



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 consistently exhibited negative PSFs under low light, and EM species tended to show more 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 generally more 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.

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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 (biotic mechanisms), nutrient availability, or allelopathic compounds (abiotic mechanisms)—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 be 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. Field

studies of sapling survival similarly show that AM-associated species are more negatively affected by conspecific neighbors than EM species, consistent with these contrasting microbial defenses (Brown et al. 2020). 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; Xi et al. 2025), 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. 2023; 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. Parallel evidence from conspecific density-dependence studies further indicates that shading amplifies negative interactions between seedlings and nearby adults, underscoring light as a central regulator of seedling–soil–neighbor dynamics (Kobe and Vriesendorp 2011). 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, shade 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 due to enhanced soil moisture (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). Because EM fungi are more host-specific (Smith and Read 2008) and structurally protective (Laliberté et al. 2015), EM seedlings are expected to gain greater benefit from conspecific soils under high light, when carbon investment supports these specialized mutualisms. 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 the majority of published PSF studies—typically ~70–95% depending on the inclusion criteria (Beals et al. 2020; Crawford et al. 2019; Forero et al. 2019; Jiang et al. 2024) have been performed in greenhouse environments. 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, because long-term PSF studies remain rare—especially for tree species—the strong negative PSFs most commonly detected in short-term experiments may not persist over longer time scales (Kardol et al. 2013). In addition, 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, and seedlings experienced natural light variation in the field and controlled light treatments in the greenhouse. We hypothesized that PSFs reflect mycorrhizal matching between seedlings and adults and are modulated by environmental context.

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; whereas EM seedlings (+PSF) show the opposite trend (Bennett et al. 2017; Kadowaki et al. 2018).

Table 1 Selected species information

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

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

2. *Light availability mediates PSFs.* AM seedlings experience stronger -PSFs under low light as carbon limitation reduces mycorrhizal colonization and increases pathogen pressure (Ibáñez and McCarthy-Neumann, 2016; Konvalinková and Jansa 2016; Liu and He 2019). In contrast, EM seedlings experience stronger +PSFs under high light, when greater carbon availability promotes ectomycorrhizal colonization, nutrient uptake and host-specific benefits in conspecific soils (Koorem et al. 2017; Laliberté et al. 2015; Xi et al. 2023).
3. *Soil microbes in conspecific soil mediate PSF directionality.* The net effect of soil microbes in conspecific soils produces negative feedbacks on AM species and positive feedbacks on EM species, reflecting differences in pathogen accumulation versus mutualist recruitment (Chen et al. 2019; Eagar et al. 2022).
4. *Environmental context modulates PSF strength and direction.* Because environmental variability influences microbial activity and plant resource allocation, we expect PSFs to differ between greenhouse and field settings, with stronger or more consistent feedbacks under controlled greenhouse conditions and weaker or more variable feedbacks in the field where abiotic and biotic interactions are more complex (Forero et al., Heinze et al. 2016; Gundale and Kardol 2021).

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). These AM and EM species span both early- and late-successional roles at this site and do not segregate cleanly by seral stage, co-occurring across generalized and mesophytic upland hardwood communities and representing a broad range of ecological strategies. *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.

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 $\geq$ 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 $\times$ 46 cm depth) were extracted using a mechanized soil corer (Giddings Machine Co., Windsor, CO, USA).

The soils used in both experiments are classified as Nester Loam (fine-loamy, mixed, active, mesic Typic Hapludalf; MacDonald et al. 1971), a moderately well-drained Alfisol developed from glacial till and common to mixed hardwood forests of central Michigan (USDA-NRCS 2023a,b). Typical surface horizon properties for Nester Loam include a pH of approximately 5.5–6.2, organic carbon content of 1.5–2.5%, and 30–40% sand, 40–50% silt, and 10–20% clay (USDA-NRCS.). To provide a quantitative index of nutrient availability, ion-exchange probes (Plant Root Simulator®; Western Ag Innovations, Saskatoon, Canada) were deployed in soils beneath adult trees that were used for soil collection and in a subset of seedling pots for the field experiment (methodology can be found in File S1). Mean nutrient supply rates ($\mu\text{g } 10 \text{ cm}^{-2} \text{ burial length}^{-1}$) are reported in Wood et al. (2023a).

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, 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 (except for NO_3^- , S^{2+} , and Zn^{2+} , which were slightly higher in pots; Supplementary Tables S1–S2; 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 ($\sim 2\%$, $\sim 15\%$, and $\sim 30\%$ 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 205 A 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 $\times$ soil source $\times$ 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 70°C to constant mass, and whole plant biomass (mg) was weighed (Supplementary Table S3).

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 $\times$ 6.6 m) spanning a light gradient from 0.032 to 0.161 Indirect Site Factor (ISF). To establish this gradient, trees were selectively felled before plot construction to create canopy openings representing low, medium, and high light. Vegetation and litter were cleared immediately before planting, and hemispherical photographs taken during the first growing season verified ISF values with HemiView software (Delta-T Devices, Ltd., Burwell, England). Although this produced a clear gradient, maximum field light ($\sim 16\%$ full sun) was lower than in the greenhouse ($\sim 30\%$) due to canopy constraints. ISF 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 $\times$ soil $\times$ plot combination). Seedlings grew for two full seasons (~ 68 weeks), after which surviving individuals were harvested, dried at 70°C 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 non-parametric 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 $\sim 2\%$ full sun and high light to $\sim 30\%$ 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 ($\pm 95\%$ 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 ($\sim 2\%$ full sun) and field (~ 3 – 7.5% full sun) were matched directly, whereas the greenhouse medium light treatment ($\sim 15\%$ 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 ($\pm 95\%$ credible intervals) in the

