Editor summary:
A controlled greenhouse study which manipulated the presence of both ectomycorrhizal fungi (EMF) and arbuscular mycorrhizal fungi (AMF) at a range of conspecific and heterospecific plant competitor densities shows that AMF promote plant species coexistence by equalizing fitness differences and stabilizing competition.

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Title: Arbuscular mycorrhizal fungi equalize differences in plant fitness and facilitate plant species coexistence through niche differentiation

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Abstract (172/200)

Mycorrhizal fungi are essential to the establishment of the vast majority of plant species but are often conceptualized with contradictory roles in plant community assembly. On one hand, host-specific mycorrhizal fungi may allow a plant to be competitively dominant by enhancing growth. On the other, host-specific mycorrhizal fungi with different functional capabilities may increase nutrient niche partitioning, allowing plant species to coexist. To resolve the balance of these two contradictory forces, we used a controlled greenhouse study to manipulate the presence of two main types of mycorrhizal fungi, ectomycorrhizal fungi (EMF) and arbuscular mycorrhizal fungi (AMF) and used a range of conspecific and heterospecific competitor densities to investigate the role of mycorrhizal fungi in plant competition and coexistence. We find that the presence of AMF equalizes fitness differences between plants and stabilizes competition to create conditions for host species coexistence. Our results show how belowground mutualisms can shift outcomes of plant competition, and that a holistic view of plant communities which incorporates their mycorrhizal partners is important in predicting plant community dynamics.

Introduction

Plants are never found in nature without their microbiomes[1]. Within plant roots, mycorrhizal fungi are a key group of microbial mutualists that form relationships with an estimated 90% of terrestrial plant species[2] and even greater percentages of plant individuals across the globe[3]. Mycorrhizal fungi have been shown to improve plant nutrient uptake, water acquisition, and defense against pathogens, often resulting in hosts that are much larger than their non-mycorrhizal counterparts[2,4,5]. Among these fungi, there are unique mycorrhizal types, which are phylogenetically, morphologically, and functionally distinct[4]. Of these, arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EMF) are by far the most ubiquitous[4]. As they differ in their enzymatic capacity to decompose organic matter, these two mycorrhizal types are thought to give rise to contrasting evolutionary strategies for plant host nutrient acquisition, where EM plants often dominate in N-limited systems and AM plants tend to dominate regions with more rapid rates of decomposition and nutrient liberation[3,6].

In conjunction with their effects on host nutrient acquisition and plant growth, mycorrhizal fungi appear to modify host demographics and alter local dominance[7–10]. For example, reduced mycorrhizal availability can decrease host competitive ability with heterospecific neighbors[8]. Biological invasions have acted as natural experiments that test the importance of mycorrhizal fungi in host demographics, demonstrating how compatible mycorrhizal partners are often required to tip the scales of coexistence to favor invading species[11]. More broadly, forests tend towards dominance by a single mycorrhizal type[12–14]. Especially where N and P are co-limiting, predictions of AMF-EMF bistability, where either AMF or EMF hosts might dominate local patches, are common[13]. Once hosts are established, these symbioses appear to generate positive con-mycorrhizal feedbacks, selecting for hosts with their own mycorrhizal strategies[14–17]. Together, these ecological patterns suggest that mycorrhizal-based competition can shape forest structure and diversity across scales[12–14]. Yet despite their strong associations with both host nutritional niches and large-scale patterns in plant community structure, mycorrhizal effects have yet to be included in an experimental framework that evaluates the multiple dimensions in which these fungi contribute to dynamics of plant competition and coexistence[7,8].

In the context of plant community assembly, these different mycorrhizal roles – expanding hosts' nutrient niche and improving host growth – may have opposing effects[18], highlighting an important gap in our understanding of the impact of mycorrhizas on plant ecology. If mycorrhizal

fungi expand the nutrient niches of plant hosts (e.g. the "mutualistic niche"[19,20]), this could stabilize plant competition and promote coexistence by increasing intra- relative to interspecific plant competition. Reciprocally, if mycorrhizal mutualisms promote large differences in plant growth, mycorrhizal relationships might exacerbate plant competition and lead to competitive exclusion (destabilization). These two mycorrhizal effects (increasing hosts' nutrient niches and promoting plant growth) could have opposing effects on plant competition and coexistence[21,22].

Modern coexistence theory (MCT) provides a useful framework for reconciling this apparent contradiction because it precisely predicts how growth differences in species' performance should help or hinder coexistence. Differences that reduce species' competitive impacts on each other consistently promote coexistence and are therefore termed stabilizing niche differences. By contrast, differences that create imbalances in competitive ability and prevent coexistence are termed unequalizing forces. Coexistence is promoted by both stabilization (i.e. high niche differentiation) and equalization (i.e. low competitive imbalance) between competitors[23–26]. Importantly, while these two possibilities are not mutually exclusive (theory suggests that the equalizing and stabilizing components are often interrelated[27]), one key strength of MCT is that it can identify how exactly these two components interact to determine coexistence[28]. As such, MCT has become an important pillar in the study of plant ecology used to predict outcomes of plant competition[23–25]. Within the MCT framework, host-specific mycorrhizal fungi may alter outcomes of competition through (un)equalizing processes if mycorrhizal fungi modify growth differences between hetero-mycorrhizal species[23,26,29]; this will determine if AMF or EMF hosts are predicted to dominate. Mycorrhizal fungi could also increase the likelihood of coexistence if fungi enable hosts to specialize in the uptake of distinct, growth-limiting nutrients, resulting in hosts co-limiting each other's growth (stabilization)[20,30].

Previous efforts to investigate how mycorrhizal fungi and other soil microbes impact plant community assembly have generally attempted to do so directly, measuring growth differences between plant hosts with mycorrhizal inoculation, or indirectly, using plant-soil feedback (PSF) experiments; others have tried to quantify the microbial effect *in vivo* by using plant invasions as natural experiments[7]. These types of studies have been critical in better understanding the role of microbes in plant competitive ability[8,19,28,31–34] and have highlighted how microbes may stabilize plant interactions[35–37]. For example, a recent meta-analysis found that fitness differences generated by microbes tended to be greater than stabilization[35]. Conversely, the development of con-

mycorrhizal networks could lead to positive feedbacks that destabilize coexistence if the presence of con-mycorrhizal individuals facilitates conspecific host growth[38,39]. Yet relatively few studies have explored how the enhanced nutrient uptake conferred by mycorrhizal fungi may directly influence heterospecific versus conspecific competitive ability of hosts[40–45], and none have investigated these interactions simultaneously for EM and AM plants or employed MCT to predict outcomes of competition. Recent theoretical developments have simplified methods to include microbial communities into plant coexistence using MCT[29,46], but they have not yet been directly applied to mycorrhizal fungi.

To help fill the need for theoretically driven tests of how positive interactions shape plant communities[18], we test how the presence of the two most common mycorrhizal types (AMF and EMF) mediate coexistence of their respective host plants. To determine the roles of these two distinct mycorrhizal types in plant coexistence, we employed the MCT framework, enabling us to disentangle the stabilizing and equalizing mechanisms of mycorrhizal fungi on plant competition. We tested these dynamics by simulating plant interactions from forest-shrubland boundaries where AMF and EMF hosts coexist at the landscape scale[47], but where at the local scale the distribution of mycorrhizal fungi is patchy[48–50] and these hosts often form monodominant stands[51]. We focused on *Baccharis pilularis* and *Pinus muricata* as focal species as they are two of the most dominant taxa in our study system and because *Baccharis* is AMF-associated and *Pinus* is EMF associated[8,51]. Using a climate-controlled growth chamber, we grew these plant hosts with and without their fungal partners as well as with differing conspecific and heterospecific competitor densities. In addition to plant growth, we also measured foliar N, δ^{15}N, and P, stomatal conductance, and photosynthesis to see how mycorrhizal fungi affected resource use under different competition scenarios and looked for mechanisms underlying the stabilizing and equalizing effects. Consistent with our expectations from the literature[2], we found that the presence of host-specific mycorrhizal fungi increased nutrient uptake and growth rates. Based on functional differences between AMF and EMF[4], we also expected that the presence of multiple mycorrhizal types would promote coexistence by shifting resource use and increasing conspecific relative to heterospecific competition. In partial support of this expectation, we found that the presence of AMF promoted coexistence by shifting patterns of host resource use in ways that increased conspecific relative to heterospecific competition. While the presence of EMF changed host resource use, EMF plants were able to grow larger without discernible changes in the strength of

conspecific versus heterospecific competition. These results illustrate a general framework for predicting when and why mycorrhizal fungi (de)stabilize coexistence and can help explain patterns in natural communities, such as the propensity for monodominance in EMF forests and the higher plant diversity often found in AMF stands[12,52]. Our study indicates that explicitly including mutualistic interactions may help reconcile differences between coexistence theory and observation[53], and that mycorrhizal fungi may provide a missing link to better understanding plant species interactions.

Results

To assess how mycorrhizal fungi contribute to dynamics of plant competition and coexistence, we established a baseline of the impacts of mycorrhizal fungi on their hosts in the absence of competition (Fig. 1). Both *Baccharis* (AMF-associated) and *Pinus* (EMF-associated) exhibited positive growth responses to their host-specific fungi (ANOVA $F_{3,45}$=5.375; p=0.003 and $F_{3,43}$=4.635; p=0.0362, respectively; Fig. 2a). We found no evidence that *Baccharis* growth was impacted by EMF inoculation when AMF were absent (Tukey's HSD, p=0.2314). In line with previous work, however, we found that even in the absence of *Baccharis,* AMF were slightly parasitic on *Pinus* growth (Tukey's HSD, p=0.0201)[54,55].

