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RESEARCH ARTICLE

Mycorrhizal nutrient acquisition strategies shape tree competition and coexistence dynamics

Michael E. Van Nuland[1] | Po-Ju Ke[2] | Joe Wan[3] | Kabir G. Peay[1]

[1]Department of Biology, Stanford University, Stanford, California, USA

[2]Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, Taiwan

[3]Department of Environmental Systems Science, ETH Zürich, Institute of Integrative Biology, Zürich, Switzerland

Correspondence
Michael E. Van Nuland
Email: vannuland.mike@gmail.com

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Abstract

1. Mycorrhizal fungi with different nutrient acquisition strategies influence plant species performance and physiology, thereby defining their trophic niche. This might drive resource competition dynamics that cumulatively impact tree species coexistence, but few manipulative experiments have directly tested this.
2. Combining surveys and experiments in a modern coexistence theory framework, we tested how variation in mycorrhizal strategies and nutrient conditions affects plant competitive outcomes. We focused on two genera of co-occurring tree species with different mycorrhizal states: *Acer* (arbuscular mycorrhizal, AM) and *Populus* (dual mycorrhizal, but often considered predominantly ectomycorrhizal, EM).
3. The EM and AM fungal responsiveness in *Populus* species varied with latitude and nitrogen (N) limitation. Host-specific soil microbiome conditioning and inorganic N fertilization combined to qualitatively affect coexistence outcomes. Lower N conditions favoured *Populus* over *Acer* trees, and N fertilization reversed this outcome for southern species, aligning with regional-scale forest mycorrhizal transitions.
4. Results from the coexistence experiment also predict competitive exclusion between the tree species pairs, which could arise, in part, from their mycorrhizal differences and is consistent with alternative stable states in dominant forest mycorrhizal strategies. Such bistability appears in natural systems as a bimodal distribution of *Populus* vs. *Acer* tree species dominance using long-term forest inventory data.
5. *Synthesis*: The magnitude and outcome of microbially mediated competition between *Populus* and *Acer* depends on soil nutrient availability, which likely relates to their mycorrhizal differentiation. These findings support the importance of mycorrhizal symbioses for contributing to large-scale biogeographical patterns of tree species trophic niche separation across soil resource gradients and bistability in forest mycorrhizal structure.

KEYWORDS
arbuscular mycorrhizal fungi, coexistence, competition, ectomycorrhizal fungi, nitrogen, plant–soil feedback, soil nutrients

1 | INTRODUCTION

The soil microbiome plays an important role in shaping plant species coexistence and community diversity as plants build relationships with microbes that influence host plant performance, competitive ability and functional separation among co-occurring species (Kandlikar et al., 2019; Ke & Wan, 2020; Peay, 2016; Silvertown, 2004). Mycorrhizal fungi are of particular importance as these root-associated microbial symbionts influence ecosystem dynamics affecting nutrient availability and plant productivity (van der Heijden et al., 2015). It is expected that nearly all tree species on Earth form symbioses with one of two main mycorrhizal types (Brundrett, 2009; Steidinger et al., 2019; but see Teste et al., 2020) that generally appear to have different nutrient acquisition capabilities: arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi. Although nutrient uptake strategies can vary within these diverse assemblages (Lilleskov et al., 2002; Maherali & Klironomos, 2007), AM fungi are generally known to scavenge soil phosphorus (P) and inorganic nutrients, while EM fungi use specialized extracellular enzymes for acquiring nutrients—especially nitrogen (N)—from complex organic sources (Bodeker et al., 2009; Kohler et al., 2015; Lindahl & Tunlid, 2015; Tisserant et al., 2013; van der Heijden et al., 2015). These mycorrhizal-mediated nutrient uptake patterns might influence the competitive balance between plant species with different mycorrhizal types and trophic niches (Aerts, 2003; Peay, 2016; Silvertown, 2004), but there has been little experimental confirmation of such potentially widespread ecological processes affecting species coexistence.

Plant communities with competing species are stabilized when within-species competition is stronger than among-species competition (Adler et al., 2018). Competitive outcomes are determined by the amount of niche differences between competitors (e.g. the differences in species' requirements and use of limiting resources) as well as underlying fitness differences (e.g. competitive hierarchies arising from differences in reproductive rates and sensitivity to competition). Modern coexistence theory describes how coexistence can be achieved based on stabilizing and equalizing mechanisms (Chesson, 2000). Specifically, conditions favouring species coexistence occur when stabilizing mechanisms increase species niche differences (or reduce niche overlap), or when equalizing mechanisms act to reduce fitness differences between competitors. Recent studies have also shown how the framework can be used to predict priority effects, a phenomenon where species arrival order determines the winner of competition, as the balance between destabilization and fitness differences (Ke & Letten, 2018). Modern coexistence theory is a promising framework because it provides a way to quantitatively link different facets of plant ecology with their ultimate goal of understanding how and why plant species coexist (Adler et al., 2006; Grainger et al., 2019; Johnson, 2021).

While modern coexistence theory continues to develop, its applications to plant ecology have been largely isolated from ecological interactions with soil microbes. By contrast, the reciprocal interactions between plants and soil microbes, and their role in biodiversity maintenance, have been more extensively studied under the framework of plant–soil feedback (van der Putten et al., 2013). Plant–soil feedbacks arise when plants experience net costs or benefits from interacting with their host-specific soil biota compared to a competitor's soil community (Bever, 2003). Negative feedbacks stabilize community diversity and promote species coexistence through negative frequency-dependent plant population dynamics (favouring species when rare), while positive feedbacks destabilize community dynamics and can lead to monodominance via priority effects (Bever et al., 1997; Eppinga et al., 2018). Plant responsiveness to various soil microbial groups (e.g. pathogens and mutualists) can drive feedbacks in different directions, and a recent study of North American trees found that negative and positive feedbacks are associated with trees that form AM vs. EM fungal symbioses, respectively (Bennett et al., 2017). However, plant–soil feedback experiments rarely account for plant–plant competition directly which makes it difficult to predict the long-term competitive outcomes from specific coexistence mechanisms (Ke & Wan, 2020; Lekberg et al., 2018). Recent theoretical studies have proposed experimental designs that combine elements from both modern coexistence theory and plant–soil feedback studies, making it possible to address this knowledge gap by incorporating soil microbial effects and plant–plant competition into the calculations of niche and fitness differences (Kandlikar et al., 2019; Ke & Wan, 2020). This opens the door to resolve long-standing hypotheses about how host-specific differences in mycorrhizal associations and soil microbiome conditioning modify plant–plant interactions and species distribution patterns.

One long-standing hypothesis is that competitive outcomes between AM and EM tree species are determined by the identity and form of major limiting nutrients (Aerts, 2003; Peay, 2016). At the global scale, AM tree species are more prevalent near the equator while EM tree species become progressively more dominant at higher latitudes, a transition which corresponds with a climatically driven shift from fast cycling, N-rich soils at low latitudes to slow cycling, N-limited soils at high latitudes (Du et al., 2020; Read, 1991; Steidinger et al., 2019). While it is generally accepted that regional-scale dominance of specific mycorrhizal symbioses is driven by adaptation to different soil nutrient environments—inorganic N for AM and organic N for EM trees and fungi (Lu & Hedin, 2019)—the assumed competitive mechanisms have not been directly tested. These competitive mechanisms centre on the mycorrhizal-mediated changes in niche and fitness differences that may drive competitive exclusions depending on whether AM or EM associations are favoured under resource competition. In addition, most studies of mycorrhizal biogeography assume that all trees within an AM or EM functional guild participate equally in their respective fungal symbiosis, even though the degree of mycorrhizal association can vary among and within plant species (Bueno et al., 2021; Gehring et al., 2006; Karst, Franklin, et al., 2021; Soudzilovskaia et al., 2015), as well as through geographical space.