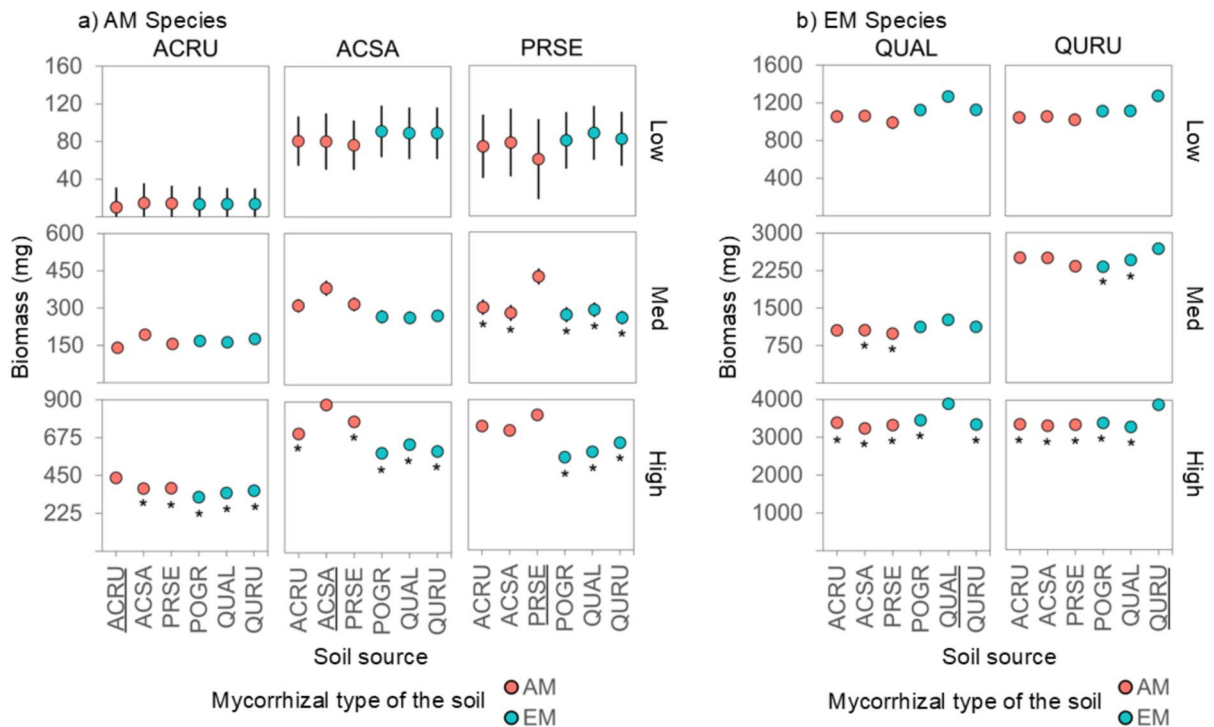


Fig. 1 Seedling biomass (mg $\pm$ standard error) for **a)** arbuscular mycorrhizal (AM) associated species and **b)** ectomycorrhizal (EM) associated species in the *greenhouse experiment* across different soil sources (denoted along the x-axes) and under low (top rows), medium (middle rows), and high (bottom rows) light levels. Error bars represent $\pm$ SE; in some cases

the variance is very low, resulting in error bars that fall within the symbol width (see Table S4 for full statistics). 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

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 (Fig. 1; Supplementary Tables S4 & 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 (Fig. 1a). At high light, *Acer rubrum* and *Acer saccharum* had 14–26% and 11–33% higher biomass, respectively, in conspecific versus heterospecific soils—the only light level where soil-source differences were significant for these species. *Prunus serotina* had 21–31% more biomass in

conspecific than EM heterospecific soils at high light, and 29–39% more biomass than in all heterospecific soils at medium light. No AM species showed significant soil source effects at low light.

Among EM species in the greenhouse experiment, biomass differences were largest at high light, with *Quercus alba* and *Q. rubra* having 11–17% and 13–15% greater biomass, respectively, in conspecific compared to all heterospecific soils (Fig. 1b). At medium light, *Q. alba* had 11% more biomass in conspecific soil than in two AM heterospecific soils, while *Q. rubra* had 13–14% more biomass in conspecific soil than in the two EM heterospecific soils. No EM species showed significant biomass differences across soil sources under low 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 S6). *Q. rubra* had higher biomass in live than sterile conspecific

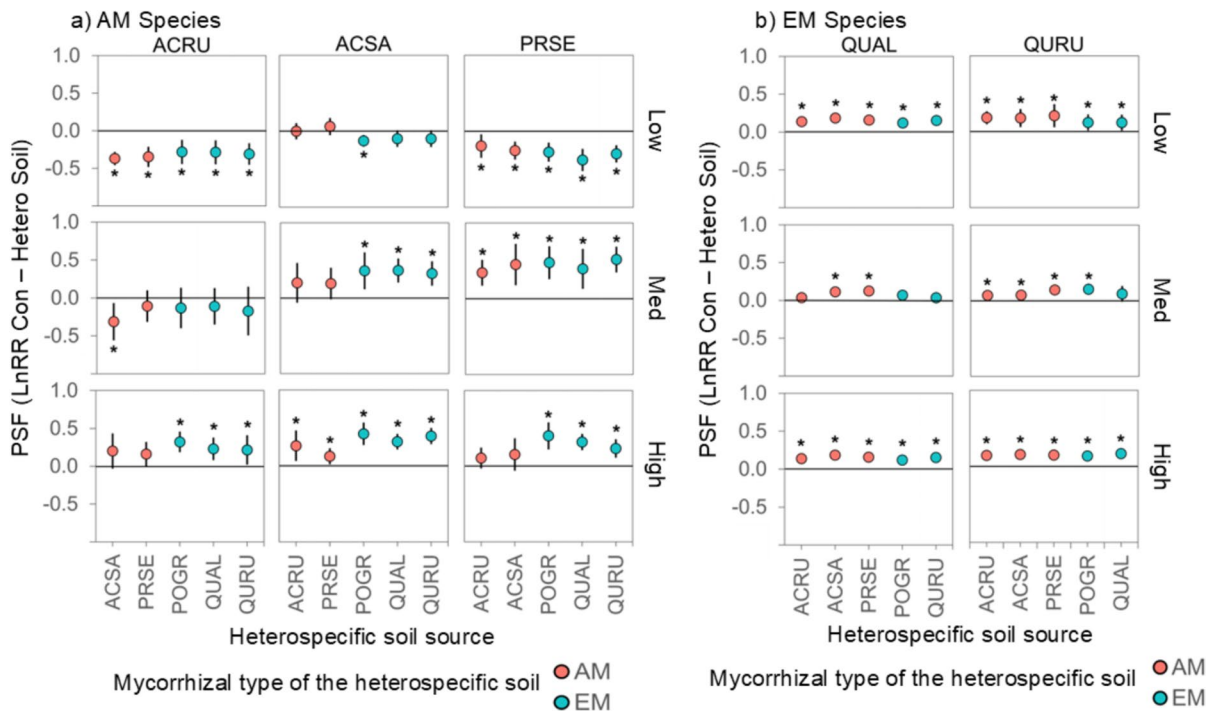


Fig. 2 Plant–soil feedbacks (PSFs) calculated as the natural log response ratio ($\ln\text{RR} \pm \text{confidence interval}$) of seedling biomass in conspecific versus heterospecific soils for **a**) arbuscular mycorrhizal (AM) associated species and **b**) ectomycorrhizal (EM) associated species in 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. Error bars represent $\pm 95\%$ CI; in some cases the

variance is very low, resulting in error bars that fall within the symbol width (see Table S4 for full statistics). 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

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.

