Mycorrhizal Identity and Light Shape Tree Seedling Biomass Responses in Plant–Soil Feedbacks

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Mycorrhizal Identity and Light Shape Tree Seedling Biomass Responses in Plant–Soil Feedbacks

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ABSTRACT

Aims - Plant–soil feedbacks (PSFs) are key drivers of forest composition and diversity, yet their direction and magnitude may depend on the mycorrhizal identity of interacting species, environmental conditions, and experimental context.

Methods - We conducted complementary greenhouse and field experiments using *Acer rubrum* L., *Acer saccharum* Marsh., *Prunus serotina* Ehrh. (all arbuscular mycorrhizal [AM] species), and *Quercus alba* L., and *Quercus rubra* L. (all ectomycorrhizal [EM] species) to test how biomass-based PSFs vary with mycorrhizal matching between seedlings and adult trees, light availability, and soil microbial communities. Seedlings were grown in soil conditioned by conspecifics, conmycorrhizal heterospecifics, or heteromycorrhizal heterospecifics under controlled and natural light regimes.

Results - Consistent with expectations, AM species generally exhibited negative PSFs and EM species positive PSFs, but this pattern was contingent on light and greenhouse versus field setting. For AM species, negative PSFs occurred primarily under low light and were neutralized or reversed under higher light. EM species showed more consistent positive PSFs across light levels and settings, although species-specific differences emerged. PSFs were driven largely by conspecific soil conditioning, with limited influence from the mycorrhizal identity of heterospecific neighbors. Results from greenhouse versus field settings diverged, with field PSFs sometimes attenuated or reversed, particularly for *Q. alba*.

Conclusions - These findings highlight that biomass-based PSFs are not fixed species traits but context-dependent outcomes influenced by mycorrhizal type, light availability, and environmental setting. Incorporating these factors is essential for predicting how PSFs influence seedling recruitment, forest dynamics, and biodiversity.

Keywords: arbuscular mycorrhizal fungi, ectomycorrhizal fungi, forest dynamics, light availability, mycorrhizal associations, plant-soil feedbacks

INTRODUCTION

Understanding the ecological processes that promote and maintain tree species diversity remains a central question in forest ecology (Chesson, 2000; Wright, 2002). Among the biotic mechanisms that regulate forest composition, plant–soil feedbacks (PSFs) have emerged as a critical driver of seedling performance, species coexistence, and long-term community dynamics (Bever et al., 1997; Crawford et al., 2019; Stein and Mangan, 2020). PSFs occur when adult trees alter the soil environment—through changes in microbial communities, nutrient availability, or allelopathic compounds—in ways that subsequently affect seedling growth and survival. Feedbacks may be positive, negative, or neutral depending on species identity and symbiotic associations. Mycorrhizal type strongly influences outcomes: trees associating with arbuscular mycorrhizal fungi (AMF; hereafter "AM trees") often experience negative feedbacks (−PSFs), whereas those associating with ectomycorrhizal fungi (EMF; hereafter "EM trees") more commonly exhibit positive feedbacks (+PSFs) (Bennett et al., 2017; Kadowaki et al.; Refsland et al., 2023). These outcomes can further shaped by whether seedlings establish in conspecific, conmycorrhizal heterospecific (same mycorrhizal type), or heteromycorrhizal heterospecific (different mycorrhizal type) soils (Kadowaki et al., 2018), particularly in mixed-mycorrhizal forests where species coexist in spatial mosaics. Light availability also modulates these dynamics: −PSFs are often strongest in low light, where survival is limited, (McCarthy-Neumann and Ibáñez, 2013), while +PSFs are more common in high light due to greater seedling biomass gains (Xi et al., 2023).

Soil microbial communities help explain these contrasting patterns. EM fungi, which form a dense sheath around roots, can physically block pathogens (Laliberté et al., 2015) and restrict nitrogen access to AM competitors (Wurzburger and Hendrick, 2009). AM fungi, by contrast, often compete with pathogens for root space but lack equivalent structural defenses (Borowicz, 2001). As a result, soils of AM trees typically harbor more pathogens and saprotrophs than EM trees (Eagar et al., 2022, 2023), and seedlings of AM trees accumulate pathogens more rapidly in conspecific soil (Chen et al., 2019). These microbial asymmetries may help explain why EM seedlings often perform better in conspecific soil, while AM seedlings perform better in heterospecific soil. Such divergent feedbacks have important consequences for forest diversity: -PSFs may promote species coexistence and diversity by increasing the likelihood that a heterospecific seedling replaces a dying adult (Bennett and Klironomos, 2019; Jiang et al., 2022; Lekberg et al., 2018), whereas +PSFs may instead favor conspecific dominance (Bennett et al., 2017; Kadowaki et al., 2018; Teste et al., 2017).

Although broad patterns of −PSFs in AM trees and +PSFs in EM trees are well documented (Bennett et al., 2017; Refsland et al., 2019; but see Jia et al., 2020), mounting evidence indicates that neighbor identity matters. The mycorrhizal type of surrounding adults—whether conspecific, conmycorrhizal heterospecific, or heteromycorrhizal heterospecific—can strongly shape microbial communities and, in turn, seedling outcomes (Averill et al., 2022; Kadowaki et al., 2018; Stein and Mangan, 2020). AMF tend to be generalists with broad host ranges, whereas EMF are often more host-specific (Smith and Read, 2008), making microbial compatibility—and thus seedling biomass accumulation—sensitive to the identity of neighboring adults. Despite this, most PSF experiments have focused on the mycorrhizal identity of the focal seedling and its conspecific adults, often simplifying heterospecific effects by pooling all non-conspecifics into a single "away" or "non-self" category (van der Putten et al., 2013). Such

simplification obscures important variation in species-specific interactions. Taken together, these insights indicate that PSFs should not be viewed as fixed traits of plant species, but as emergent outcomes shaped by the specific composition and mycorrhizal strategies of the surrounding plant community. Whether a seedling encounters compatible or incompatible soil biota may be especially important in driving growth responses and shaping competitive outcomes in systems where AM and EM trees coexist (Delavaux et al., 2023; Mao et al., 2024).

