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ARTICLE

Do plant–soil feedbacks promote coexistence in a sagebrush steppe?

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Abstract

Recent studies have shown the potential for negative plant–soil feedbacks (PSFs) to promote stable coexistence, but have not quantified the stabilizing effect relative to other coexistence mechanisms. We conducted a field experiment to test the role of PSFs in stabilizing coexistence among four dominant sagebrush steppe species that appear to coexist stably, based on previous work with observational data and models. We then integrated the effects of PSF treatments on focal species across germination, survival, and first-year growth. To contribute to stable coexistence, soil microbes should have host-specific effects that result in negative feedbacks. Over two replicated growing seasons, our experiments consistently showed that soil microbes have negative effects on plant growth, but these effects were rarely host-specific. The uncommon host-specific effects were mostly positive at the germination stage, and negative for growth. Integrated effects of PSF across early life-stage vital rates showed that PSF-mediated self-limitation occasionally had large effects on projected plant biomass, but occurred inconsistently between years. Our results suggest that while microbially-mediated PSF may not be a common mechanism of coexistence in this community, it may still affect the relative abundance of dominant plant species via changes in host fitness. Our work also serves as a blueprint for future investigations that aim to identify underlying processes and test alternative mechanisms to explain important patterns in community ecology.

KEYWORDS
coexistence, negative feedback, plant–microbe interactions, plant–soil feedbacks, sagebrush steppe, stabilizing mechanisms

INTRODUCTION

Understanding the coexistence of species and the maintenance of diversity has fascinated ecologists since the beginning of the discipline (Gause, 1932; Lotka, 1932; Volterra, 1926). Classically, these efforts focused on qualitative tests of individual mechanisms such as spatial habitat partitioning (MacArthur, 1958) or resource partitioning (McKane et al., 2002). However, such tests of single mechanisms are difficult to place into a real-world context where multiple mechanisms interact to determine coexistence. Therefore, these classical studies could not identify which mechanisms are most essential to diversity maintenance in specific communities, or address the relative importance of multiple mechanisms working simultaneously and interactively. Chesson (2000) pioneered a theoretical synthesis that provided a way to assess the simultaneous contributions of multiple coexistence mechanisms. Coexistence mechanisms stabilize population dynamics by causing species to limit themselves more than they limit other species, and the magnitude of such stabilizing effects on population growth can be quantified by analyzing invasion growth rates.

When applied to a sagebrush steppe community, this theoretical framework produced evidence for stable coexistence based on strong stabilization among the dominant plant species (Adler et al., 2010). Phenomenological multispecies population models fit with long-term observational data projected high invasion growth rates, reflecting interspecific limitations that were very weak relative to intraspecific limitations. Importantly, the intraspecific limitations that most promoted coexistence occurred during seed production and recruitment, did not exhibit strong interannual variation, and acted at local (<1 m^2) spatial scales (Adler et al., 2010; Chu & Adler, 2015).

These results are based on models that represent intra- and interspecific interactions phenomenologically, begging the question, what is the underlying mechanism generating such stable coexistence? What is happening in the recruitment process to cause intraspecific interactions to be so much more limiting than interspecific interactions? Identifying the mechanism would not only give us more confidence in the phenomenological results, but would also make it possible to predict how future environmental change might affect coexistence. Here, we evaluate one plausible mechanism that could decrease seedling establishment next to conspecific relative to heterospecific neighbors: microbially-mediated negative plant–soil feedbacks (PSFs) (Bever, 2003; Crawford et al., 2019).

PSFs occur when host-specific microbial communities cultivated by different plant species regulate plant population growth and performance (Bever, 2003; Bever et al., 1997). Such PSFs are often negative, where plant hosts promote microbial associates that are more detrimental to themselves compared to other plant species in the community (Kulmatiski et al., 2008). PSFs have been shown to correlate with plant community dynamics such as secondary succession, stability, and species' relative abundances (Chung, Collins, & Rudgers, 2019; Kardol et al., 2006; Klironomos, 2002; Mangan et al., 2010). In addition, both theory (Bever, 2003; Revilla et al., 2013) and empirical work indicate that these negative feedbacks could play key roles in stabilizing coexistence by enhancing self-limitation in plant populations (Burns & Brandt, 2014; Chung & Rudgers, 2016; Siefert et al., 2018; Stein & Mangan, 2020). However, in the tradition of classical, mechanistic coexistence research, the majority of these studies were conducted under greenhouse conditions and specifically targeted the contribution of competition and PSFs to stable coexistence, ignoring other mechanisms (Chung & Rudgers, 2016; Siefert et al., 2018; Stein & Mangan, 2020). The role of microbially-mediated PSF in stabilizing coexistence under natural field conditions, relative to other mechanisms, remains unknown.

We conducted a field experiment using seedling transplants to investigate microbially-mediated PSF among the four dominant plant species in a semi-arid sagebrush steppe that, according to our previous work (Chu & Adler, 2015), coexist stably. Our manipulations compared the relative effects of microbially-mediated PSF, direct root competition, and other background niche mechanisms on germination, growth, and survival. If plants in this experimental study reflect long-term, observed dynamics, individuals in the "control" condition that experience all niche mechanisms should perform worse near intraspecific relative to interspecific neighbors. For microbially-mediated PSF to play an important role in coexistence relative to other simultaneously operating mechanisms, microbes must have a strong negative impact on host performance and those impacts must be strongly host-specific. If PSFs are driving the strong stabilizing effects emerging at the recruitment stage for coexisting study species, we should find that germination, seedling growth, and survival are much lower for seedlings interacting with intraspecific soil microbial communities than for seedlings interacting with interspecific soil microbial communities (Crawford et al., 2019). The absence of strongly negative, host-specific microbial effects on plant seedlings would imply that coexistence in this sagebrush steppe community is stabilized by other mechanisms, not microbially-driven PSFs.

METHODS

Study system

Field experiments were conducted at the USDA-ARS Sheep Experimental Station (USSES) 9.6 km north of Dubois, Idaho (44.2° N, 112.1° W, elevation 1500 m). Mean annual precipitation is 300 mm and mean temperatures range from −6.5°C (January) to 20°C (July) (Dubois Experimental Station weather station 44.2° N, 112.2° W). The 2 years of our study period differed strongly in annual precipitation: 2018 water year precipitation was 359 mm (September 2017 to August 2018), and 2019 water year precipitation was 207 mm (September 2018 to August 2019).

Soils are fine-loamy Calcic Argixerolls over basalt bedrock (Seefeldt & McCoy, 2003). The vegetation at this site is sagebrush steppe, dominated by the shrub *Artemisia tripartita* (ARTR), and C_3 perennial grasses *Pseudoroegneria spicata* (PSSP), *Hesperostipa comata* (HECO), and *Poa secunda* (POSE). These four species were the focus of the previous studies based on population models fit to long-term observational data (Adler et al., 2010; Chu & Adler, 2015). The experiments reported here were conducted in the same livestock exclosure where six of the historical quadrats are located, as well as a recent removal experiment (Adler, Kleinhesselink, et al., 2018).

