been acknowledged for decades (Amarasekare, 2000; Antonovics, 1976, 1992, 2003; Booth & Philip Grime, 2003; Chave, 2004; Fridley & Philip Grime, 2010; Kassen, 2002; Lankau & Strauss, 2007; Whitlock et al., 2007), and a growing body of theoretical work has proposed mechanisms that could link these fundamental levels of biodiversity (Eck et al., 2019; Vellend, 2006,

2008; Vellend & Geber, 2005). For example, genetic and species diversity may positively influence each other if different genotypes of a focal species have a competitive advantage against different species in the community, and reciprocally, if different species have a competitive advantage against different genotypes of a common focal species (Vellend, 2006, 2008; Vellend & Geber, 2005). Alternatively, genetic and species diversity may negatively influence each other if high genetic diversity reduces available niche space for heterospecifics, and if high species diversity reduces available niche space for genotypes within species (Vellend & Geber, 2005).

While linkages between genetic and species diversity have so far been considered primarily through the mechanism of competition, other types of species interactions, like the interaction between plants and their soil microbiota, also may contribute. Microbe-mediated plant–soil feedback (PSF hereafter, although we note that PSF can also be mediated by abiotic factors [Ehrenfeld et al., 2005]) is a ubiquitous mechanism of plant coexistence. The effects of PSF on plant growth are similar in magnitude to those of competition (Lekberg et al., 2018), and plant competition for soil resources is in fact a form of abiotic-mediated PSF (Smith-Ramesh & Reynolds, 2017). PSF occurs when different plant species attract and stimulate the growth of different soil microbial communities, and these microbial communities then feed back to differentially affect the fitness of plant species through species-specific pathogens or mutualists. Negative PSF occurs when plant species have lower fitness in their own soil microbial community relative to other members of the plant community, leading to negative density-dependence, increased likelihood of coexistence, and the maintenance of species diversity (Bever et al., 1997). Positive PSF, on the other hand, occurs when species have higher fitness when grown with their own soil microbial community relative to other members of the plant community, resulting in positive density dependence, reduced likelihood of coexistence, and ultimately species diversity declines (Bever et al., 1997).

While most work has focused on microbe-mediated interspecific PSF as a mechanism for maintaining species diversity, some studies have found significant intraspecific PSF that can affect the coexistence of genotypes within species (Bever et al., 1997; Bukowski et al., 2018; Bukowski & Petermann, 2014; Felker-Quinn et al., 2011; Liu et al., 2015). For example, when pathogens differentially affect genotypes of a species, as has been found in both agricultural (Croll & McDonald, 2017; Neupane et al., 2015; Walters et al., 2018) and natural (Eck et al., 2019; Laine, 2004; Laine et al., 2011) populations, then the pathogens most harmful to a common genotype will accumulate and reduce the fitness of that genotype in the next generation. As with interspecific PSF, these

dynamics lead to negative density dependence and the maintenance of genetic diversity through negative intraspecific PSF. On the other hand, if mutualists differentially affect genotypes of a species, then mutualists most beneficial to a common genotype may accumulate and increase the fitness of that genotype in the next generation. Such positive intraspecific PSFs, which lead to positive density dependence and the erosion of genetic diversity, have also been demonstrated (Bever et al., 1996; Bukowski et al., 2018; Bukowski & Petermann, 2014).

Because PSF can influence the maintenance of both species diversity and genetic diversity, it may also mediate linkages between the two. Analogous to theory regarding competition as a mediator of linkages between genetic diversity and species diversity, we may expect PSF to cause genetic and species diversity to positively influence each other if (1) some species perform better with the microbial communities associated with one genotype of a focal species, while other species perform better with the microbial communities associated with different genotypes, and (2) some genotypes of a focal species perform better with the microbial communities associated with one species, while other genotypes perform better with the microbial communities associated with different species (Figure 1a). These dynamics could occur, for example, if a legume species that is highly dependent on nitrogen-fixing rhizobia benefits from co-occurring with a heterospecific legume genotype that strongly promotes rhizobia growth, while another plant species may benefit instead from the microbes associated with a different genotype of the legume, perhaps through associational resistance to an enemy.

On the other hand, PSF may cause genetic diversity and species diversity to negatively influence each other if (1) high genetic diversity in a focal species dilutes conspecific pathogens that would otherwise promote negative interspecific PSF and (2) high species diversity dilutes the congenotypic pathogens of a common genotype that would otherwise promote negative intraspecific PSF (Figure 1b). Recent theoretical work found support for the dilution of conspecific pathogens, showing that when pathogens were genotype specific, simulated communities with low genetic diversity supported more species diversity by promoting more negative interspecific PSF relative to simulated communities with high genetic diversity (Eck et al., 2019). The reciprocal effects of species diversity on intraspecific PSFs may also occur, although this was not tested in the Eck et al. (2019) model.

Here, we tested empirically whether PSF can mediate linkages between genetic diversity and species diversity in a simplified two-population, two-species system. We tested how one- or two-species treatments, and how one- or two-population (within species) treatments, affected

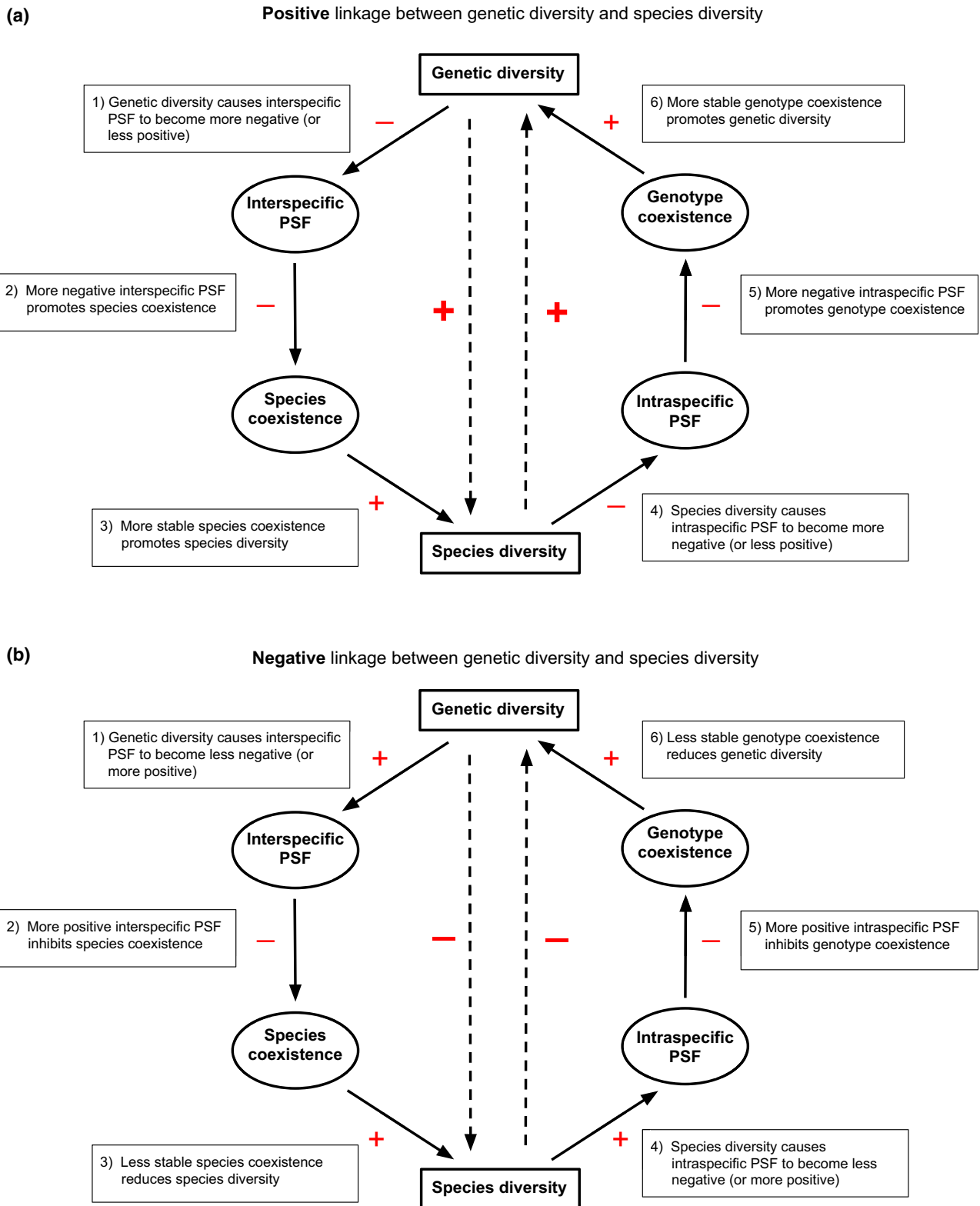


FIGURE 1 Legend on next page.