Consistent with H1, AM tree species in the greenhouse experiment exhibited -PSFs and EM species exhibited +PSFs (Fig. 2; Table S5). However, this pattern was observed for AM species only under low light, which is consistent with stronger -PSF impacts expected in low light under H2 (Fig. 2a). EM species displayed PSFs consistent with expectations across all light levels, with seedlings generally performing better in conspecific than heterospecific soils (Fig. 2b). 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 comparison with a conmycorrhizal soil.

In the field experiment, the two EM species showed opposing biomass and PSF patterns (Fig. 3a; Table S6 & S7). *Q. alba* had 22–30% lower biomass in conspecific than heterospecific soils under low light, 74–77% less in medium light, and 20–25% less in high light. 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. These biomass patterns were reflected in species' PSF responses: *Q. rubra* experienced +PSF as expected, whereas *Q. alba* experienced -PSFs, contrary to predictions (Fig. 3b; Table S7). All PSFs occurred regardless

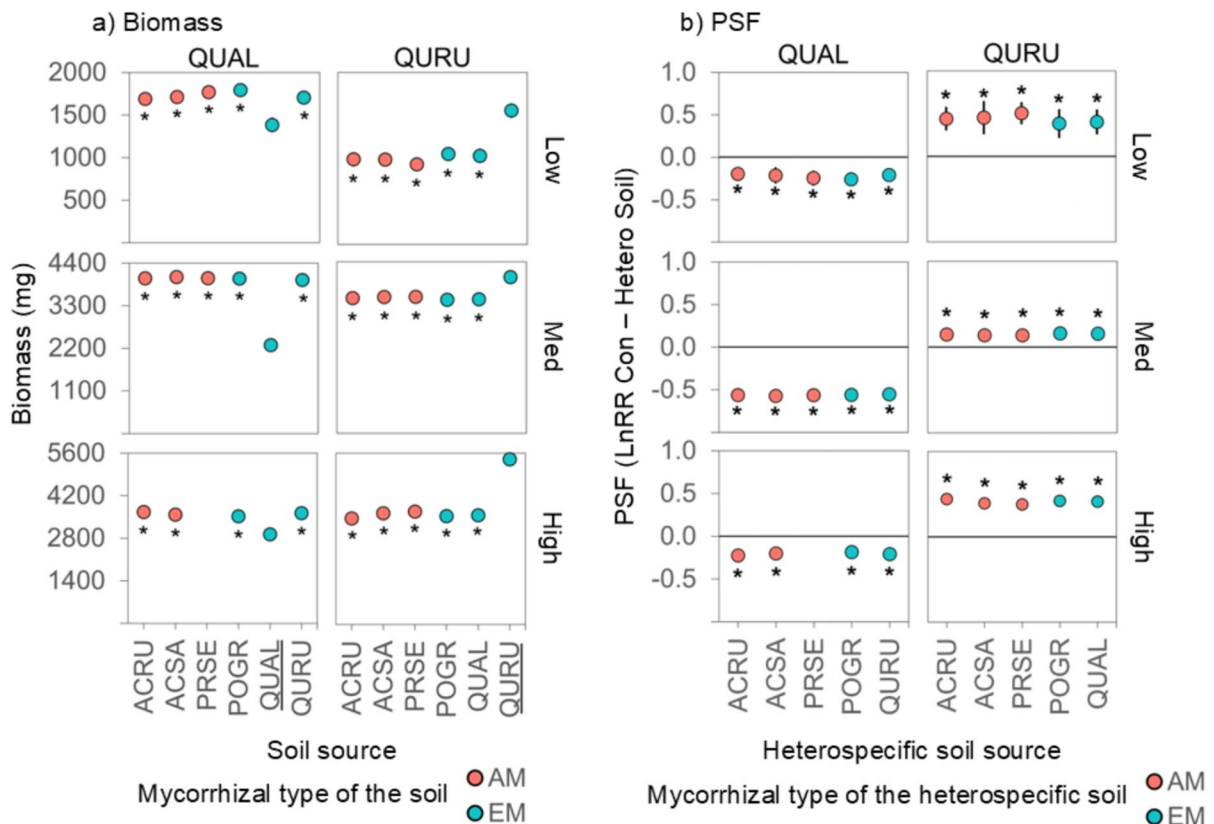


Fig. 3 a) Seedling biomass (mg $\pm$ standard error) and b) plant-soil feedbacks (PSFs; natural log response ratio, $\lnRR \pm 95\%$ confidence interval) for ectomycorrhizal (EM)-associated species in the *field experiment* across different soil sources (denoted along the x-axes) and under low (top rows), medium (middle rows), and high (bottom rows) light levels. Error bars represent $\pm$ SE (Biomass) and $\pm 95\%$ CI (PSF); in some cases the variance is very low, resulting in error bars that fall within the symbol width (see Table S5 for full statistics). 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

of the mycorrhizal identity of the heterospecific soil source.

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). This pattern highlights stronger light sensitivity of AM seedlings, which shifted from negative to neutral PSFs with increasing light, while EM species remained stable.