Seedling preparation

We germinated seeds collected from the field site in 2016 for transplant into the field experiment in late August each year (2017 and 2018). Due to their small size, we sowed ARTR seeds directly into conetainers (~15 seeds/pot) filled with silica sand (Granusil industrial quartz 7030, CoviaCorp, OH, USA) and misted daily. For the three grass species, we sowed seeds into germination boxes containing moist silica, covered with blotting paper, and transplanted seedlings into silica-filled conetainers as they germinated. All seedlings were watered with a weak nutrient solution each week (0.03% FloraGro and 0.015% FloraMicro, General Hydroponics, CA, USA), and maintained in a growth chamber with 12-h days, 20/15°C day/night temperature, and 75% relative humidity to start. To better prepare seedlings for transplanting outside, we lowered chamber temperature every 3–4 days to mimic field conditions, ending at 15/9°C day/night temperature after 6 weeks of growth and prior to transplant in the field.

Field PSF experiment

To measure PSF for focal species in the field, we reciprocally transplanted seedlings for each of the four species into five soil environments in the late fall (October) before each target growing season. These five environments represented soils influenced by each of the four species, and "bare" soil that was unvegetated at time of transplant (Figure 1B). Each year, we selected soil environment locations along three 40 m transects, 10 m apart, in 10 replicate blocks (3–4 blocks per transect). For the plant-associated soil environments, we selected naturally-occurring donor plants that formed a distinct single-species bunch (Figure 1C). Sites for 2017–2018 and 2018–2019 experiments were within the same 600 × 150 m livestock exclosure, but in different locations (Figure 1A).

To isolate microbially-driven effects from other belowground stabilizing mechanisms, we crossed reciprocal transplants with three microbial treatments (Figure 1D): (1) microbial and root exclusion ("exclusion"), (2) microbial feedback ("feedback"), and (3) all niches control ("control"). The "exclusion" treatment tests the performance of transplant seedlings in sterilized soils with decreased microbial colonization and no direct root competition. The "feedback" treatment tests the performance of transplant seedlings in live soil, but still excludes direct root competition from neighboring plants. The "control" treatment tests transplant seedling performance directly in the field environment, with live soils and root competition. At each microbial environment location, seedlings in the "exclusion" and "feedback" treatments were planted inside belowground cylinders, which were then installed <5 cm from donor plants in each soil environment, and >30 cm from other nearby plants of focal species (Figure 1C). Cylinders were constructed using 0.45 μm nylon mesh which allowed exchange of water, solutes, and small bacteria, but prevented hyphal and root penetration (Santa Cruz Biotech) (15 cm tall bag attached to 5 cm diameter polyvinyl chloride [PVC] ring). At each planting location, a 5 cm diameter 15 cm deep soil core was extracted and sieved at 5 mm to remove rocks. For the "feedback" treatment, we used the live, sieved soil to fill the cylinder installed in the same coring location. For the "exclusion" treatment, sieved soil was sterilized (autoclave 121°C 2× 60 min, 24 h rest period), before using it to fill the cylinder. All implements and gloves were cleaned with a 10% bleach solution in between each sample. For the all niches "control" treatment, we similarly extracted and sieved a soil core as in the other treatments. The sieved soil was then directly returned to the coring location, and a PVC ring collar installed at the soil surface. The full design of the experiment each year included: 4 species × 5 microbial environments × 3 treatments × 10 reps = 600 plants total.

We washed seedlings of silica, transplanted into cylinders and PVC ring-marked locations, and watered to aid initial establishment. Seedlings of grass species were protected with a 5 mm wire mesh cage to prevent grasshopper herbivory. In the first week after transplant, seedlings were watered 20 mL every 2 days to facilitate establishment and reduce transplant shock. Two weeks after transplant, we replaced any dead seedlings. As ARTR seedlings were small at transplant and susceptible to mortality, we transplanted three seedlings to ensure at least one live plant persisted. Any extra (>1) surviving ARTR seedlings were removed during the first spring census the next year. In fall 2018, we could not successfully germinate HECO in the growth chamber. Thus, we used the first HECO seedling that germinated from the seeds added for the field germination test in