In this study, we use the framework of modern coexistence theory to test how nutrient availability and symbiont responsiveness affects the outcome of competition between trees with different

mycorrhizal strategies. We manipulated competitive environments under different nutrient regimes between two genera—*Acer* (AM) and *Populus* (dual mycorrhizal, but predominately EM; Brundrett & Tedersoo, 2020)—and congeneric species with differing geographical and climatic ranges (*P. tremuloides* and *P. deltoides*). Both genera are often described as having similar habitat characteristics (e.g. moist temperature zones and riparian areas) yet frequently occur as monodominant forest patches (Braatne et al., 1996; Frelich et al., 1993). This means that testing their coexistence mechanisms is relevant for understanding the possibility of biogeochemical priority effects as mycorrhizal differences may drive broader patterns of bistability and alternative stables states in forest ecosystems (Averill et al., 2022; Lu & Hedin, 2019). We hypothesized that:

1. The balance between EM vs. AM symbioses within *Populus* trees changes with latitude and N limitation such that EM root colonization is greater for *Populus* species with more northern geographical distributions and decreases with inorganic N fertilization.
2. The strength and direction of plant–soil feedbacks differ among plant mycorrhizal types, with AM trees creating negative feedbacks and EM trees creating positive feedbacks.
3. The competitive advantages of AM and EM associations depend on soil N availability such that EM tree species gain an advantage under low N (varying with EM responsiveness levels) and inorganic N fertilization tips the competitive balance in favour of AM over EM symbioses.

Overall, we show that mycorrhizal type, responsiveness and nutrient availability interactively affect plant competition and coexistence outcomes that match host species distributions and bimodal transitions in forest mycorrhizal states.

2 | MATERIALS AND METHODS

2.1 | Sample collection and mycorrhizal measurements

In the field survey, we examined mycorrhizal affinity in two widespread *Populus* species (*P. tremuloides* and *P. deltoides*) that have latitudinally divergent species ranges (Figure 1a). Such trees are well-known dual mycorrhizal hosts (Teste et al., 2020; but see Brundrett & Tedersoo, 2020), which means we can measure how EM and AM associations vary while limiting confounding factors of host identity and phylogeny. In Summer 2018, we collected *P. deltoides* roots from 24 sites covering Mississippi to Minnesota, and *P. tremuloides* roots from 13 sites in the Rocky Mountains and upper Midwest. At each site, we collected soil samples (5 cm diameter, 10 cm depth) and ~12 cm long root sections from five separate trees (5–7 samples/tree, pooled at the site level). Soil samples were thoroughly mixed, air-dried, sieved at 2 mm and sent to A&L Western Laboratories, Inc for analysis (soil organic matter [% rating], NH_4, NO_3, P and pH). Root samples were gently washed before measuring percent root length colonized by EM fungi using the gridline intersect method (Giovannetti & Mosse, 1980). A separate portion of each washed root sample was collected and stored in 70% ethanol at 4°C for AM fungal processing. These root samples were placed in tissue cassettes, autoclaved in 10% KOH (45 min cycle) and transferred to fresh 10% KOH overnight. Cassettes were then placed in 2% HCl for 40 min, followed immediately by staining with Trypan Blue dye and stored in DI water at 4°C. AM fungal colonization was measured in the same manner as EM fungi, using any AM structure as a positive count for colonization (sensu Karst, Franklin, et al., 2021). See Supplemental Figure S1 for examples of EM and AM fungal structures.

We extracted mean annual temperature and annual precipitation from GPS coordinates taken at the centre of each site (WorldClim database, 30 arcsec resolution; Fick & Hijmans, 2017) which were used to estimate site-level decomposition coefficients predicted by the Yasso07 model of climate controls on mass-loss rates of different leaf litter nutrient pools (Tuomi et al., 2009). These decomposition constants have been the best predictors of mycorrhizal dominance in tree communities (Steidinger et al., 2019) as they approximate the speed with which nutrients move from organic matter into more easily accessible inorganic forms, and thus whether systems are 'fast' or 'slow' regarding nutrient cycles. Finally, we used long-term forest inventory data to measure the frequency of forest sites dominated by *Populus* vs. *Acer* species based on basal area estimates (rFIA R package; Stanke et al., 2020).

2.2 | Growth room competition experiment

For the growth room experiment, we collected material from the same two *Populus* species and two *Acer* species that form AM symbioses and generally have northern vs. southern distributions: *A. saccharum* and *A. saccharinum* (Figure 1a). In early Fall 2019, we re-collected soils and roots beneath trees from two previously visited sites: one northern site where *P. tremuloides* and *A. saccharum* co-occur (elevation = 370 m; mean temperature = 6.6° C; annual precipitation = 802 mm; soil pH = 6.9, soil organic matter = 4.6% rating), and one southern site where *P. deltoides* and *A. saccharinum* co-occur (elevation = 221 m; mean temperature = 12.9° C; annual precipitation = 956 mm; soil pH = 7.4; soil organic matter = 3.1% rating). Five pairs of *Populus* and *Acer* trees were sampled at each of the sites (10 total trees per site), with each pair serving as an experimental replicate (i.e. samples were not pooled for the inoculum treatments; Reinhart & Rinella, 2016). We collected enough field soil and fine root material to be used for Live and Sterilized inoculum treatments (sterilized by two 45-minute autoclave cycles with a 12-h rest period in between), as well as sterilized background soil that we purposefully enriched with sterilized plant leaf material to create a baseline of enriched soil organic nutrient sources (see Supplemental Information for more details).

To test how plant–soil and plant–plant interactions modify tree species competitive outcomes, we created a manipulative