the strength and direction of interspecific and intraspecific PSF. While we acknowledge that it is difficult to generalize about genetic diversity and species diversity based

on our simplified system, our goal was to test whether PSF has the potential to mediate linkages between genetic and species diversity. To manipulate genetic

diversity, we used individuals from one or two populations that are divergent in several growth traits. For species diversity, our treatments compare one versus two species communities. Specifically, we asked:

1. Does genetic diversity (two populations vs. one) alter the strength of interspecific PSF?
2. Does species diversity (two species vs. one) alter the strength of intraspecific PSF?

If genetic diversity causes interspecific PSF to become more negative (or less positive) and species diversity causes intraspecific PSF to become more negative (or less positive), then genetic and species diversity will positively influence each other in this simplified system such that diversity begets diversity (Figure 1a). On the other hand, if genetic diversity causes interspecific PSF to become more positive (or less negative) and species diversity causes intraspecific PSF to become more positive (or less negative), then genetic and species diversity will negatively influence each other such that diversity at one level of biological organization reduces diversity at the other level (Figure 1b).

METHODS

Experimental design overview

To test how genetic diversity influences interspecific plant–soil feedback (PSF) and how species diversity influences intraspecific PSF, we conducted a two-phase PSF experiment (Bever, 1994) in the greenhouse in the fall of 2017. In this method, a plant or group of plants conditions the soil microbial community in the first phase (Phase I), and the effects of those microbial communities on plant growth are then assessed in a second phase (Phase II). We calculated PSF as the net-pairwise feedback, I_s , a measure that allows us to make predictions about the (de)stabilizing effects of PSF on community or population diversity (Bever et al., 1997). Additionally,

we estimated the ln-response ratio for each species and each population, which is a direct measure of that species' or population's relative growth in its own soil microbial community versus heterospecific or hetero-population soil.

We manipulated genetic diversity (one or two populations) and species diversity (one or two species) in Phase I to test their influence on the strength and direction of inter- and intraspecific PSF, respectively. We manipulated species diversity by planting pairs of plants in each pot that were either two individuals of the same species or one individual of each of two species, and we manipulated genetic diversity within each species in a similar way, except we planted two individuals from the same population or one individual from each of two populations (note that each population includes numerous genotypes; Figure 2). We assume that the genetic distance between two genotypes from the same population is lower than the genetic distance between two genotypes from different populations. Thus, pots planted with two species represent higher species diversity than pots planted with a single species, and pots planted with two populations represent higher genetic diversity than pots planted with a single population. We refer to these lower and higher species diversity treatments as “one-species” and “two-species,” respectively, and we refer to the lower and higher genetic diversity treatments as “one-population” and “two-population,” respectively. We used these two levels of diversity within each pot because including more levels would have made the experiment unfeasibly large, and the largest effects of increasing species or genotype richness are often observed at relatively low richness (Tilman et al., 1996, 1997).

Feedback experiment

Phase I: Conditioning soil

We used two commonly co-occurring perennial prairie plant species: *Echinacea purpurea* (Asteraceae; “*Echinacea*” hereafter) and *Coreopsis lanceolata* (Asteraceae;

FIGURE 1 Conceptual diagram showing how the effects of genetic and species diversity on coexistence have the potential to lead to (a) positive and (b) negative linkages between genetic diversity and species diversity that are mediated by plant–soil feedback (PSF). (a) If genetic diversity causes interspecific PSF to become more negative (or less positive) (a1), and species diversity causes intraspecific PSF to become more negative (or less positive) (a4), then genetic diversity and species diversity will increase the potential for PSF-mediated coexistence of competing species and genotypes, respectively. If stronger coexistence leads to greater diversity, this could then cause genetic and species diversity to positively influence each other such that diversity begets diversity. (b) Reciprocally, if genetic diversity causes interspecific PSF to become more positive (or less negative) (b1), and species diversity causes intraspecific PSF to become more positive (or less negative) (b4), then genetic diversity and species diversity may negatively influence each other such that diversity at one level of biological organization reduces diversity at the other level. The positive and negative symbols on the solid arrows indicate how an increase in the variable at the arrow's tail affects the variable at the arrow's head. The resulting net effect of each level of diversity on the other is summarized by the vertical dotted lines and is determined by multiplication of the individual effects. Note that here we assume that more positive inter- and intraspecific PSF always inhibit species coexistence and genotype coexistence, respectively (a2, a5, b2, b5), and coexistence always promotes the maintenance of species and genetic diversity, respectively (a3, a6, b3, b6)

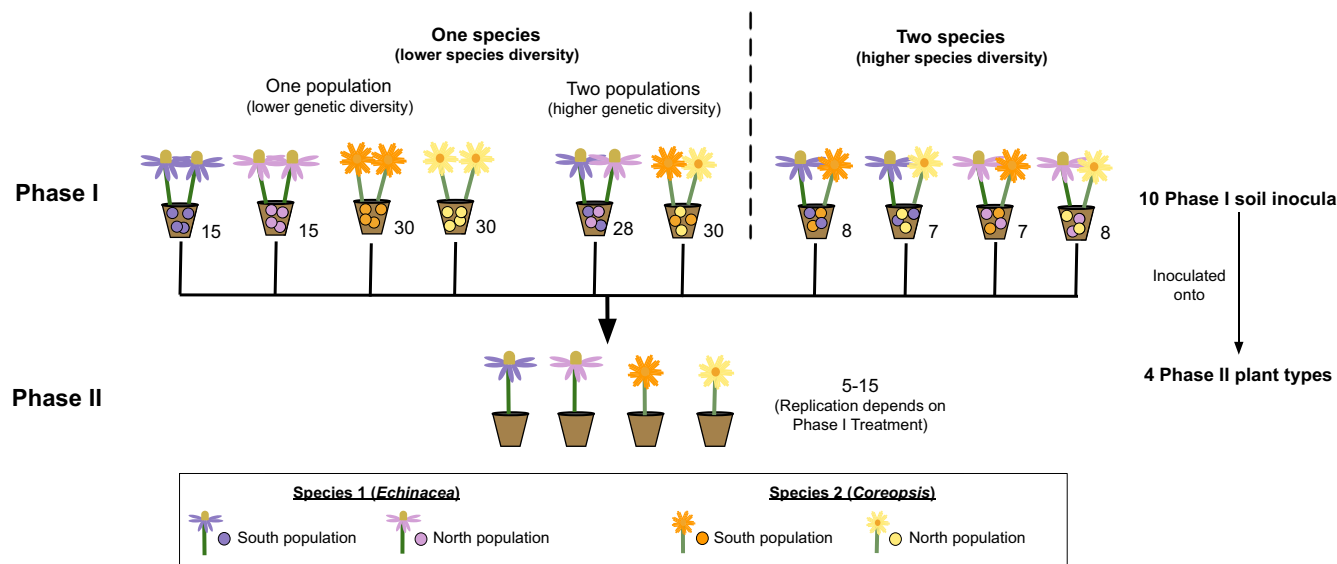


FIGURE 2 Experimental design. Small colored circles represent the soil microbial communities conditioned by different plant pairs in Phase I, which were inoculated onto new plants in Phase II. We planted 30 replicates of each of seven treatments (shown left to right): 1–4, one species, one population (*Echinacea* South, *Echinacea* North, *Coreopsis* South, *Coreopsis* North); 5–6, one species, two populations (*Echinacea* South + North, *Coreopsis* South + North); and 7, two species (all possible pairwise combinations of *Echinacea* and *Coreopsis* populations). The number next to each pot represents the final number of replicates for each soil inoculum, which were reduced in the one-species *Echinacea* treatments because of low germination