Consistent with the paradigm of mycorrhizal fungi as nutritional symbioses, host-specific mycorrhizal fungi increased total baseline P uptake for both *Baccharis* (ANOVA $F_{3,26}$=5.164, p=0.0062; Fig. 2b) and *Pinus* (ANOVA $F_{3,20}$=6.612, p=0.0028). Mycorrhization improved total N uptake for *Pinus* (ANOVA $F_{3,20}$=5.105, p=0.0087; Fig. 2c), but not for *Baccharis* (ANOVA $F_{3,20}$=1.139, p=0.3570). To test if mycorrhizal fungi enabled hosts to utilize different sources of N (e.g. organic versus mineral), we compared values of δ^{15}N by treatment. δ^{15}N was not impacted by mycorrhization for *Baccharis* (ANOVA $F_{3,20}$=0.518; p=0.674), however, we did find evidence for differences in δ^{15}N values across mycorrhizal treatments for *Pinus* (ANOVA; $F_{3,20}$=4.532; p=0.0140), indicating that the presence of EMF increased the variety of N sources available to *Pinus* and/or host dependence on mycorrhizal N as EMF preferentially pass on lighter isotopes to their hosts (fractionation), resulting in more negative values of δ^{15}N [56] (Tukey's HSD p=0.1179 and p=0.0118 for EMF and EMF+AMF, respectively). Curiously, though there was no difference in the amount of N uptake for *Pinus* in the AMF compared to nonmycorrhizal treatment (Tukey's HSD p=0.8406), δ^{15}N values for *Pinus* in the AMF treatment were lower than those observed for

nonmycorrhizal *Pinus* (Tukey's HSD p=0.0529), indicating that AMF may directly impact *Pinus* N uptake/utilization. N:P ratios differed across mycorrhizal treatments for both *Baccharis* (ANOVA; $F_{3,20}$=45.683; p=0.0055) and *Pinus* (ANOVA; $F_{3,20}$=11.06; p=0.0002). Specifically, alleviation of P limitation led to increases in N limitation for *Baccharis* (Tukey's HSD p=0.0594 and p=0.0979 for AMF and AMF+EMF treatments, respectively; Fig. 2d). In contrast, EMF+ treatments reduced P limitation for *Pinus* while simultaneously increasing N uptake, resulting in more optimal nutritional ratios (Tukey's HSD p=0.0022 and p=0.0009 for EMF and AMF+EMF treatments, respectively). The availability of limiting nutrients associated with mycorrhization also had functional consequences for plant physiological performance. As EMF colonization promoted both N and P uptake, we observed increased photosynthetic capacity of *Pinus* in the presence of EMF (ANOVA; $F_{3,19}$= 6.891; p= 0.0025, Fig. S1). Conversely, while AMF enhanced *Baccharis* growth by increasing P uptake, we found that photosynthesis eventually became constrained, likely as a result of N limitation, as there were no significant differences in photosynthetic capacity across mycorrhizal treatments (ANOVA; $F_{3,18}$= 1.532; p= 0.2404, Fig. S1).

Baseline EMF percent root length colonization (PRLC) rates ranged from 31.1 ± 14.7% to 26.5 ± 8.66% in the EMF and AMF+EMF treatments, respectively; colonization did not differ between these groups (Tukey's HSD, p=0.5396) and no EM colonization was observed in EMF- treatments. *Pinus* biomass increased with EMF colonization (linear mixed effects; marginal R^2=0.198, slope=0.6209, p=0.0462; Fig. S2). For *Baccharis,* we confirmed colonization by spot-checking samples; observed PRLC ranged from 84.0 ± 21.8 % (n=16) to 15.8 ± 34.4 % (n=13) in the AMF+ and AMF- treatments, respectively. Despite soil sterilization (see Methods), two samples in AMF- treatments were well-colonized (98% and 87% PRLC, respectively). While arbuscules:vesicles ratios ranged from 1:1 and 1:2 for AMF+ treatments, we observed a 1:10 ratio of arbuscules:vesicles and only vesicles (0 arbuscles) in these two samples. Accordingly, this contamination likely derived from a less mutualistic AMF species from the background soil. Neither sample was a statistical outlier for any measurements compared to other nonmycorrhizal controls; consequently, we retained these samples in their original treatment groups. Background colonization excluding these samples otherwise remained low (1.9 ± 4.49 %).

In the presence of competition, mycorrhizal fungi had important consequences for plant fitness (Fig. 3). When no mycorrhizal fungi were present, the intensity of competition for *Baccharis* was similar between heterospecific and conspecific competitors (Fig. 3a). When AMF

were present, *Baccharis* was more sensitive to conspecific compared to heterospecific competition; these patterns held when EMF were added (see Fig. 3c). Though the average biomass of *Pinus* was consistently lower than that of *Baccharis, Pinus* was also generally less sensitive to competition (Fig. 3e-h). With no mycorrhizae, there was little difference in *Pinus* biomass across competition treatments (Fig. 3e). The addition of EMF slightly relaxed conspecific competition for *Pinus* relative to heterospecific competition (Fig. 3f) and these results were consistent even with the addition of AMF (Fig. 3h). With only EMF, both *Pinus* biomass and EMF colonization slightly increased under low-density conspecific competition, prompting us to test for potential conspecific facilitation. However, model selection favored the simpler models showing a steady decline in both *Pinus* biomass (AIC: 38.5048 on 6 DF for the higher-order model versus 31.5118 on 5 DF for the simple model) and EMF colonization with increasing competitor density (AIC: 5.1662 on 6 DF for the higher-order model versus -3.6461 on 5 DF for the simple model). In the AMF treatment, *Pinus* was relatively insensitive to either heterospecific or conspecific competition, likely because the plants were already so small due to slight parasitism of AMF on *Pinus*.

We also found evidence that mycorrhizal fungi might help shape host niches under competition by shifting their nutrient uptake profiles and physiology. Foliar P data indicate that AMF enabled *Baccharis* to specialize in P uptake, where the concentration of foliar P significantly differed by both mycorrhizal treatment and competition type for *Baccharis* (ANOVA $F_{3,56}=16.295$, $p<0.0001$ and $F_{2,56}=39.941$, $p<0.0001$, respectively; Fig. 4b) and we observed strong evidence of an interaction between these factors; P uptake was higher for *Baccharis* in heterospecific compared to conspecific competition where AMF were present (ANOVA $F_{6,56}=3.051$, $p=0.0118$). For *Pinus,* we found strong evidence that mycorrhizal treatment (ANOVA $F_{3,46}=28.306$, $p<0.0001$; Fig. 4b), but not competition treatment (ANOVA $F_{2,56}=0.037$, $p=0.6922$) impacted P uptake and we observed moderate evidence for an interaction between these factors ($F_{6,56}=2.192$, $p=0.0572$) where P was higher in heterospecific competition when only EMF were present, but lower when both mycorrhizal types were present. Altogether, we found that AMF enabled *Baccharis* to better compete for P, limiting the growth of *Pinus* in heterospecific competition and limiting itself under conspecific competition. Our data further indicate that N uptake also increased for *Baccharis* in heterospecific compared to conspecific competition when both mycorrhizal types were present (Tukey's HSD $p=0.0066$; Fig. 4a), perhaps as AMF

colonization of *Baccharis* induced some degree of P limitation for *Pinus* (Fig. 4d), resulting in decreased competitive ability of *Pinus* for N. Consistent with this interpretation, δ^{15}N data for *Baccharis* revealed differences in isotopic leaf N across competition treatments (ANOVA $F_{2,56}$= 60.279, p<0.0001; Fig. 4c), but not across mycorrhizal treatment (ANOVA $F_{3,56}$= 0.724, p=0.5420), indicating that while the quantity of N taken up by *Baccharis* shifted, the source of N remained consistent.

Patterns of water use further indicate how mycorrhizal fungi influenced host competition for resources (Fig. S3). While we found little evidence that mycorrhizal fungi influence *Baccharis* stomatal conductance in the absence of competition (g_s; ANOVA; $F_{3,62}$ = 2.107, p = 0.1084), we observed that g_s was significantly lower in conspecific compared to heterospecific competition, indicating greater competition for water resources amongst conspecifics versus heterospecifics for *Baccharis* (Tukey's HSD p = 0.0208163). In *Pinus*, we found strong evidence that transpiration increases with mycorrhization (ANOVA; $F_{3,53}$ = 6.787, p = 0.0005) and varies across competition type (ANOVA; $F_{2,53}$ = 3.480, p = 0.0380). Additionally, we observed an interaction between these mycorrhizal treatment and competition types for *Pinus* (ANOVA; $F_{6,53}$ = 2.389, p = 0.0407) where when only EMF were present, g_s was higher for *Pinus* in heterospecific compared to conspecific competition, but when both mycorrhizal types were present, g_s was lower for *Pinus* in heterospecific compared to conspecific competition (Fig. S3). Together, these data indicate that AMF helped *Baccharis* compete with *Pinus* for water resources, thus potentially helping to limit the growth of *Pinus* where AMF were present.

Whereas EM colonization declined with increasing heterospecific competitor density (linear mixed effects; marginal R^2=0.237, slope=-0.03566, p=0.0009; Fig. S1a), EMF colonization rates remained consistent with an increasing density of conspecific competitors (linear mixed effects; marginal R^2=0.237, slope=-0.0004, p=0.9636), suggesting that the presence of con-mycorrhizal hosts facilitated conspecific colonization. *Pinus* biomass and P and N uptake were positively correlated with EMF colonization (linear mixed effects; marginal R^2=0.477, slope=0.820, p<0.0001; linear mixed effects; marginal R^2=0.464, slope=1.7233, p=0.0006; Fig. S1b; linear mixed effects; marginal R^2=0.440, slope=5.0903, p= 0.0058; Fig. S1c, respectively). δ^{15}N declined with increasing EMF colonization (linear mixed effects; marginal R^2=0.157, slope=-4.3727, p=0.0465; Fig. S1d), suggesting that hosts were either outsourcing N uptake to fungal

partners as lighter isotopes (lower δ^{15}N values) were likely being passed from fungal mutualists to hosts, and/or that different N sources were being accessed.

To integrate the diversity of mycorrhizal effects on plant growth and resource use, we utilized a recent derivation of modern coexistence theory to predict how mycorrhizal fungi might mediate processes of plant coexistence[29] (Fig. 5, Table 1). In the absence of mycorrhizal fungi, our models predicted that *Pinus* has a strong fitness advantage against *Baccharis* (f_{Pi}/f_{Ba} = 1.6670). This effect was largely driven by the low sensitivity of *Pinus* to competition from either species (α_{PiBa}= -0.0619 and α_{PiPi} = -0.0591) relative to *Baccharis* (α_{BaPi}= -0.0994 and α_{BaBa} = -0.1022) in this treatment. Adding each mycorrhizal type promoted the fitness of its host: EMF slightly affected fitness ratio in favor of *Pinus* (f_{Pi}/f_{Ba} = 1.8100), while AMF reversed the fitness hierarchy in favor of *Baccharis* (f_{Pi}/f_{Ba} = 0.8234). Finally, when both mycorrhizal types were present, we observed nearly equal fitness between hosts (f_{Pi}/f_{Ba} = 0.9597). Meanwhile, niche difference was lowest in the nonmycorrhizal treatment (1-ρ = 0.0090), followed by the EMF treatment (1-ρ = 0.0716), which in both cases was insufficient for coexistence due to strong fitness imbalances. On the other hand, niche difference was higher in the AMF+EMF treatment (1-ρ = 0.1597) and highest in the AMF treatment (1-ρ = 0.2681), both of which were sufficient for coexistence. These differences in the treatments involving AMF were largely driven by *Baccharis*'s greatly reduced sensitivity to heterospecific competition (α_{BaPi}= -0.0444 in the AMF+EMF and α_{BaPi}= -0.0363 in the AMF treatment versus α_{BaPi}= -0.0994 in the nonmycorrhizal treatment). Using non-parametric bootstrapping to understand the effect of experimental variation on our inferences, we found considerable uncertainty in niche/fitness metrics and inferred coexistence outcomes (Figure 5; Table 1) due to underlying demographic variation captured by our experimental biomass measurements. Nonetheless, results from the bootstrapping distribution support our inference that AMF may create the possibility of coexistence in this system: coexistence was predicted in 60% of bootstrap samples for the AMF treatment, compared to 42% from AMF+EMF treatments, and only 0.83% and 0.67% in the nonmycorrhizal and EMF treatments, respectively (Table S1).