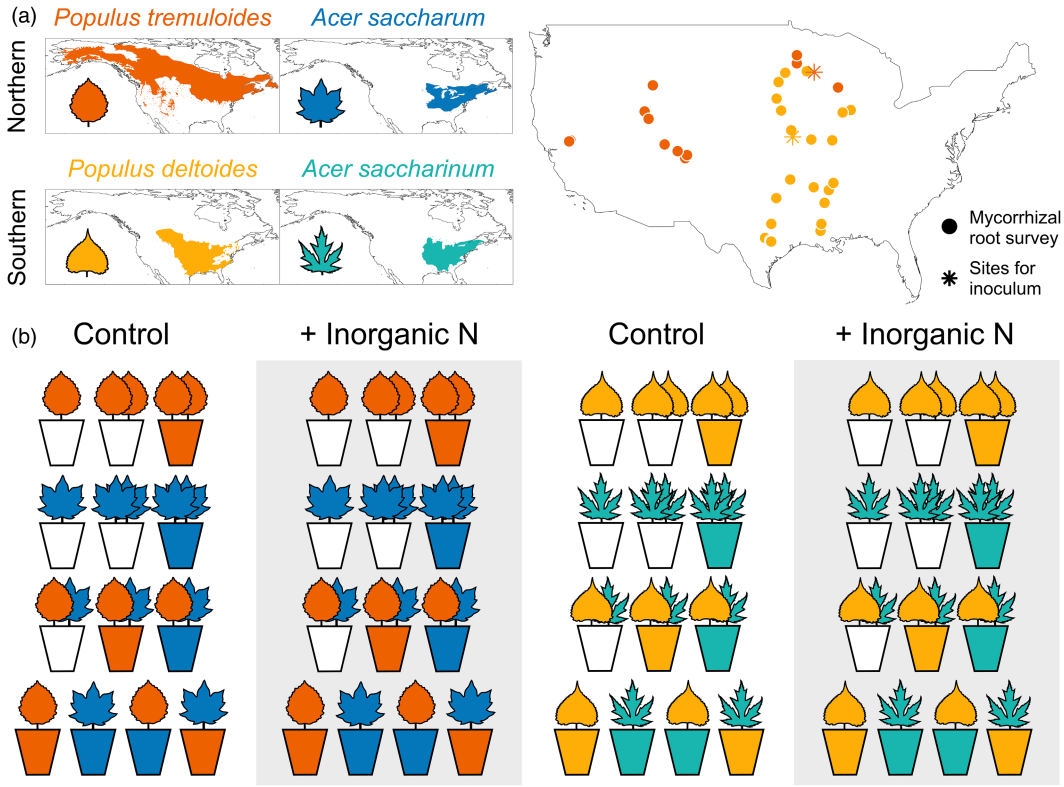

FIGURE 1 Tree species range maps, sampling locations and experimental design. (a) Range maps of the *Populus* (EM) and *acer* (AM) species included in this study, grouped into northern and southern pairs. Locations of sites across the US where *Populus* roots were collected for mycorrhizal measurements (circles) and soil/root samples were collected for experimental inoculum (stars). (b) Outline of the experimental design with soil inoculum, plant competition and nitrogen (N) fertilization treatments applied to the northern and southern tree species pairs. Coloured pots represent live inoculum and empty pots show sterilized inoculum that serve as uncultivated 'reference' soil treatments (this design was replicated without pooling soil inoculum). Plants were grown either alone (single individual), in intraspecific competition (two individuals of the same species), or in interspecific competition (one focal individual plus a competitor belonging to the other species). The first two rows are used to calculate intraspecific effects, the third row is used for interspecific effects and the final row comprises treatments for plant–soil feedback measurements.

experiment based on a design that efficiently measures the impact of soil microbes on plant competition and coexistence (Ke & Wan, 2020). For each geographical pair of *Populus* (EM) and *Acer* (AM) species, plants were first grown either alone (single individual), in intraspecific competition (two individuals of the same species), or in interspecific competition (one focal individual plus a competitor belonging to the other species) with Sterilized inoculum. For the competition pairs, we also included additional treatments where Live soil cultivated by the competitor were added as inoculum. For example, when the focal *Acer* species was growing in interspecific competition treatments with *Populus*, soils conditioned by the *Populus* species were added. This allowed us to quantify the combined impact of a competitor individual through both plant–plant interaction and plant–soil interaction pathways. We also included four additional treatments with each tree species grown alone with Live inoculum in a reciprocal Home and Away plant–soil feedback design (Bever et al., 2010). This design (in total 13 planting combinations; Figure 1b) was replicated five times using the separate inoculum sources from each of the five pairs of *Populus* and *Acer* trees sampled at each site. In addition, we replicated all competition and soil inoculum treatments across two soil nutrient conditions, unfertilized control treatments and inorganic N fertilization with NH_4NO_3 (5 ml doses at 20 mg N kg^{-1} soil), which we confirmed using Plant Root Simulator resin membrane probes (see Supplemental Information for more details). Note that the fertilization treatment mainly reflects how N addition affects plant–soil microbe interactions but not the development of microbial communities; the latter would require implementing N fertilization during the soil conditioning process (e.g. Manning et al., 2008).

We used a randomized block design (one block for each soil inoculum replicate per N fertilization treatment) with plants grown in D16L Deepots (262 ml; Stuewe and Sons, Tangent, OR) in racks on different shelves in the growth chamber (20°C, 60% humidity, 16:8-hour light–dark cycle). Plants were transferred into the experiment at approximately the same size, and soil inoculum was applied as ~5% total soil volume (consistent with other plant–soil feedback designs, Crawford et al., 2019; see Supplemental Information for more details). The experiment lasted 35 weeks, after which harvesting occurred by clipping plants at their base and drying the shoots at 60°C for 72 h before weighing the

above-ground biomass (mg). We gently rinsed roots to remove soil particles and stored root samples in DI water at 4°C for up to 48 hours. EM fungal colonization was measured on *Populus* roots (as above) on ~25 randomly cut 1–2 cm long root segments. A subset of *Populus* root samples from the experiment were processed for AM fungal colonization (n = 93). The full experimental setup had two geographical pairs (run separately for each pair) × two soil nutrient treatments × five replicates × 13 planting combinations comprising the various soil inoculum and competition treatments. However, we were only able to grow enough *P. tremuloides* seedlings of similar sizes for four replicates. This resulted in 234 total pots containing 360 total plants from which we made 288 plant measurements based on the plant competition x soil inoculum design (the two plant measurements in intraspecific competition treatments were averaged). Further details on the design and setup of the growth room experiment are provided in the Supplemental Information.

2.3 | Analysis

We analysed *Populus* mycorrhizal root colonization levels from the field and the growth room experiment to test Hypothesis 1. For field-collected roots, we created a linear model with *Populus* species as a fixed effect and EM or AM fungal colonization as the response (logit transformed). We calculated a standardized log ratio of EM:AM colonization to evaluate the importance of environmental gradients for explaining changes in the balance between EM vs. AM associations (RELAIMPO R package; Grömping, 2006; R Core Team, 2021). We first calculated the partial residuals of EM:AM colonization after accounting for tree species effects before including the following fixed effects in a multiple regression model: projected litter decomposition rate, soil organic matter (%), NH_4, NO_3, P and pH. We used Moran's I to test for spatial autocorrelation on the residuals of the multiple regression model (SPDEP R package; Bivand & Wong, 2018). For *Populus* root samples collected from the growth room experiment, we used mixed-effects models with the NLME package (Pinheiro et al., 2021). Focusing on Live *Populus* inoculum treatments (anticipating that *Acer* inoculum would not produce appreciable EM fungal colonization on *Populus* roots; Supplemental Figure S2), we created a model with EM colonization as the response variable (logit transformed), tree species (*P. deltoides* or *P. tremuloides*), N fertilization, competition type and all interactions as fixed effects, and block as a random effect. Because Live *Populus* and *Acer* inoculum could both provide a source for AM fungal colonization (Supplemental Figure S2), we created a similar model with AM colonization as the response (logit transformed), inoculum type (i.e. *Populus* or *Acer* inoculum), tree species (*P. deltoides* or *P. tremuloides*), N fertilization, competition type and all interactions as fixed effects, and block as a random effect.

We compared plant growth responses between soil inoculum treatments to test Hypothesis 2. Our experiment used a Home vs. Away soil inoculum design: 'Home' treatments refer to soil inoculum sources matched with the same plant species and 'Away' treatments refer to the mismatch between plant species and soil inoculum source. Using only the single plant treatments (Figure 1b bottom row), we created a mixed-effects model with above-ground biomass as the response (log transformed for normality), soil inoculum source (Home or Away), plant species, N fertilization and their interactions as fixed effects, and block as a random effect. We calculated individual plant–soil feedback effects for each species as the log ratio growth response between Home vs. Away soil inoculum in each replicate. To characterize the net effect of soil communities on plant community dynamics, we calculated pairwise plant–soil feedback coefficients (I_S) for each replicate as

$$I_S = \ln(G_{A,A}) - \ln(G_{A,P}) - \ln(G_{P,A}) + \ln(G_{P,P}),$$

where $G_{i,j}$ represents the biomass of plant i when grown in soil cultivated by plant j (i and j being A = *Acer* or P = *Populus*). Therefore, $G_{A,A}$ and $G_{P,P}$ are growth responses of *Acer* and *Populus* to their conspecific soil community, respectively, and $G_{A,P}$ and $G_{P,A}$ are growth responses of *Acer* and *Populus* to the heterospecific soil community, respectively. Negative I_S values are considered to stabilize species interactions and promote coexistence through negative frequency-dependent feedback cycles, and positive I_S values indicate destabilizing interactions that may lead to single species monoculture (Bever et al., 1997; Eppinga et al., 2018).