“*Coreopsis*” hereafter). For each of these species we used two populations: one from the southern Midwestern United States (South; *Coreopsis*, Missouri Wildflower Nursery, originally collected from Joplin County, Missouri, USA; *Echinacea*, Hamilton Native Outpost, cultivated in Putnam County, Missouri, USA but likely originating from populations in Iowa) and one from the upper Midwestern United States (North; *Coreopsis*, Agrecol, originally collected from Kenosha, Wisconsin, USA; *Echinacea*, Agrecol, originally collected from Madison, Iowa, USA). These populations differ in several traits, including relative growth rate, supporting our assumption that genetic distances are greater between than within populations (Lau et al., 2019; Zirbel & Brudvig, 2020a, 2020b; Appendix S1: Table S1).

We inoculated all pots with a common field soil inoculum at the time of planting. The inoculum was comprised of soils collected from beneath *Echinacea* and *Coreopsis* plants in August 2017 at each of four restored prairie sites at the W. K. Kellogg Biological Station (Hickory Corners, Michigan). These sites were sown with 12 common prairie species in Fall, 2015, and two sites were planted with South populations of *Echinacea* and *Coreopsis* while two were planted with North populations. Specifically, we used a 1.9 cm diameter core to collect soil to a depth of 15 cm from beneath the *Echinacea* and *Coreopsis* individual located closest to every 5-m mark along two 30-m transects, except for one site where we used the first 12 plants we could find because our species were rare at this site. We sieved the soil

(2-mm mesh) to remove rocks and roots, then homogenized it to create a single inoculum that we stored at 4°C until Phase I was planted (maximum 20 days).

We sterilized and filled 656 ml Deepots (Stuewe and Sons, Tangent, Oregon, USA) with a sterile base soil composed of a 9:1 mixture of untreated sand (Quickrete All Purpose Sand, Atlanta, Georgia, USA, included for drainage) and sifted, sterilized (autoclaved at 121°C for two periods of 45 min with a 48-h rest between) field soil that we collected from a restored prairie that received a similar seed mix and management as the experimental prairies described in the previous paragraph. We then inoculated each pot with a 40-ml layer of the common inoculum and topped with a thin layer of sterile base soil to reduce contamination between pots. We planted four seeds into each pot, later thinning to two seedlings, in the combinations described in the Experimental Design Overview (Figure 2). We planted 30 replicates of each treatment, but due to poor germination of the *Echinacea* South population we ended up with 15 replicates of each *Echinacea* one-population treatment and 28 replicates of the *Echinacea* two-population treatment (Phase I $N = 178$).

We harvested all plants after 18 weeks and dried and weighed aboveground biomass to account for Phase I productivity in our analyses (see below). Roots of the plant pairs could not be separated, and so were discarded. We stored conditioned soil at 4°C until we planted Phase II (approximately 1 week).

Phase II: Quantifying plant growth effects of conditioned soil

To test for the effect of each soil microbial community from Phase I on plant growth, we inoculated single individuals of each population of each species with soils from each Phase I treatment in a full factorial design (Figure 2; $N = 384$, 5–15 replicates of each Phase I inoculum \times 10 Phase I inocula \times 2 species \times 2 populations per species). In the one-population treatments, where we were testing the growth of a species in heterospecific soil, we only planted five replicates of each population because the two populations were combined to represent the species. For example, to represent the growth of *Coreopsis* in soil conditioned by *Echinacea*, we planted five replicates each of *Coreopsis* South in soil conditioned by *Echinacea* South, *Coreopsis* South in soil conditioned by *Echinacea* North, *Coreopsis* North in soil conditioned by *Echinacea* South, and *Coreopsis* North in soil conditioned by *Echinacea* North, for a total of 20 plants (see Appendix S1: Tables S2 and S3 for additional replication details).

We filled pots with a sterile base soil as described for Phase I (except we sterilized the sand for Phase II) and inoculated them with a 40-ml layer of conditioned soil originating from a single Phase I pot (soil from each Phase I pot was inoculated onto 2–4 Phase II pots). Maintaining independence of replicates in this way is essential because mixing soils from multiple pots produces falsely precise estimates of PSF (Reinhart & Rinella, 2016). We then sprinkled a thin layer of twice-autoclaved Turface (calcined clay, Profile Products, Illinois) on top of the inoculum layer to improve drainage and reduce contamination between pots. To improve germination, we cold-stratified *Echinacea* seeds in wet quartz sand in a plastic bag for 4 weeks. We surface sterilized all seeds for 2 min in 5% bleach, followed by three rinses in DI water, and then planted three seeds into each pot, which were later thinned to one seedling. We planted *Coreopsis* as seeds but transplanted *Echinacea* as seedlings at the two-leaf stage because of germination concerns (we planted *Echinacea* seeds into Metro Mix 360 in 350-ml plastic tray cells at the same time that we planted our experiment, and selected seedlings at the two-leaf stage from those that germinated to transplant). After 14 weeks above- and belowground biomass was harvested, dried at 65°C, and weighed.

Statistical analyses

Does genetic diversity alter the strength of interspecific PSF?

To determine whether genetic diversity (two populations vs. one) affects the strength or direction of interspecific

PSF, we fit linear mixed models using the lme4 package (Bates et al., 2015) in R, version 3.5.2 (R Core Team, 2018). Phase II biomass (the sum of aboveground and belowground biomass) was the response variable; and Phase II species (i.e., species planted in Phase II: *Echinacea* or *Coreopsis*), Phase I species (i.e., species that conditioned the soil: *Echinacea* or *Coreopsis*), Phase I genetic diversity (i.e., number of populations that conditioned soil: one or two), and all interactions were included as fixed effects. Phase I pot (the pot from which conditioned soil was taken) and Phase II greenhouse bench (the spatial location in the greenhouse) were included as random effects. To control for potential confounding effects of microbial density or nutrient draw-down being greater in soil conditioned by larger plants, Phase I pot biomass (the sum of aboveground biomass for both individuals, scaled to a mean of zero) was included as a covariate. Interspecific PSF is calculated as the coefficient $I_s = G(A)_\alpha - G(A)_\beta - G(B)_\alpha + G(B)_\beta$, where α is soil conditioned by species *A*, β is soil conditioned by species *B*, and *G* represents growth (Bever et al., 1997). Whether this coefficient (i.e., PSF) differs significantly from zero is indicated by a statistical test of the interaction between Phase II species and Phase I species. Therefore, a significant Phase II species \times Phase I species \times Phase I genetic diversity interaction would indicate that interspecific PSF differs between the one- and two-populations treatments. We assessed statistical significance using Type III ANOVA with Satterthwaite's approximation of denominator degrees of freedom using the package lmerTest (Kuznetsova et al., 2015).