Discussion

Microbial communities are critical to the function of diverse ecosystem processes[57]. Within plant roots, microbial mutualists, especially mycorrhizal fungi, mediate host access to key limiting

329 nutrients and have important repercussions for plant growth[2]. By simultaneously measuring the
330 stabilizing and equalizing effects of mycorrhizal fungi on plant competition, we provide a
331 framework for investigating and predicting how the presence of different types of mycorrhiza
332 (AMF and EMF) regulate processes of plant coexistence. In particular, we find that EMF enable
333 hosts to maintain heterospecific exclusion. While AMF boosted host competitive ability, they also
334 promoted stabilizing effects that were large enough to increase the frequency of coexistence
335 predicted between the two hosts in this system. The presence of both types of mycorrhiza nullified
336 fitness differences between hosts, but stabilizing forces were dampened from the AMF-only
337 treatment. As a result, in the AMF+EMF treatment, predictions for coexistence were slightly less
338 favored compared to AMF alone. The results of our study demonstrate that different mycorrhizal
339 fungi can fundamentally alter plant competitive strategies and thus should be considered as
340 potential explanations for community assembly patterns observed in natural systems[21,22].
341 A number of recent studies have demonstrated that forest stands tend to be dominated by
342 trees of a single mycorrhizal type[13,30], perhaps the most extreme case of which is monodominant
343 EMF tree stands that occur in otherwise diverse (and AMF-dominated) tropical rainforests[12,58].
344 Previous studies have provided evidence that such differences can arise from feedback loops. For
345 example, positive feedbacks can develop when EMF trees with recalcitrant litter modify soil
346 nutrients in a way that favors EMF[12]. Similarly, while susceptibility to host-specific pathogens can
347 create negative feedbacks that promote diverse AMF tree communities[15,31,59], EMF provide a
348 physical shield that reduces pathogen-induced negative feedbacks[60]. In the present study, we used
349 sterilized and homogenized soil to isolate the nutrient and growth benefits of mycorrhiza on
350 dynamics of plant competition and coexistence. Consequently, our results add to this picture by
351 showing that intrinsic demographic differences may arise from EMF and AMF, even in the absence
352 of external factors such as leaf chemistry or soil pathogens. While our model predicts coexistence
353 in the presence of AMF, we demonstrate how the tendency of EMF to promote host-specific
354 growth and decrease conspecific competition is likely a major contributor to EM monodominance,
355 especially where the viability or density of AMF inoculum is low, for example following fire[61].
356 Though our study was not designed to test why differences in negative conspecific density
357 dependence arise between plant associations with AMF and EMF, there are some well-established
358 biological differences between mycelial network potential and dispersal capacity between these
359 mycorrhizal types that may explain these observations. EMF produce extensive extra-radical

mycelium that can link root systems[38] and may translocate nutrients over large scales[62]. While there is debate about the extent to which EMF transfer nutrients between hosts[63], the low sensitivity of EMF-associated *Pinus* to conspecific competition may be explained by these mycorrhizal networks. For example, at low competitor densities, EM colonization declined with increasing heterospecific competitor density, however, colonization was maintained and potentially weakly facilitated with conspecific competition. Thus, greater EMF host density may enhance host colonization (and subsequently, host growth) by enabling the development of more robust mycorrhizal networks[64,65]. In contrast, while *Baccharis* growth was quite responsive to AMF colonization, AMF also intensified conspecific competition. Findings of AMF disfavoring conspecific growth have been reported in other systems[31,60]. Our data indicate that by enhancing host growth, AMF also intensify conspecific competition, disfavoring monodominance. While AMF networks are not as well studied, these networks are generally considered less robust than those formed by EMF[63]. Consequently, while EMF networks may facilitate conspecific colonization and access to nutrients, AMF colonization may better promote individual host growth, thus exacerbating conspecific nutrient stress. Recent work also suggests that coordinated evolutionary strategies between plant traits and mycorrhizal fungi[66]. This evolutionary coordination may extend beyond foliar or root traits to life history strategies[67]. For example, EMF hosts are perhaps adapted to the more limited availability of EMF partners in landscapes, employing a strategy of resisting diverse types of competition, but growing very little in the absence of EMF (the "waiting for the fungi" hypothesis[68]). By contrast, AMF are more broadly distributed[3,4], conceivably enabling plants to more readily depend on them for their growth benefits, but with less capacity for functional differentiation.

Though mycorrhizal fungi are broadly known to improve host growth through increased nutrient uptake, we show the potential for mycorrhizal diversity to facilitate coexistence through niche partitioning (i.e. the "mutualistic niche"[19,34]). Our results are consistent with previous work, with EMF increasing plant access to organic nutrients that are otherwise not plant-available[6], and AMF generally improving P uptake relative to N[69]. However, linking these differences to coexistence depended on the nuances of nutrient uptake in different competitive scenarios. For example, N uptake conferred to *Pinus* by EMF was relatively insensitive to the presence of competitors. Thus, while a large literature has developed around the capacity for EMF to access novel organic N sources relative to AMF[3,12,30,70–72], EMF may simply be better all-around N

391 competitors. In contrast, while AMF promoted P uptake for *Baccharis*, they also intensified
392 conspecific competition for nutrients. However, when both mycorrhizal types were present, we
393 found that this facilitated niche differentiation, promoting uptake of N and P for *Baccharis* in
394 heterospecific relative to conspecific competition. Our $\delta^{15}N$ results indicate that while AMF-hosts
395 enhance the draw-down of inorganic N in conspecific competition[69,73], EMF potentially enabled
396 *Pinus* competitors to access organic N, thereby relieving competition for inorganic N. While our
397 study used a single AMF plant and fungus, these host-specific effects on nutrient and competition
398 are consistent with similar experiments showing that increased mycorrhizal diversity leads to
399 higher plant diversity[32]. A better link between specific fungal genes and patterns of host nutrient
400 uptake during competition will help to connect mycorrhizal diversity to observed diversity in plant
401 communities.
402 Our measurements of plant water use based on g_s also demonstrated how AMF might help
403 *Baccharis* better compete for water resources, as g_s declined for *Pinus* when growing in
404 competition with *Baccharis* only when AMF were present. AMF have recently been shown to
405 transport water to host plants[5], highlighting an important, but less well studied aspect of the
406 mycorrhizal niche. The ways in which mycorrhizal fungi impact plant competition for water is an
407 important area of future research.
408 Adding to our understanding of the role of plant-soil feedbacks in shaping plant
409 communities, recent theoretical work has highlighted the importance of identifying how these
410 feedbacks arise from specific underlying mechanisms[74]. By better understanding the dynamics of
411 the mutualistic and pathogenic organisms responsible for feedbacks[18,75,76], researchers may be
412 better able to classify and predict the consequences of feedbacks. Our data add to a growing
413 recognition that apparently complicated dynamics contributing to coexistence can be better
414 understood by identifying underlying mechanisms[77]. In conducting an empirical study to
415 investigate both the equalizing and stabilizing mechanisms of mycorrhizal fungi on coexistence,
416 we were able to better understand some of the patterns which occur in nature (e.g. EMF
417 monodominance). Although our study focused on local interactions between plants and their
418 mycorrhizal partners, not on how these interactions might vary over time and space, our results
419 also provide a starting point from which future work could address the additional stabilizing role
420 of temporal or spatial heterogeneity in nutrients or mycorrhizal fungi[23,26]. Additionally, while we
421 have implicitly focused on competition from the plant perspective, direct competition for resources

must occur between AM and EM fungi and is a topic requiring further investigation[78]. We emphasize that modern coexistence theory offers important tools for connecting mycorrhizal effects to their consequences for ecological communities[29,79,80].

While we cannot generalize as to whether all EMF and AMF alter host demography in this way more globally, the principles that we have identified will apply when fungi are host-specific and functionally differentiated, as they generally appear to be for plants forming relationships with AMF and EMF[60,81,82]. Our findings should also apply to differences within plants that share the same mycorrhizal type and have host-specific fungi[32], or when shared fungal partners have host-specific effects on niche or fitness differences. In the present experiment, we were able to examine the relationships between two co-dominant hosts in a relatively simplified community, however, approaches which are able to assess coexistence in multispecies communities will be important in better understanding the role of mycorrhizal fungi in landscape-scale dynamics of plant assembly[83]. Because, as our results show, plant competition depends on the composition of the local mycorrhizal community, whether plant species successfully migrate to new climates or persist in changed environments should depend on both their own physiological capabilities but also the ecological details of local partnerships with mycorrhizal fungi. More generally, because microbial communities are not evenly distributed across landscapes or environments[84,85], results from plant competition studies may be misleading without explicit consideration of the spatial distribution of mycorrhizal fungi.

Materials and Methods

Study system

Point Reyes National Seashore (Point Reyes), USA is located in coastal Northern California characterized by a Mediterranean climate, maritime fog in the summer[86] and a high severity fire regime[47]. Dominant plant species include coyote brush (*Baccharis pilularis* DC), Bishop pine (*Pinus muricata* D. Don), blue blossom (*Ceanothus thyrsiflorus* Eschsch.), and Douglas-fir (*Pseudotusga menziesii* [Mirb.] Franco)[47]. For the present study, we specifically chose to work with *Baccharis* and *Pinus* as: (1) these two plant species associate with different mycorrhizal types (*Baccharis* associates with AMF and *Pinus* associates with EMF); (2) the dynamics of EMF dispersal are well-studied at this site[84,85]; (3) the presence of EMF have previously been linked to increased competitive ability of *Pinus* with *Baccharis*[8]. Additionally, Point Reyes is dominated by

only a few plant species, which allows us to articulate the mechanisms of plant species coexistence more fully across this landscape. In this way, Point Reyes acts as a natural lab in which we can test the role of mycorrhizal fungi in plant ecological dynamics.