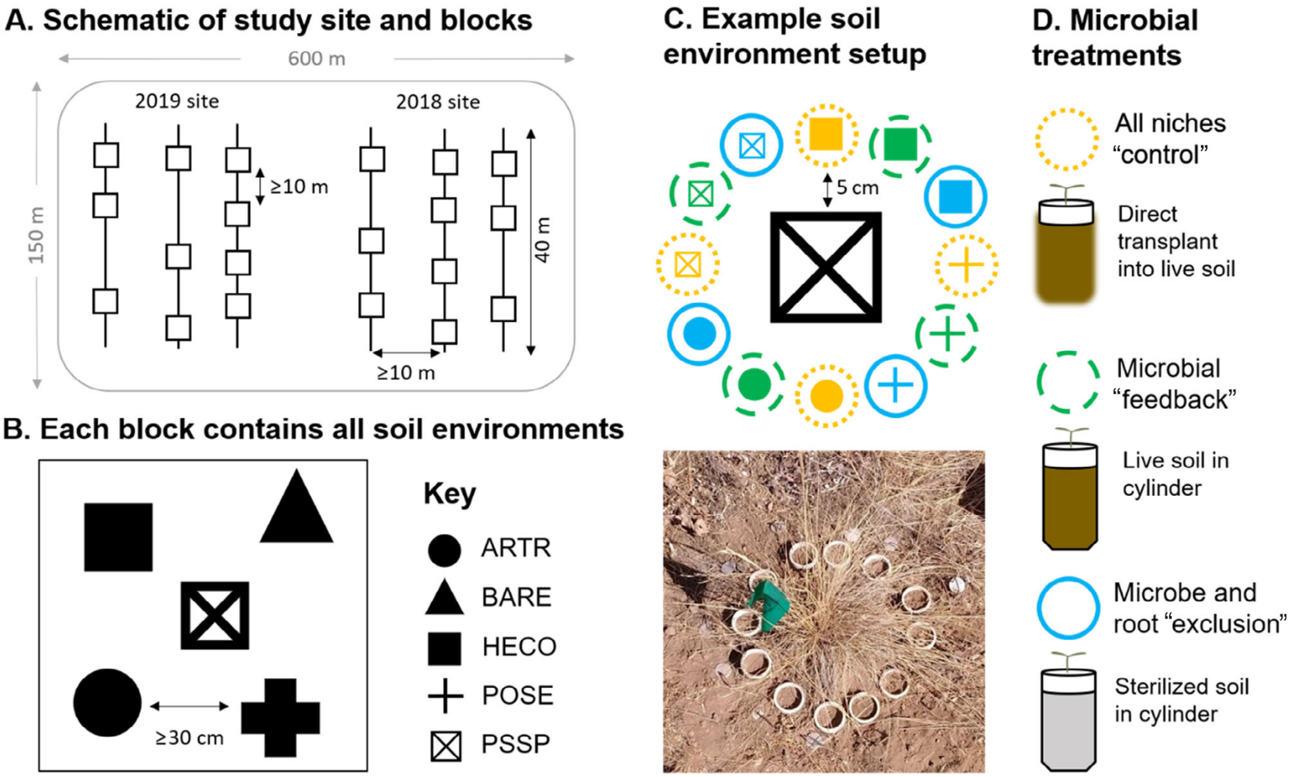

FIGURE 1 Experimental design: (A) Schematic of study sites within the exclosure (gray box). Within each site, replicate blocks (squares) are arranged along three transects (vertical lines). (B) Within each replicate block, we identified locations for all five soil environments. (C) Each soil environment location contained 12 focal plant seedlings (4 species × 3 microbial treatments). This example shows a PSSP soil environment location, matching the example photo of a PSSP soil environment location in the field (photo credit: Y. Anny Chung). Polyvinyl chloride (PVC) collars mark transplanting locations. Center plant is an existing PSSP adult acting as soil environment donor. (D) Explanation of microbial treatments. Symbols (plant species) and colors (microbial treatments) are similarly used throughout the following figures. ARTR, *Artemisia tripartita*; BARE, bare; HECO, *Hesperostipa comata*; POSE, *Poa secunda*; PSSP, *Pseudoroegneria spicata*.

each cylinder or PVC ring location (see next paragraph) as the focal plant.

To measure the effects of soil environments on germination and emergence, we added 10 seeds of the same species as the transplant seedling. Individual seeds were glued onto plastic toothpicks (Elmer's liquid glue, OH, USA), and inserted into the soil within each cylinder or PVC collar-marked location. We began censusing transplant seedlings survival and emergence from added seeds every 2 weeks at the start of the next growing season (late April). Each year in early July, cylinders were gently loosened from the soil, and transplant biomass extracted. Thus, each field PSF experiment phase lasted 10 months, allowing ample time for experimental transplants to respond to the effects of microbial environments. The "control" transplants were removed using a large auger to preserve belowground biomass. Aboveground biomass was stored in paper bags and dried at 60°C for 7 days and weighed. Belowground biomass was washed clean of soil, and a portion reserved for microscopy.

PSF analyses

To investigate the general underlying mechanism, direction, and magnitude of PSFs, and their implication for coexistence, we conducted four main analyses. First, we used generalized linear models to compare transplant species, soil environment, and treatment effects on transplant demographic performance (germination, survival, or growth). This analysis gives insight into soil environments and treatment combinations that could be mechanisms underlying PSFs. Second, we calculated single-species PSF as the log-response ratio of each species' growth or germination in an intraspecific soil environment versus each of the other four interspecific microsites (including "bare" soil), for each treatment. This metric compares whether each species performs worse in its own soil environment (negative feedback) or worse in an interspecific environment (positive feedback) in a way that is directly comparable to the phenomenological interaction coefficients estimated for these species using observational data (Adler et al., 2010). This metric also provides information about the individual components of the next analysis. Third, to evaluate net pairwise PSF, we calculated pairwise interaction strengths (*Is*) for all species pair combinations, which allow inference about coexistence in the absence of competition (Bever, 2003; Bever et al., 1997). This metric considers the effects of PSF for both plant species to determine whether net pairwise feedbacks will contribute to stable coexistence between the species pair (negative *Is*). However, each of these three analyses consider plant responses such as germination, survival, and growth separately. In the fourth analysis, we used a bootstrap approach to integrate the effects of soil environment microsite and treatments on all demographic responses to determine net effects on the seed to first-year seedling transition. Details for each analysis are as follows.

To investigate the effects of soil environment and treatment on focal plant species' demographic rates, we first fit separate models for aboveground biomass at harvest (a measure of growth), survival, and germination. Each model contained the effects of soil environment, treatment, transplant species, all two-way and the three-way interaction among those factors, as well as the effect of experiment year (treated as factor) as predictors. Aboveground biomass was ln-transformed prior to analysis with a general linear model, whereas germination (number of germinants from 10 added seeds) and transplant survival were analyzed using a generalized linear model with binomial error distribution. Marginal means and multiple pairwise comparisons were estimated using package "emmeans" (Lenth, 2019). We removed one aboveground biomass record from our dataset prior to all analyses due to the mass being too small to be reliably measured by the balance (≤ 0.0001 g). We also investigated an alternative mixed model approach by including block as a random intercept in each model. The random effect did not explain a lot of variation in any case and results were not different from the approach above (Appendix S1: Table S2).

We calculated the log-response ratio of each species' performance in an intraspecific soil environment versus each of the other four microsites to determine single-species feedback. For aboveground biomass, these ratios were calculated for pairs of individuals within each treatment and replicate, and only for pairs where both individuals survived. For germination, we added 1 to all samples to avoid division by zero. We did not calculate response ratios for survival, as it was uniformly high for all treatments and species. We determined if log-response ratios differed according to treatment or soil environment microsite type using ANOVA, with main effects of treatment, soil environment, year, and all interactions. Log-response ratios for each unique treatment by soil environment type combination were then tested for significant difference from zero using coefficient *p*-values with the model fitted using means parameterization instead of effects parameterization (offsetting intercept to zero). In this case, each fitted coefficient corresponds to the estimated group means for each unique treatment by soil environment type combination. A significantly negative log-response ratio suggests that effects of intraspecific soil environments is more detrimental than interspecific, or no neighbor, environments.

To calculate *Is*, we summed the calculated log-ratios for each pairwise combinations of species (six pairs total) within each treatment and replicate, and only for pairs where both log-ratios were available. For example, the *Is* between ARTR and POSE = ln(ARTR in ARTR soil/ARTR in POSE soil) + ln(POSE in POSE soil/POSE in ARTR soil) (Bever et al., 1997). We determined if *Is* differed according to treatment or species pair using ANOVA, with main effects of treatment, species pair, year, and all interactions. Pairwise interaction strengths for each unique treatment by plant species pair combination were then tested for significant difference from zero using means parameterization in a linear model as above. A significantly negative *Is* suggests that solely considering the effects of PSFs, the plant species in the pair should stabilize. We calculated *Is* for biomass and germination responses in the 2 years separately. We did not calculate *Is* for survival because it was uniformly high for all treatments and species.