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

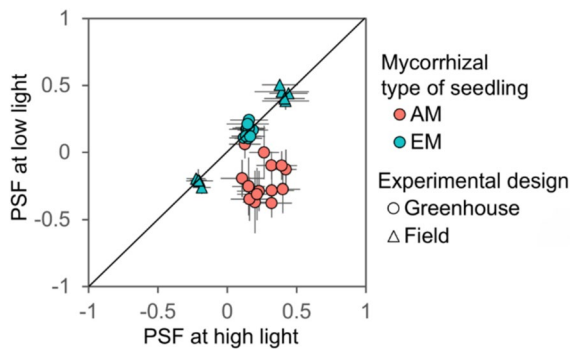


Fig. 4 Plant–soil feedbacks (PSFs) at high versus low light in greenhouse (2% vs. 30% full sun) and field experiments (3–7.5% vs. 11.8–16.1%) are presented, showing means for each species $\times$ soil combination (means $\pm$ 95% credible intervals). Sterilized conspecific soils are excluded. The solid line represents a 1:1 relationship between PSFs at high and low light. A key takeaway is that AM seedlings exhibit more negative PSFs in low light but shift toward neutral or positive PSFs under higher light, whereas EM species show consistent PSFs across light levels—indicating greater light sensitivity of AM-mediated feedbacks

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.

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.

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

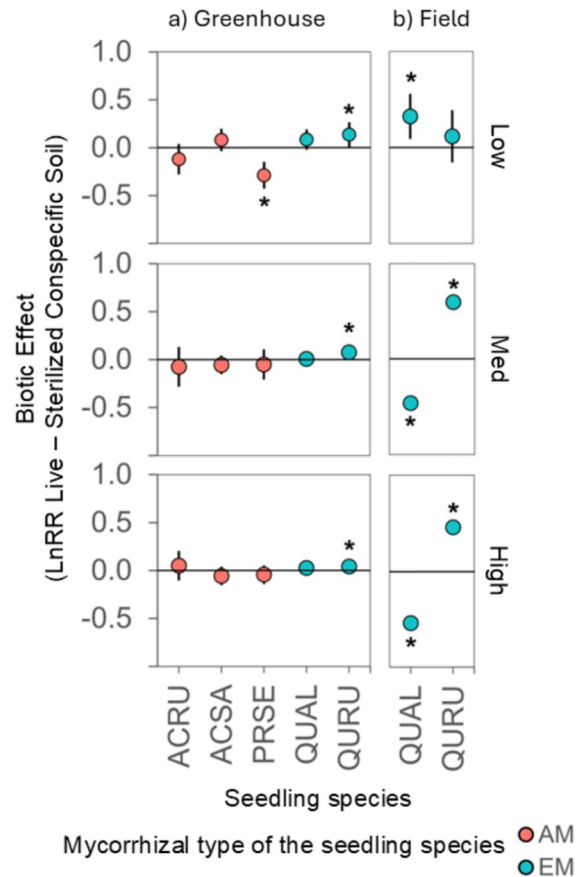


Fig. 5 Biotic effect of conspecific soil, calculated as the natural log response ratio ($\ln\text{RR} \pm$ confidence interval) of seedling biomass in live versus sterilized conspecific soil for a) greenhouse and b) field experiments across light levels for each seedling species. Error bars represent $\pm$ 95% CI; in some cases the variance is very low, resulting in error bars that fall within the symbol width (see Table S4 & S6 for full statistics). 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

(greenhouse vs. field). While AM species generally exhibited more -PSFs and EM species more +PSFs, as predicted (H1), these guild-level patterns masked strong species-and context-dependence. In particular,—PSFs for AM species only occurred under low light, highlighting the role of light in modulating PSFs (H2). In addition, *Q. alba* shifted from +PSFs in the greenhouse to strongly -PSFs in the field, demonstrating that environmental context can override

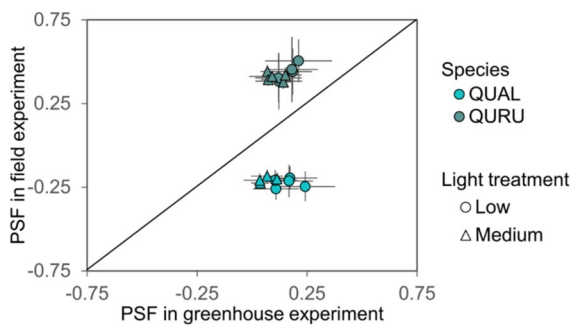


Fig. 6 Plant–soil feedbacks (PSFs) in greenhouse versus field experiments across light treatments, showing means for each EM species $\times$ soil combination (means $\pm$ 95% credible intervals). Treatments were matched as follows: greenhouse low (2%) vs. field low (3–7.5% full sun); greenhouse medium (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

broad mycorrhizal expectations (H4). 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 from organic sources and reducing pathogen pressure through improved defense and tolerance (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. Thus, our results do not support a universal positive PSF for EM species; instead, EM responses range from strongly positive (*Q. rubra*) to negative (*Q. alba* in the field) depending on environment. Taken together, these patterns suggest that conspecific soils tend to be more detrimental for AM species and more beneficial for EM species (Bennett et al. 2017; Eagar et al. 2024; Kadowaki et al. 2018), while still allowing for substantial species- and context-specific variation. This pattern mirrors Brown et al. (2020), who found that AM species were more susceptible to density-dependent mortality than EM species, consistent with stronger negative PSFs among AM seedlings under low light.

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., unpublished data), 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. More broadly, several studies have reported phylogenetic signals in PSFs (Crawford et al. 2019; Wandrag et al. 2020), whereas others have found weak or inconsistent relationships (Mehrabi and Tuck 2015; Sweeney et al. 2025).

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 (Augsburger 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; Wood et al. 2023b). In addition, AM seedlings commonly experience a transient growth depression under low light because carbon supply is insufficient to support both host growth and fungal partners; this constraint typically weakens as plants mature and carbon availability increases (Konvalinková and Jansa 2016). As light increases, pathogen pressure likely declines and seedling traits for recovery and defense become more effective (McCarthy-Neumann et al., unpublished data; Wood et al. 2023a,b), shifting AMF symbioses from parasitism to mutualism and resulting in +PSFs under high light (Ibáñez and McCarthy-Neumann, 2016; Konvalinková and Jansa 2016; Wood et al. 2023b).