A key environmental mediator of PSF outcomes is light availability (McCarthy-Neumann and Ibáñez 2013; Xi et al., 2023). Light directly influences seedling carbon balance and shapes soil biotic interactions by affecting both mutualist colonization and pathogen abundance. In higher light environments, seedlings can invest more carbon into mycorrhizal associations (Bereau et al., 2000; Shi et al., 2014; Koorem et al., 2017), benefiting from improved nutrient acquisition and defense, which can shift PSFs in a more positive direction (Xi et al., 2023). In contrast, shaded, moist conditions can limit the supply of photosynthetic carbon and reduce colonization rates (Ibáñez and McCarthy-Neumann, 2016; Konvalinková and Jansa, 2016), while simultaneously promoting the proliferation of pathogens such as fungi, oomycetes, and bacteria (Liu and He, 2019), which can drive widespread seedling mortality (Terborgh, 2012). These effects are particularly pronounced for AM species, which are more susceptible to pathogen buildup and may derive fewer benefits from mycorrhizal symbionts under carbon-limited conditions (Ibáñez and McCarthy-Neumann 2016). The direction of PSFs therefore reflects the net effect of mutualistic and antagonistic soil-borne microbes (van der Putten et al., 2013), both of which vary with light. These microbial effects can operate through both conspecific and heterospecific soils: +PSFs may arise from greater mutualist abundance or reduced pathogen pressure in conspecific soils and/or lower mutualist abundance or higher pathogen pressure in heterospecific soils, while -PSFs may result from the opposite patterns (Bever 2002; McCarthy-Neumann and Ibáñez 2012).

Most PSF research has been conducted under controlled greenhouse conditions, which facilitate isolation of microbial effects by reducing environmental variability. Indeed, meta-analyses indicate that 83–95% of published PSF studies are greenhouse-based (Beals et al., 2020; Crawford et al., 2019; Forero et al., 2019). These studies have repeatedly shown that PSFs are often negative and driven largely by soil biota (Bennett et al., 2017; Klironomos, 2002; Petermann et al., 2008). However, such experiments may overestimate the magnitude of microbial effects due to artificial inoculation techniques, altered soil physical structure, increased nutrient availability, and disruption of mycorrhizal networks (Forero et al., 2019). In contrast, field-based PSF studies, which remain rare, account for natural variability in light, competition, herbivory, climate, and biotic interactions, and thus should better reflect the conditions seedlings encounter in nature. Notably, the limited number of complementary studies suggests that PSFs observed in greenhouse settings do not always translate to the field, with microbial effects often attenuated or even reversed (Heinze et al., 2016; Schittko et al., 2016). Furthermore, field experiments are uniquely suited to disentangle the context dependency of PSFs by incorporating spatial heterogeneity and temporal fluctuations in resource availability, disturbance, and microbial dynamics. As such, field studies are essential for assessing how PSFs influence seedling performance in situ and for evaluating their relative contribution to community assembly compared to other drivers such as light, nutrients, and herbivory (Gundale and Kardol, 2021; Kulmatiski and Kardol, 2008).

To investigate how PSFs vary with mycorrhizal associations, light availability, and experimental setting, we conducted complementary greenhouse and field experiments using seedlings of AM and EM tree species grown in soils cultured by conspecific and heterospecific adults. Heterospecific soils included both conmycorrhizal and heteromycorrhizal species. Seedlings experienced natural variation in light in the field and controlled light treatments in the greenhouse. Our overarching hypothesis is that PSFs reflect mycorrhizal matching between seedlings and adults and are modulated by environmental context. Specifically, we test four hypotheses:

1. *PSF directionality depends on mycorrhizal matching.* AM seedlings (-PSFs) exhibit lowest biomass in conspecific soil, intermediate in heterospecific EM soil, and highest in heterospecific AM soil. EM seedlings (+PSFs) exhibit highest biomass in conspecific soil, intermediate in heterospecific EM soil, and lowest in heterospecific AM soil.
2. *Light availability mediates PSFs.* AM seedlings experience stronger -PSFs under low light; EM seedlings experience stronger +PSFs under high light.
3. *Soil-borne microbes in conspecific soil mediate PSF directionality.* Soil-borne microbes from conspecific soils have negative effects on biomass for AM species and positive effects on biomass for EM species.
4. *PSF effects differ between greenhouse and field settings.* Greenhouse experiments detect stronger PSFs due to controlled conditions; field PSFs are weaker or more variable due to interacting abiotic and biotic influences.

MATERIALS AND METHODS

To evaluate how soil microbial communities and light availability influence seedling biomass across species, we conducted a greenhouse experiment and a complementary field transplant experiment. Both experiments tested tree seedling species in seven soil sources (including conspecific live, conspecific sterilized, and five heterospecific soils) under varying light conditions. Whole plant biomass (mg) was recorded for all surviving seedlings at the conclusion of each experiment.

Shared Methods

Study species - We selected six tree species differing in shade tolerance, seed size, and mycorrhizal association: *Acer rubrum* L., *A. saccharum* Marsh., *Prunus serotina* Ehrh., *Populus grandidentata* Michx., *Quercus alba* L., and *Q. rubra* L. (Table 1). *P. grandidentata* seedlings were not grown due to poor seed availability, and *A. rubrum* seedlings were not included in the field experiment because of low germination; soils cultured by these species were retained as treatments.

Table 1 Selected species information. [1]Local adult abundance (± standard deviation) was calculated as the number of individuals ≥ 5cm diameter at breast height per ha. [2]Shade tolerance (± standard deviation) was reported on a standardized scale from 1 (very intolerant) to 5 (very tolerant), following Niinemets and Valladares (2006). [3]Seed weight (± standard deviation) was taken from Kattge et al. (2020). [4]EM tree species can also be colonized by AMF as seedlings.

Species (Acronym)	Local adult abundance[1]	Shade tolerance[2]	Seed weight (mg)[3]	Primary mycorrhizal association[4]
Acer rubrum (ACRU)	120 (71)	Intermediate (3.44 ± 0.23)	22.85 (12.83)	AMF
Acer saccharum (ACSA)	262 (63)	very tolerant (4.76 ± 0.11)	64.16 (23.54)	AMF
Prunus serotina (PRSE)	4 (4)	intolerant (2.46 ± 0.34)	95.36 (33.17)	AMF
Populus grandidentata (POGR)	82 (31)	intolerant (1.21 ± 0.27)	0.14 (0.02)	EMF
Quercus alba (QUAL)	13 (3)	tolerant (2.85 ± 0.17)	3000.48 (625.03)	EMF
Quercus rubra (QURU)	72 (8)	intermediate (2.75 ± 0.18)	2997.37 (827.86)	EMF

Soil collection and preparation - Soils were collected from beneath mature trees in a mixed hardwood forest that has not been logged since 1897 at Alma College's Ecological Field Station (Vestaburg, MI, USA; 43.4°N, 84.9°W) in August 2017 for the greenhouse experiment and from May to June 2016 and April to May 2017 for the field experiment. We sampled the upper 15 cm of soil within 1 m of the trunk from six randomly selected adult trees per species (diameter at breast height ≥ 75th percentile), each located within a 3-ha mapped stand and at least two crown diameters from other study species to minimize multi-species culturing. Soil from each adult was kept as separate replicates (Reinhart and Rinella, 2016; Rinella and Reinhart, 2018). For the greenhouse experiment, soil was sieved (1-cm mesh), and fine roots were retained and homogenized. For the field experiment, intact soil cores (9 cm diameter × 46 cm depth) were extracted using a mechanized soil corer (Giddings Machine Co., Windsor, CO, USA).