Finally, we used a bootstrap model to integrate the effects of soil environment microsite and treatments across the seed to first-year seedling transition. We asked, if we started with 100 seeds, how much total biomass should we expect from the resulting 1-year old seedlings? To do this, we first obtained bootstrapped samples of germination rate, survival probability, and biomass at the end of the growing season for all plant–soil environment-treatment combinations in each year by randomly resampling our data with replacement ($N = 10$ per sample as in the experiment for each plant–soil-environment-treatment combination). We then calculated the mean germination rate, survival probability, and biomass for the bootstrapped sample. Finally, for each bootstrapped sample, we calculated the expected biomass of seedlings coming from 100 seeds in each plant–soil environment-treatment combination using Equation (1).

$$M_{i,P,E,T} = 100 \times \overline{g}_{i,P,E,T} \times \overline{s}_{i,P,E,T} \times \overline{b}_{i,P,E,T}, \tag{1}$$

where M is the total biomass of first-year seedlings for bootstrap sample i for plant species P, in soil environment E, and treatment T. $\overline{g}$ is the mean germination rate of the bootstrapped sample, $\bar{s}$ is mean seedling survival, and $\bar{b}$ is mean seedling biomass. We repeated this for $i = 5000$ estimates of M for each plant species P, soil environment E, and treatment T combination, separately using data from 2018 to 2019. To assess whether estimated biomass contributions in intraspecific soil environments were significantly different from the interspecific environments for each plant in each microbial treatment each year, we calculated the 95% confidence interval (CI) for the difference in M in each comparison. Those comparisons with differences whose 95% CI did not include zero were deemed significantly different from each other.

Abiotic covariates and fungal colonization

We conducted additional measurements and sampling to determine whether spatial variation in soil water and nutrient availability differed among soil environments. We also compared soil chemistry in live versus autoclaved soils to ensure that the sterilization process did not alter nutrient concentrations. Finally, we randomly sampled a 25% subset of root tissue samples for root fungal colonization microscopy to determine the efficacy of the fungal cylinder treatments. Detailed methods are in Appendix S1: Section S1.

RESULTS

Abiotic covariates and treatment efficacy

Soil moisture did not consistently differ among soil environments or follow consistent spatial patterns. During the 2018 growing season, we found no effect of soil environment on soil moisture, and only a small spatial effect in the April measurement where soil moisture increased from south to north in transect 3. In 2019, we found some spatial patterns that changed from May to June. During this year, HECO soil environments consistently had the highest soil moisture (mean 14.4% in May and 9.1% in June). Detailed results can be found in Appendix S1: Section S2.

Soil chemistry analyses revealed that our sterilization method did not result in a nutrient flush, and the main difference in soil environment was significantly lower organic matter content under HECO ($p = 0.006$) (Appendix S1: Section S2; Table S1). While it was impossible to completely exclude fungi as the tops of cylinders were open to airborne spore colonization during the experiment, our treatments successfully manipulated fungal colonization of transplant roots. In general, hyphal colonization of arbuscular mycorrhizal fungi (AMF) and dark septate endophytes (DSE) were highest in "control," intermediate in "feedback," and lowest in "exclusion" (Appendix S1: Table S2). AMF hyphal colonization ranged from 48% (±1.7 SE) in "control" transplants, 31% (±2.2 SE) in "feedback," to 27% (±1.8 SE) in "exclusion" ($F_{2,283} = 34.21$, $p < 0.0001$). DSE hyphal colonization ranged from 17% (±1.0 SE) in "control" transplants, 10% (±1.0 SE) in "feedback," to 5% (±0.6 SE) in "exclusion" ($F_{2,283} = 66.67$, $p < 0.0001$). While "feedback" transplants received live soil, their lower colonization compared to controls may reflect the lack of continuous propagule and hyphal penetration belowground throughout the experiment.

Overall effects of soil environment and microbial treatments on transplant performance

Germination differed significantly among treatments ($\chi^2 = 11.28$, df = 2, $p = 0.0035$), soil environments ($\chi^2 = 52.06$, df = 4, $p < 0.0001$), transplant species ($\chi^2 = 284.32$, df = 3, $p < 0.0001$), and years ($\chi^2 = 798.55$, df = 1, $p < 0.0001$). Germination was highest in the microbe present but root excluded "feedback" treatment, intermediate in "exclusion," and lowest in "control" (Figure 2A). However, these differences were not large, with mean germination rates for each treatment group ranging from 22% to 5%. Among soil environments, germination was lowest in the "bare soil" environment (mean 18.5%) compared to environments next to plants (25%–29%). We found a significant interaction between soil environment and transplant species ($\chi^2 = 15.44$, df = 12, $p = 0.0171$), and no support for the three-way interaction between soil environment, microbial treatment, and transplant species ($p = 0.8385$).

We found that survival was generally high and significantly differed among transplant species ($\chi^2 = 89.43$, df = 3, $p < 0.0001$), with *Poa secunda* (POSE) having the lowest survival at harvest (Figure 2B). We found no evidence that survival differed among treatments, soil environments, or years ($p = 0.2913$, 0.4878, 0.2484, respectively).

Aboveground biomass differed significantly among treatments ($F_{2,1038} = 319.58$, $p < 0.0001$), soil environments ($F_{4,1038} = 6.71$, $p < 0.0001$), transplant species ($F_{3,1038} = 180.25$, $p < 0.0001$), and years ($F_{1,1038} = 89.78$, $p < 0.0001$). Specifically, plant biomass was highest in the root and microbe "exclusion," intermediate in the microbe-present but root-excluded "feedback" treatment, and lowest in the all niche mechanisms "control" (Figure 2C). On average, plants in the exclusion treatment were 2.4× the size of those in the feedback