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 highlight the mechanisms through which light regulates seedling–soil interactions. Under shaded conditions, limited photosynthetic carbon restricts root exudation and mycorrhizal colonization, reducing the availability of carbon for mutualists and thereby weakening symbiotic benefits while allowing pathogens to dominate the rhizosphere (Ibáñez and McCarthy-Neumann 2016; Konvalinková and Jansa 2016; Liu and He 2019). This carbon limitation likely underlies the stronger -PSFs expressed by AM seedlings in low light, as reduced defense and higher pathogen pressure amplify conspecific inhibition. Higher moisture levels in shaded environments may intensify pathogen pressure and interact with light to shape PSF outcomes (Liu and He 2019). Patterns from field studies also show that seedling mortality increases with both shading and conspecific density (Kobe and Vriesendorp 2011), supporting the view that light limitation intensifies biotic stress through density-dependent pathogen accumulation. In contrast, increased

irradiance enhances carbon supply to roots, promoting mycorrhizal colonization, nutrient uptake, and pathogen defense (Bereau et al. 2000; Shi et al. 2014; Koorem et al. 2017), which can shift toward more positive or neutral outcomes over time as mutualist benefits outweigh pathogen costs (Xi et al. 2023). Importantly, study duration and performance metric influence the observed direction of PSFs: short-term survival-based studies tend to detect stronger -PSFs under shade when seedlings are most vulnerable to pathogens (McCarthy-Neumann and Kobe 2010a, b; McCarthy-Neumann and Ibáñez 2013; McCarthy-Neumann et al., unpublished data), whereas longer-term, biomass-based studies often report -PSFs under high light that weaken or become neutral as light availability decreases (Smith and Reynolds 2015; Xi et al. 2020). Together, these findings support a carbon-allocation framework in which light governs the balance between antagonistic and mutualistic soil biota, thereby determining the direction and magnitude of PSFs—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. Abiotic changes such as localized nutrient depletion, altered soil chemistry, or shifts in resource stoichiometry may therefore also contribute to PSF outcomes, particularly when microbial effects are weak or context dependent (Bennett and Klironomos 2019; Png et al. 2018).

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. For both AM and EM species, discrepancies between PSFs based on contrasts with heterospecific soils and biotic effects from sterilization underscore that our PSF metric integrates both biotic and abiotic differences among soil sources, whereas the sterilization treatment isolates only the net microbial effect of conspecific soils.

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* using soils collected from the same adult trees, allowing a rare test of environmental context on PSF outcomes. *Q. rubra* exhibited stronger +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 appeared most pronounced.

This divergence highlights the need to evaluate PSFs across environmental contexts rather than rely solely on controlled conditions. Greenhouse studies can overestimate PSF strength due to reduced variability and disruption of belowground interactions (Forero et al. 2019), whereas field experiments capture natural heterogeneity in competition, herbivory, and resource availability, providing a more realistic

measure of biotic and abiotic interactions (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, we found that PSF direction and strength shifted with light and soil source. In our experiment, 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. 2020), 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 benefitted 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., unpublished data) 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 importance of integrating survival and growth to fully understand how PSFs influence forest structure, diversity, and resilience.

Caveats and future directions

We were unable to compare all species across greenhouse and field settings due to high mortality of AM seedlings in the field after the first growing season (Wood et al. 2023a). Thus, our direct comparisons are limited to *Q. rubra* and *Q. alba* after two years of field growth. While the *Q. rubra* results were consistent across settings, the contrasting responses of *Q. alba* point to context dependency that warrants further investigation.

Our greenhouse experiment lasted 12 weeks and captured only the earliest seedling stage. Because PSFs often weaken or shift direction over time—and long-term studies remain rare for trees—short-term experiments may overrepresent negative feedbacks (Kardol et al. 2013). Longer-duration studies are therefore necessary to determine whether early PSFs persist, weaken, or reverse through later life stages. Although we found no evidence that nutrient availability mediated PSFs (based on root simulator probe data and lack of differences between sterilized and unsterilized soil; Wood et al. 2023a), nutrient × microbial interactions may still play subtle roles that warrant exploration. More broadly, PSFs can emerge through both biotic and abiotic pathways, and our design did not allow us to isolate the relative contributions of these mechanisms. Pairing nutrient addition with microbial manipulations could help disentangle these effects.

Finally, because our sterilization treatment removed both pathogenic and mutualistic organisms, we could not disentangle their individual contributions to PSF directionality or assess microbial effects in heterospecific soils. Future experiments incorporating selective inoculation or microbial community sequencing would help separate pathogen-driven versus mutualist-driven components of biotic PSFs.

Conclusions

This study demonstrates that PSFs are not intrinsic species traits, but rather dynamic outcomes shaped by mycorrhizal type, environmental context, and species-specific interactions. Crucially, PSFs were driven primarily by conspecific soil conditioning, with limited influence from the mycorrhizal type of heterospecific neighbors. While general patterns, such as more -PSFs for AM species in low light and more +PSFs for EM species across light levels, held broadly, notable exceptions (especially the context-dependent responses of *Q. alba*) highlight the complexity of plant–soil–environment relationships. These findings underscore the importance of context-aware PSF research that incorporates light availability, microbial mediation, and differences between greenhouse and field conditions to improve predictions of forest composition and diversity.

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Data availability All data associated with this study have been deposited in Dryad and are publicly available at DOI:<https://doi.org/10.5061/dryad.rfj6q57qj>

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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References