Soil, seed, and tool sterilization and nutrient controls - To isolate microbial effects, a subset of conspecific soils was sterilized using gamma irradiation (greenhouse: 43.7 ± 7.6 kGy in December 2017; field: 44.6 ± 6.9 kGy in July 2017; Sterigenics International, Schaumburg, IL, USA), a method that eliminates soil biota while minimizing changes to soil chemistry and structure (McNamara et al., 2003). Mycorrhizal colonization remained low in sterilized soils (greenhouse: 0.02% AMF, 3% EMF; field: 8% AMF, 4% EMF at 3 weeks; 10% AMF, 7% EMF at 68 weeks). Nutrient availability, measured with Plant Root Simulator probes (Western Ag Innovations Inc., Saskatchewan, Canada), did not differ significantly between sterilized and non-sterilized soils, nor between seedling pot soils at planting and undisturbed soils beneath the source adult trees (Wood et al., 2023a). These results suggest

that our experimental design did not introduce unintended changes to nutrient availability. To minimize non-experimental contamination, Seeds were surface-sterilized in 0.6% NaOCl before stratification, and tools/surfaces contacting soil or roots were disinfected with 10% NaOCl or 70% ethanol and rinsed with deionized water between uses.

Greenhouse Experiment

We conducted the greenhouse study at Michigan State University's Tree Research Center (East Lansing, MI, USA; 42.7°N, 84.5°W), growing five species (*A. rubrum*, *A. saccharum*, *P. serotina*, *Q. alba*, *Q. rubra*) in seven soil types (sterile and live conspecific, and five heterospecific) under three light regimes (~2%, ~15%, and ~30% full sunlight). Shade treatments were created with layered black shade cloth and reflective poly-aluminum sheeting (BFG Supply, Burton, OH, USA) and verified with a LI-COR 205A quantum sensor.

Pots (volume = 655 cm^3) filled with a 1:1 mixture of processed field soil and Fafard #2 potting mix were arranged across nine greenhouse benches, with three benches allocated per light treatment. We included 30 seedlings per species × soil source × light level combination, totaling 3,150 seedlings. A single seed with a newly emerged radicle was planted in each pot in January 2018. Seedlings were grown for 12 weeks across nine greenhouse benches (three per light level), then harvested, dried at 70ºC to constant mass, and whole plant biomass (mg) was weighed (Supplementary Table S1).

Field Experiment

For complete methodological details, refer to Wood et al. (2023a). The field experiment was conducted in a 100-ha hardwood forest at Alma College's Ecological Field Station (43.4°N, 84.9°W), where *Q. alba* and *Q. rubra* seedlings (N = 1,512) were grown in the same seven soil types as above. Seedlings were planted in custom pots created from intact soil cores, with two 7.5 cm side holes covered with 0.5 µm nylon mesh to permit water and nutrient exchange (Allison et al., 2013) while blocking roots and pathogens (McGuire, 2007; Teste et al., 2017). Although we initially included two additional species (*A. saccharum* and *P. serotina*), their low survival rates in the first growing season (Wood et al., 2023a) precluded biomass evaluations.

In June 2018, 64 cm^3 of a 1:1 mix of peat moss and soil inoculum (live or sterilized) was added to each core to enhance transplant success and provide fresh inoculum. The inoculum was collected in late May 2018 to minimize the effects of long-term storage. Seedlings were planted in 18 field plots (8.4 m × 6.6 m) spanning a natural light gradient from 0.032 to 0.161 Indirect Site Factor (ISF). ISF, quantified from hemispherical canopy photographs, represents the proportion of diffuse (indirect) solar radiation reaching a given location relative to an open site; multiplying ISF by 100 yields the equivalent percent full sunlight. Plots were categorized as low light (0.032–0.075 ISF; ~3–7.5% full sun), medium light (0.075–0.118 ISF; ~7.5–11.8% full sun), and high light (0.118–0.161 ISF; ~11.8–16.1% full sun). Each plot was fenced with 1.8-m tall galvanized hardware cloth to exclude deer, and top mesh coverings were glued to PVC cores to prevent seedling excavation. A total of 84 seedlings were planted per plot, evenly distributed by species and soil source (N = 6 replicates per species × soil × plot

combination). Seedlings grew for two full seasons (~68 weeks), after which surviving individuals were harvested, dried at 70ºC to constant mass, and whole plant biomass (mg) was weighed (Table S1).

Statistical analysis

All statistical analyses were conducted in R version 3.5.1 (R Core Team, 2020). We used the *lme4* package (Bates et al., 2015) to fit linear models assessing the effects of soil source and light availability on seedling biomass. Separate models were developed for each species, with soil source and light availability specified as fixed effects. Significance of main effects and interactions was evaluated using likelihood ratio tests via the "Anova" function from the *car* package (Fox and Weisberg, 2019). Holm-adjusted pairwise comparisons and estimated marginal means were obtained using the *emmeans* package (Hothorn et al., 2008; Lenth, 2020).

To evaluate Hypothesis 1 (PSF directionality depends on mycorrhizal matching), we examined species-specific biomass patterns across soil sources. PSFs were quantified using the natural log-transformed response ratio (lnRR) of biomass in conspecific versus heterospecific soils, following Bates et al. (2020). Specifically, PSF was calculated as the difference between mean natural log-transformed biomass in conspecific soil and heterospecific soils. Uncertainty around PSF estimates was quantified via nonparametric bootstrapping with 10,000 resamples.

Hypothesis 2 (light availability mediates PSFs) was tested by comparing PSF values for each species across low and high light environments, calculated separately for the greenhouse and field experiments. In the greenhouse, low light corresponded to ~2% full sun and high light to ~30% full sun, while in the field, low light ranged from ~3–7.5% full sun and high light from ~11.8–16.1% full sun. For each species–soil combination, we plotted mean PSF values (± 95% credible intervals) at high versus low light. Deviations from the 1:1 line and non-overlap of credible intervals with this line were interpreted as evidence of light-modulated PSFs.

To assess Hypothesis 3 (soil-borne microbes mediate PSF directionality), we compared seedling biomass in non-sterile versus sterilized conspecific soils using the same lnRR and bootstrapping approach described above.

To evaluate Hypothesis 4 (PSF effects differ between greenhouse and field settings), we compared PSF values between experiment types across all three light treatments. For cross-experiment comparisons, low light treatments in the greenhouse (~2% full sun) and field (~3–7.5% full sun) were matched directly, whereas the greenhouse medium light treatment (~15% full sun) was compared to high light plots in the field (~11.8–16.1% full sun) due to their similar light availability. For each EM species, we plotted mean PSFs (± 95% credible intervals) in the greenhouse versus the field, using a 1:1 reference line. Deviations from this line, especially where credible intervals did not overlap with it, indicated differences in PSFs between controlled and natural conditions.