We then estimated interspecific PSF at each genetic diversity level as the coefficient for the Phase II species \times Phase I species interaction (Bever et al., 1997) in two separate models: one for the one-population treatment and one for the two-population treatment. Phase I pot and Phase II greenhouse bench were again included as random effects, and Phase I pot biomass was again included as a covariate. For the one-population treatment, our estimation of a species' growth in conspecific soil only included treatments where each population was grown in soil conditioned by its own population (e.g., growth of *Echinacea* North in soil conditioned by *Echinacea* North, but not by *Echinacea* South).

To quantify plant growth responses to con- versus heterospecific soil, we estimated the ln-response ratio for each species within each level of genetic diversity using identical models to those described above, but on ln-transformed total biomass (Bates et al., 2019). We then calculated the ln-response ratio for each species by subtracting the model estimate in heterospecific soil from the estimate in conspecific soil. Because we included the interaction between main effects in our model, we

needed to do an additional adjustment to propagate the standard error estimates, which we did according to Hedges et al. (1999).

Does species diversity alter the strength of intraspecific PSF?

To test for the effect of species diversity (two species vs. one) on intraspecific PSF, we fit linear mixed models separately for each species. We built both models as described above, except the fixed effects were Phase II population (i.e., population planted in Phase II: North or South), Phase I population (i.e., population that conditioned soil: North or South), and Phase I species diversity (i.e., number of species that conditioned soil: one or two). Here, a significant Phase II population × Phase I population × Phase I species diversity interaction would indicate that intraspecific PSF differs between the one- and two-species treatments.

Using methods similar to those above, we estimated intraspecific PSF separately for each level of species diversity as the coefficient I_s for the Phase II population × Phase I population interaction (Bever et al., 1997) for each species. For the one-species treatment, we only included one-population treatments to avoid confounding species diversity with genetic diversity (i.e., because all two-species treatments included only one population within a species, we only included one-species treatments that also included only one population).

To quantify plant growth responses to con- versus heteropopulation soil, we estimated the ln-response ratio for each population of each species within each level of species diversity using the model fitting method as described above (Bates et al., 2019).

RESULTS

Does genetic diversity alter the strength of interspecific PSF?

Interspecific plant–soil feedback (PSF) was significantly more positive (or less negative) in the two-population treatment (soil conditioned by two populations) than in the one-population treatment (soil conditioned by one population), indicating that genetic diversity may weaken the ability of PSF to maintain species diversity (Phase II species × Phase I species × Phase I genetic diversity: $F_{1,143} = 5.73, p = 0.02$; Figure 3). Interspecific PSF was negative in the one-population treatment (Phase II species × Phase I species: $F_{1,90} = 5.40, p = 0.02$) but did not significantly differ from zero in the two-population

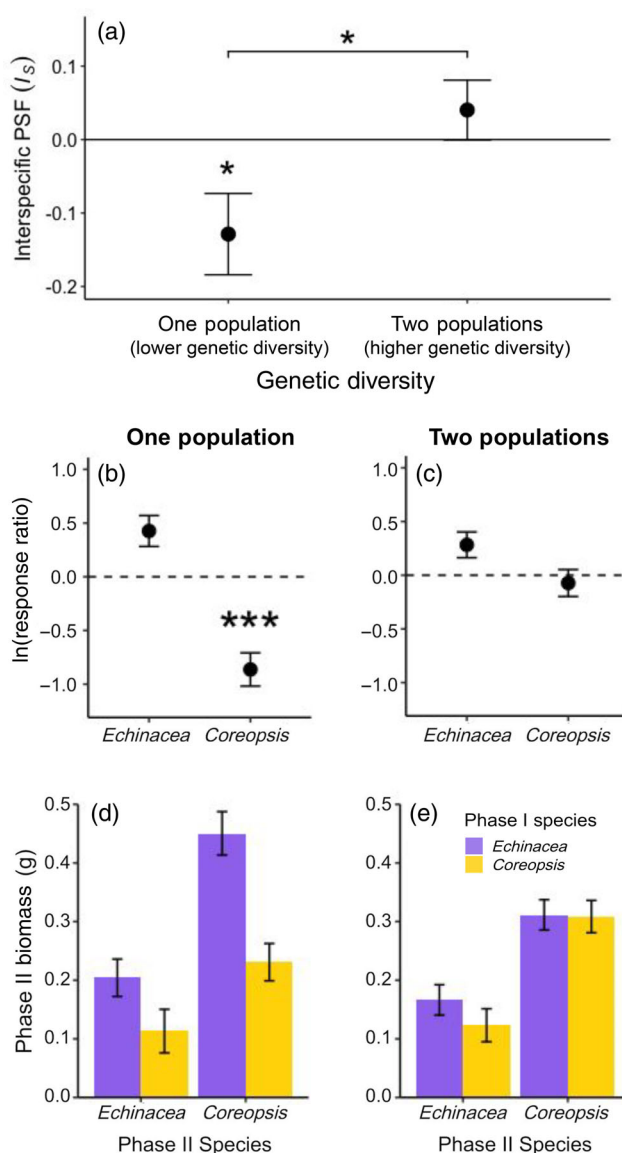


FIGURE 3 Interspecific microbe-mediated plant–soil feedback (PSF) between *Echinacea* and *Coreopsis* grown in soil conditioned by pairs of plants representing one population (lower genetic diversity, left column) or two populations (higher genetic diversity, right column). The top panel shows the net pairwise interspecific PSF (I_s) between *Echinacea* and *Coreopsis* (a). The middle row shows the ln-response ratio of biomass produced in conspecific soil compared to biomass produced in heterospecific soil [(b), (c)], and the bottom row shows the biomass produced by each species when grown in soil conditioned by each species [(d), (e)]. The interaction coefficient of the biomass plots in (d) and (e) are depicted as the interspecific PSF for each level of genetic diversity in (a) (I_s ; Bever et al., 1997). Error bars are fitted SE. Asterisk above bar in (a) indicates significant difference between groups; asterisk above treatment indicates that (a) PSF or (b) ln-response ratio differs significantly from zero; * $p < 0.05$, *** $p < 0.001$

treatment (Phase II species × Phase I species: $F_{1,84} = 1.00, p = 0.33$; Figure 3a), suggesting that PSF would contribute to the coexistence of these two species

only at low levels of genetic diversity. The negative interspecific PSF in the one-population treatment was driven by *Coreopsis* producing substantially more biomass when grown in soil conditioned by *Echinacea* than in soil conditioned by conspecifics (Figure 3b,d). *Coreopsis* was also more responsive to the genetic diversity treatments, which drove the difference in interspecific PSF between one- and two-population treatments (comparing *Coreopsis* In-response ratios in Figure 3b,c). Note that the greater absolute growth of *Coreopsis* relative to *Echinacea* may have contributed to the negative PSF observed in the one-population treatment (Figure 3a,d), but it should not influence the effects of genetic diversity on interspecific PSF. There was no relationship between Phase I pot biomass and Phase II biomass (Phase I Pot biomass: $F_{1,210} = 2.1$, $p = 0.15$; Appendix S1: Figure S1), suggesting that these effects cannot be explained by differences in plant biomass (which could affect things like nutrient drawdown) among Phase I treatments.

Does species diversity alter the strength of intraspecific PSF?

For *Coreopsis*, intraspecific PSF was marginally significantly more positive (or less negative) in the two-species treatment (conditioned by both *Coreopsis* and *Echinacea*) than in the one-species treatment (conditioned by *Coreopsis* alone), indicating that species diversity may weaken the ability of intraspecific PSF to maintain genetic diversity (Phase II population \times Phase I population \times Phase I species diversity: $F_{1,54} = 3.95$, $p = 0.052$; Figure 4a–e). This effect was primarily driven by the North population, which tended to produce more biomass in heteropopulation (South) soil in the one-species treatment, but switched to producing more biomass in conpopulation (North) soil in the two-species treatment (Figure 4d,e). For *Echinacea*, species diversity did not influence intraspecific PSF (Phase II population \times Phase I population \times Phase I species diversity: $F_{1,54} = 0.43$, $p = 0.52$; Figure 4f–j).