- Allison SD, Lu Y, Weihe C, Goulden ML, Martiny AC, Treseder KK, Martiny JBH (2013) Microbial abundance and composition influence litter decomposition response to environmental change. *Ecol* 94:714–725. <https://doi.org/10.1890/12-1243.1>
- Augsburger CK, Kelly CK (1984) Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia* 61:211–217. <https://doi.org/10.1007/BF00396763>
- Averill C, Fortunel C, Maynard DS, van den Hoogen J, Dietze MC, Bhatnagar JM, Crowther TW (2022) Alternative stable states of the forest mycobiome are maintained through positive feedbacks. *Nat Ecol Evol* 6:375–382. <https://doi.org/10.1038/s41559-022-01663-9>
- Bates D, Machler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48
- Bates SE, Wandrag EM, Duncan RP (2020) Calculating the uncertainty associated with log response ratios in plant-soil feedback studies. *Plant Ecol* 221:829–836. <https://doi.org/10.1007/s11258-019-00981-6>
- Beals KK, Moore JAM, Kivlin SN, Bayliss SLJ, Lumibao CY, Moorhead LC, Patel M, Summers JL, Ware IM, Bailey JK et al (2020) Predicting plant-soil feedback in the field: meta-analysis reveals that competition and environmental stress differentially influence PSF. *Front Ecol Evol*. <https://doi.org/10.3389/fevo.2020.00191>
- Bennett JA, Klironomos J (2019) Mechanisms of plant-soil feedback: interactions among biotic and abiotic drivers. *New Phytol* 222:91–96. <https://doi.org/10.1111/nph.15603>
- Bennett JA, Maherali H, Reinhart KO, Lekberg Y, Hart MM, Klironomos J (2017) Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science* 355:181–184. <https://doi.org/10.1126/science.aai8212>
- Bureau M, Barigah TS, Louisanna E, Garbaye J (2000) Effects of endomycorrhizal development and light regimes on the growth of *Dicorynia guianensis* Amshoff seedlings. *Ann For Sci* 57:725–733. <https://doi.org/10.1051/forest:2000153>
- Bever JD (2002) Negative feedback within a mutualism: host-specific growth of mycorrhizal fungi reduces plant benefit. *Proc Biol Sci* 269:2595–2601. <https://doi.org/10.1098/rspb.2002.2162>
- Bever JD, Westover KM, Antonovics J (1997) Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *J Ecol* 85:561. <https://doi.org/10.2307/2960528>
- Borowicz VA (2001) Do arbuscular mycorrhizal fungi alter plant-pathogen relations? *Ecology* 82:3057–3068. <https://doi.org/10.2307/2679834>
- Brown AJ, Payne CJ, White PS, Peet RK (2020) Shade tolerance and mycorrhizal type may influence sapling susceptibility to conspecific negative density dependence. *J Ecol* 108:325–336. <https://doi.org/10.1111/1365-2745.13237>
- Chen L, Swenson NG, Ji N, Mi X, Ren H, Guo L, Ma K (2019) Differential soil fungus accumulation and density dependence of trees in a subtropical forest. *Science* 366:124–128. <https://doi.org/10.1126/science.aau1361>
- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Evol Syst* 31:343–366. <https://doi.org/10.1146/annurev.ecolsys.31.1.343>
- Crawford KM, Bauer JT, Comita LS, Eppinga MB, Johnson DJ, Mangan SA, Queenborough SA, Strand AE, Suding KN et al (2019) When and where plant-soil feedback may promote plant coexistence: a meta-analysis. *Ecol Lett* 22:1274–1284. <https://doi.org/10.1111/ele.13278>
- Delavaux CS, LaManna JA, Myers JA, Phillips RP, Aguilar S, Allen D, Alonso A, Anderson-Teixeira KJ, Baker ME, Baltzer JL et al (2023) Mycorrhizal feedbacks influence global forest structure and diversity. *Commun Biol* 6:1066. <https://doi.org/10.1038/s42003-023-05410-z>
- Eagar AC, Mushinski RM, Horning AL, Smemo KA, Phillips RP, Blackwood CB (2022) Arbuscular mycorrhizal tree communities have greater soil fungal diversity and relative abundances of saprotrophs and pathogens than ectomycorrhizal tree communities. *Appl Environ Microbiol* 88:e01782-21. <https://doi.org/10.1128/AEM.01782-21>
- Eagar AC, Smemo KA, Phillips RP, Blackwood CB (2023) Context-dependence of fungal community responses to dominant tree mycorrhizal types in Northern hardwood forests. *Soil Biol Biochem* 178:108971. <https://doi.org/10.1016/j.soilbio.2023.108971>
- Eagar AC, Abu PH, Brown MA, Moledor SM, Smemo KA, Phillips RP, Case AL, Blackwood CB (2024) Setting the stage for plant-soil feedback: mycorrhizal influences over conspecific recruitment, plant and fungal communities, and coevolution. *J Ecol* 112:1–18. <https://doi.org/10.1111/1365-2745.14393>
- Forero LE, Grenzer J, Heinze J, Schittko C, Kulmatiski A (2019) Greenhouse- and field-measured plant-soil feedbacks are not correlated. *Front Environ Sci* 7:184. <https://doi.org/10.3389/fevns.2019.00184>
- Fox J, Weisberg S (2019) An R companion to applied regression. SAGE, Thousand Oaks, CA
- Gundale MJ, Kardol P (2021) Multi-dimensionality as a path forward in plant-soil feedback research. *J Ecol* 109:3446–3465. <https://doi.org/10.1111/1365-2745.13679>
- Heinze J, Sitte M, Schindhelm A, Wright J, Joshi J (2016) Plant-soil feedbacks: a comparative study on the relative importance of soil feedbacks in the greenhouse versus the field. *Oecologia* 181:559–569. <https://doi.org/10.1007/s00442-016-3591-8>
- Hersh MH, Vilgalys R, Clark JS (2012) Evaluating the impacts of multiple generalist fungal pathogens on temperate tree seedling survival. *Ecology* 93(3):511–520. <https://doi.org/10.1890/11-0598.1>
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biom J* 50:346–363. <https://doi.org/10.1002/bimj.200810425>