RESULTS

Seedling biomass varied by mycorrhizal type, soil source, and light availability, with patterns differing between greenhouse and field settings (Fig. 1 and 2A; Supplementary Tables S2–S5). In the greenhouse, all three AM species had significantly greater biomass in conspecific than heterospecific soils, though the pattern varied by species and light. *Acer rubrum* and *Acer saccharum* had 14–26% and 11–33% higher biomass, respectively, in conspecific soil at high light than at low and medium light. *Prunus serotina* had 21–31% more biomass in conspecific than EM

heterospecific soils and 29–39% more biomass than in all heterospecific soils at medium light. No species showed significant biomass differences across soil sources under low light.

Among EM species, *Quercus alba* and *Quercus rubra* had greater biomass in conspecific than heterospecific soils at high light. *Q. alba* had 11–17% more biomass in conspecific soil at high light and 11% more than two of the three AM heterospecific soils at medium light. *Q. rubra* had 13–15% more biomass in conspecific than heterospecific soils in both medium and high light.

Only *P. serotina* showed a negative biotic effect in conspecific soil, with 34% lower biomass in live versus sterile soil under low light (Supplementary Table S4). *Q. rubra* had higher biomass in live than sterile conspecific soil at all light levels, but the biotic effect declined from 13% in low light to 7% and 4% in medium and high light, respectively.

In the field, species showed opposing biomass patterns (Fig. 2A; Table S5). *Q. alba* had 22–30% lower biomass in conspecific than heterospecific soil(s) under low light, 74–77% less in medium light, and 20–25% less in high light. Biomass was 21% higher in live than sterile conspecific soil under low light, but 59% and 72% lower in live soil under medium and high light, respectively. In contrast, *Q. rubra* had 32–40% more biomass in conspecific soils under low light, 13–15% more in medium, and 32–36% more in high light, with positive biotic effects of 44% and 37% in live soil under medium and high light, respectively.

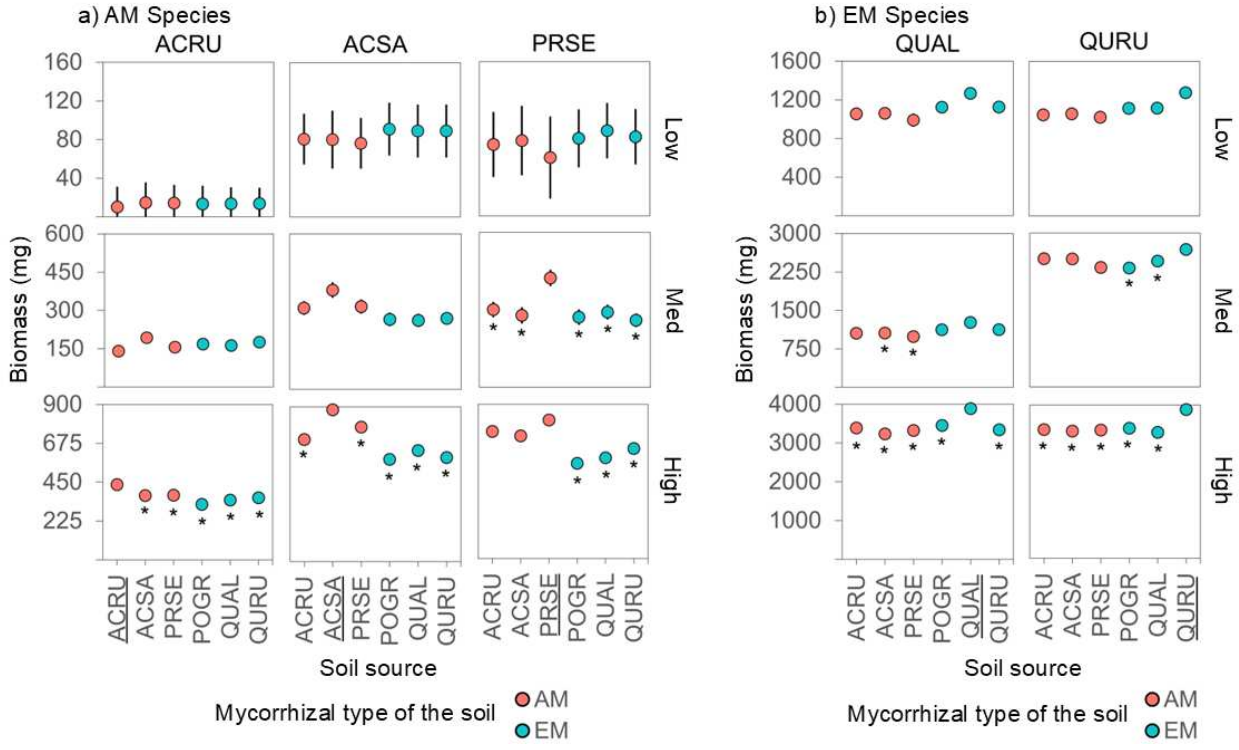

Fig. 1 Seedling biomass (mg ± standard error) for a**)** arbuscular mycorrhizal (AM) associated species and b) ectomycorrhizal (EM) associated species in the *greenhouse experiment* across different soil sources (denoted along the x-axes) and under low (top rows), medium (middle rows), and high (bottom rows) light levels. Conspecific seedling species codes are underlined. Asterisks indicate statistically significant differences ($p < 0.05$) in biomass between conspecific and heterospecific soils. Species and soil source codes are defined in Table 1