Seed origin and germination

Baccharis seeds were collected from Point Reyes in 2018 from various location at Point Reyes and multiple individual plants. The achene was removed from the pappus via physical perturbation, separated based on density, and stored at 4°C prior to germination. *Pinus* seeds were ordered from Sheffield's seeds, which were sourced from California-based populations, and stored at 4°C prior to germination. Seeds were germinated in 6 cohorts as both planting and harvesting seedlings took approximately 6 and 8 weeks, respectively. *Pinus* seeds were soaked in distilled water in a covered auto stirrer for 24 hours. Seeds were then soaked in 30% H_2O_2 for 30 minutes, washed thoroughly in distilled water, and then let to soak in distilled water in a covered auto stirrer for an additional 24 hours. Seeds were then plated onto 1% water agar and placed in growth chamber with a 16-hour photoperiod to germinate. *Baccharis* seeds are very small and fragile, and we had little success recovering them from sterilization trials. Consequently, we chose to plate *Baccharis* seeds directly onto water agar as above and allowed these seeds to germinate in a 16-hour photoperiod. Seeds were allowed to germinate for approximately 7 days prior to planting.

Experimental design and planting

This experiment utilized a fully factorial design with 4 mycorrhizal treatments, 2 focal plant species, conspecific/heterospecific competition, and 4 different competition densities (Fig. 1). This experimental design (across the different microbial treatments, densities, and competitors) was selected as it enabled us to employ recently developed models which incorporate microbial communities into modern coexistence theory[29,87,88], allowing us to explicitly test the role of EMF and AMF in plant species coexistence. With each focal seedling, we planted 0, 1, 4, or 8 either conspecific or heterospecific competitors. Each planting combination was performed across 4 different mycorrhizal treatments: (1) no mycorrhizal fungi, (2) EMF, (3) AMF, (4) both EMF and AMF. Each unique combination was replicated 6 times for a total of 2 focal plant species * 4 planting densities * 2 competitor types * 4 mycorrhizal treatments * 6 replicates = 384 pots.

Field and biological collections

Field soils were collected from Point Reyes in November 2019 from a mixed scrub-grassland site previously established to have a low density of ectomycorrhizal fungi (at least 4.2 km away from the nearest edge of *Pinus* stands)[84]. We specifically selected EMF-free soils as EMF spores are often more heat resistant and thus more likely to carry over into our different mycorrhizal treatments than AMF spores, even after autoclaving[89]. Soils were collected using ethanol-sterilized shovels and stored at 4°C. To characterize the nutrient availability from these soils, we planted PRS probes (plant root simulators; Western Ag. Innovations Inc., Saskatoon, Saskatchewan) in the same pots used for the experiment for 9 weeks; soil nutrient data can be found in Table S2.

For the EMF inoculum, we used *Suillus pungens*, an EMF species with the capacity for long-distance dispersal, which is found especially on young *Pinus* seedlings and trees[84,85]. In this way, *S. pungens* likely plays a role in the establishment of *Pinus* stands throughout Point Reyes. Different populations of *Suillus pungens* fruiting bodies were collected from San Francisco and Marin counties in CA, USA and prepared for spore collection (see section on Mycorrhizal treatments below). DNA was extracted from fruiting body populations using Extract 'N Amp buffer and the ITS region was sequenced using fungal-specific primers ITS-1F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS-4 (5′-TCCTCCGCTTATTGATATGC-3′) to ensure that collections were from the target species[90]. For AMF inoculum, we selected *Rhizophagus intraradices*, which was previously found to be a top colonizer of *Baccharis*[91]. A total of 2 L of AMF inoculum was obtained from the International Collection for (Vessicular) Arbuscular Mycorrhizal Fungi (INVAM; *R. intraradices* Accessions: WV115A, WV116, WV229, SW101; combined and well-mixed).

Soil preparation, mycorrhizal treatments, and growth conditions

Field collected soils were sieved to 2 mm to homogenize soils and remove rocks and coarse roots. Soils were placed into autoclave containers and spread about 4 cm deep. Autoclave tape was placed in Eppendorf tubes at the lowest soil layer to confirm sterilization across the soil depth. After autoclaving soils, we allowed them to rest for 24 hours and then repeated the same autoclave process. Soils were then mixed 50:50 with autoclaved coarse sand and this mixture was used for planting.

Pots were randomized across all treatments and planted in this randomized design over the course of 6 weeks. For planting, we used Deepots (Stuewe & Sons, Tangent, OR, USA; D27L, volume 444 ml) with polyfill placed at the bottom of each pot and the filled with the 50:50 mix of autoclaved field soils and sand. AMF inoculum consisted of a mixture of spores, fine roots, and soil obtained through trap culture (grown using sudangrass, *Sorghum drummondii* at INVAM). We chopped fine roots into smaller 1-2 cm fragments and homogenized the inoculum prior to adding it to our AMF+ treatments. Because we were adding roots and soils to these AMF pots, we wanted to ensure that the potential effects seen in the experiment were not related to a fertilization effect from adding this root mixture or due to other components of the microbial community present in the AMF inoculum. Accordingly, for AMF- treatments, we used a bacterial/viral wash to collect these components of the AMF inoculum and then autoclaved the remaining root and soil slurry using 2*40-minute cycles to kill the AMF and the autoclave slurry and bacterial/viral wash were added to AMF- treatments in equivalent volumes to the live inoculum. To do so, we first filtered the inoculum in a series of steps; first, through a 20 µm mesh overnight and then, through filter paper (#1 Whatman) for about 8 hours (total volume was allowed to filter). The 20 µm mesh was selected as this diameter of filter should remove most species of fungal spores and many hyphae. The #1 Whatman filter maintains an approximately 10 µm diameter, which was aimed to remove additional hyphal fragments or any AMF spores that might have gotten through. The filtrate was then kept at 4°C prior to using for inoculations. The control inoculum (what remained after filtering) was autoclaved for 30 minutes, allowed to sit overnight, and then re-autoclaved the next day. The control inoculum was then allowed to dry at 60°C overnight to help reduce any phytotoxic compounds that might have been released through autoclaving process. All pots that did not receive live AMF inoculum (the EMF and non-mycorrhizal treatments) received an equivalent volume of autoclaved inoculum plus the bacterial filtrate.

For treatments with live AMF, 5 mL of AMF inoculum was added to each pot and mixed into the top layer of soil. For treatments that did not include live AMF, we added 5 mL of sterilized AMF inoculum. In addition to the sterilized AMF inoculum used in non-AMF treatments, we added 2 mL of the bacterial filtrate to these pots and treatments with live AMF received 2 mL of DI water as a control. *S. pungens* spores were obtained from field collections by placing the hymenial layer of the fruiting body onto tin foil, letting the spores drop, and then collecting them into distilled water and storing at 4°C prior to inoculation. Because EMF spores were collected

into distilled water, no root or soil biomass was added for these treatments and the relative volume of other microbes on collected on the spores was assumed to be quite low. Consequently, for EMF-treatments, we used an equivalent volume of DI water as a negative control. We added 2 mL of EMF inoculum at a concentration of 500,000 spores per mL to the appropriate pots. For treatments that did not include EMF, we added the equivalent volume of DI water.

Germinated seedlings were planted into each Deepot using sterilized forceps with the appropriate focal plant and competitors. Seedlings were monitored and individuals that did not survive transplantation were replanted for up to 2 weeks following initial cohort planting. Seedlings were grown in a controlled-environment walk-in growth chamber (R.W. Smith & Co., San Diego, CA, USA) for 8 months. Relative humidity was set at 60.0% and temperature was at 20.0°C for an 18-hour photoperiod from 5a to 11p. Pots were kept well-watered by watering plants with approximately 10 mL of tap water three times per week.

Plant harvesting

For each pot, aboveground biomass was separated from the belowground biomass for focal plants and competitors. For *Pinus* seedlings, we assessed extent of EMF colonization for all treatments by sectioning entire fine root systems into small root fragments and counting the number of EMF root tips using the grid intersect method[8]. For *Baccharis*, approximately 0.25-0.5 g of fine roots were collected from a random subset of focal seedlings throughout the harvest (both where live AMF and sterilized AMF inoculum were added) to assess AMF colonization. The wet mass of the *Baccharis* total root system was recorded along with the wet mass of the fine roots subset for assessment of AMF colonization and wet:dry biomass ratios were used to estimate the total dry root biomass for *Baccharis* root systems as described below. Fine roots for assessment of AMF colonization were stored in 70% ethanol and kept at 4°C prior to clearing and staining (enumerated below). For the high-density conspecific treatments, it was often difficult to distinguish if roots belonged to competitors or focal plant, particularly for the conspecific competition treatments. In these cases, the roots remaining after separating the competitor seedlings from the focal plant root system were weighed and then that mass was subdivided based on the total number of competitors plus the focal plant. Root systems, stems, and leaf tissue for focal plants and competitors were placed in separate coin envelopes and dried at 65°C for at least one week to ensure that they were fully dried. Dried biomass was measured for each of these components on an electronic balance

with accuracy to 0.001 g (model XS205, Mettler Toledo, Columbus, OH, USA). After these steps were completed, AMF root colonization was measured by clearing roots in 10% KOH in a 20-minute autoclave cycle, acidifying roots in 2% HCl for 30 minutes, and boiling roots in Trypan blue dye solution for 30 minutes[92]. Roots were left in DI water for at least 5 days to remove excess dye prior to fixing the roots on glass slides with Polyvinyl-Lacto-Glycero (PVLG). The gridline-insect method was then used to access percent mycorrhizal root length[93].

Nutrient content and stable isotope analyses

Dried leaf material was used to assess carbon ($\delta^{13}C$ and % C) and nitrogen ($\delta^{15}N$ and % N) content and total leaf nutrient content. Briefly, leaf samples were ground into a fine powder and approximately 7 mg of dried leaf material were weighed into tin capsules for analysis using an elemental analyzer/continuous flow isotope ratio mass spectrometer at the University of California, Berkeley Center for Stable Isotope Biogeochemistry. This facility uses an Isoprime100 continuous flow mass spectrometer using dual-element analysis mode interfaced with a CHNOS elemental analyzer. Long-term precision for C and N isotope determinations is ±0.10‰ and ±0.20‰, respectively. The $\delta^{13}C$ results were reported in values relative to the Vienna Pee Dee Belemnite standard and the $\delta^{15}N$ measure of the ratio of the two stable isotopes of nitrogen, 15N:14N and the standard is atmospheric N^2 (0.3663 atom% ~ ^{15}N).

Dried and homogenized samples were also used to determine leaf P content at University of California, Davis Analytical Lab using a closed vessel microwave digestion in nitric acid/hydrogen peroxide and Inductively Coupled Plasma Atomic Emission Spectrometry (ICP-AES). Long-term method detection limits for P at this lab is 0.01%.