- Ibáñez I, McCarthy-Neumann S (2016) Effects of mycorrhizal fungi on tree seedling growth: quantifying the parasitism–mutualism transition along a light gradient. *Can J Forest Res* 46:48–57. <https://doi.org/10.1139/cjfr-2015-0327>
- Jia S, Wang X, Yuan Z, Lin F, Ye J, Lin G, Hao Z, Bagchi R (2020) Tree species traits affect which natural enemies drive the Janzen–Connell effect in a temperate forest. *Nat Commun* 11:286. <https://doi.org/10.1038/s41467-019-14140-y>
- Jiang J, Abbott KC, Baudena M, Eppinga MB, Umbanhowar JA, Bever JD (2020) Pathogens and mutualists as joint drivers of host species coexistence and turnover: implications for plant competition and succession. *Am Nat* 195:591–602. <https://doi.org/10.1086/707355>
- Jiang J, Wang Z, Chu C, Kembel SW, He F (2022) Phylogenetic dependence of plant–soil feedback promotes rare species in a subtropical forest. *J Ecol* 110:1237–1246. <https://doi.org/10.1111/1365-2745.13879>
- Jiang J, Bennett JA, Crawford KM, Heinze J, Pu X, Luo A, Wang Z (2024) Global patterns and drivers of plant–soil microbe interactions. *Ecol Lett* 27:e14364. <https://doi.org/10.1111/ele.14364>
- Johnson NC, Graham JH, Smith FA (1997) Functioning of mycorrhizal associations along the mutualism–parasitism continuum. *New Phytol* 135:575–586. <https://doi.org/10.1046/j.1469-8137.1997.00729.x>
- Kadowaki K, Yamamoto S, Sato H, Tanabe AS, Hidaka A, Toju H (2018) Mycorrhizal fungi mediate the direction and strength of plant–soil feedbacks differently between arbuscular mycorrhizal and ectomycorrhizal communities. *Commun Biol* 1:1–11. <https://doi.org/10.1038/s42003-018-0201-99>
- Kardol P, De Deyn GB, Laliberté E, Mariotte P, Hawkes DV (2013) Biotic plant–soil feedbacks across temporal scales. *J Ecol* 101:309–315. <https://doi.org/10.1111/1365-2745.12046>
- Kattge J, Boenisch G, Diaz S et al (2020) TRY plant trait database – enhanced coverage and open access. *Glob Change Biol* 26:119–188. <https://doi.org/10.1111/gcb.14904>
- Klironomos JN (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417:67–70. <https://doi.org/10.1038/417067a>
- Kobe RK, Vriesendorp RK (2011) Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest. *Ecol Lett* 14:503–510. <https://doi.org/10.1111/j.1461-0248.2011.01612.x>
- Konvalinková T, Jansa J (2016) Lights off for arbuscular mycorrhiza: on its symbiotic functioning under light deprivation. *Front Plant Sci*. <https://doi.org/10.3389/fpls.2016.00782>
- Koorem K, Tulva I, Davison J, Jarius T, Õpik M, Vasar M, Zobel M, Moora M (2017) Arbuscular mycorrhizal fungal communities in forest plant roots are simultaneously shaped by host characteristics and canopy-mediated light availability. *Plant Soil* 410:259–271. <https://doi.org/10.1007/s11104-016-3004-0>
- Kulmatiski A, Kardol P (2008) Getting plant–soil feedbacks out of the greenhouse: Experimental and conceptual approaches. In: Lüttge U, Beyschlag W, Murata J (eds) *Prog. Bot.* Springer Berlin Heidelberg, Berlin, Heidelberg, pp 449–472
- Laliberté E, Lambers H, Burgess TI, Wright SJ (2015) Phosphorus limitation, soil-borne pathogens and the coexistence of plant species in hyperdiverse forests and shrublands. *New Phytol* 206:507–521. <https://doi.org/10.1111/nph.13203>
- Lekberg Y, Bever JD, Bunn RA, Callaway RM, Hart MM, Kivlin SN, Klironomos J, Larkin BG, Maron JL, Reinhart KO et al (2018) Relative importance of competition and plant–soil feedback, their synergy, context dependency and implications for coexistence. *Ecol Lett* 21:1268–1281. <https://doi.org/10.1111/ele.13093>
- Lenth R (2020) emmeans: estimated marginal means, aka least-squares means. R Package Version 1(5):1
- Liu Y, He F (2019) Incorporating the disease triangle framework for testing the effect of soil-borne pathogens on tree species diversity. *Funct Ecol* 33:1211–1222. <https://doi.org/10.1111/1365-2435.13345>
- MacDonald RL, Delcourt PA, Kapp RO (1971) Plant communities of the MacCurdy ecological tract, Montcalm County, Michigan. *Mich Acad* 4:17–28
- Mao Z, Wiegand T, Corrales A, Fang S, Hao S, Lin F, Ye J, Yuan Z, Wang X (2024) Mycorrhizal types regulate tree spatial associations in temperate forests: ectomycorrhizal trees might favour species coexistence. *Ecol Lett* 27:e70005
- McCarthy-Neumann S, Ibáñez I (2012) Tree range expansion may be enhanced by escape from negative plant–soil feedbacks. *Ecology* 93:2637–2649. <https://doi.org/10.1890/11-2281.1>
- McCarthy-Neumann S, Ibáñez I (2013) Plant–soil feedback links negative distance dependence and light gradient partitioning during seedling establishment. *Ecology* 94:780–786. <https://doi.org/10.1890/12-1338.1>
- McCarthy-Neumann S, Kobe RK (2010) Conspecific plant–soil feedbacks reduce survivorship and growth of tropical tree seedlings. *J Ecol* 98:396–407. <https://doi.org/10.1111/j.1365-2745.2009.01619.x>
- McCarthy-Neumann S, Kobe RK (2010) Conspecific and heterospecific plant–soil feedbacks influence survivorship and growth of temperate tree seedlings. *J Ecol* 98:408–418. <https://doi.org/10.1111/j.1365-2745.2009.01620.x>
- McCarthy-Neumann S, Wood K.E.A., Ibáñez I, Kobe RK (2026) Mycorrhizal identity of neighboring trees shapes seedling survival and plant–soil feedbacks through trait and light interactions. Unpublished manuscript.
- McGuire KL (2007) Common ectomycorrhizal networks may maintain monodominance in a tropical rain forest. *Ecology* 88:567–574. <https://doi.org/10.1890/05-1173>
- McNamara NP, Black HJJ, Beresford NA, Parekh NR (2003) Effects of acute gamma irradiation on chemical, physical and biological properties of soils. *Appl Soil Ecol* 24:117–132. [https://doi.org/10.1016/S0929-1393\(03\)00073-8](https://doi.org/10.1016/S0929-1393(03)00073-8)
- Mehrabi Z, Tuck SL (2015) Relatedness is a poor predictor of negative plant–soil feedbacks. *New Phytol* 205:1071–1075. <https://doi.org/10.1111/nph.13238>
- Niinemets Ü, Valladares F (2006) Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecol Monogr* 76:521–547. [https://doi.org/10.1890/0012-9615\(2006\)076\[0521:TTSDAW\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2)
- Petermann JS, Fergus AJF, Turnbull LA, Schmid B (2008) Janzen–Connell effects are widespread and strong enough