We tested Hypothesis 3 by examining how plant–soil interactions relate to species niche and fitness differences. Following the timescale-separated formulas of Ke and Wan (2020), which assume that microbial population dynamics are fast relative to plant population dynamics, we used the full set of plant–soil and plant–plant treatments to calculate and partition interaction coefficients into different terms for plant competition or soil microbial effects. Assuming that biomass at the end of the experiment serves as a proxy for (e.g. is proportional to) population growth, we calculated interaction coefficients using plant biomass measurements (averaged across soil replicates) when species i was grown with or without competition from species j in either Live or Sterilized soil inoculum treatments (denoted as $B_{i,j,k}$, with $j = 0$ indicating no competitors and k assigned the category of live or sterilized soil inoculum). These interaction coefficients reflect the per-capita effects of j on the biomass of i relative to the biomass of i when grown individually in sterilized soil. Microbial effects can be quantified by comparing interaction coefficients calculated from competition treatments using either Live or Sterilized soils of species j. Here, we quantify microbial effects using plant performance in sterilized soil as a reference, thereby capturing the overall impact of soil microbes (see also recent discussion on the usage of other reference soils such as unconditioned field soil, Abbott et al., 2021; Yan et al., 2022). Plant–plant interaction, in the presence of soil microbial effects, can be calculated as:

$$\alpha_{i,j,\text{live}} = \left(B_{i,j,\text{live}} - B_{i,0,\text{sterilized}}\right) / \left(\Delta N_j \times B_{i,0,\text{sterilized}}\right),$$

and in the absence of microbial effects as:

$$\alpha_{i,j,\text{sterilized}} = \left(B_{i,j,\text{sterilized}} - B_{i,0,\text{sterilized}}\right) / \left(\Delta N_j \times B_{i,0,\text{sterilized}}\right),$$

where $B_{i,j,\text{live}}$ and $B_{i,j,\text{sterilized}}$ represent the biomass of species i under the competitive impact of species j in Live and Sterilized inoculum of soil j, respectively, $B_{i,0,\text{sterilized}}$ represents the biomass of species i grown individually in Sterilized inoculum, and ΔN_j represents the density of species j competitors (in this case, $\Delta N_j = 1$). Values of α have units of individuals^{-1}, interpreted as the density needed to prevent new individuals from establishing, and thus to suppress population growth (see Appendix A). Here, it is important that the Live soil treatments are cultivated by the competitor to correctly account for their impact via both plant–plant competition and plant–soil interactions (Ke & Wan, 2020). This approach was also used to calculate the relevant interaction coefficients from intraspecific competition pairs (i.e. $B_{i,i,k}$ and $B_{j,j,k}$). For each species pair and soil treatment combination, we quantified niche overlap (ρ, or the magnitude of niche difference, $1 - \rho$) as the relative difference between interspecific and intraspecific interaction coefficients (Ke & Wan, 2020):

$$\rho = \sqrt{\frac{\alpha_{i,j}\alpha_{j,i}}{\alpha_{i,i}\alpha_{j,j}}}.$$

We quantified fitness ratios (a form of fitness differences; Ke & Wan, 2020) as:

$$\frac{f_j}{f_i} = \sqrt{\frac{\alpha_{i,i}\alpha_{i,j}}{\alpha_{j,j}\alpha_{j,i}}}.$$

Under modern coexistence theory, competitive outcomes depend on two mechanisms related to niche differences and fitness ratios: stabilizing forces increase niche differences, while equalizing forces reduce fitness ratios. Boundaries where f_j/f_i equals ρ and $1/\rho$ define four regions in the parameter space that represent different competitive outcomes: coexistence, competitive exclusion by species i, competitive exclusion by species j, and priority effects (Ke & Letten, 2018; Ke & Wan, 2020).

3 | RESULTS

Under field conditions, *P. tremuloides* formed more EM root symbioses than *P. deltoides* (28.7% vs. 12.1% mean root colonization; $F_{1,35} = 10.5$, $p = 0.003$), but this trend reversed for AM symbioses (7.6% vs. 21.0% mean root colonization; $F_{1,33} = 24.1$, $p < 0.001$; Figure 2a). Root colonization of EM and AM fungi was negatively correlated ($r^2 = 0.49$, $p < 0.001$; Supplemental Figure S3). After accounting for tree species effects using partial residuals, the ratio of *Populus* EM:AM colonization was better predicted by projected litter decomposition rates compared with local soil nutrient conditions ($F_{1,28} = 4.2$, $p = 0.05$; Figure 2a; Supplemental Figure S4). Decomposition rates strongly correlated with latitude and climate (Supplemental Figure S4), and EM:AM ratios showed weak evidence of spatial autocorrelation (Moran's I test on multiple regression residuals: $p = 0.06$). Cumulatively, these patterns show that *Populus* mycorrhizal strategies transition from AM to EM symbioses in areas with slower nutrient turnover (e.g. colder, drier climates at higher latitude/elevation).

In the growth room experiment, *P. tremuloides* averaged higher EM root colonization (45.4% vs. 36.7%), and lower AM colonization

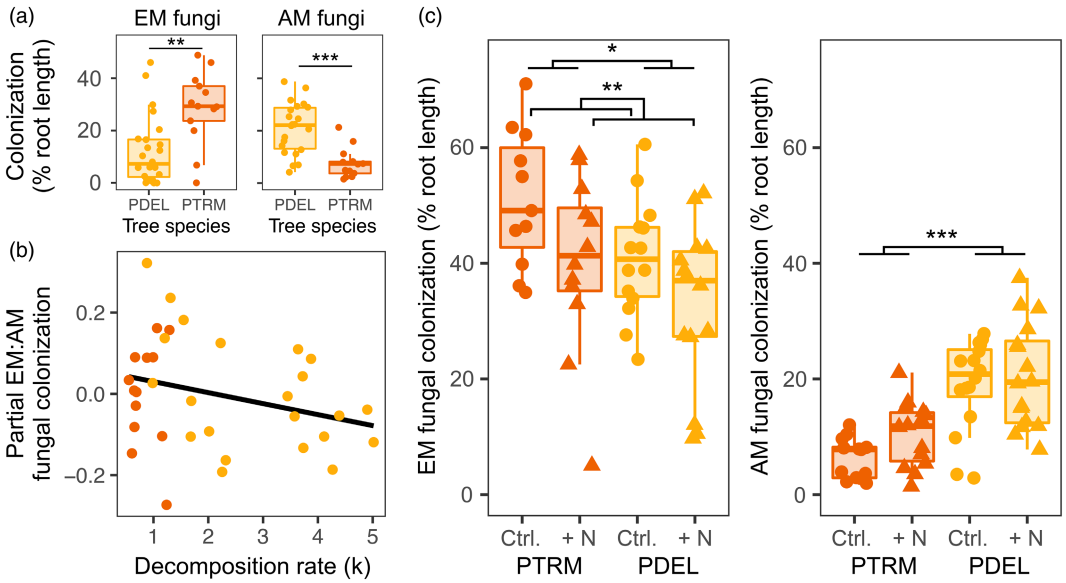

FIGURE 2 Pattens of ectomycorrhizal and arbuscular mycorrhizal fungal prevalence on *Populus* roots. (a) Field samples show that *P. tremuloides* and *P. deltoides* differ in the percent root length colonized by EM and AM fungi overall. After accounting for tree species effects, the balance of *Populus* EM:AM strategies was best explained by projected litter decomposition rates. Partial residuals of EM:AM fungal colonization decreased with faster decomposition. (b) In the experiment, mycorrhizal colonization varies between the two *Populus* in the same direction as field patterns (EM: *P. tremuloides* > *P. deltoides*; AM: *P. tremuloides* < *P. deltoides*). Inorganic nitrogen (N) fertilization reduced EM colonization in both tree species but did not affect AM colonization. Triangles show N fertilizer treatments, circles show unfertilized control treatments, PDEL = *P. deltoides*, PTRM = *P. tremuloides*. Percent root colonization data was logit transformed in the analyses.