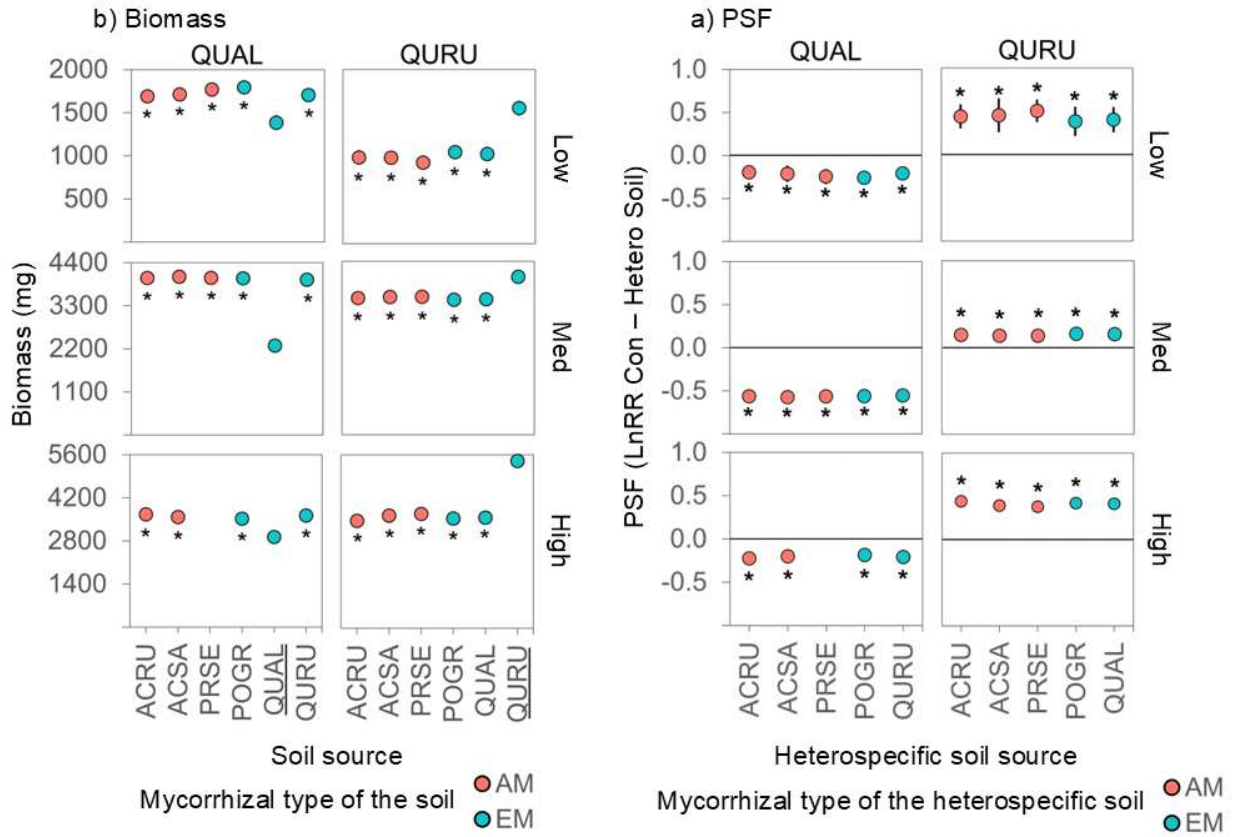

Fig. 2 a) Seedling biomass (mg ± standard error) and b) plant–soil feedbacks (PSFs; natural log response ratio, lnRR ± confidence interval) for ectomycorrhizal (EM)-associated species in the *field experiment* across different soil sources (denoted along the x-axes) and under low (top rows), medium (middle rows), and high (bottom rows) light levels. PSFs were calculated as the lnRR of seedling biomass in conspecific versus heterospecific soils. Asterisks in panel A indicate statistically significant differences ($p < 0.05$) in biomass between conspecific and heterospecific soils. Asterisks in panel B indicate statistically significant PSFs, where confidence intervals do not overlap zero. *Note: no PSF value is shown for Q. alba seedlings grown in P. serotina soil in high light because no seedlings in that treatment survived to the end of the experiment.* The horizontal line at zero indicates no PSF. Positive values indicate +PSFs (greater biomass in conspecific soils), and negative values indicate −PSFs (lower biomass in conspecific soils). Species and soil source codes are defined in Table 1

Consistent with H1, AM tree species in the greenhouse experiment exhibited -PSFs and EM species exhibited +PSFs. However, this pattern was observed for AM species only under low light (Fig. 3; Table S4), which is consistent with stronger -PSF impacts expected in low light under H2. EM species displayed PSFs consistent with expectations across all light levels, with seedlings generally performing better in conspecific than heterospecific soils. Another facet of H1 posited that the mycorrhizal type of the adult tree culturing heterospecific soil would influence PSF directionality, for which there was negligible support. In the greenhouse, 9 of 15 species-by-light combinations exhibited PSFs regardless of the mycorrhizal type of the heterospecific soil. In five combinations, PSF directionality aligned with predictions based on mismatches between the seedling and heterospecific adult mycorrhizal type. Only one case, *A. rubrum* in medium light, showed PSFs that were contingent on a comparison with a conmycorrhizal soil. In the field, EM species exhibited PSFs regardless of the mycorrhizal identity of the

heterospecific soil source (Fig. 2B; Table S5). For *Q. rubra* this was a +PSF as expected; however, *Q. alba* experienced -PSFs, contrary to predictions.