Determination of leaf-level gas exchange

After 8 months, seedlings were harvested by cohort for a period of approximately 6 weeks. Prior to cutting stems, leaf-level gas exchange was determined for each focal plant using a LI-COR 6800 with the conifer chamber attachment (LI-COR, Lincoln, NE, USA). Conifer chamber conditions were set to match the growth chamber conditions as closely as possible where chamber relative humidity was set to 60%, CO_2 concentrations were set at 400 ppm, light was set at 1000 µmols/m^2s, and the fan speed was set at 5000 rpm. As the leaves for both species were not able to fill the entirety of the chamber, leaf area encapsulated by the chamber was marked using permanent

marker and this leaf area was subsequently digitally scanned for determination of leaf area using a silhouette leaf area method[94] and Leafscan v1.3.21[95]. Where Leafscan was unable to process photos due to continuity of leaf area or errors identifying leaf boundaries, leaf area was measured using ImageJ2[96] and the scale bars from the Leafscan guide used for the digital scans. These values were then adjusted in the LI-COR 6800 datasheet to reflect the actual leaf area measured with the LI-COR 6800. To try to minimize differences in measurement error, we standardized the amount and type of tissue measured as much as possible, encapsulating as much of the terminal end of the *Pinus* shoots as possible and encapsulating ~5 of the most terminal leaves/stem of the *Baccharis* seedlings.

Statistical analysis

All data were analyzed in R version 4.2.2[97]. Prior to analysis, to correct for the small proportion fresh root mass that was needed to assess AMF colonization on a subset of samples for *Baccharis*, we ran a linear regression between wet:dry fine root mass to then back-calculate the corrected total dry mass for these plants. These data corrections are all included in our analysis pipeline.

Our first expectation was that, in the absence of competition, host-specific mycorrhizal fungi would increase plant growth, which is often a proxy for overall plant fitness. To assess this, we compared total plant biomass data across mycorrhizal treatments using an ANOVA with the 'aov' function. We also expected that mycorrhizal fungi would increase host access to soil nutrients, expanding host's nutritional niche. We tested this prediction by comparing plant nutrient status across mycorrhizal treatments. Differences within treatments were then assessed with a post-hoc Tukey's HSD test using the 'TukeyHSD' function.

Because EMF form more robust mycorrhizal networks[4,63] and potentially enable hosts to access novel sources of N , our second prediction was that EMF would reduce the strength of conspecific relative to heterospecific competition. Additionally, we predicted that AMF would have the opposite effect, improving host growth in isolation, but exacerbating conspecific competition as conspecific hosts would become better competitors for the same pool of nutrients[39]. To test this prediction, we first employed linear mixed effects models via the 'lmer' function from the lme4 package[98], allowing us to compare changes in focal plant biomass across increasing densities of both conspecific and heterospecific competitors. For these models, we included a random effect of tray location in the growth chamber to account for microclimatic variability

within the growth chamber. Additionally, because the y-intercept for these linear mixed-effects models represented the condition when no competitors were present, we forced a shared intercept and only included an interaction term between competitor density and competition treatment (heterospecific versus conspecific competition)[88]. The biomass data for this study were right-skewed, so prior to fitting these models, the data were transformed by taking the square root of plant total biomass for all models and model residuals were visually inspected to for normality[88].

To test the role of mycorrhizal fungi in modifying niche and fitness differences of their hosts simultaneously, we used the MCT framework to examine the response of focal plant biomass to both con and heterospecific competition across increasing competitor densities relative to the biomass of the plant growing without mycorrhizal fungi and with no plant competition. We calculated competition coefficients according to the following formulas[29]:

$$\alpha_{\text{BaPi, MYCO}} = \frac{M_{BaPi,MYCO} - M_{Ba,0,None}}{\Delta N_{Pi} * M_{Ba,0,None}} \quad (1)$$

$$\alpha_{\text{BaBa, MYCO}} = \frac{M_{BaPi,MYCO} - M_{Ba,0,None}}{\Delta N_{Ba} * M_{Ba,0,None}} \quad (2)$$

Here, (Ba) is *Baccharis* as the focal plant and (Pi) is *Pinus* as its heterospecific competitor, ΔN_{Ba} and ΔN_{Pi} respectively represent the change in density of competitors Ba and Pi relative to the no competitor treatment (in our case, we used the values for our highest density treatment where N=8). $M_{\text{Ba,0,None}}$ represents the biomass of a single focal plant growing in the nonmycorrhizal treatment; α_{BaPi} and α_{BaBa} represent the per capita effect of *Pinus* on *Baccharis* and *Baccharis* on *Baccharis*, respectively. The values for focal plant *Pinus* (Pi) can be calculated analogously across each of the mycorrhizal treatments (MYCO; no mycorrhizal fungi, AMF, EMF, and AMF&EMF). The choice to use the nonmycorrhizal treatment as a reference assumes the availability of mutualists to be part of the density-dependent competitive effect of plants (i.e. PSF; mutualists are nearly absent when their hosts are rare)[29]. On the other hand, using the single individual biomass from the same inoculum treatment as a reference assumes that mutualist availability is fixed and thus not part of density-dependent competitive effects (i.e. mutualists remain just as available even when their hosts are rare). As we were interested in the conditioning effect in the former scenario, we use the nonmycorrhizal treatment as a reference here. In addition to this approach, we also tried calculating alpha values from our regression analysis using the full competition gradient[88]. However, we found

poor model fits for some treatments, so we instead applied the formula with solo/competitor biomass using the maximum number of competitors as this provides the best approximation of competitive dynamics near the monoculture equilibrium[29].

Assuming that plant performance responds linearly to competitor density[88], we were then able to we were then able to use a modified model from modern coexistence theory to calculate niche overlap (ρ) and fitness differences $\left(\frac{f_{Pi}}{f_{Ba}}\right)$ across these treatments based on the calculated α values[88]:

$$\rho = \sqrt{\frac{\alpha_{BaPi}\alpha_{PiBa}}{\alpha_{BaBa}\alpha_{PiPi}}} \quad (3)$$

$$\frac{f_{Pi}}{f_{Ba}} = \sqrt{\frac{\alpha_{BaPi}\alpha_{BaBa}}{\alpha_{PiBa}\alpha_{PiPi}}} \quad (4)$$

where coexistence occurs when $\rho < \frac{f_{Pi}}{f_{Ba}} < \frac{1}{\rho}$ and an alternative stable state occurs when $\frac{1}{\rho} < \frac{f_{Pi}}{f_{Ba}} < \rho$. These data were then plotted using the original MCT formulation of niche and fitness differences[99]. We evaluated the effect of experimental variation on coexistence metrics and outcomes using non-parametric bootstrapping. Stratifying by all levels of the experimental design, we sampled 10,000 bootstrap replicates and recalculated competition coefficients, niche difference, fitness ratio, and predicted outcome using the resampled data, generating 95% confidence intervals using the percentile method[100]. We then visualized the distribution of outcomes (the bootstrapping distribution) as contours on the MCT phase plane plot and tabulated the proportion of coexistence outcomes for each treatment[35,101].

In addition to calculating these niche and fitness differences within the MCT framework, we also examined the possible biological basis for niche and fitness differences by measuring leaf nutrient content and leaf-level photosynthesis. These data were compared using ANOVA and post-hoc tests as described above. Additionally, while we were unable to assess AMF colonization across all treatments due to logistical constraints, we were able to compare rates of EMF colonization across mycorrhizal and competition treatments using this linear mixed-effects modeling approach, enabling us to compare how rates of colonization corresponded to nutrient uptake and were impacted by the different competition treatments.

Data Availability: All data are available via the Dryad Digital Repository: https://doi.org/10.5061/dryad.rxwdbrvjb

Code Availability: All code for analysis is available via Github: https://github.com/ClaireWilling/MycorrhizaCoexist.git

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Author Contributions Statement: C.E.W. and K.G.P. planned and designed the research. C.E.W. and K.G.P. conducted field work and C.E.W., J.J.Y., A.M.C. conducted the lab work. C.E.W. analyzed and interpreted the data with critical contributions from J.W., J.J.Y., A.M.C., and K.G.P. The manuscript was written by C.E.W. and all coauthors provided important contributions and critical revisions. All authors approve of the final version of this manuscript.

Competing Interests Statement: The authors declare no competing interests.

Tables

Table 1. Modern coexistence theory interaction coefficients (α) and niche (1-ρ) and fitness differences $\left(\frac{f_{Pi}}{f_{Ba}}\right)$ calculated from Ke and Wan (2020) based on n=8 competitors. (Ba) refers to *Baccharis* and (Pi) refers to *Pinus*, where α_{BaPi} refers to the growth of *Baccharis* growing in heterospecific competition and where α_{BaBa} refers to the growth of *Baccharis* growing in conspecific competition. We sampled 10,000 bootstrap replicates and recalculated competition coefficients, niche differences, fitness ratios; 95% confidence intervals using the percentile method[102].

Mycorrhizal Treatment	α_{BaBa}	α_{BaPi}	α_{PiBa}	α_{PiPi}	Fitness Ratio $log\left(\frac{f_{Pi}}{f_{Ba}}\right)$	Niche Difference log(1-ρ)
None	-0.1022 ± 0.0058	-0.0994 ± 0.0070	-0.0619 ± 0.0102	-0.0591 ± 0.0199	0.5110 ± 0.3456	-0.0090 ± 0.7531
EMF	-0.1034 ± 0.0039	-0.1119 ± 0.0078	-0.0530 ± 0.0157	-0.0666 ± 0.0201	0.5931 ± 0.3687	0.0716 ± 0.3909
AMF	-0.0889 ± 0.0113	-0.0363 ± 0.0196	-0.0790 ± 0.0218	-0.0602 ± 0.0168	-0.1943 ± 0.4395	0.2681 ± 0.3411
AMF& EMF	-0.0915 ± 0.0129	-0.0444 ± 0.0176	-0.0801 ± 0.0192	-0.0551 ± 0.0175	-0.0411 ± 0.4414	0.1597 ± 0.3598

Figure Captions

Fig. 1. Experimental design for quantifying competitive ability[29,87]. The two focal species were grown with either 0, 1, 4, or 8 competitors; competitors were either of conspecific (identical to the focal species) or heterospecific identity (the competitor species). This design was fully factorial across 4 different mycorrhizal treatments as shown above with n=6 replicates. Art by Karly Nobuko Chin.