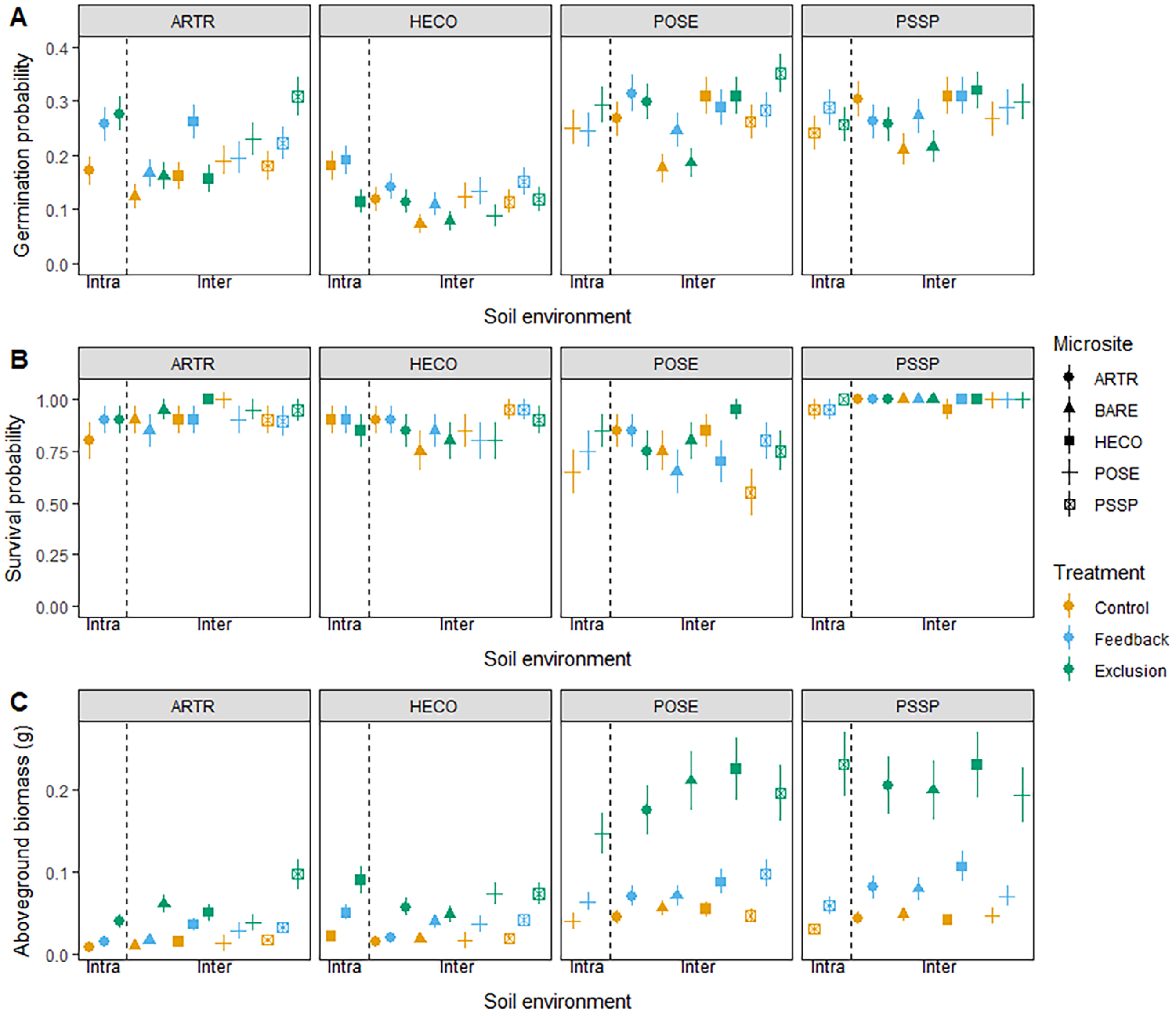

FIGURE 2 Germination, survival, and aboveground biomass of focal species (panel titles) under all soil environment and treatment combinations. Soil environment microsites are distinguished by symbol shapes, and plotted such that the conspecific soil environment microsite for each species (Intra) is always on the left-hand side of the dashed line in each panel to facilitate comparisons of intra- versus interspecific effects. Microbial treatments are distinguished by colors. Plotted values and error bars are estimated marginal means and standard errors, respectively, across both experimental years. Note different *y* axis scales. ARTR, *Artemisia tripartita*; BARE, bare; HECO, *Hesperostipa comata*; POSE, *Poa secunda*; PSSP, *Pseudoroegneria spicata*.

treatment, and 4.1× the size of control plants. We found a significant interaction between soil environment and transplant species ($F_{12,1038} = 2.52$, $p = 0.0028$), suggesting that the effect of soil environment on plant growth differed among species, lending strength to the potential for PSFs. However, we did not find support for the three-way interaction among soil environment, transplant species, and treatment ($F_{24,1038} = 0.87$, $p = 0.6514$), which suggests that the species-specific soil environment effects were not dependent on microbial treatments, and may be abiotic in nature.

Treatment effects on single-species PSFs

In germination, we found significant effects of year and marginally significant effects of treatment for HECO and PSSP (Appendix S1: Figure S1). Specifically, HECO germination response ratios were more positive in 2019 ($F_{1,212} = 7.92$, $p = 0.0097$), and less positive in the exclusion treatment ($F_{2,212} = 7.92$, $p = 0.0498$). This suggests that HECO-specific microbes may play a role in its self-facilitation. PSSP germination response ratios were more positive in 2018 ($F_{1,212} = 7.92$, $p = 0.0001$), and more positive in the feedback treatment ($F_{2,212} = 7.92$, $p = 0.0563$). Of the 24 types of comparisons in log-response ratios for each species, all ratios significantly different from zero were positive, indicating higher germination in intraspecific soils. These included two for HECO, one for POSE, and five for PSSP (Appendix S1: Figure S1).

In general, log-response ratios of plant biomass in intraspecific compared to interspecific/bare soils rarely differed systematically among treatments or soil environments (Figure 3). PSSP was the only species for which log-response significantly differed by treatment ($F_{2,211} = 7.92$, $p = 0.0005$). Specifically, PSSP log-response ratios were negative in the "control" and "feedback" treatments, but positive in the "exclusion" treatment, showing evidence of microbially-mediated negative PSFs. For ARTR, HECO, and POSE, we found no significant main effects of treatment, soil environment, or year on log-response. When considering each log-response value, we found only a few that were significantly different from zero (Figure 3). Of the 24 log-response values calculated for each species (4 soil environment types × 3 treatments × 2 years), only four were significantly negative for ARTR, two were significantly positive for HECO, six were significantly negative for POSE, and three were significantly negative for PSSP (Figure 3). We did not find that seedling growth or germination were more likely depressed in intraspecific soil environments (negative log-response ratios) in the all niches "control" treatment (Appendix S1: Figure S1, Figure 3).

Net pairwise PSFs

In general, net pairwise PSFs were neutral, with few statistically significant deviations from zero. We did not find any pairwise feedbacks that significantly differed from zero in germination (Appendix S1: Figure S2). Net pairwise feedbacks in biomass were significantly negative between ARTR and PSSP in the "feedback" treatment in 2018, and in the "control" in 2019 (Figure 4). Net pairwise feedbacks in germination and biomass did not differ consistently based on year, treatment, or species pair (all $p > 0.05$).