(8.5% vs. 19.8%), compared to *P. deltoides* (EM: $F_{1,39} = 4.8$, $p = 0.04$; AM: $F_{1,38} = 24.0$, $p < 0.001$; Figure 2b). Experimental soils in the N addition treatment had 48% greater inorganic N supply rates compared to control soils (N addition mean = 1488 ± 151 μg N/10 cm^2/8 weeks, Control mean = 912 ± 58 μg N/10 cm^2/8 weeks). Adding inorganic N also shifted the balance of other limiting nutrients (Supplemental Table S1), including soil P which was 112% lower in N addition treatments compared to control soils (N addition mean = 2.9 ± 0.2 μg P/10 cm^2/8 weeks, Control mean = 10.3 ± 0.9 μg P/10 cm^2/8 weeks). Fertilizer treatments decreased *Populus* EM fungal colonization overall by 23% compared to control treatments ($F_{1,39} = 7.4$, $p = 0.01$) but did not affect AM fungal colonization levels ($p = 0.3$; Figure 2b; Supplemental Table S2). Both *Populus* species had similar amounts of EM colonization when grown alone (~36%–41% root length), but showed different responses to the competition treatments (species × competition interaction: $F_{2,39} = 4.2$, $p = 0.02$; Supplemental Table S2). In their Home soil, EM colonization on *P. tremuloides* roots increased by more than a third in competition pairs—regardless of the competitor's identity—compared to plants grown alone, while *P. deltoides* showed no changes in EM affinity when alone or in competition treatments (Supplemental Figure S5). As expected, the sterilized soil inoculum treatments resulted in very little to no EM and AM root colonization for either *Populus* species (Supplemental Figure S2).

Plant above-ground biomass varied by a significant interaction between plant species × soil inoculum source (Live Home vs. Away inoculum; $F_{3,52} = 8.0$, $p < 0.001$; Figure 3a, Supplemental Table S3). For the northern species, both *P. tremuloides* and *A. saccharum* performed better when inoculated with *P. tremuloides* conditioned soil (Tukey's post-hoc $p < 0.001$). This created a positive individual plant–soil feedback effect for *P. tremuloides* (mean = 0.39 ± 0.15 *SE*; *t*-test difference from zero: $t_{1,7} = 2.6$, $p = 0.02$) and a marginally negative feedback effect for *A. saccharum* (mean = −0.26 ± 0.16 SE; $t_{1,7} = 1.6$, $p = 0.07$; Figure 3b). Both southern species (*P. deltoides* and *A. saccharinum*) showed no growth differences between the reciprocal inoculum treatments (neutral individual feedbacks). However, calculating pairwise plant–soil feedback effects showed a negative I_S for the southern species pair that persisted in both N treatments (mean = −0.47 ± 0.09 SE; $t_{1,9} = 5.3$, $p < 0.001$; Figure 3c). In contrast, the northern species feedback I_S was slightly positive overall (mean = 0.29 ± 0.22 SE; $t_{1,7} = 1.4$, $p = 0.11$) and changed with N addition: control treatments had positive I_S (mean = 0.67 ± 0.23; $t_{1,3} = 3.0$, $p = 0.03$) but N fertilization caused neutral I_S ($t_{1,3} = 0.4$, $p = 0.4$). Both *P. tremuloides* and *A. saccharum* responded negatively to the N fertilization treatments while *A. saccharinum* performed better with added N (species × N fertilization interaction: $F_{3,52} = 8.1$, $p < 0.001$; Supplemental Table S3).

For the northern pair (*P. tremuloides* and *A. saccharum*), the net effect of soil microbes destabilized plant species interactions by causing niche differences to become increasingly negative (Table 1; Figure 4a). In the unfertilized control treatments, Sterilized inoculum predicts *A. saccharum* will win because of its stronger interspecific effect on *P. tremuloides* ($\alpha_{P,A}$) (Supplemental Figure S6). Incorporating Live soil microbes weakened the competitive impact imposed by *P. tremuloides* ($\alpha_{P,P}$ and $\alpha_{A,P}$). This caused interspecific competition ($\alpha_{A,P}$) to become slightly stronger than intraspecific competition ($\alpha_{P,P}$) for *P. tremuloides* in the more N-limited control soils, driving the interaction to be governed by priority effects where the first plant to arrive wins as neither species can successfully invade the other at their equilibrium (Figure 4a). With inorganic N fertilization, Sterilized treatments predicted stable coexistence, but adding Live soil microbes resulted in competitive dominance by *P. tremuloides*. Specifically, N fertilization in Sterilized treatments caused the strong interspecific competitive impacts of *A. saccharum* to become weaker ($\alpha_{P,A}$) and this led to coexistence (Figure 4a). However, adding inorganic N in Live inoculum treatments caused *P. tremuloides* to inflict a stronger interspecific effect on *A. saccharum* ($\alpha_{A,P}$) and drove their competitive exclusion. We estimated the individual contribution of each plant species' soil conditioning effects on the net competitive outcome by sequentially replacing each species interaction coefficients from Live treatments with the corresponding Sterilized coefficients and recalculating niche and fitness differences. Here, *P. tremuloides* soil microbes had the greatest influence on the competitive balance between the two northern tree species. Soil conditioning by *A. saccharum* either promoted their competitive dominance (low N) or maintained coexistence (high N), but strong destabilizing effects from *P. tremuloides* soil conditioning ultimately pushed the interaction towards priority effects (low N) or *P. tremuloides* competitive dominance (high N).

The net effect of soil microbes on the southern tree species competition pair (*P. deltoides* and *A. saccharinum*) was weaker compared to northern species overall (Table 1; Figure 4b). In low N control treatments, *P. deltoides* showed competitive dominance over the co-occurring *A. saccharinum* regardless of soil microbial effects from either species (Supplemental Figure S6). Specifically, *P. deltoides* wins under low N in Sterilized treatments because of its stronger interspecific impact on *A. saccharinum* ($\alpha_{A,P}$), and the relative strength of intraspecific and interspecific competition showed little change with Live microbes such that the competitive outcome remained the same. As with the northern pair, N fertilization enabled coexistence between the southern species pair in Sterilized inoculum treatments. This was caused by N addition weakening the otherwise strong interspecific competitive impact of *P. deltoides* on *A. saccharinum* ($\alpha_{A,P}$). With Live inoculum, N fertilization reduced *A. saccharinum* intraspecific effects ($\alpha_{A,A}$) resulting in the competitive exclusion of *P. deltoides* as *A. saccharinum* microbial conditioning effects exacerbate species fitness differences under higher N conditions.

Long-term forest inventory data from across the eastern US show a bimodal distribution of sites dominated by the *Populus* and *Acer* species pairs in this study (Figure 5). Using approximately 2000 forest sites, we identified two distinct frequency peaks in the distribution of tree species abundance based on basal area. The opposing peaks at 0% and 100% show it is much more common that a given forest is dominated by a single *Populus* or *Acer* species as opposed to them co-occurring in relatively equal abundance.