In our model for *Coreopsis*, we detected a four-way interaction with the Phase I pot biomass covariate (Phase II population \times Phase I population \times Phase I species diversity \times Phase I pot biomass: $F_{1,51} = 5.29$, $p = 0.03$). Including the interaction with the covariate in our models caused one term to shift from non-significant to significant and one term to shift from significant to marginally significant, despite a loss of statistical power (Appendix S1: Figure S2). Here we present results from the more conservative model that excludes interactions with the covariate, but we provide results and an interpretation of the model with covariate interactions in the supplement (Appendix S1: Figures S2 and S3, Table S4).

Estimated intraspecific PSFs did not differ significantly from zero in any treatment for either species, despite being similar in magnitude to those of interspecific PSF.

DISCUSSION

Genetic diversity, which is the fuel for adaptation, and species diversity, which is the main driver of ecosystem functions, are typically studied in isolation. However, theory predicts they may be linked: species diversity may influence the maintenance of genetic diversity and, reciprocally, genetic diversity may influence the maintenance of species diversity (Vellend & Geber, 2005). Here, we found that higher genetic diversity (two populations vs. one) reduced the stabilizing effect of interspecific plant–soil feedback (PSF), thus reducing the ability of PSF to promote coexistence and contribute to the maintenance of plant species diversity. We also found that, for one of our two species, higher species diversity (two species vs. one) reduced the stabilizing effect of intraspecific PSF, thus reducing the ability of PSF to promote the coexistence of competing populations or genotypes and the maintenance genetic diversity within species. If these patterns hold for other plant species and are exemplary of more diverse communities (see *Caveats*), then our work illustrates that genetic and species diversity may be negatively linked through microbe-mediated plant–soil feedback (Figure 1b).

Potential mechanisms of PSF-mediated linkages between genetic diversity and species diversity

Consistent with our results that genetic diversity reduced the ability of interspecific PSF to promote species diversity, recent theoretical work has shown that when pathogens are genotype specific, species diversity in the host plant community is best maintained when plant genetic diversity is low (Eck et al., 2019). Using a simulation model that included four species and three levels of genetic diversity, Eck et al. (2019) found that plant genetic diversity weakened the stabilizing effects of negative interspecific PSF through a pathogen dilution effect. When plant genetic diversity was low, seeds of a focal species were more likely to land in soil previously occupied by their same genotype, resulting in strong negative interspecific PSF that promoted plant species diversity. On the other hand, when genetic diversity was high, seeds more often landed in heterogenotypic soil, resulting in less negative interspecific PSF and dominance of the focal plant species. By contrast, if

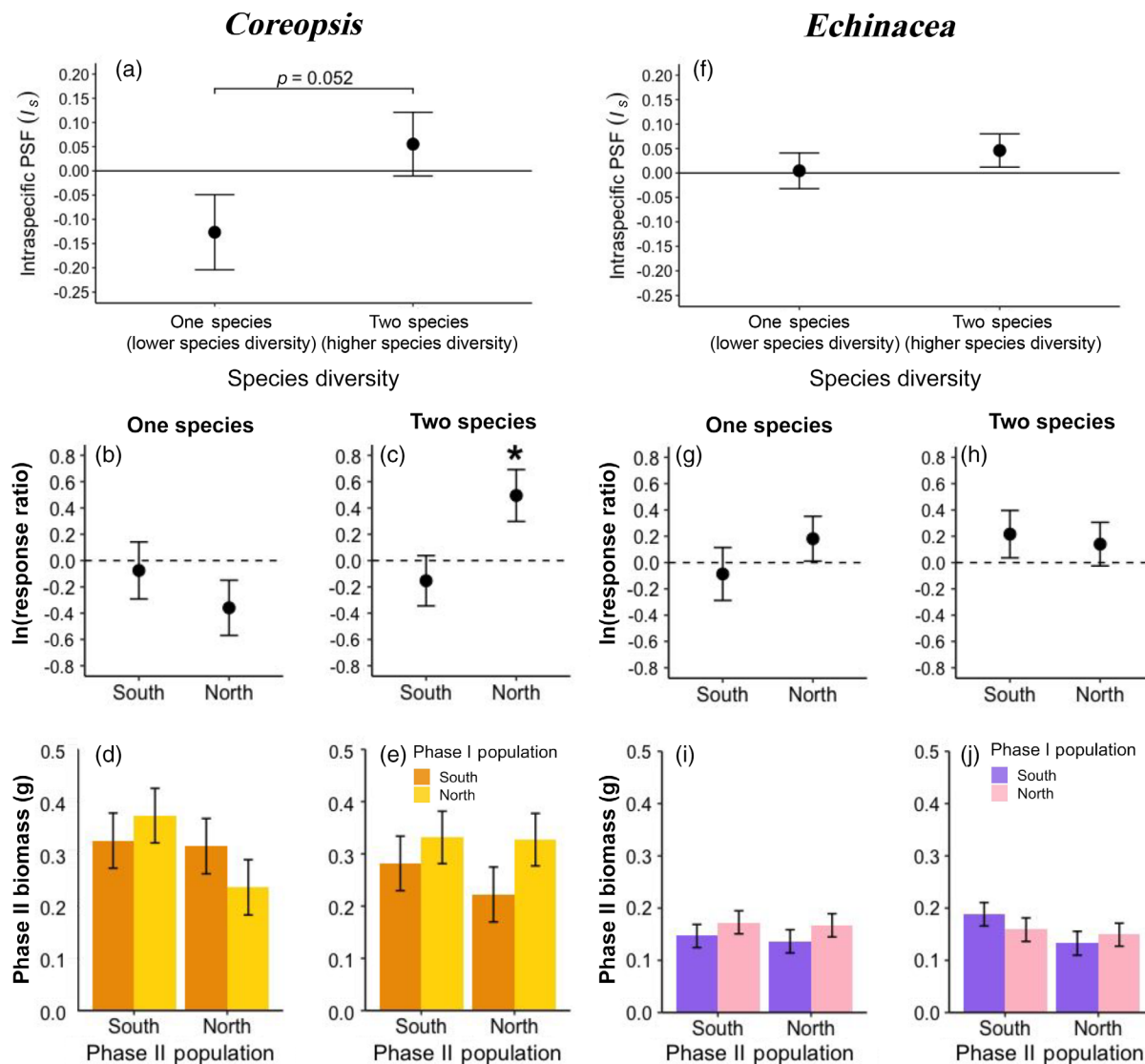


FIGURE 4 Intraspecific microbe-mediated plant-soil feedback (PSF) between South and North populations of *Coreopsis* (left) and *Echinacea* (right) grown in soil conditioned by pairs of plants representing one species (lower species diversity, left column under each species) or two species (higher species diversity, right column under each species). The top row shows the net pairwise intraspecific PSF (I_s) between South and North populations [(a), (f)]. The middle row shows the ln-response ratio of biomass produced in conpopulation soil compared to biomass produced in heteropopulation soil [(b), (c), (g), (h)], and the bottom row shows the biomass produced by each population when grown in soil conditioned by each population [(d), (e), (i), (j)]. The interaction coefficient of the biomass plots in (d) and (e) are depicted as the intraspecific PSF for each level of species diversity in (a) and (f) (I_s , Bever et al., 1997). Error bars are fitted SE. Asterisk above treatment in (c) indicates that ln-response ratio differs significantly from zero; * $p < 0.05$

mutualists were mediating these patterns, then low genetic diversity would cause seeds to frequently land in soil containing their genotype-specific mutualists, leading to more positive interspecific PSF that would erode species diversity. Thus, while we did not test whether genetic diversity-mediated shifts in interspecific PSF were caused by pathogens versus mutualists, our results are consistent with a pathogen dilution effect.