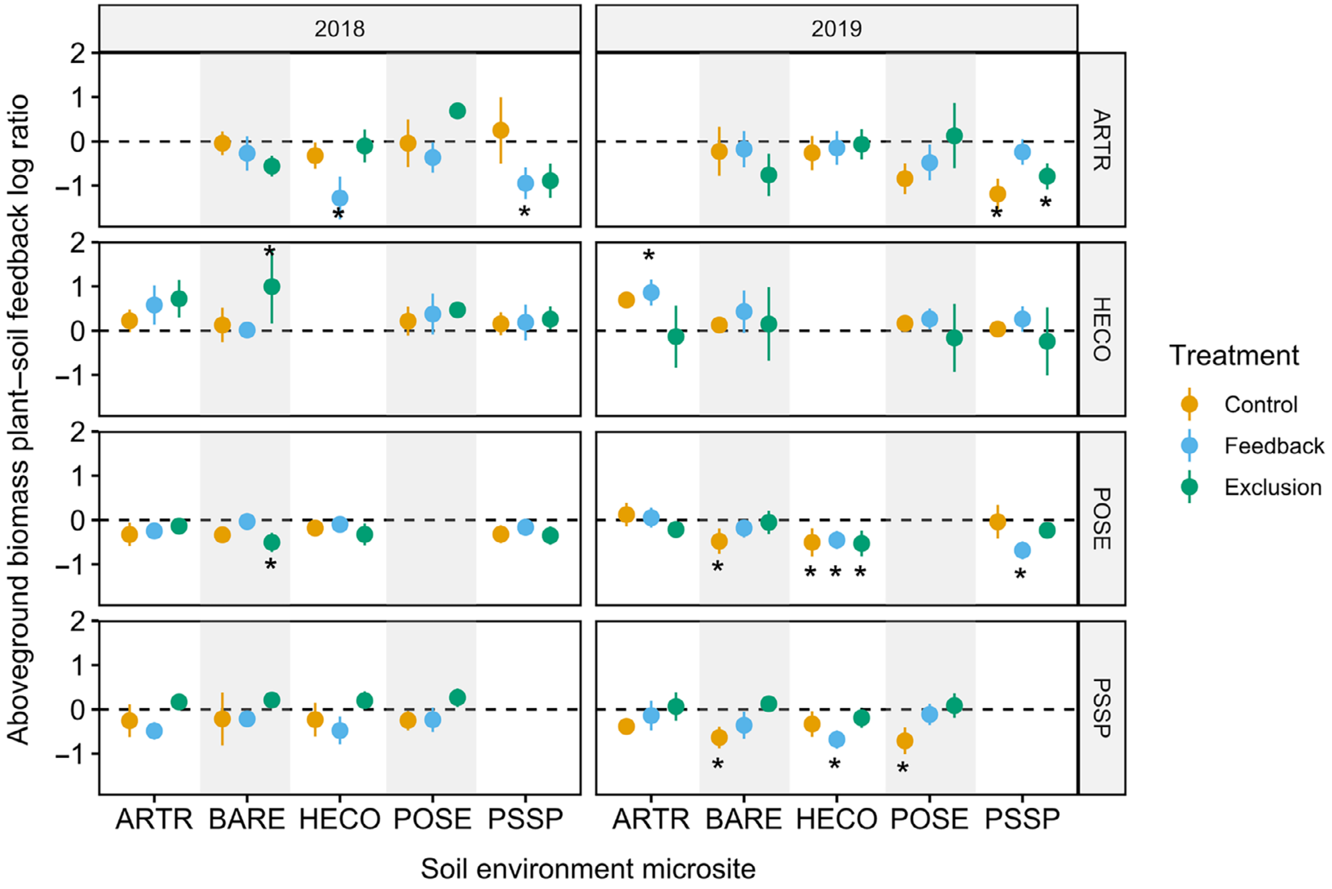

FIGURE 3 Feedback ratio (SE) for each species' biomass in its own soil environment compared to each of the other four soil environments. * marks ratios that are significantly different from zero (horizontal dashed line). ARTR, *Artemisia tripartita*; BARE, bare; HECO, *Hesperostipa comata*; POSE, *Poa secunda*; PSSP, *Pseudoroegneria spicata*.

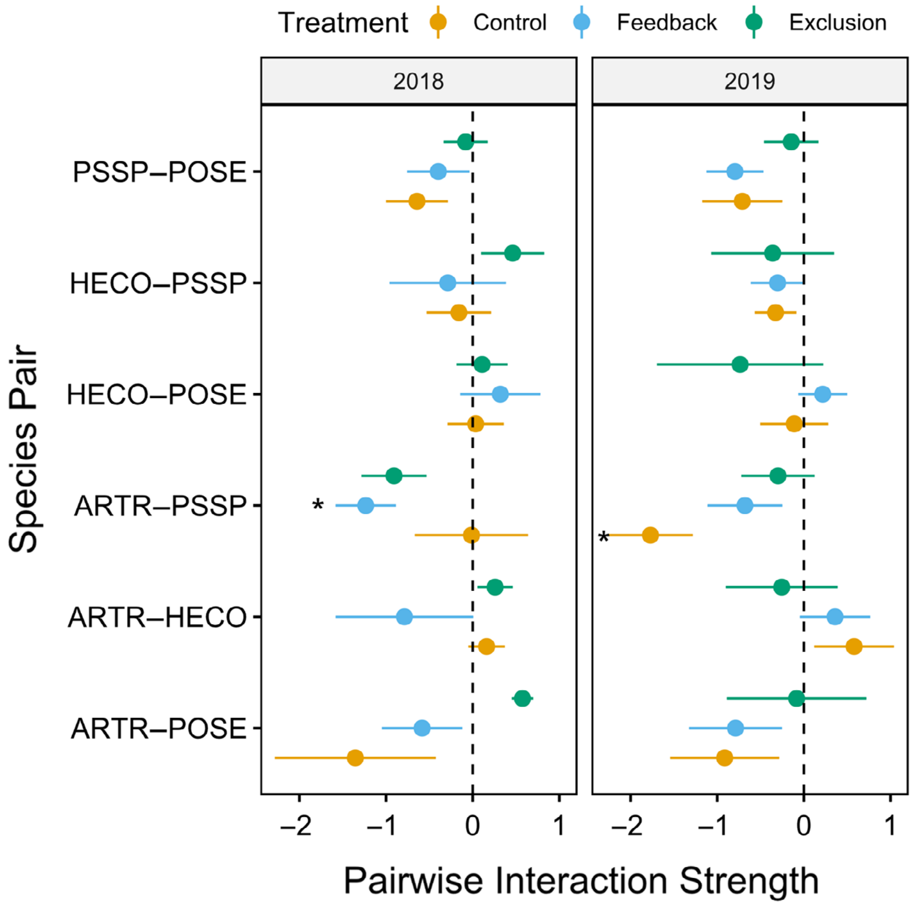

FIGURE 4 Calculated pairwise interaction strengths (*Is*, ±SE) in aboveground biomass for all plant species pairs from experiments in growing season 2018 and 2019. * indicates significant difference from zero (vertical dashed line). ARTR, *Artemisia tripartita*; HECO, *Hesperostipa comata*; POSE, *Poa secunda*; PSSP, *Pseudoroegneria spicata*.

Integrated effects across first year of seedling life history

We found strong microbial treatment effects that were consistent between growing seasons in the bootstrap model (Figure 5). The same number of seeds led to the greatest amount of biomass in the sterile soil "exclusion" treatment, and the least amount of biomass in the all niches "control." We found that there were more significant differences in projected biomass contributions in intraspecific versus interspecific microbial environments during 2019 (15 of 48 comparisons) than in 2018 (6 of 48 comparisons). Of these, HECO consistently exhibited self-facilitation (up to a 536% increase in mean biomass contribution in the 2018 control treatment when compared to the BARE microbial environment). In contrast, the significant differences in the other three species mostly indicated self-limitation (lower biomass contribution in intraspecific vs. interspecific environments). For example, based on 2018 data, ARTR in "feedback" treatments are projected to contribute on average 65% and 67% less biomass in intraspecific soil environments compared to HECO and PSSP environments respectively. The size of this effect was similar for the 10 (of 15) significant pairwise comparisons that indicated negative feedbacks in 2019 (labeled in Figure 5), which ranged from 50% to 83% biomass reduction in intraspecific microbial environments in those significant comparisons. In 2019, when more significant differences were present, only 1 of 15 significant comparisons occurred in the "exclusion" treatment, suggesting that microbes played a role in the majority of cases of significant negative feedbacks.