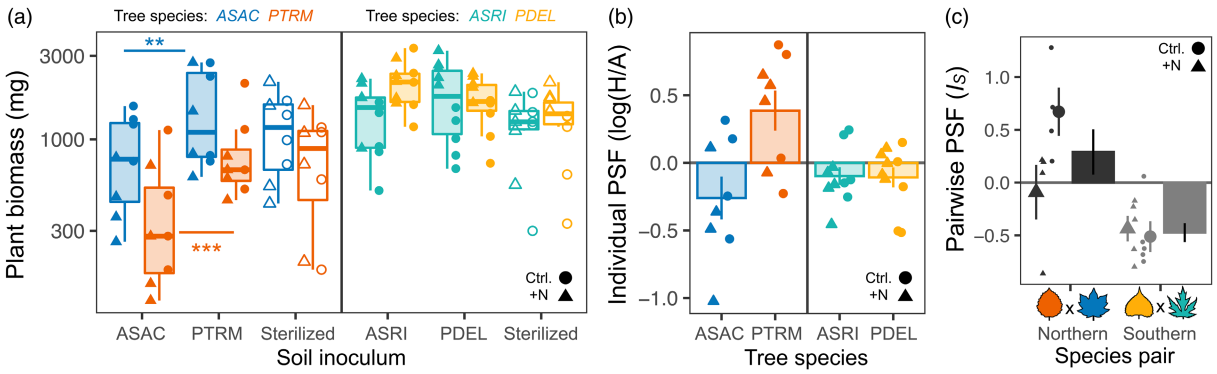

FIGURE 3 Soil microbial effects on plant growth and plant–soil feedbacks. (a) Above-ground biomass differences between soil inoculum treatments show plant growth benefits of interacting with (*P. tremuloides*) or without (*A. saccharum*) their conditioned soil microbial communities. There were no clear growth differences between soil inocula for the southern species pair. (b) Individual plant–soil feedback calculations for each replicate indicate stronger and more divergent effects in the northern species pair (ASAC and PTRM) compared to the neutral effects in the southern species pair. Bars show overall mean ± 1 SE. (c) Pairwise plant–soil feedbacks calculated for each species pair show differential responses to soil microbial communities result in negative coefficients that stabilize southern tree species coexistence ($I_s < 0$), while northern species interactions are moderately destabilized from positive plant–soil feedbacks ($I_s > 0$). Large points show nitrogen fertilization treatment means ±1 SE, bars show overall mean ± 1 SE. Triangles show nitrogen fertilizer treatments, circles show unfertilized control treatments, ASAC = *A. saccharum*, ASRI = *A. saccharinum*, PDEL = *P. deltoides*, PTRM = *P. tremuloides*.

TABLE 1 Interaction coefficients (α_{ii} and α_{ij}) of *Populus* and *acer* tree species competition pairs

	Northern pair (PTRM × ASAC)				Southern Pair (PDEL × ASRI)			
Control (low N)	$\alpha_{P,P}$	$\alpha_{P,A}$	$\alpha_{A,P}$	$\alpha_{A,A}$	$\alpha_{P,P}$	$\alpha_{P,A}$	$\alpha_{A,P}$	$\alpha_{A,A}$
Sterilized soil	−0.581	−0.793	−0.461	−0.476	−0.268	−0.340	−0.541	−0.599
Live soil	−0.048	−0.691	−0.065	−0.343	−0.236	−0.233	−0.516	−0.303
Microbial effect	0.533	0.102	0.396	0.133	0.032	0.107	0.025	0.296
N addition (high N)	$\alpha_{P,P}$	$\alpha_{P,A}$	$\alpha_{A,P}$	$\alpha_{A,A}$	$\alpha_{P,P}$	$\alpha_{P,A}$	$\alpha_{A,P}$	$\alpha_{A,A}$
Sterilized soil	−0.413	−0.416	−0.328	−0.598	−0.343	−0.309	−0.214	−0.400
Live soil	−0.077	−0.151	−0.718	−0.256	−0.486	−0.188	−0.363	−0.159
Microbial effect	0.336	0.265	−0.390	0.342	−0.143	0.121	−0.149	0.241

Note: Interaction coefficients represent intraspecific competition with conspecific soil inoculum ($\alpha_{P,P}$ and $\alpha_{A,A}$), and interspecific competition with heterospecific soil inoculum ($\alpha_{P,A}$ and $\alpha_{A,P}$).Abbreviations are PTRM = *P. tremuloides*, ASAC = *A. saccharum*, PDEL = *P. deltoides*, ASRI = *A. saccharinum*. High and low inorganic N refer to the N fertilization and control treatments, respectively. Microbial effects are the difference between Live and Sterilized soil treatments.

4 | DISCUSSION

Studies of geographical variation in root symbioses tend to treat plant mycorrhizal type as monolithic functional classes (Bueno et al., 2017; Lu & Hedin, 2019; Soudzilovskaia et al., 2015; Steidinger et al., 2019). However, our results show that the extent of mycorrhizal associations within a functional class can also show large geographical changes, and that these within-group patterns match expectations from studies comparing mycorrhizal nutrient uptake strategies. Previous work has shown that *Populus* can vary in the degree of EM and AM symbioses (Gehring et al., 2006; Karst, Franklin, et al., 2021), and here we demonstrate why such patterns might arise based on geographical differences in mycorrhizal strategies and soil nutrient availability. In support of Hypothesis 1, the more northern species (*P. tremuloides*) had greater EM colonization and less AM colonization than the more southern species (*P. deltoides*), aligning with global patterns of increasing EM dominance with latitude and climate controls on nutrient cycling (Steidinger et al., 2019). The climate-projected litter decomposition rate was an important environmental gradient explaining *Populus* mycorrhizal variation, which could reflect a causal driver of colonization on a given fine root section but may also represent a coarse proxy for other unmeasured variables (e.g. local forest mycorrhizal composition). Still, stronger soil N-limitation favours EM symbioses to become more prevalent as plants increasingly rely on these fungi to mine nutrients from organic sources (Lu & Hedin, 2019), and here we found evidence supporting this within a single plant genus across geographical scales. Our experimental results support this further as experimental N addition reduced *Populus* EM colonization levels, consistent with past work demonstrating the negative effects of nutrient fertilization