Fig. 2. The effects of mycorrhizal fungi on plant growth and nutritional niche in the absence of competition. (a) Total plant biomass was significantly different across mycorrhizal treatments for both *Baccharis* (P=0.0030) and *Pinus* (*P*=0.0362) based on ANOVA (n=6). (b) mg of leaf P per plant; %P was similarly standardized to total leaf dry biomass. (c) mg of leaf N per plant; %N was standardized to total leaf dry biomass in order to determine total plant N accumulated through the experiment across treatments. (d) N:P ratios by treatment; 15:1 is generally considered the optimal N:P ratio for plant growth and plants tend to become either N limited below 14:1 or P limited above 16:1. For each plot, the boxplots show the 25–75% quantile range and the 50% quantile center line. Whiskers depict data points within 1.5 times the interquartile range. Different letters indicate significant differences between mycorrhizal treatments ($P < 0.05$) according to *post hoc* Tukey HSD tests (n=6) for each plant host species, respectively.

Fig. 3. The role of mycorrhizal fungi in the competitive dynamics between plant species. Biomass is plotted against number of competitors and colors represent competition treatment (no competitors, conspecific competitors, or heterospecific competitors). Regression lines are shown from linear mixed-effects models for each treatment and shading represent 95% C.I. bands; includes jittered data points (n=6).

Fig. 4. The effects of mycorrhizal fungi on plant nutritional niche under different types of competition. (a) mg of leaf N per plant; % N was standardized to total leaf dry biomass in order to determine total plant N accumulated through experiment across treatments. (b) mg of leaf P per plant; %P was similarly standardized to total leaf dry biomass. (c) $\delta^{15}N$ across mycorrhizal treatments and competition types. (d) N:P ratios by treatment; 15:1 is generally considered the optimal N:P ratio for plant growth and plants tend to become either N limited below 14:1 or P limited above 16:1. Each boxplot shows the 25–75% quantile range and the 50% quantile center line. Whiskers depict data points within 1.5 times the interquartile range. Different letters indicate significant differences ($P < 0.05$) across mycorrhizal treatments and competition type (no competitors, 8 heterospecific competitors, 8 conspecific competitors) according to *post hoc* Tukey HSD tests (n=6) for each host plant species, respectively.

Fig. 5. Symbiotic mutualisms help to structure dynamics of plant coexistence. (a) Results are visualized on the parameter space of niche difference (-log ρ, x-axis) and fitness ratio (log f_{Pi}/f_{Ba}, y-axis); note here that we have used log-transformed versions of these metrics to improve visualization[102]. Areas shaded in gray represent where coexistence versus priority effects are predicted to occur and areas where *Pinus* versus *Baccharis* are predicted to occur are labeled in the top and bottom portions of the phase plane. (b) A stacked bar plot displaying the proportion of predicted outcomes; we sampled 10,000 bootstrap replicates and recalculated competition coefficients, niche difference, fitness ratio, and predicted outcome using the resampled data, generating 95% confidence intervals using the percentile method[102]. When no mycorrhizal fungi are present or when only EMF are present, *Pinus* is predicted to invade. The addition of AMF, however, drives the system towards stable coexistence through both equalizing (decreasing the fitness differences between hosts) and stabilizing forces (increasing niche differentiation between hosts).

References:

1. Vandenkoornhuyse, P., Quaiser, A., Duhamel, M., Le Van, A. & Dufresne, A. The importance of the microbiome of the plant holobiont. *New Phytologist* **206**, 1196–1206 (2015).
2. Smith, S. E. & Read, D. J. *Mycorrhizal Symbiosis*. (Academic Press, 2010).
3. Steidinger, B. S. *et al.* Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature* **569**, 404–408 (2019).
4. van der Heijden, M. G. A. van der, Martin, F. M., Selosse, M.-A. & Sanders, I. R. Mycorrhizal ecology and evolution: the past, the present, and the future. *New Phytologist* **205**, 1406–1423 (2015).
5. Kakouridis, A. *et al.* Routes to roots: direct evidence of water transport by arbuscular mycorrhizal fungi to host plants. *New Phytologist* **236**, 210–221 (2022).

6. Pellitier, P. T. & Zak, D. R. Ectomycorrhizal fungi and the enzymatic liberation of nitrogen from soil organic matter: why evolutionary history matters. *New Phytologist* **217**, 68–73 (2018).
7. Hodge, A. & Fitter, A. H. Microbial mediation of plant competition and community structure. *Functional Ecology* **27**, 865–875 (2013).
8. Peay, K. G. Timing of mutualist arrival has a greater effect on Pinus muricata seedling growth than interspecific competition. *Journal of Ecology* **106**, 514–523 (2018).
9. Wagg, C., Jansa, J., Stadler, M., Schmid, B. & van der Heijden, M. G. A. Mycorrhizal fungal identity and diversity relaxes plant–plant competition. *Ecology* **92**, 1303–1313 (2011).
10. Scheublin, T. R., Van Logtestijn, R. S. P. & Van Der Heijden, M. G. A. Presence and identity of arbuscular mycorrhizal fungi influence competitive interactions between plant species. *Journal of Ecology* **95**, 631–638 (2007).
11. Hoeksema, J. D. *et al.* Ectomycorrhizal Plant-Fungal Co-invasions as Natural Experiments for Connecting Plant and Fungal Traits to Their Ecosystem Consequences. *Front. For. Glob. Change* **3**, 84 (2020).
12. Corrales, A., Mangan, S. A., Turner, B. L. & Dalling, J. W. An ectomycorrhizal nitrogen economy facilitates monodominance in a neotropical forest. *Ecology Letters* **19**, 383–392 (2016).
13. Lu, M. & Hedin, L. O. Global plant–symbiont organization and emergence of biogeochemical cycles resolved by evolution-based trait modelling. *Nature Ecology & Evolution* **3**, 239–250 (2019).
14. Averill, C. *et al.* Alternative stable states of the forest mycobiome are maintained through positive feedbacks. *Nat Ecol Evol* **6**, 375–382 (2022).

15. Laliberté, E., Lambers, H., Burgess, T. I. & Wright, S. J. Phosphorus limitation, soil-borne pathogens and the coexistence of plant species in hyperdiverse forests and shrublands. *New Phytologist* **206**, 507–521 (2015).
16. Bever, J. D. *et al.* Rooting theories of plant community ecology in microbial interactions. *Trends in Ecology & Evolution* **25**, 468–478 (2010).
17. Bever, J. D., Platt, T. G. & Morton, E. R. Microbial Population and Community Dynamics on Plant Roots and Their Feedbacks on Plant Communities. *Annual Review of Microbiology* **66**, 265–283 (2012).
18. Hart, S. P. How does facilitation influence the outcome of species interactions? *Journal of Ecology* **Advance online publication**, (2023).
19. Peay, K. G. The Mutualistic Niche: Mycorrhizal Symbiosis and Community Dynamics. *Annu. Rev. Ecol. Evol. Syst.* **47**, 143–164 (2016).
20. Van Nuland, M. E. & Peay, K. G. Symbiotic niche mapping reveals functional specialization by two ectomycorrhizal fungi that expands the host plant niche. *Fungal Ecology* **46**, 100960 (2020).
21. Chomicki, G., Weber, M., Antonelli, A., Bascompte, J. & Kiers, E. T. The Impact of Mutualisms on Species Richness. *Trends in Ecology & Evolution* **34**, 698–711 (2019).
22. Tedersoo, L., Bahram, M. & Zobel, M. How mycorrhizal associations drive plant population and community biology. *Science* **367**, eaba1223 (2020).
23. Chesson, P. Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and Systematics* **31**, 343–366 (2000).
24. Westoby, M. & Wright, I. J. Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution* **21**, 261–268 (2006).

25. Kraft, N. J. B., Godoy, O. & Levine, J. M. Plant functional traits and the multidimensional nature of species coexistence. *Proc Natl Acad Sci USA* **112**, 797–802 (2015).
26. Barabás, G., D'Andrea, R. & Stump, S. M. Chesson's coexistence theory. *Ecological Monographs* **88**, 277–303 (2018).
27. Song, C., Barabás, G. & Saavedra, S. On the Consequences of the Interdependence of Stabilizing and Equalizing Mechanisms. *The American Naturalist* **194**, 627–639 (2019).
28. Kandlikar, G. S., Johnson, C. A., Yan, X., Kraft, N. J. B. & Levine, J. M. Winning and losing with microbes: how microbially mediated fitness differences influence plant diversity. *Ecology Letters* **22**, 1178–1191 (2019).
29. Ke, P.-J. & Wan, J. Effects of soil microbes on plant competition: a perspective from modern coexistence theory. *Ecological Monographs* **90**, e01391 (2020).
30. Averill, C., Turner, B. L. & Finzi, A. C. Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature* **505**, 543–545 (2014).
31. Bever, J. D. Negative feedback within a mutualism: host-specific growth of mycorrhizal fungi reduces plant benefit. *Proc Biol Sci* **269**, 2595–2601 (2002).
32. van der Heijden, M. G. A. *et al.* Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396**, 69–72 (1998).
33. Bever, J. D. Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New Phytologist* **157**, 465–473 (2003).
34. Afkhami, M. E., McIntyre, P. J. & Strauss, S. Y. Mutualist-mediated effects on species' range limits across large geographic scales. *Ecology Letters* **17**, 1265–1273 (2014).
35. Yan, X., Levine, J. M. & Kandlikar, G. S. A quantitative synthesis of soil microbial effects on plant species coexistence. *PNAS* **119**, e2122088119 (2022).

873 36. Crawford, K. M. *et al.* When and where plant-soil feedback may promote plant coexistence:
874 a meta-analysis. *Ecology Letters* **22**, 1274–1284 (2019).
875 37. Xi, N. *et al.* Relationships between plant–soil feedbacks and functional traits. *Journal of*
876 *Ecology* **109**, 3411–3423 (2021).
877 38. Beiler, K. J., Durall, D. M., Simard, S. W., Maxwell, S. A. & Kretzer, A. M. Architecture of
878 the wood-wide web: Rhizopogon spp. genets link multiple Douglas-fir cohorts. *New*
879 *Phytologist* **185**, 543–553 (2010).
880 39. Hart, M. M., Reader, R. J. & Klironomos, J. N. Plant coexistence mediated by arbuscular
881 mycorrhizal fungi. *Trends in Ecology & Evolution* **18**, 418–423 (2003).
882 40. Endlweber, K. & Scheu, S. Interactions between mycorrhizal fungi and Collembola: effects
883 on root structure of competing plant species. *Biol Fertil Soils* **43**, 741–749 (2007).
884 41. Guo, Y. *et al.* The interspecific competition presents greater nutrient facilitation compared
885 with intraspecific competition through AM fungi interacting with litter for two host plants in
886 karst soil. *Journal of Plant Ecology* **15**, 399–412 (2022).
887 42. Hartnett, D. C., Hetrick, B. A. D., Wilson, G. W. T. & Gibson, D. J. Mycorrhizal Influence
888 on Intra- and Interspecific Neighbour Interactions among Co-Occurring Prairie Grasses.
889 *Journal of Ecology* **81**, 787–795 (1993).
890 43. Marler, M. J., Zabinski, C. A. & Callaway, R. M. Mycorrhizae Indirectly Enhance
891 Competitive Effects of an Invasive Forb on a Native Bunchgrass. *Ecology* **80**, 1180–1186
892 (1999).
893 44. Moora, M. & Zobel, M. Effect of arbuscular mycorrhiza on inter- and intraspecific
894 competition of two grassland species. *Oecologia* **108**, 79–84 (1996).