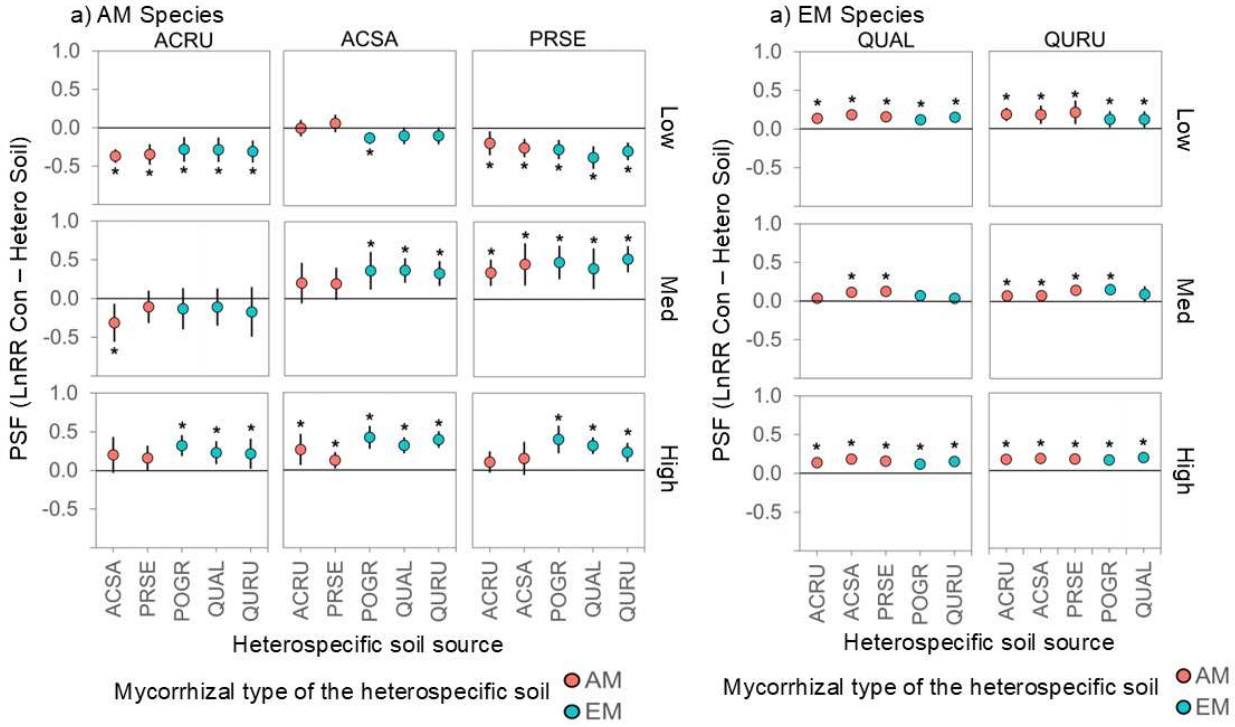

Fig. 3 Plant–soil feedbacks (PSFs) calculated as the natural log response ratio (lnRR ± confidence interval) of seedling biomass in conspecific versus heterospecific soils for a) arbuscular mycorrhizal (AM) associated species and b) ectomycorrhizal (EM) associated species in the *greenhouse experiment* across different soil sources (denoted along the x-axes) and under low (top rows), medium (middle rows), and high (bottom rows) light levels. The horizontal line at zero indicates no PSF. Asterisks indicate statistically significant PSFs, where intervals do not overlap the zero line. Positive values indicate +PSF (greater biomass in conspecific soils), while negative values indicate –PSF (lower biomass in conspecific). Species and soil source codes are defined in Table 1

Partially supporting H2 (that light availability mediates PSF strength and direction), AM seedlings in the greenhouse shifted from -PSFs in low light to neutral or +PSFs in higher light (Fig. 4). EM species, in contrast, experienced similar PSFs across light levels (Fig. 4).

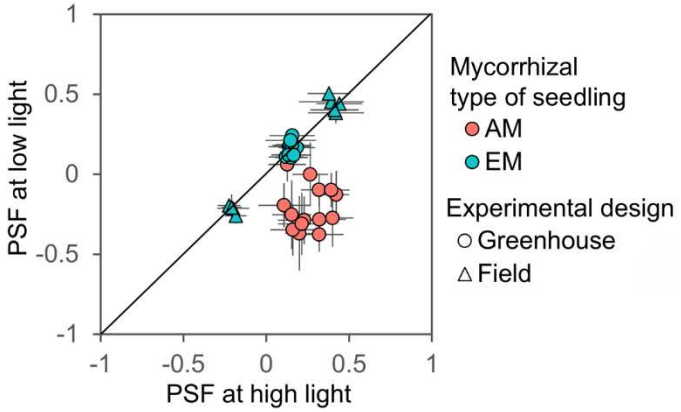

Fig. 4 Plant–soil feedbacks (PSFs) at high versus low light in greenhouse (2% vs. 30% full sun) and field experiments (3-7.5% vs. 11.8-16.1%) are presented, showing means for each species × soil combination (means ±

95% credible intervals). Sterilized conspecific soils are excluded. The solid line represents a 1:1 relationship between PSFs at high and low light

We found limited evidence for H3 (that PSF directionality is mediated by soil-borne microbes in conspecific soils) (Fig. 5). All AM species exhibited -PSFs in low light, but only *P. serotina* showed reduced biomass in live versus sterile conspecific soil under those conditions. At higher light levels, although AM species exhibited +PSFs, seedling biomass in live conspecific soil did not exceed that in sterile soil. For *Q. rubra*, PSFs were consistently positive across light levels in the greenhouse, with higher biomass in live conspecific soil. In the field, *Q. rubra* seedlings also showed +PSFs across light levels, and biomass increased in live conspecific soil at medium and high light. In contrast, *Q. alba* exhibited -PSFs across light levels, but increased biomass in live conspecific soil was only observed at low light; at medium and high light, conspecific soil microbes reduced biomass, although seedlings still exhibited +PSFs.

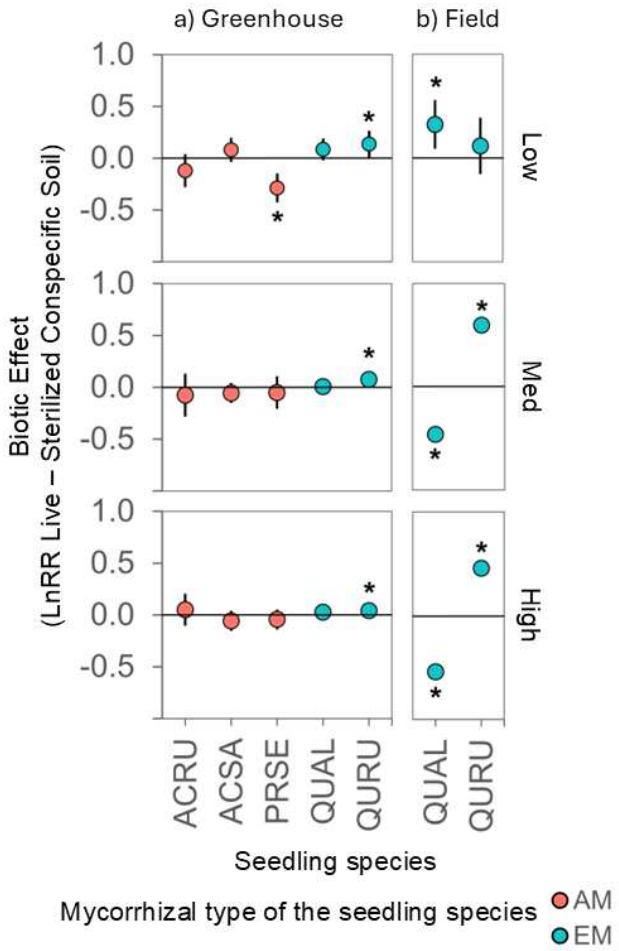

Fig. 5 Biotic effect of conspecific soil, calculated as the natural log response ratio (lnRR ± confidence interval) of seedling biomass in live versus sterilized conspecific soil for a) greenhouse and b) field experiments across light levels for each seedling species. The horizontal line at zero indicates no PSF. Asterisks indicate statistically significant biotic effects, where confidence intervals do not overlap zero. Positive values indicate positive biotic effect (greater biomass in live soil), while negative values indicate negative biotic effect (lower biomass in live soil). Seedling species codes are defined in Table 1

Consistent with H4, PSFs differed between greenhouse and field experiments for both *Q. rubra* and *Q. alba* (Fig. 6). For these comparisons, greenhouse low light (~2% full sun) was matched to field low light (~3–7.5% full sun), and greenhouse medium light (~15% full sun) was compared to field high light (~11.8–16.1% full sun). Across both species, PSFs were generally more positive in the field than in the greenhouse. For *Q. rubra*, this pattern held under both matched light treatments, with field PSFs consistently higher than greenhouse values. In contrast, *Q. alba* showed the opposite trend, with positive PSFs in the greenhouse shifting to negative PSFs in the field under both matched light treatments.