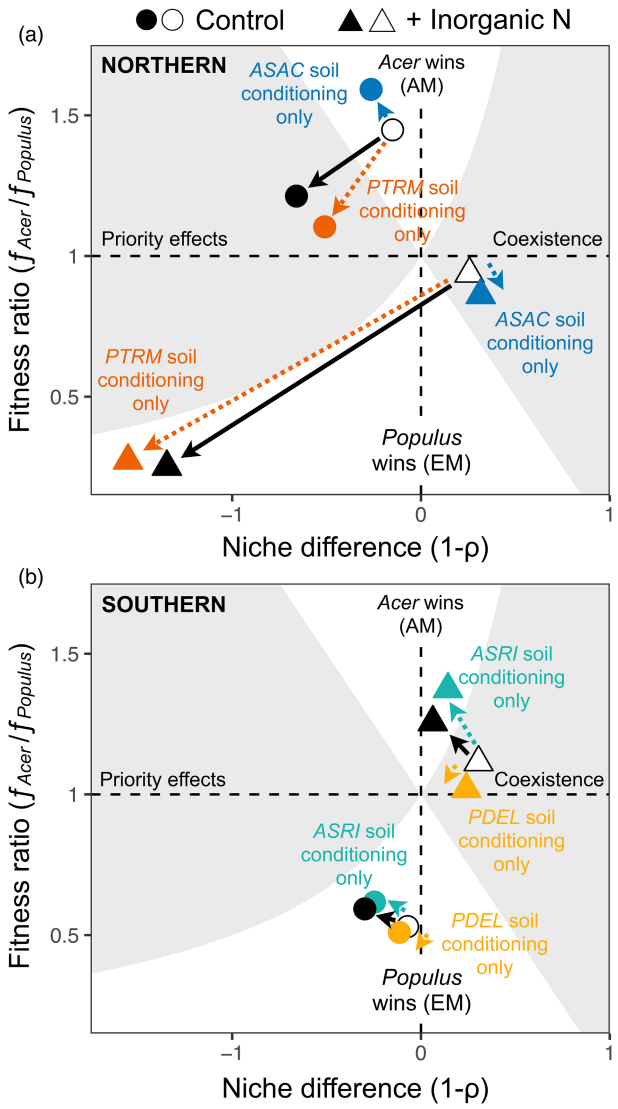

FIGURE 4 Soil microbial effects on the outcomes of plant competition under different soil nutrient conditions. The parameter space shows the niche difference (i.e. stabilization potential, *x*-axis) and fitness ratio (*y*-axis) of the northern (a) and southern (b) plant species interactions. Shaded areas indicate regions where coexistence (right) or priority effects (left) are expected to occur, and unshaded regions show competitive exclusion by *Acer* (top) or *Populus* (bottom). Circles show Control (unfertilized) treatments and triangles show inorganic N fertilization treatments. Open and closed symbols indicate Sterilized and Live soil inoculum, respectively, with solid arrows showing the net effect of soil microbes on plant competitive outcomes. Dashed arrows show the influence of species-specific soil conditioning effects on plant competition (blue = *A. saccharum*, orange = *P. tremuloides*, green = *A. saccharinum*, yellow = *P. deltoides*).

on mycorrhizal associations, symbiotic benefits and EM community composition (Johnson, 1993; Morrison et al., 2016; van der Linde et al., 2018; but see Karst, Wasyliw, et al., 2021).

There is likely a limit on how flexible plants can be regarding the intensity of mycorrhizal colonization. For instance, *P. deltoides* lacks specific genetic loci found in other poplars that promote the recognition and formation of EM symbioses with *Laccaria bicolor* (Labbé et al., 2019). If this extends to other fungi, it could be another reason why *P. deltoides* had lower EM affinity. Such inflexibility might occur in the opposite direction too if highly EM plants are unable to advantageously lower their symbiotic associations down to a more cost-effective level under weak N-limitation. The decline of EM trees with N pollution across US forests might be one potential example of this phenomena (Averill et al., 2018). Even if plants can reduce EM colonization slightly (as found here), it may not be enough to remain competitively viable in communities with differing plant–mycorrhizal strategies. This raises questions about the functional consequences of variation in mycorrhizal responsiveness across plant species or genotypes as soil resources change.

Diverse mycorrhizal strategies have been shown to influence the mechanisms underlying plant coexistence by affecting niche partitioning and relative fitness differences (Peay, 2018; Stanescu & Maherali, 2017; van der Heijden et al., 2003, 2008), but the nature and design of these studies made them largely incapable of predicting whether plant–soil interactions lead to stable coexistence or species exclusion. Our results demonstrate the usefulness of modern coexistence theory to understand how soil microbiome and nutrient variation interactively shape the outcomes of plant–plant competition. We find that competitive outcomes between plants with different mycorrhizal fungi is contingent on their geographical origin and the soil nutrient context. Adding soil microbes did not promote stable coexistence among *Populus* and *Acer* tree species—Live inoculum always had destabilizing effects (i.e. decreasing niche differences) and sometimes contributed to competitive exclusion by intensifying fitness differences. This strong tendency for microbially driven destabilization and competitive exclusion among tree species may help explain the bimodal signature in models of EM vs. AM competitive strategies (Lu & Hedin, 2019) and the abrupt latitudinal transitions in forest mycorrhizal states (Steidinger et al., 2019). A broader test of competitive interactions among many tree species pairs with different and shared mycorrhizal associations would help clarify whether these findings are specific to *Populus–Acer* pairs or evidence of a general tendency towards competitive exclusion between EM and AM mycorrhizal types.

The approach we apply here predicts whether the balance between plant–plant and plant–microbe interactions during the seedling stage promotes coexistence or competitive exclusion. Approaches that explicitly incorporate plant demography (e.g. Chu & Adler, 2015) may eventually shed light upon how microbes affect competition across the entire life cycle of tree species. A clear drawback of this study is the relatively short timeframe of the experiment for interpreting ecological interactions among tree species with long life spans. Nonetheless, given the difficulty of experimentally manipulating communities of long-lived plants, short-term approaches focusing on seedling performance provide an important starting point for understanding mycorrhizal effects on plant community dynamics. Comparing projections based on these short-term experiments to long-term observational data can help evaluate their insight into drivers of coexistence. For example, our experimental

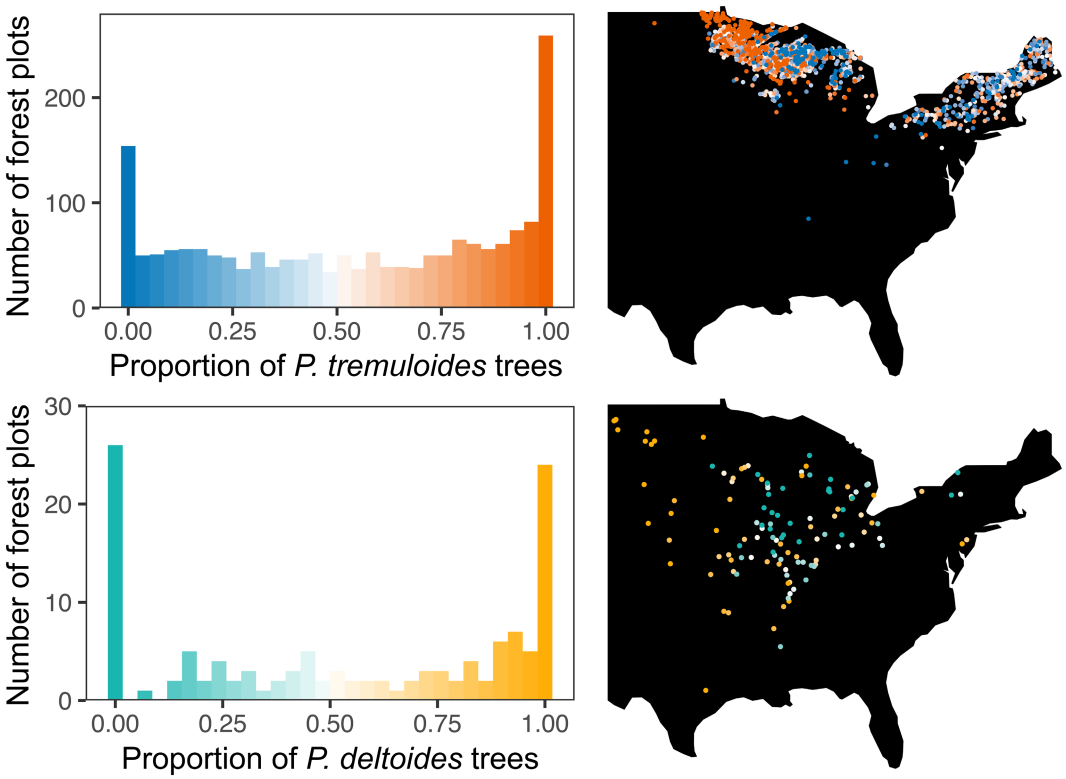

FIGURE 5 Bimodality of *Populus* (EM) versus *Acer* (AM) forests on the landscape. Histograms show the frequency distribution of forest plots as the proportion of *Populus* to *acer* trees by basal area. Values of 1 are forest sites dominated by *P. tremuloides* (orange) or *P. deltoides* (yellow) (i.e. comprising >90% of the total forest basal area) and the respective *acer* species pair is absent. Values of 0 are sites dominated by *A. saccharum* (blue) or *A. saccharinum* (green) and the *Populus* species pair is absent. Values between 0 and 1 show the proportion of *Populus* to *Acer* basal area in sites where the tree species pairs co-occur. Maps show the spatial distribution of the 1967 forest inventory plots across the eastern US used in this analysis (1841 northern pair, 126 southern pair), with colours reflecting the relative abundance of *Populus* vs. *Acer* trees by basal area.