45. Schroeder-Moreno, M. S. & Janos, D. P. Intra- and inter-specific density affects plant growth responses to arbuscular mycorrhizas. *Botany* **86**, 1180–1193 (2008).

46. Kandlikar (□□□□ □□□□□□□□), G. S., Yan (严心怡), X., Levine, J. M. & Kraft, N. J. B. Soil Microbes Generate Stronger Fitness Differences than Stabilization among California Annual Plants. *The American Naturalist* **197**, E30–E39 (2021).

47. Forrestel, A. B., Moritz, M. A. & Stephens, S. L. Landscape-Scale Vegetation Change Following Fire in Point Reyes, California, USA. *Fire Ecol* **7**, 114–128 (2011).

48. A. Dickie, I. & Reich, P. B. Ectomycorrhizal fungal communities at forest edges. *Journal of Ecology* **93**, 244–255 (2005).

49. Peay, K. G. & Bruns, T. D. Spore dispersal of basidiomycete fungi at the landscape scale is driven by stochastic and deterministic processes and generates variability in plant–fungal interactions. *New Phytologist* **204**, 180–191 (2014).

50. Smith, G. R., Steidinger, B. S., Bruns, T. D. & Peay, K. G. Competition–colonization tradeoffs structure fungal diversity. *The ISME Journal* **12**, 1758–1767 (2018).

51. Harvey, B. J. & Holzman, B. A. Divergent successional pathways of stand development following fire in a California closed-cone pine forest. *Journal of Vegetation Science* **25**, 88–99 (2014).

52. Teste, F. P. *et al.* Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands. *Science* **355**, 173–176 (2017).

53. Simha, A., Pardo-De la Hoz, C. J. & Carley, L. N. Moving beyond the "Diversity Paradox": The Limitations of Competition-Based Frameworks in Understanding Species Diversity. *The American Naturalist* **200**, 89–100 (2022).

54. Horton, T. R., Cázares, E. & Bruns, T. D. Ectomycorrhizal, vesicular-arbuscular and dark septate fungal colonization of bishop pine (Pinus muricata) seedlings in the first 5 months of growth after wildfire. *Mycorrhiza* **8**, 11–18 (1998).
55. Wagg, C., Antunes, P. M. & Peterson, R. L. Arbuscular mycorrhizal fungal phylogeny-related interactions with a non-host. *Symbiosis* **53**, 41–46 (2011).
56. Hobbie, E. A., Macko, S. A. & Shugart, H. H. Insights into nitrogen and carbon dynamics of ectomycorrhizal and saprotrophic fungi from isotopic evidence. *Oecologia* **118**, 353 (1999).
57. Banerjee, S., Schlaeppi, K. & van der Heijden, M. G. A. Keystone taxa as drivers of microbiome structure and functioning. *Nat Rev Microbiol* **16**, 567–576 (2018).
58. Peh, K. S.-H., Lewis, S. L. & Lloyd, J. Mechanisms of monodominance in diverse tropical tree-dominated systems. *Journal of Ecology* **99**, 891–898 (2011).
59. Mangan, S. A. *et al.* Negative plant–soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* **466**, 752–755 (2010).
60. Bennett, J. A. *et al.* Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science* **355**, 181–184 (2017).
61. Enright, D. J., Frangioso, K. M., Isobe, K., Rizzo, D. M. & Glassman, S. I. Mega-fire in redwood tanoak forest reduces bacterial and fungal richness and selects for pyrophilous taxa that are phylogenetically conserved. *Molecular Ecology* **n/a**, (2022).
62. Klein, T., Siegwolf, R. T. & Körner, C. Belowground carbon trade among tall trees in a temperate forest. *Science* **352**, 342–344 (2016).
63. Karst, J., Jones, M. D. & Hoeksema, J. D. Positive citation bias and overinterpreted results lead to misinformation on common mycorrhizal networks in forests. *Nat Ecol Evol* 1–11 (2023) doi:10.1038/s41559-023-01986-1.

64. Kretzer, A. M., Dunham, S., Molina, R. & Spatafora, J. W. Microsatellite markers reveal the below ground distribution of genets in two species of Rhizopogon forming tuberculate ectomycorrhizas on Douglas fir. *New Phytologist* **161**, 313–320 (2004).
65. Bergemann, S. E. & Miller, S. L. Size, distribution, and persistence of genets in local populations of the late-stage ectomycorrhizal basidiomycete, Russula brevipes. *New Phytologist* **156**, 313–320 (2002).
66. Averill, C., Bhatnagar, J. M., Dietze, M. C., Pearse, W. D. & Kivlin, S. N. Global imprint of mycorrhizal fungi on whole-plant nutrient economics. *PNAS* **116**, 23163–23168 (2019).
67. Grime, J. P. Vegetation classification by reference to strategies. *Nature* **250**, 26–31 (1974).
68. Collier, F. A. & Bidartondo, M. I. Waiting for fungi: the ectomycorrhizal invasion of lowland heathlands. *Journal of Ecology* **97**, 950–963 (2009).
69. Thirkell, T. J., Cameron, D. D. & Hodge, A. Resolving the 'nitrogen paradox' of arbuscular mycorrhizas: fertilization with organic matter brings considerable benefits for plant nutrition and growth. *Plant Cell Environ* **39**, 1683–1690 (2016).
70. Shah, F. *et al.* Ectomycorrhizal fungi decompose soil organic matter using oxidative mechanisms adapted from saprotrophic ancestors. *New Phytologist* **209**, 1705–1719 (2016).
71. Terrer, C., Vicca, S., Hungate, B. A., Phillips, R. P. & Prentice, I. C. Mycorrhizal association as a primary control of the CO2 fertilization effect. *Science* **353**, 72–74 (2016).
72. Phillips, R. P., Brzostek, E. & Midgley, M. G. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon–nutrient couplings in temperate forests. *New Phytologist* **199**, 41–51 (2013).

73. Herman, D. J., Firestone, M. K., Nuccio, E. E. & Hodge, A. Interactions between an arbuscular mycorrhizal fungus and a soil microbial community mediating litter decomposition. *FEMS Microbiology Ecology* **80**, 236–247 (2012).
74. Abbott, K. C., Eppinga, M. B., Umbanhowar, J., Baudena, M. & Bever, J. D. Microbiome influence on host community dynamics: Conceptual integration of microbiome feedback with classical host–microbe theory. *Ecology Letters* **24**, 2796–2811 (2021).
75. Jiang, J. *et al.* Pathogens and Mutualists as Joint Drivers of Host Species Coexistence and Turnover: Implications for Plant Competition and Succession. *The American Naturalist* **195**, 591–602 (2020).
76. Collins, C. D., Bever, J. D. & Hersh, M. H. Community context for mechanisms of disease dilution: insights from linking epidemiology and plant–soil feedback theory. *Annals of the New York Academy of Sciences* **1469**, 65–85 (2020).
77. Letten, A. D. & Stouffer, D. B. The mechanistic basis for higher-order interactions and non-additivity in competitive communities. *Ecology Letters* **22**, 423–436 (2019).
78. Fernández, N., Knoblochová, T., Kohout, P., Janoušková, M. & Rydlová, J. Asymmetric Interaction Between Two Mycorrhizal Fungal Guilds and Consequences for the Establishment of Their Host Plants. *Front. Plant Sci.* **13**, (2022).
79. Letten, A. D., Ke, P.-J. & Fukami, T. Linking modern coexistence theory and contemporary niche theory. *Ecological Monographs* **87**, 161–177 (2017).
80. Ellner, S. P., Snyder, R. E., Adler, P. B. & Hooker, G. Toward a “modern coexistence theory” for the discrete and spatial. *Ecological Monographs* **92**, e1548 (2022).

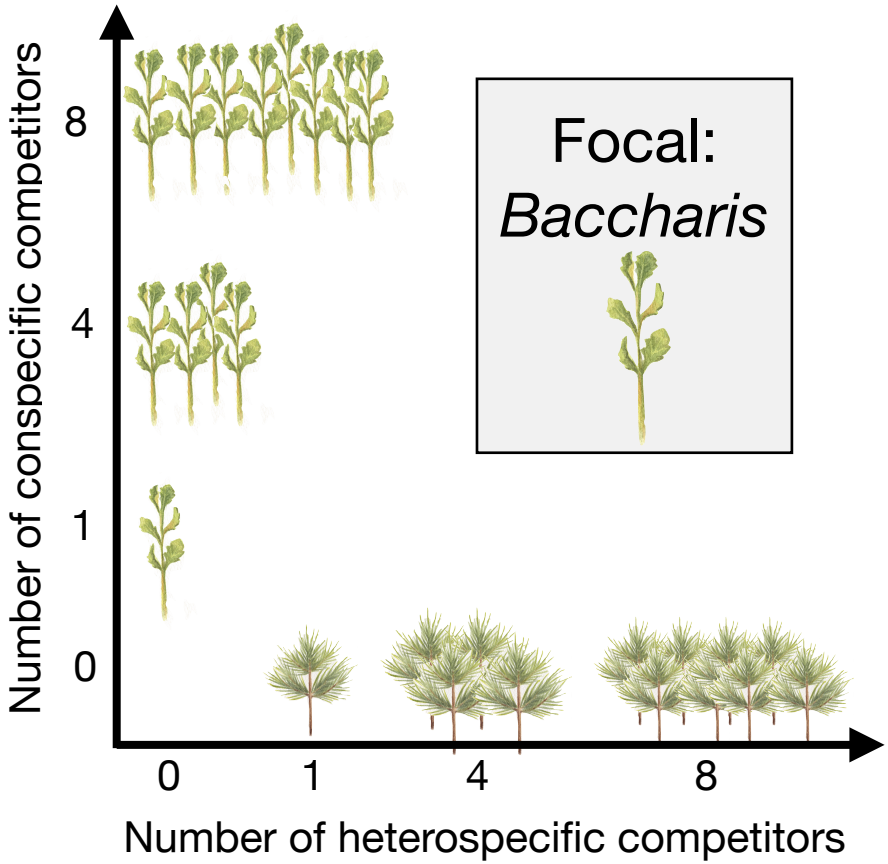
81. Van Der Heijden, M. G. A. & Horton, T. R. Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *Journal of Ecology* **97**, 1139–1150 (2009).
82. Delavaux, C. S. *et al.* Mycorrhizal feedbacks influence global forest structure and diversity. *Commun Biol* **6**, 1–11 (2023).
83. Chang, C.-Y., Bajić, D., Vila, J. C. C., Estrela, S. & Sanchez, A. Emergent coexistence in multispecies microbial communities. *Science* **381**, 343–348 (2023).
84. Peay, K. G., Schubert, M. G., Nguyen, N. H. & Bruns, T. D. Measuring ectomycorrhizal fungal dispersal: macroecological patterns driven by microscopic propagules. *Molecular Ecology* **21**, 4122–4136 (2012).
85. Peay, K. G., Bruns, T. D., Kennedy, P. G., Bergemann, S. E. & Garbelotto, M. A strong species–area relationship for eukaryotic soil microbes: island size matters for ectomycorrhizal fungi. *Ecology Letters* **10**, 470–480 (2007).
86. Dawson, T. E. Fog in the California redwood forest: ecosystem inputs and use by plants. *Oecologia* **117**, 476–485 (1998).
87. Hart, S. P., Freckleton, R. P. & Levine, J. M. How to quantify competitive ability. *Journal of Ecology* **106**, 1902–1909 (2018).
88. Ke, P.-J. & Wan, J. A general approach for quantifying microbial effects on plant competition. *Plant and Soil* 1–14 (2022).
89. Bruns, T. D., Hale, M. L. & Nguyen, N. H. *Rhizopogon olivaceotinctus* increases its inoculum potential in heated soil independent of competitive release from other ectomycorrhizal fungi. *Mycologia* **111**, 936–941 (2019).