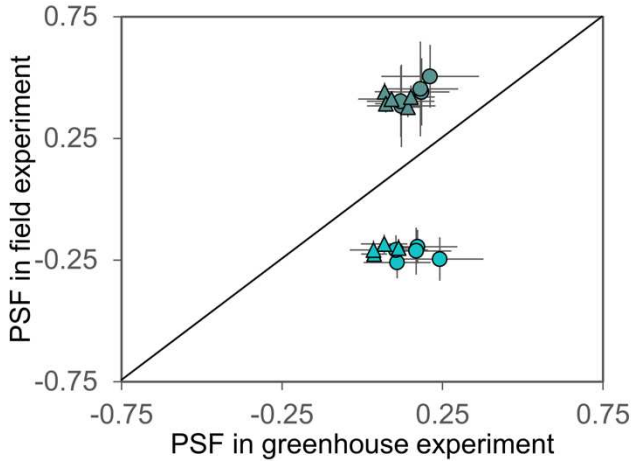

Fig. 6 Plant–soil feedbacks (PSFs) in greenhouse versus field experiments across three light treatments, showing means for each EM species × soil combination (means ± 95% credible intervals). Treatments were matched as follows: greenhouse low (2%) vs. field low (3–7.5% full sun); greenhouse medium (15%) vs. field high (11.8–16.1% full sun). Sterilized conspecific soils are excluded. The solid line represents a 1:1 relationship between PSFs in the greenhouse and field experiment

DISCUSSION

Understanding the mechanisms driving plant–soil feedbacks (PSFs) is essential for predicting forest dynamics and diversity. Our results show that PSF direction and magnitude vary with seedling mycorrhizal type, light availability, and environmental context (greenhouse vs. field). While AM species generally exhibited -PSFs and EM species +PSFs, as predicted (H1), this pattern held for AM species only under low light, highlighting the role of light in modulating PSFs (H2). PSFs also differed between greenhouse and field settings (H4), particularly for *Q. alba*, which showed a reversal in PSF direction. We found limited support that soil-borne microbes in conspecific soils were the primary drivers of PSFs (H3), as biotic effects were inconsistent across species and light levels. Additionally, PSFs occurred regardless of the mycorrhizal type of heterospecific trees, suggesting conspecific identity—rather than mycorrhizal mismatches—was the stronger determinant of PSF direction and strength.

H1: PSF Direction Reflects Mycorrhizal Matching

Consistent with expectations, AM seedlings exhibited -PSFs (reduced biomass in conspecific soils), especially under low light. This result is consistent with the idea that pathogen buildup in AM-conditioned soils drives conspecific inhibition (Bennett et al., 2017; Chen et al., 2019; Eagar et al., 2022). As light increased, AM PSFs became neutral

or positive, suggesting mutualist benefits from AM fungi outweighed pathogen costs under higher carbon availability. Greater light boosts AMF colonization and allows fungi to outcompete pathogens for root-derived carbon (Borowicz, 2001). Under high light, seedlings may also allocate carbon to more beneficial fungi, enhancing nutrient returns (Zheng et al., 2015), consistent with carbon-rich conditions strengthening AMF mutualisms (Johnson et al., 1997). Our results, together with previous studies, suggest that mutualisms dominate under high light. Additionally, surviving seedlings may reflect individuals that escaped early pathogen mortality, amplifying the observed biomass benefits.

In contrast, EM seedlings generally showed +PSFs across all light levels in the greenhouse, consistent with the role of EM fungi in nutrient acquisition and pathogen defense (Laliberté et al., 2015; Smith and Read, 2008). *Q. rubra* displayed strong +PSFs in both experiments, but *Q. alba* deviated from this pattern in the field, exhibiting -PSFs. This may reflect antagonistic effects, as *Q. alba* biomass was lower in live than sterilized conspecific soil under medium and high light. Aside from *Q. alba* in the field, these results support the hypothesis that conspecific soils are detrimental for AM species and beneficial for EM species (Bennett et al., 2017; Eagar et al., 2024; Kadowaki et al., 2018; McCarthy-Neumann et al., in review).

The mycorrhizal type of heterospecific adult trees did not influence PSFs. Most PSFs occurred regardless of whether heterospecific soils were conditioned by AM or EM trees, suggesting that for growth-based PSFs, conspecific effects outweigh heterospecific microbial mismatches. This contrasts with seedling survival patterns in a companion study (McCarthy-Neumann et al., in review), where PSFs were stronger when seedlings and neighboring adults differed in mycorrhizal type. It also diverges from Delavaux et al. (2023), who found conmycorrhizal heterospecifics reduced density dependence in global forest datasets.

H2: Light Availability Mediates PSFs

Light strongly influenced PSFs, particularly for AM species. In the greenhouse, all three AM species shifted from -PSFs in low light to +PSFs in higher light. This matches findings that seedlings are more disease-prone under shade (Augspurger and Kelley, 1984; Liu and He, 2019; McCarthy-Neumann and Ibáñez, 2013), likely due to higher pathogen abundance (Hersh et al., 2012; Reinhart et al., 2010) and potential parasitism by AMF (Ibáñez and McCarthy-Neumann, 2016; Konvalinková and Jansa, 2016; Wood et al., 2023b). As light increases, pathogen pressure likely declines and seedling traits for recovery and defense become more effective (McCarthy-Neumann et al., in review; Wood et al., 2023a,b), shifting AMF symbioses from parasitism to mutualism and resulting in +PSFs under high light.

In contrast, EM seedlings maintained +PSFs across light levels, suggesting EMF confer consistent benefits even under carbon-limited, low-light conditions. Their greater enzymatic capacity, host specificity, and pathogen protection—including root sheathing—likely contribute to this consistency (Laliberté et al., 2015; Smith and Read, 2008). The fact that EM seedlings maintained higher biomass in conspecific soils even in shade supports that EM associations are more stable mutualisms than those involving AMF (Ibáñez and McCarthy-Neumann, 2016; Johnson et al., 1997).

These light-dependent PSF differences also help explain conflicting outcomes across studies. Survival-based studies often find stronger PSFs in low light due to high seedling sensitivity to pathogen pressure (McCarthy-Neumann and Kobe 2010a,b; McCarthy-Neumann and Ibáñez 2013; McCarthy-Neumann et al., in review, but see McCarthy-Neumann and Kobe 2019). Pathogen-induced seedling mortality typically begins around week three and peaks four to six weeks after germination (McCarthy-Neumann and Ibáñez, 2012), suggesting that survival metrics primarily capture early-stage dynamics. In contrast, studies measuring biomass—usually at the end of the growing season—often find more -PSFs in high light, which may turn neutral or positive as light availability decreases (Smith and Reynolds, 2015; Xi et al., 2020). Under high light, greater plant biomass and nutrient demand increase root-soil contact and exudation, promoting stronger soil conditioning, pathogen buildup, and competition for nutrients, which can intensify -PSFs (Smith and Reynolds, 2015). These effects are amplified under interspecific competition and linked to shifts in microbial communities (Xi et al., 2020). Conversely, in low light, smaller seedlings condition soil less, weakening -PSFs. However, biomass-based +PSFs have been observed in high light as seedlings benefit from mycorrhizal mutualists and more readily recover from biotic stress (Xi et al., 2023), which aligns with our findings, particularly for AM species.