- to maintain diversity in grasslands. *Ecology* 89:2399–2406. <https://doi.org/10.1890/07-2056.1>
- Png GK, Lambers H, Kardol P, Turner BL, Wardle DA, Laliberté E (2018) Biotic and abiotic plant-soil feedback depends on nitrogen acquisition strategy and shifts during long-term ecosystem development. *J Ecol* 107:142–153. <https://doi.org/10.1111/1365-2745.13048>
- R Core Team (2020) R: A language and environment for statistical computing, version 4.0.2. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Refsland TK, Adams B, Bronson D, Kern CC, Marquardt P, McGraw AM, Royo AA, Miesel JR (2023) Synthesis of plant-soil feedback effects on eastern North American tree species: implications for climate-adaptive forestry. *Front Ecol Evol* 11:1073724. <https://doi.org/10.3389/fevo.2023.1073724>
- Reinhart KO, Rinella MJ (2016) A common soil handling technique can generate incorrect estimates of soil biota effects on plants. *New Phytol* 210:786–789. <https://doi.org/10.1111/nph.13822>
- Reinhart KO, Royo AA, Kageyama SA, Clay K (2010) Canopy gaps decrease microbial densities and disease risk for a shade-intolerant tree species. *Acta Oecol* 36:530–536. <https://doi.org/10.1016/j.actao.2010.07.006>
- Rinella MJ, Reinhart KO (2018) Toward more robust plant-soil feedback research. *Ecology* 99:550–556. <https://doi.org/10.1002/ecy.2146>
- Schittko C, Runge C, Strupp M, Wolff S, Wurst S (2016) No evidence that plant-soil feedback effects of native and invasive plant species under glasshouse conditions are reflected in the field. *J Ecol* 104:1243–1249. <https://doi.org/10.1111/1365-2745.12603>
- Shi G, Liu Y, Johnson NC, Olsson PA, Mao L, Cheng G, Jiang S, An L, Du G, Feng H (2014) Interactive influence of light intensity and soil fertility on root-associated arbuscular mycorrhizal fungi. *Plant Soil* 378:173–188. <https://doi.org/10.1007/s11104-014-2022-z>
- Shinohara N, Kobayashi Y, Nishizawa K, Kadowaki K, Yamawo A (2024) Plant-mycorrhizal associations may explain the latitudinal gradient of plant community assembly. *Oikos* 2024(6):e10367. <https://doi.org/10.1111/oik.10367>
- Smith S, Read D (2008) Mycorrhizal symbiosis. (3rd ed.). Academic Press, London.
- Smith LM, Reynolds HL (2015) Plant-soil feedbacks shift from negative to positive with decreasing light in forest understory species. *Ecology* 96:2523–2532. <https://doi.org/10.1890/14-2150.1>
- Stein C, Mangan SA (2020) Soil biota increase the likelihood for coexistence among competing plant species. *Ecology* 101:e03147. <https://doi.org/10.1002/ecy.3147>
- Sweeney CJ, Semchenko M, de Vries FT, van Dongen BE, Bardgett RD (2025) Plant phylogeny, traits and fungal composition as drivers of plant-soil feedbacks. *J Ecol* 113:608–620. <https://doi.org/10.1111/1365-2745.14481>
- Terborgh J (2012) Enemies maintain hyperdiverse tropical forests. *Am Nat* 179:303–314. <https://doi.org/10.1086/664183>
- Teste FP, Kardol P, Turner BL, Wardle DA, Zemunik G, Renton M, Laliberté E (2017) Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands. *Science* 355:173–176. <https://doi.org/10.1126/science.aai8291>
- USDA–NRCS (2023a) Official Soil Series Description (OSD) for Nester Series. U.S. Department of Agriculture, Natural Resources Conservation Service, National Cooperative Soil Survey. Available at <https://casoilresource.lawr.ucdavis.edu/sde/?series=nester#osd>. Accessed 7 Nov 2025.
- USDA–NRCS (2023b) Soil Data Explorer – Nester Series Laboratory Data. UC Davis Soil Resource Laboratory. Available at <https://casoilresource.lawr.ucdavis.edu/sde/?series=nester#lab-data>
- van der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, Kardol P, Klironomos JN, Kulmatiski A, Schweitzer JA et al (2013) Plant-soil feedbacks: the past, the present and future challenges. *J Ecol* 101:265–276. <https://doi.org/10.1111/1365-2745.12054>
- Wandrag EM, Bates SE, Barrett LG, Catford JA, Thrall PH, van der Putten WH, Duncan RP (2020) Phylogenetic signals and predictability in plant-soil feedbacks. *New Phytol* 228:1440–1449. <https://doi.org/10.1111/nph.16768>
- Wood KEA, Kobe RK, McCarthy-Neumann S, Ibáñez I (2023) Tree seedling functional traits mediate plant-soil feedback survival responses across a gradient of light availability. *PLoS ONE* 18:e0293906. <https://doi.org/10.1371/journal.pone.0293906>
- Wood KEA, Kobe RK, McCarthy-Neumann S (2023) Tree seedling shade tolerance arises from interactions with microbes and is mediated by functional traits. *Front Ecol Evol* 11:1224540. <https://doi.org/10.3389/fevo.2023.1224540>
- Wright JS (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130:1–14. <https://doi.org/10.1007/s004420100809>
- Wurzbarger N, Hendrick RL (2009) Plant litter chemistry and mycorrhizal roots promote a nitrogen feedback in a temperate forest. *J Ecol* 97:528–536. <https://doi.org/10.1111/j.1365-2745.2009.01487.x>
- Xi N, Bloor JMG, Chu C (2020) Soil microbes alter seedling performance and biotic interactions under plant competition and contrasting light conditions. *Ann. Bot.* 126:1089–1098. <https://doi.org/10.1093/aob/mcaa134>
- Xi N, McCarthy-Neumann S, Feng J, Wu H, Wang W, Semchenko M (2023) Light availability and plant shade tolerance modify plant-microbial interactions and feedbacks in subtropical trees. *New Phytol* 238:393–404. <https://doi.org/10.1111/nph.18737>
- Xi N, De Long JR, Davison J, Kardol P, Forero LE, Zobel M, Semchenko M (2025) Plant-soil microbial interactions as modulators of species coexistence and productivity. *Trends Ecol Evol* 40:673–686. <https://doi.org/10.1016/j.tree.2025.04.013>
- Zheng CY, Ji BM, Zhang JL, Zhang FS, Bever JD (2015) Shading decreases plant carbon preferential allocation towards the most beneficial mycorrhizal mutualist. *New Phytol* 205:361–368. <https://doi.org/10.1111/nph.13025>