results predict mycorrhizal-mediated competitive exclusion and the emergence of alternative stable states, which aligns with the bimodal signal of *Populus* vs. *Acer* dominance from large-scale forest inventory data. Recent models have shown that such bimodality in forest structure is more likely the result of mycorrhizal differences than environmental filtering (Averill et al., 2022), though we cannot rule out some potential filtering effects here. For example, these *Populus* and *Acer* species may differ in shade tolerance or occupy different points along successional gradients, which could be working in concert with mycorrhizal-mediated resource competition to generate bimodality in species dominance. The connection between experimental prediction and observed forest composition exists even though we used soil inoculum from a small number of sites, but an experimental approach using soil inoculum from a broader range of sites might provide better spatial inference for extrapolating mycorrhizal effects on plant competitive dynamics across forest systems. Although we did not directly manipulate mycorrhizal fungi in the experiment, our whole microbiome inoculum approach mirrors how plants compete in nature by recruiting into competitor soils, and which clearly affected EM and AM colonization rates in our experiment.

Most conceptualizations of the functional differences between AM and EM symbioses focus on nutrient competition (Averill et al., 2019; Corrales et al., 2016; Phillips et al., 2013), and we find evidence that inorganic N fertilization switches *Acer* (AM) vs. *Populus* (EM) competitive outcomes (often in the expected direction). In Sterilized inoculum, *Populus* and *Acer* have enough niche separation to coexist with high N availability. Incorporating soil microbiome effects for the southern species pair matches the AM-EM nutrient competition framework (support for Hypothesis 3): *A. saccharinum* and *P. deltoides* were superior competitors in high and low inorganic N conditions, respectively. Higher latitude soils are typically characterized as N-limited (Du et al., 2020), meaning that the competitive outcomes between northern species in unfertilized control treatments are more likely to reflect the actual soil nutrient properties in the field. Under these conditions, *P. tremuloides*-cultivated microbes pushed the interaction to be governed by priority effects, which allow for alternative stable states depending on the initial species density. This exactly fits the bimodal patterns found in *Populus* and *Acer* forests (Figure 5) as well as other large-scale observations of AM and EM tree species prevalence across US forests that emerge from con-mycorrhizal feedbacks and evolutionary stable state

models of plant–mycorrhizal nutrient economies (Averill et al., 2022; Lu & Hedin, 2019). Overall, soil microbiome effects weakened the competitive impact imposed by *P. tremuloides* (Table 1), and we speculate that EM symbioses formed in Live inoculum gave *P. tremuloides* greater access to the organic nutrient pool, thereby relaxing resource competition with competitors.

However, *P. tremuloides* does not completely fit the plant–mycorrhizal nutrient competition paradigm as this northern, highly EM species was projected to be competitively superior with greater inorganic N levels. Some evidence indicates EM fungi may have the potential to hoard N (Franklin et al., 2014; Nasholm et al., 2013), meaning that *P. tremuloides* could have captured a competitive advantage by monopolizing soil resources in the fertilization treatments. This unexpected pattern may also be related to the controlled conditions in which the interactions took place (i.e. missing an important detail from natural systems or the methods for establishing plants in the experiment), or that soil P limitation played an important role. Adding inorganic N reduced soil P, which may have increased host reliance on AM fungal symbionts in ways that affected plant performance or competitive tolerance. For instance, *Populus* AM fungal colonization did not respond to N fertilization, suggesting that plant hosts could be maintaining these associations to combat higher soil P demand even if some EM fungal species can specialize in providing plant growth benefits under strong soil P limitation (e.g. *Thelephora terrestris*; Van Nuland & Peay, 2020). More generally, the dual colonized strategy of *Populus* could have impacted nutrient competition in ways that disadvantaged *Acer* more than might be expected if we had used a tree species with a single, fixed EM strategy. We likely do not fully understand how mycorrhizal fungi affect nutrient competition, and this unexpected outcome reinforces the need for further mechanistic experiments between mycorrhizal associations (including single vs. dual colonized strategies).

We used multiple approaches to characterize soil microbial effects on plant coexistence, from which there were both complementary and contradictory lines of evidence. The plant–soil feedback and modern coexistence frameworks converged on the same pattern for the northern species pair. Specifically, positive plant–soil feedbacks (pairwise I_S>0) should lead to positive frequency dependence and priority effects (dominance of either species). This was confirmed in the modern coexistence theory approach as adding *P. tremuloides* soil microbes destabilized the overall interaction leading to priority effects (low N) and the competitive exclusion of *A. saccharum* (high N). Plant–soil interactions in the southern species pair were predicted to stabilize coexistence with net negative pairwise feedback effects (I_S<0). However, analysing their interaction coefficients in a modern coexistence framework showed destabilizing effects with the two species never predicted to coexist and, instead, that they should competitively exclude one another under different soil nutrient conditions. Recently, the field of modern coexistence theory has started to estimate confidence ellipse around the point estimates of niche difference and fitness ratio (e.g. via sampling from the posterior distribution; Bowler et al., 2022). The southern species pair showed a relatively small net effect of soil microbes that sit right near the transition boundaries (Figure 4b), and it is possible that the uncertainty around these estimates might overlap both zones for a less clear distinction between coexistence and exclusion. Moreover, the large shift in Figure 4b between low vs. high N treatments suggests that plant characteristics beyond microbial interactions also contribute to their adaptation to different soil environments. For instance, EM and AM associating plants have trait syndromes that likely function in concert with their belowground symbioses (Averill et al., 2019), and tropical EM trees specialized on low and high fertility soils were found to associate with similar EM fungi (Peay et al., 2015), pointing to other demographic features that operate in concert to generate edaphic specialization.

The mismatch between plant–soil feedback direction and the projected competitive outcome arises because the I_S pairwise feedback index uses plant biomass measurements when individuals were grown alone in different soils, whereas the other interaction coefficient calculations incorporate both plant–soil and plant–plant effects. Even though both southern species performed slightly worse when grown alone in their Home inoculum, each species benefited from conspecific soil conditioning in a net competitive sense across the N treatments (e.g. mostly positive *Microbial effects* in Table 1). In other words, microbial effects ameliorated competition for the resident plant species more than for the invader. Thus, the integrated approach captures an element of positive microbial effects that is missed by traditional plant–soil feedback calculations. In fact, only the modern coexistence approach gave predictions that matched our intuition—a shift towards AM competitive dominance with higher N in the southern pair. Such discrepancies underscore that the plant–soil feedback approach alone may be insufficient to accurately predict coexistence outcomes without explicitly incorporating plant–plant competition (Ke & Wan, 2020). Collectively, our findings empirically support emerging theoretical work on how mutualisms alter species coexistence and fit large-scale observations of mycorrhizal bistability and biogeography across resource gradients, further emphasizing the importance of incorporating plant–mycorrhizal associations into the mechanisms of biodiversity maintenance.

AUTHOR CONTRIBUTIONS

Michael E. Van Nuland and Kabir G. Peay designed the experiment. Michael E. Van Nuland created the experiment, collected data, conducted the analyses, and wrote the initial manuscript draft. Po-Ju Ke and Joe Wan helped with the analysis and results interpretation. All authors contributed significant manuscript edits.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data and code are archived and publicly available on Zenodo https://doi.org/10.5281/zenodo.7324408 (Van Nuland et al., 2022).

ORCID

Michael E. Van Nuland https://orcid.org/0000-0002-3333-0212
Po-Ju Ke https://orcid.org/0000-0002-8371-7984
Kabir G. Peay https://orcid.org/0000-0002-7998-7412

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SUPPORTING INFORMATION

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