H3: Soil Microbes Mediate PSF Directionality in a Context-Dependent Manner

We found limited evidence that conspecific soil microbes directly mediated PSFs. In the greenhouse, only *Prunus serotina* showed reduced biomass in live versus sterilized conspecific soil under low light, suggesting microbial antagonism under shaded conditions (Reinhart et al., 2010; Ibáñez and McCarthy-Neumann, 2016; Liu and He, 2019). *Acer rubrum* and *Acer saccharum*, however, displayed PSFs across light levels without corresponding biotic effects, pointing to possible roles for abiotic feedbacks or mutualists in heterospecific soils.

Among EM species, *Quercus rubra* consistently exhibited greater biomass in live conspecific soil, in both experiments, implicating mutualistic microbes in its +PSFs. This aligns with the lower carbon demands and pathogen-blocking abilities of EM fungi (Smith and Read, 2008; Laliberté et al., 2015). *Q. rubra* also performed better in conspecific versus heterospecific EM soils, suggesting strong host specificity. In contrast, *Quercus alba* showed no biotic effects in the greenhouse, but in the field had lower biomass in live conspecific soil under medium and high light, indicating antagonistic microbial effects not present under greenhouse conditions.

These species- and context-dependent outcomes suggest that while conspecific microbes can drive PSFs, their effects vary by species and environment. *Q. rubra* benefitted consistently, while *Q. alba* and *P. serotina* showed neutral or negative effects. This highlights the value of field studies in capturing complex microbial dynamics (Kulmatiski and Kardol, 2008; Forero et al., 2019).

Since only conspecific soils were sterilized, we could not assess whether heterospecific soil effects were biotic or abiotic. Positive PSFs could result from more mutualists in conspecific soils—or more pathogens or abiotic stress in heterospecific ones. Likewise, -PSFs may stem from conspecific pathogens or beneficial microbes in heterospecific soils. Future work should include sterilized heterospecific soils to isolate these effects, though we recognize this adds substantial logistical complexity.

H4: Experimental Setting Alters PSF Outcomes

Our study directly compared PSFs in greenhouse and field settings for *Q. rubra* and *Q. alba*. *Q. rubra* exhibited more +PSFs in the field under low and high light, suggesting that EMF benefits persist or even strengthen under natural conditions. In contrast, *Q. alba* shifted from +PSFs in the greenhouse to -PSFs in the field, especially under medium light, where microbial antagonism was most pronounced.

This divergence underscores the importance of evaluating PSFs in both controlled and natural environments. Greenhouse studies may overestimate PSF strength due to reduced environmental variability and disruption of belowground interactions (Forero et al., 2019). In contrast, field studies capture more realistic dynamics, incorporating competition, herbivory, and spatial heterogeneity in light and moisture (Kulmatiski and Kardol, 2008; Gundale and Kardol, 2021).

Ecological Implications

Our findings reinforce that PSFs are not fixed species traits, but dynamic outcomes shaped by mycorrhizal identity, environmental context, and biotic interactions. For AM species, PSF direction and strength shifted with light and soil source. Seedlings established best in heterospecific EM soils under low light, where conspecific soils likely promoted pathogen buildup or AMF parasitism, but benefitted from conspecific soils under high light, when mutualistic AMF effects became more prominent. These patterns support the idea that -PSFs in shade may limit conspecific recruitment and promote diversity via negative density dependence (Bennett et al., 2017; Jiang et al., 2021), while high light may reverse these effects and allow AM seedlings to capitalize on conspecific microbial mutualists.

In contrast, EM species—particularly *Q. rubra*—consistently benefited from conspecific soils across light levels, suggesting that EMF associations are more stable mutualisms across environmental gradients. These persistent +PSFs may reinforce local dominance and facilitate conspecific recruitment (Shinohara et al., 2024), potentially shaping forest composition and oak persistence. However, species-specific responses within the EM guild—such as the contrast between *Q. rubra* and *Q. alba*—demonstrate that even closely related species can exhibit divergent PSFs depending on site conditions and microbial communities.

Results from a companion greenhouse study on seedling survival (McCarthy-Neumann et al., in review) diverged from growth-based PSFs in important ways, underscoring distinct ecological roles. Survival-based PSFs were strongest under low light and occurred primarily when seedlings grew in soils cultured by heterospecifics with mismatched mycorrhizal types. While AM seedlings often showed survival-based -PSFs and EM seedlings positive ones, these effects were neutralized under high light, likely due to increased mycorrhizal colonization and trait expression. Notably, survival was consistently higher in EM soils, regardless of seedling type, highlighting a broader facilitative role of EM-associated soil communities.

Together, these differences suggest that survival and growth-based PSFs influence different stages of forest dynamics: survival shapes seedling recruitment and community assembly, while growth affects succession rate and long-term demographic trends. Our findings caution against relying on a single performance metric and highlight the

467 importance of integrating survival and growth to fully understand how PSFs influence forest structure, diversity, and
468 resilience.
469
470 **Caveats and Future Directions**
471 We were unable to compare all species across greenhouse and field settings due to high mortality of AM seedlings in
472 the field after the first growing season (Wood et al., 2023a). Thus, our direct comparisons are limited to *Q. rubra*
473 and *Q. alba* after two years of field growth. While the *Q. rubra* results were consistent across settings, the
474 contrasting responses of *Q. alba* point to context dependency that warrants further investigation.
475 Although we found no evidence that nutrient availability mediated PSFs (based on root simulator probe
476 data and lack of differences between sterilized and unsterilized soil; Wood et al., 2023a), nutrient × microbial
477 interactions may still play subtle roles that warrant exploration. Pairing nutrient addition with microbial
478 manipulations could help disentangle these effects.
479
480 **Conclusions**
481 This study demonstrates that PSFs are not intrinsic species traits, but rather dynamic outcomes shaped by
482 mycorrhizal type, environmental context, and species-specific interactions. Crucially, PSFs were driven primarily by
483 conspecific soil conditioning, with limited influence from the mycorrhizal type of heterospecific neighbors. While
484 general patterns, such as -PSFs for AM species in low light and +PSFs for EM species across light levels, held
485 broadly, notable exceptions highlight the complexity of plant–soil–environment relationships. These findings
486 underscore the importance of context-aware PSF research that incorporates light availability, microbial mediation,
487 and differences between greenhouse and field conditions to improve predictions of forest composition and diversity.

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