The Eck et al. (2019) simulation model did not test the effect of species diversity on intraspecific PSF, but we

would expect by analogy that the dilution of species-specific pathogens by the presence of other species would have a similar effect as the dilution of genotype-specific pathogens had on interspecific PSF, leading to less negative intraspecific PSF (provided that genotype-specific pathogens are generating intraspecific PSF). Our results that species diversity reduced the ability of intraspecific PSF to promote genetic diversity were consistent with such a pathogen dilution effect in *Coreopsis*, but not in *Echinacea*.

Relative strengths of intra- and interspecific PSF

Although we did not detect any significant intraspecific PSF, the parameter estimates of intraspecific PSF rivaled those of interspecific PSF (the strongest estimate for both was $I_s = -0.13$ while weaker estimates were likewise similar, ranging from $I_s = 0.005$ to 0.06 ; Figures 3a and 4a,f), indicating that the effects of intraspecific PSF on genetic diversity may be similar in magnitude to the effects of interspecific PSF on species diversity. In contrast, a prior study that measured both inter- and intraspecific PSF in four plant species (but that did not investigate linkages between genetic and species diversity) found that interspecific PSF was five times stronger than the strongest estimate of intraspecific PSF (Bever et al., 1996). While the difference in outcome between studies could be due to species-specific differences in interspecific PSF, it may also reflect differences in the degree of trait divergence among studied genotypes (Crawford et al., 2019). Bever et al. (1996) compared genotypes co-occurring within a small field, so these genotypes were likely closely related and therefore similar in their traits. By contrast, our results suggest that divergence in relevant PSF traits between our geographically distant populations rival the divergence of those traits between our two species, leading to intra- and interspecific PSF's similar in strength.

Our interspecific PSF results were driven primarily by one of our two species, *Coreopsis*. According to our data, *Coreopsis* would limit itself when common in soil trained by a single population, while *Echinacea* would be unresponsive to soil conditioning. Yet, based on the PSF coefficients we obtained, theory predicts that PSF would stabilize coexistence between these species despite this asymmetry (Bever et al., 1997). There are several possible reasons for this asymmetric soil response. First, *Echinacea*-specific pathogens may have been less abundant than *Coreopsis*-specific pathogens in these recently established prairie restorations, resulting in low host specificity between plants and soil pathogens, which often weakens negative interspecific PSF (Cortois et al., 2016). Second, transplanting *Echinacea* into conditioned soil as seedlings, rather than as seeds, could have protected *Echinacea* from the negative effects of pathogens since plants are generally more susceptible to pathogens earlier in development (Develey-Rivière & Galiana, 2007). Last, species differences could be related to successional dynamics as later successional species like *Echinacea* generally experience weaker negative PSF than early successional species (Bauer et al., 2015; Kardol et al., 2006) due to being more defended against pathogens and more responsive to mutualists (Koziol & Bever, 2015; Reynolds et al., 2003; Van der Putten, 2003).

Similarly, *Coreopsis*' intraspecific PSF results were driven primarily by one population, although neither population exhibited significant growth responses to con- versus heteropopulation soil (Figure 4b,c). Intraspecific PSF strength has been shown to differ among populations (Felker-Quinn et al., 2011), families (Eck et al., 2019), and genotypes (Bever et al., 1996; Bukowski et al., 2018; Bukowski & Petermann, 2014), so it is not surprising that our populations responded differently to soil microbes. While we do not know what caused these differences, intraspecific variation is common in plant traits that are likely to contribute to PSF, including plant defenses (Moore et al., 2014) and root exudation (Binns et al., 2002; Micallef et al., 2009).

Caveats

We have shown that interactions between plants and their soil microbes can link genetic diversity and species diversity in the study species and populations that we chose, but we do not know how patterns would differ if we had used different plant species or populations, especially given that the effects were primarily driven by one species (*Coreopsis*) and one population (the North population). Was *Coreopsis*' strong response the exception or the norm? And were our intraspecific PSF results driven by species diversity and the dilution of genotype-specific pathogens, or were they a function of unique properties of *Coreopsis* and *Echinacea*? In this preliminary work, we set out to test whether PSF could mediate linkages between genetic and species diversity in principle, and we showed that it is possible, at least with these species. PSF might commonly link genetic and species diversity if the dilution effect is indeed driving these patterns, at least in systems where genotype-specific microbes dominate (Eck et al., 2019).

It also remains to be seen whether and how these effects will scale up to more diverse communities. In our two-species community, theory predicts that negative interspecific PSF would promote the coexistence of these species when genetic diversity is low, but not when genetic diversity is high (Bever et al., 1997). Although empirical work has shown that results in simplified communities may be predictive of more complex community outcomes (Hawkes et al., 2013; Klironomos, 2002; Lankau et al., 2011; Mangan et al., 2010), it is unclear how commonly such effects can be extrapolated to the diverse communities found in nature, and even less is known about how the influence of genetic diversity on interspecific PSF may scale in more speciose communities. However, scaling up may be facilitated by the local scale at which PSF dynamics play out. There simply is

not much physical room in the zones where roots intermingle for very many plants to condition a patch of soil (i.e., each soil patch is likely conditioned by a small number of genotypes or species). As a result, our two-species and two-genotype “higher diversity” treatments may not be as unrealistically low as they might appear given that soil is unlikely to be conditioned by exceptionally high numbers of species or genotypes. Similarly, the small spatial scale of root intermingling means that diversity is most likely to affect PSF outcomes in natural communities not by increasing the number of species conditioning small patches of soil, but by increasing the number of potential species combinations available to condition soils. Accordingly, whether our results scale up to natural communities depends on whether the study species we used exemplify typical dynamics, or if instead they are unique properties of these particular species. We hope that future empirical studies will explore the generality of our findings by investigating additional taxa and potentially higher diversity communities. That said, we generally expect PSF-mediated feedbacks between genetic diversity and species diversity to be strongest in populations and communities where strong PSF would be neutralized by a strong dilution effect, as may occur in diverse communities and populations.

Finally, while negative PSFs certainly cause negative density dependence and, therefore, can be stabilizing mechanisms that promote coexistence, their ultimate effects on the maintenance of diversity also will depend on microbially mediated mean fitness differences between species or genotypes (Kandlikar et al., 2019). In some cases, like the annual plant communities studied by Kandlikar et al. (2019), the effects of the microbial communities on mean fitness differences may overwhelm the stabilizing effects of negative density dependence, leading to competitive exclusion rather than coexistence.

Implications

If our findings apply to more diverse communities and to a variety of species, then our result that genetic diversity can influence the strength of interspecific PSF may explain variation in the strength and direction of PSF observed across species, as well as variation within species observed across studies (Bezemer et al., 2006; Crawford et al., 2019; Kardol et al., 2006; Klironomos, 2002). While there are certainly true differences among species in their PSF, estimates of interspecific PSF may be artificially increased (i.e., measured as more positive) in studies where species are experimentally represented by a genetically diverse population, while estimates may be artificially decreased (i.e., measured as more negative) in studies

where species are represented by a less genetically diverse population.

Just like many studies of PSF ignore genetic diversity, studies of interactions between species and genotypes often ignore soil microbes, but our study and others have shown that microbes can alter these interactions. For example, the outcome of competition between *Trifolium repens* and co-occurring grass species depended on the genotypes of each species (Turkington, 1989; Turkington & Aarssen, 1984; Vavrek, 1998), but this genotype specificity was driven by the particular *Rhizobia* strain inoculated onto the plants (Chanway et al., 1989). Such microbe-mediated competitive interactions could generate linkages between genetic and species diversity. More generally, microbe-mediated linkages between genetic and species diversity (including those due to PSF) may be common but cryptic, since few studies have tested for them.