DISCUSSION

Contrasting experimental results with expectations based on long-term observations and modeling

Models fit to long-term observations (Adler et al., 2010; Chu & Adler, 2015) predict that small individuals

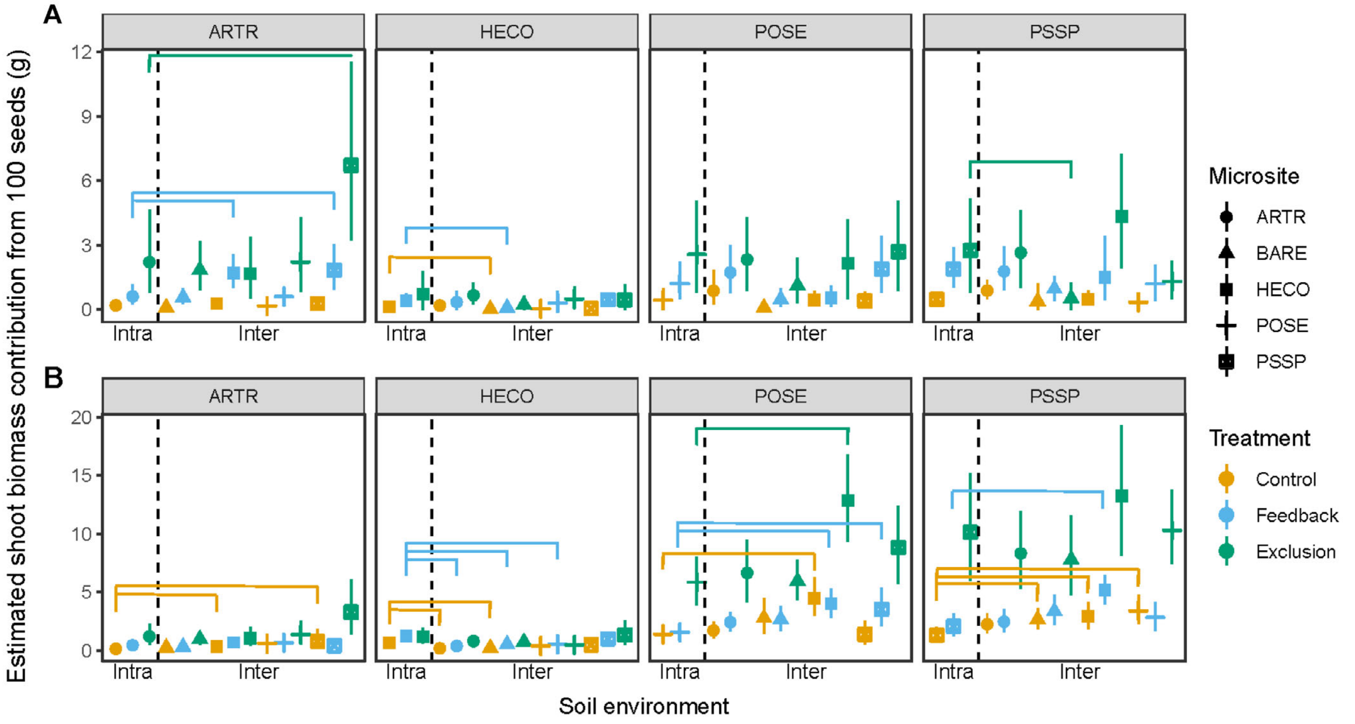

FIGURE 5 Boot-strapped estimates (mean and 95% CI) of aboveground biomass contribution from 100 seeds of each foundation plant species given treatment and soil environment effects on germination, survival, and final biomass in 2018 (A) and 2019 (B). Soil environment microsites are distinguished by symbol shapes, and plotted such that the conspecific soil environment microsite for each species (Intra) is always on the left-hand side of the dashed line in each panel to facilitate comparisons of intra- versus interspecific effects. Microbial treatments are distinguished by colors. Significant pairwise intraspecific versus interspecific soil environment comparisons based on permutational 95% CI are marked with brackets. Note different *y* axis scales. ARTR, *Artemisia tripartita*; BARE, bare; HECO, *Hesperostipa comata*; POSE, *Poa secunda*; PSSP, *Pseudoroegneria spicata*.

growing close to neighbors of the same species should perform significantly worse than individuals with no neighbors or neighbors of different species. These same models also predict that such self-limiting stabilizing effects are consistent across years. But our experimental results showed that even in the all niches "control" treatment transplants rarely performed worse in intraspecific compared to interspecific soil environments (Figures 3 and 5). What could explain this discrepancy?

One explanation could be that analyses of observational data give biased estimates of interaction coefficients between plants. This could result from measurement error (Detto et al., 2019), or an effect of the "ghost of competition present" (Tuck et al., 2018). This concept hypothesizes that, in the observational datasets, plant individuals may have already sorted into the microsites in which they compete the best. This spatial sorting would lead to an overestimation of intraspecific competition compared to an experimental approach where plants are grown across all different microsites available (Adler, Smull, et al., 2018). Another consideration is that our field experiment did not capture the stabilization mechanisms operating in the long-term data. In the observational dataset, species interaction coefficients were estimated based on changes in individual basal area as a function of distance to neighbors. In our field experiment, seeds and seedlings were transplanted <5 cm from an established adult plant. It is possible that the adult-seedling interaction dynamics differ from interactions among adult plants due to differing rooting depths. Furthermore, the "recruitment" process estimated from the observational dataset integrates seed production, germination and emergence, and seedling survival and growth. In the field experiment, we focused only on germination and emergence from seed, and then the survival and growth of transplants. However, even though the observational analyses and this experiment measured slightly different responses, the magnitude of the difference in intra- and interspecific effects in the observational data is so large that the lack of such differences in the experimental results is surprising. The discrepancy adds to growing evidence that experimental approaches show less of a difference between intra- and interspecific interactions than observational approaches (Adler, Kleinhesselink, et al., 2018; Adler, Smull, et al., 2018).

Microbe-mediated PSFs as a stabilizing coexistence mechanism

Given the absence of strong stabilizing niche mechanisms in general in our temporally-replicated experiment, we found mixed evidence to support our hypothesis that PSFs were important mechanisms for stable coexistence in this sagebrush steppe community. Here, we evaluated the "importance" of a mechanism based on its commonness among community members and magnitude of effect. To contribute to stable coexistence of plant hosts, soil microbes should have strongly host-specific effects that result in self-limitation (Crawford et al., 2019). Over two replicated field seasons, our field experiments consistently showed that soil microbes have negative effects on focal plant species growth. However, these impacts were rarely host-specific, leading to few examples of negative pairwise PSFs measured in our field experiments (Figure 4). Nonetheless, in instances where plants were more limited by intraspecific rather than interspecific soil environments, the effects were large and occurred in treatments that included soil microbes (Figure 5).