CONCLUSIONS

We found that higher genetic diversity (two populations vs. one) weakened the stabilizing effect of interspecific PSF, and that higher species diversity (two species vs. one) weakened the stabilizing effect of intraspecific PSF for one of our two species. If our results from this simplified system generalize to more complex systems and to more plant species, then these patterns suggest that PSF may cause genetic diversity and species diversity to negatively influence one another (Figure 1b). If PSF is a major driver of coexistence, then these dynamics point to two contrasting outcomes: a plant community with few species but high genetic diversity within those species, or a community with many species but low genetic diversity within species. For example, if plant species diversity is eroded by human-caused extinction, then genetic diversity may remain high due to the strengthened stabilizing effects of intraspecific PSF. Conversely, if genetic diversity is lost because of strong selection or drift, then species diversity may remain high due to the strengthened stabilizing effects of interspecific PSF. While the outcomes of diversity loss are certain to depend on other ecological and evolutionary processes, our results suggest that PSF may dampen the negative effects of diversity loss by promoting diversity at other levels of biological organization.

AUTHOR CONTRIBUTIONS

Lana G. Bolin and Jennifer A. Lau designed the study, and Lana G. Bolin performed the research and analyzed the data. Lana G. Bolin wrote the first draft of the manuscript, and Jennifer A. Lau contributed substantially to the revisions.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Bolin & Lau, 2022) are available in Dryad at <https://doi.org/10.5061/dryad.cfxpvnv6w>.

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REFERENCES

- Amarasekare, P. 2000. "The Geometry of Coexistence." *Biological Journal of the Linnean Society* 71(1): 1–31.
- Antonovics, J. 1992. "Toward Community Genetics." In *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution, and Genetics*, edited by R. S. Fritz and E. L. Simms, 426–49. Chicago: University of Chicago Press.
- Antonovics, J. 1976. "The Input from Population Genetics: 'The New Ecological Genetics.'" *Systematic Botany* 1(3): 233–45.
- Antonovics, J. 2003. "Toward Community Genomics?" *Ecology* 84(3): 598–601.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-effects Models Using lme4." *Journal of Statistical Software* 67: 1–48.
- Bates, S. E., E. M. Wandrag, and R. P. Duncan. 2019. "Calculating the Uncertainty Associated with Log Response Ratios in Plant–Soil Feedback Studies." *Plant Ecology* 221: 829–36.
- Bauer, J. T., K. M. L. Mack, and J. D. Bever. 2015. "Plant–Soil Feedbacks as Drivers of Succession: Evidence from Remnant and Restored Tallgrass Prairies." *Ecosphere* 6(9): 1–12.
- Bever, J. D. 1994. "Feedback between Plants and their Soil Communities in an Old Field Community." *Ecology* 75: 1965–77.
- Bever, J. D., K. M. Westover, and J. Antonovics. 1997. "Incorporating the Soil Community into Plant Population Dynamics: The Utility of the Feedback Approach." *Journal of Ecology* 85(5): 561–73.
- Bever, J. D., J. Morton, J. Antonovics, and P. Schultz. 1996. "Host Specificity and Diversity of Glomalean Fungi: An Experimental Approach in an Old-Field Community." *Journal of Ecology* 84: 71–82.
- Bezemer, T. M., C. S. Lawson, K. Hedlund, A. R. Edwards, A. J. Brook, J. M. Igual, S. R. Mortimer, and W. H. Van Der Putten. 2006. "Plant Species and Functional Group Effects on Abiotic and Microbial Soil Properties and Plant–Soil Feedback Responses in Two Grasslands." *Journal of Ecology* 94(5): 893–904.
- Binns, S. E., J. T. Arnason, and B. R. Baum. 2002. "Phytochemical Variation within Populations of *Echinacea Angustifolia* (Asteraceae)." *Biochemical Systematics and Ecology* 30(9): 837–54.
- Bolin, L. G., and J. A. Lau. 2022. "Linking Genetic Diversity and Species Diversity through Plant–Soil Feedback." Dryad, data set. <https://doi.org/10.5061/dryad.cfxpvnv6w>.
- Booth, R. E., and J. Philip Grime. 2003. "Effects of Genetic Impoverishment on Plant Community Diversity." *Journal of Ecology* 91(5): 721–30.
- Bukowski, A. R., and J. S. Petermann. 2014. "Intraspecific Plant–Soil Feedback and Intraspecific Overyielding in *Arabidopsis Thaliana*." *Ecology and Evolution* 4(12): 2533–45.
- Bukowski, A. R., C. Schittko, and J. S. Petermann. 2018. "The Strength of Negative Plant–Soil Feedback Increases from the Intraspecific to the Interspecific and the Functional Group Level." *Ecology and Evolution* 8(4): 2280–9.
- Chanway, C. P., F. B. Holl, and R. Turkington. 1989. "Effect of Rhizobium Leguminosarum Biovar Trifolii Genotype on Specificity between *Trifolium Repens* and *Lolium Perenne*." *Journal of Ecology* 77: 1150–60.
- Chave, J. 2004. "Neutral Theory and Community Ecology." *Ecology Letters* 7(3): 241–53.
- Cortois, R., T. Schröder-Georgi, A. Weigelt, W. H. van der Putten, and G. B. De Deyn. 2016. "Plant–Soil Feedbacks: Role of Plant Functional Group and Plant Traits." *Journal of Ecology* 104(6): 1608–17.
- Crawford, K. M., J. T. Bauer, L. S. Comita, M. B. Eppinga, D. J. Johnson, S. A. Mangan, S. A. Queenborough, et al. 2019. "When and where Plant–Soil Feedback May Promote Plant Coexistence: A Meta-Analysis." *Ecology Letters* 22(8): 1274–84.
- Croll, D., and B. A. McDonald. 2017. "The Genetic Basis of Local Adaptation for Pathogenic Fungi in Agricultural Ecosystems." *Molecular Ecology* 26(7): 2027–40.
- Develey-Rivière, M.-P., and E. Galiana. 2007. "Resistance to Pathogens and Host Developmental Stage: A Multifaceted Relationship within the Plant Kingdom." *The New Phytologist* 175(3): 405–16.
- Eck, J. L., S. M. Stump, C. S. Delavaux, S. A. Mangan, and L. S. Comita. 2019. "Evidence of within-Species Specialization by Soil Microbes and the Implications for Plant Community Diversity." *Proceedings of the National Academy of Sciences USA* 116(15): 7371–6.
- Ehrenfeld, J. G., B. Ravit, and K. Elgersma. 2005. "Feedback in the Plant–Soil System." *Annual Review of Environment and Resources* 30(1): 75–115.

- Felker-Quinn, E., J. K. Bailey, and J. A. Schweitzer. 2011. "Soil Biota Drive Expression of Genetic Variation and Development of Population-Specific Feedbacks in an Invasive Plant." *Ecology* 92(6): 1208–14.
- Fridley, J. D., and J. Philip Grime. 2010. "Community and Ecosystem Effects of Intraspecific Genetic Diversity in Grassland Microcosms of Varying Species Diversity." *Ecology* 91(8): 2272–83.
- Hawkes, C. V., S. N. Kivlin, D. Jennifer, and V. T. Eviner. 2013. "The Temporal Development and Additivity of Plant-Soil Feedback in Perennial Grasses." *Plant and Soil* 369(1): 141–50.
- Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. "The Meta-Analysis of Response Ratios in Experimental Ecology." *Ecology* 80(4): 1150–6.
- Kandlikar, G. S., C. A. Johnson, X. Yan, N. J. B. Kraft, and J. M. Levine. 2019. "Winning and Losing with Microbes: How Microbially Mediated Fitness Differences Influence Plant Diversity." *Ecology Letters* 22(8): 1178–91.
- Kardol, P., T. M. Bezemer, and W. H. Van Der Putten. 2006. "Temporal Variation in Plant-Soil Feedback Controls Succession." *Ecology Letters* 9(9): 1080–8.
- Kassen, R. 2002. "The Experimental Evolution of Specialists, Generalists, and the Maintenance of Diversity." *Journal of Evolutionary Biology* 15(2): 173–90.
- Klironomos, J. N. 2002. "Feedback with Soil Biota Contributes to Plant Rarity and Invasiveness in Communities." *Nature* 417(6884): 67–70.
- Koziol, L., and J. D. Bever. 2015. "Mycorrhizal Response Trades off with Plant Growth Rate and Increases with Plant Successional Status." *Ecology* 96(7): 1768–74.
- Kuznetsova, A., P. B. Brockhoff, and R. H. Bojesen Christensen. 2015. "lmerTest Package: Tests in Linear Mixed Effects Models." *Journal of Statistical Software* 82: 1–26.
- Laine, A.-L. 2004. "Resistance Variation within and among Host Populations in a Plant-Pathogen Metapopulation: Implications for Regional Pathogen Dynamics." *Journal of Ecology* 92(6): 990–1000.
- Laine, A.-L., J. J. Burdon, P. N. Dodds, and P. H. Thrall. 2011. "Spatial Variation in Disease Resistance: From Molecules to Metapopulations." *Journal of Ecology* 99(1): 96–112.
- Lankau, R. A., and S. Y. Strauss. 2007. "Mutual Feedbacks Maintain both Genetic and Species Diversity in a Plant Community." *Science* 317(5844): 1561–3.
- Lankau, R. A., E. Wheeler, A. E. Bennett, and S. Y. Strauss. 2011. "Plant-Soil Feedbacks Contribute to an Intransitive Competitive Network that Promotes both Genetic and Species Diversity." *Journal of Ecology* 99(1): 176–85.
- Lau, J. A., S. M. Magnoli, C. R. Zirbel, and L. A. Brudvig. 2019. "The Limits to Adaptation in Restored Ecosystems and How Management Can Help Overcome Them." *Annals of the Missouri Botanical Garden* 104(3): 441–54.
- Lekberg, Y., J. D. Bever, R. A. Bunn, R. M. Callaway, M. M. Hart, S. N. Kivlin, J. Klironomos, et al. 2018. "Relative Importance of Competition and Plant-Soil Feedback, their Synergy, Context Dependency and Implications for Coexistence." *Ecology Letters* 21(8): 1268–81.
- Liu, X., R. S. Etienne, M. Liang, Y. Wang, and Y. Shixiao. 2015. "Experimental Evidence for an Intraspecific Janzen-Connell Effect Mediated by Soil Biota." 96: 662–71. <https://doi.org/10.1890/14-0014.1>.
- Mangan, S. A., S. A. Schnitzer, E. A. Herre, K. M. L. Mack, M. C. Valencia, E. I. Sanchez, and J. D. Bever. 2010. "Negative Plant-Soil Feedback Predicts Tree-Species Relative Abundance in a Tropical Forest." *Nature* 466: 752–5.
- Micallef, S. A., M. P. Shiaris, and A. Colón-Carmona. 2009. "Influence of Arabidopsis Thaliana Accessions on Rhizobacterial Communities and Natural Variation in Root Exudates." *Journal of Experimental Botany* 60(6): 1729–42.
- Moore, B. D., R. L. Andrew, C. Külheim, and W. J. Foley. 2014. "Explaining Intraspecific Diversity in Plant Secondary Metabolites in an Ecological Context." *The New Phytologist* 201(3): 733–50.
- Neupane, A., P. Tamang, R. S. Brueggeman, and T. L. Friesen. 2015. "Evaluation of a Barley Core Collection for Spot Form Net Blotch Reaction Reveals Distinct Genotype-Specific Pathogen Virulence and Host Susceptibility." *Phytopathology* 105(4): 509–17.
- R Core Team. 2018. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation For Statistical Computing.
- Reinhart, K. O., and M. J. Rinella. 2016. "A Common Soil Handling Technique Can Generate Incorrect Estimates of Soil Biota Effects on Plants." *The New Phytologist* 210(3): 786–9.
- Reynolds, H. L., A. Packer, J. D. Bever, and K. Clay. 2003. "Grassroots Ecology: Plant-Microbe-Soil Interactions as Drivers of Plant Community Structure and Dynamics." *Ecology* 84(9): 2281–91.
- Smith-Ramesh, L. M., and H. L. Reynolds. 2017. "The Next Frontier of Plant-Soil Feedback Research: Unraveling Context Dependence across Biotic and Abiotic Gradients." *Journal of Vegetation Science* 28(3): 484–94.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. "The Influence of Functional Diversity and Composition on Ecosystem Processes." *Science* 277(5330): 1300–2.
- Tilman, D., D. Wedin, and J. Knops. 1996. "Productivity and Sustainability Influenced by Biodiversity in Grassland Ecosystems." *Nature* 379(6567): 718–20.
- Turkington, R. 1989. "The Growth, Distribution and Neighbour Relationships of Trifolium Repens in a Permanent Pasture. V. the Coevolution of Competitors." *Journal of Ecology* 77: 717–33.
- Turkington, R., and L. W. Aarssen. 1984. "Local-Scale Differentiation as a Result of Competitive Interactions." In *Perspectives on Plant Population Ecology*, edited by R. Dirzo and J. Sarukhan. Sunderland, MA: Sinauer Associates Inc. <http://agris.fao.org/agris-search/search.do?recordID=US201301469085>.
- Van der Putten, H. W. 2003. "Plant Defense Belowground and Spatiotemporal Processes in Natural Vegetation." *Ecology* 84(9): 2269–80.
- Vavrek, M. C. 1998. "Within-Population Genetic Diversity of Taraxacum Officinale (Asteraceae): Differential Genotype Response and Effect on Interspecific Competition." *American Journal of Botany* 85(7): 947–54.
- Vellend, M. 2006. "The Consequences of Genetic Diversity in Competitive Communities." *Ecology* 87(2): 304–11.
- Vellend, M. 2008. "Effects of Diversity on Diversity: Consequences of Competition and Facilitation." *Oikos* 117(7): 1075–85.
- Vellend, M. 2010. "Conceptual Synthesis in Community Ecology." *The Quarterly Review of Biology* 85(2): 183–206.

- Vellend, M., and M. A. Geber. 2005. "Connections between Species Diversity and Genetic Diversity." *Ecology Letters* 8(7): 767–81.
- Walters, W. A., Z. Jin, N. Youngblut, J. G. Wallace, J. Sutter, W. Zhang, A. González-Peña, et al. 2018. "Large-Scale Replicated Field Study of Maize Rhizosphere Identifies Heritable Microbes." *Proceedings of the National Academy of Sciences USA* 115(28): 7368–73.
- Whitlock, R., J. Phil Grime, R. Booth, and T. Burke. 2007. "The Role of Genotypic Diversity in Determining Grassland Community Structure under Constant Environmental Conditions." *Journal of Ecology* 95(5): 895–907.
- Zirbel, C. R., and L. A. Brudvig. 2020a. "Trait-Environment Interactions Affect Plant Establishment Success during Restoration." *Ecology* 101(3): e02971.
- Zirbel, C. R., and L. A. Brudvig. 2020b. "Data from: Trait-Environment Interactions Affect Plant Establishment Success

during Restoration." Dryad Digital Repository. <https://doi.org/10.5061/dryad.bnzs7h46q>.

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