That we found few instances of host-specific negative feedbacks is surprising because meta-analyses have demonstrated that negative PSFs are common, not rare (Crawford et al., 2019; Kulmatiski et al., 2008). However, these synthesis studies often obscure the reality that PSF measurements are notoriously context-dependent (De Long et al., 2019), and depend on which "other" species are studied (Crawford et al., 2019). Past studies that have included our focal species have found variable positive or negative PSFs for *Pseudoroegneria spicata* (Kulmatiski et al., 2017; Perkins & Nowak, 2013), strongly negative feedbacks for *Hesperostipa comata* (Reinhart, 2012), and neutral feedbacks for *Poa secunda* (Reinhart, 2012). Whether co-occurring plant species exhibit significant PSFs depends on the presence, abundance, and level of association with host-specific pathogens or mutualists. Future work to sequence root and soil microbiomes of experimental transplants could yield more insight into specific taxa that may underlie PSF (or the lack thereof) in this ecosystem (e.g., Chung, Jumpponen, & Rudgers, 2019).

Despite the uncommon occurrence of microbially-mediated negative feedbacks in our experiments, when they did occur their magnitude was large, resulting in >50% reductions in projected biomass in intraspecific compared to interspecific soil environments (Figure 5). Our results suggest that, while microbially-mediated PSF may not be a common stabilizing mechanism of coexistence in this sagebrush steppe community, it could still have strong impacts on the relative abundances of species that are more susceptible to host-specific microbes via changes in host fitness (frequency-independent growth rate) differences (Kandlikar et al., 2019; Ke & Wan, 2020). For example, a recent meta-analysis provided support for the microbe-mediated growth-defense trade-off hypothesis, where "faster" species (such as those with greater specific leaf area and specific root length) were more susceptible to negative interactions with microbes than "slower" species (Xi et al., 2021). Additionally, across multiple experiments, microbes in PSFs were more likely to drive plant host exclusion rather than coexistence by increasing the fitness difference between plant competitors (Yan et al., 2022). Thus, soil microbes alter the parameter space for coexistence and the relative importance of other, simultaneously acting, coexistence mechanisms. While we could not adequately test for the relative contributions of niche versus fitness differences to coexistence with this current dataset (see Appendix S1: Figure S6), it could be a fruitful avenue for future work.

Effects of soil microbial environments are variable across early seedling vital rates and years

A frequent criticism of PSF studies is that experiments conducted in the greenhouse may not reflect field plant–microbe interactions (Chung, Jumpponen, & Rudgers, 2019; Forero et al., 2019), and also that experiments often only focus on one plant response, such as biomass or survival, instead of considering multiple vital rates. Those studies which have considered multiple plant responses have often found that measured PSFs are not consistent through time or among vital rates (Dudenhöffer et al., 2018; Hawkes et al., 2013). Our experiment uniquely addresses both issues by considering feedbacks in seedling germination, growth, and survival, and by replicating the same experiment over two field seasons.

We found remarkable consistency in the response of seedling growth to microbes despite 2018 having 73% higher water year precipitation compared to 2019. For all four focal plant species, treatments that included microbes consistently decreased biomass up to 80% compared to the "exclusion," suggesting that belowground plant–fungal interactions were overwhelmingly pathogenic. Interactions between plants and microbial associates are highly context-dependent, especially to abiotic conditions (Hoeksema et al., 2010; Rudgers et al., 2020). That we saw strong, consistent, community-level pathogenicity that was not host specific suggests that there is likely high functional redundancy in the microbial community in this ecosystem with respect to plant–microbe interactions (Louca et al., 2018).

Our results also support previous work that showed feedbacks are variable depending on the plant response measured. Germination, survival, and growth responses to microbial and soil environment treatments were not correlated, and neither were their feedbacks (Appendix S1: Figures S3 and S4). When we combined the effects across these three responses to derive bootstrapped estimates of overall treatment effects, we found that the resulting patterns were dominated by the growth response. The difficulty of manipulating microbes for long periods in the field has been the primary barrier to understanding the population-level effects of PSFs. While combining PSF measurements with long-term population data can be one way to address this issue, our study demonstrates some of the difficulties of this approach, as well as the necessity of considering the spatiotemporal aspects of PSF (Chung, 2023b; Ke et al., 2021).

What's next in unraveling coexistence mechanisms from observed phenomena?

Going from pattern to process is a necessary and difficult step in gaining ecological insight (Magurran, 2005; Murrell et al., 2001; Shea et al., 2004). Our experiment did not capture the self-limiting effects seen from long-term observational data, and suggests that microbially-driven PSFs are unlikely to be a strong mechanism for stabilization, and consequently coexistence. What alternative hypotheses could explain the observed differences in intraspecific versus interspecific interaction strengths? Our measurements of abiotic covariates did not reveal consistent species-specific differences. Our measurement of soil moisture was based on 0- to 15-cm depth, which is appropriate for understanding seed to seedling transitions, but may not reflect the most important water dynamics in the sagebrush steppe. Recent work in the same ecosystem suggests that species-specific water uptake patterns differed most in 11- to 38-cm depth, and the depth to 50% water uptake correlated well with species cover on the landscape (Kulmatiski et al., 2020). Another alternative niche axis that we did not measure could be microsite variation in soil depth, which has been shown to determine coexistence and abundance dynamics in a calcareous grassland (Fridley et al., 2011).

Unpacking the Hutchinsonian *n*-dimensional niche hypervolume (Hutchinson, 1957) to understand the mechanisms driving patterns of relative abundance and coexistence is inherently difficult. Our work serves as a blueprint for the "top-down" approach, in which phenomenological outcomes and natural history knowledge are combined to inform hypotheses for important coexistence mechanisms. Next, well-replicated field experiments directly test the contribution of the hypothesized mechanism to observed coexistence. Even if results do not provide evidence for the importance of the hypothesized mechanism, as in our case, they can point to alternative mechanisms for future study. We argue that this mechanism-based approach is crucial to the next chapter of understanding the role of PSFs in mediating coexistence in natural ecosystems.

AUTHOR CONTRIBUTIONS

Y. Anny Chung and Peter B. Adler conceived of and designed the study. Y. Anny Chung conducted experiments with help from Thomas A. Monaco, Peter B. Adler, and J. Bret Taylor. Y. Anny Chung analyzed data. Y. Anny Chung and Peter B. Adler wrote the manuscript, with input from Thomas A. Monaco and J. Bret Taylor.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Chung, 2023a) are available in Dryad at https://doi.org/10.5061/dryad.b5mkkwhhg.

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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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