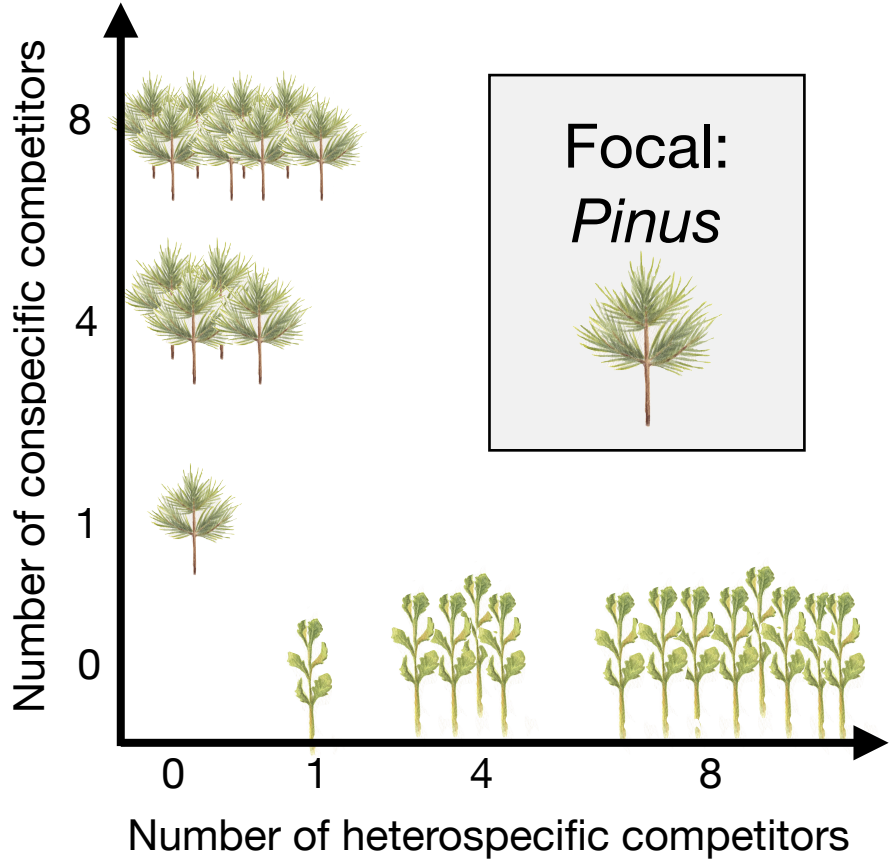
90. Gardes, M. & Bruns, T. D. ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rusts. *Molecular Ecology* **2**, 113–118 (1993).
91. Duhamel, M. *et al.* Plant selection initiates alternative successional trajectories in the soil microbial community after disturbance. *Ecological Monographs* **89**, e01367 (2019).
92. Phillips, J. M. & Hayman, D. S. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. *Transactions of the British Mycological Society* **55**, 158-IN18 (1970).
93. Giovannetti, M. & Mosse, B. An Evaluation of Techniques for Measuring Vesicular Arbuscular Mycorrhizal Infection in Roots. *New Phytologist* **84**, 489–500 (1980).
94. Smith, W. K., Schoettle, A. W. & Cui, M. Importance of the method of leaf area measurement to the interpretation of gas exchange of complex shoots. *Tree Physiology* **8**, 121–127 (1991).
95. Anderson, C. J. R. & Rosas-Anderson, P. J. Leafscan. (2017).
96. Rueden, C. T. *et al.* ImageJ2: ImageJ for the next generation of scientific image data. Preprint at https://doi.org/10.48550/arXiv.1701.05940 (2017).
97. R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing (2022).
98. Bates, D., Mächler, M., Bolker, B. & Walker, S. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* **67**, 1–48 (2015).
99. Chesson, P. & Kuang, J. J. The interaction between predation and competition. *Nature* **456**, 235–238 (2008).

100. Rousselet, G. A., Pernet, C. R. & Wilcox, R. R. The Percentile Bootstrap: A Primer With Step-by-Step Instructions in R. *Advances in Methods and Practices in Psychological Science* **4**, (2021).

101. Terry, J. C. D. & Armitage, D. W. Widespread analytical pitfalls in empirical coexistence studies and a checklist for improving their statistical robustness. 2023.07.04.547661 Preprint at https://doi.org/10.1101/2023.07.04.547661 (2023).

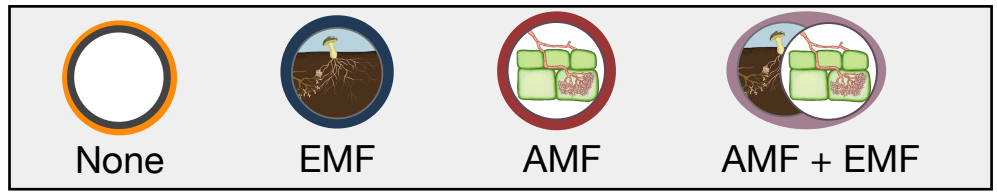
102. Johnson, C. A., Dutt, P. & Levine, J. M. Competition for pollinators destabilizes plant coexistence. *Nature* **607**, 721–725 (2022).

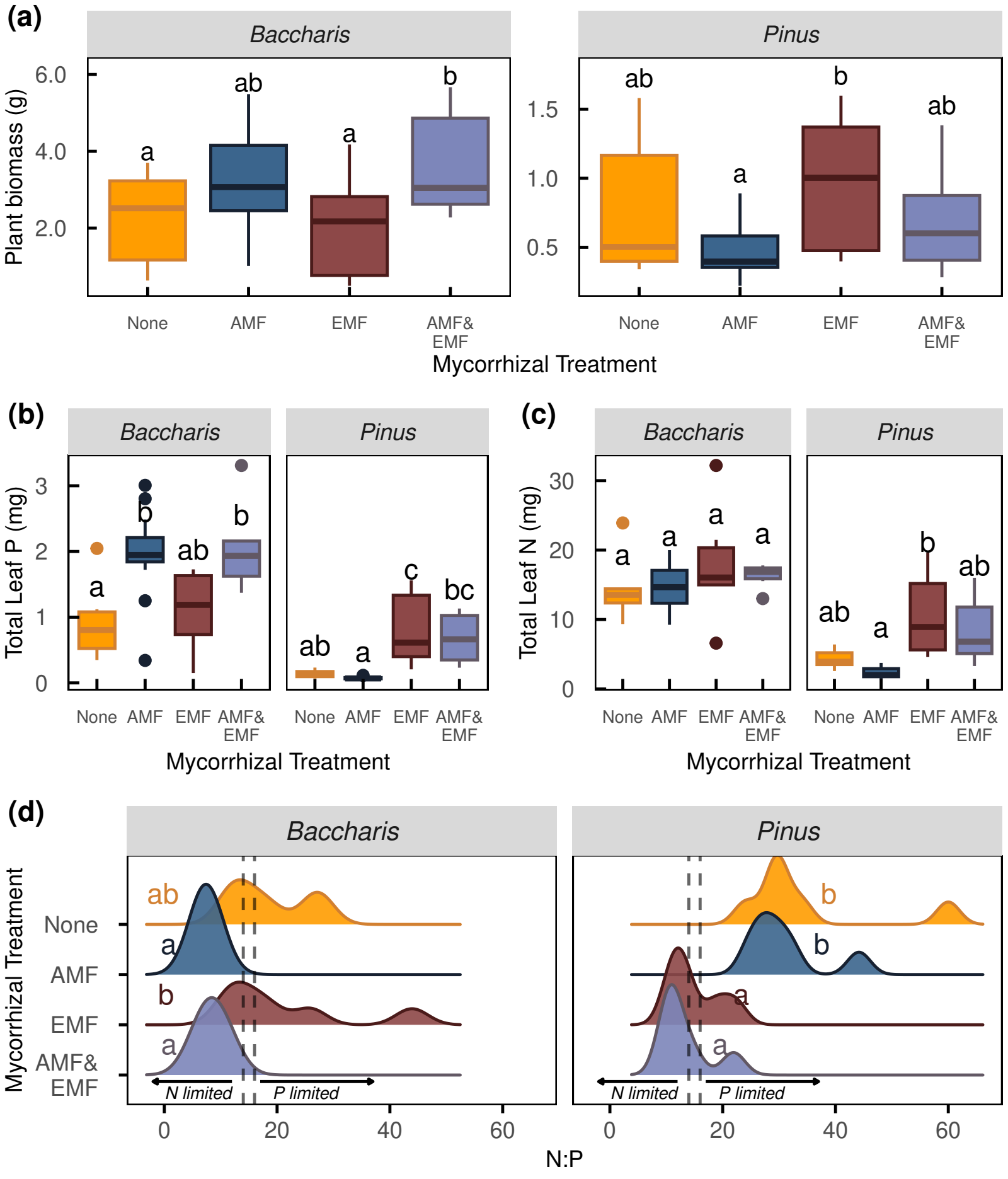


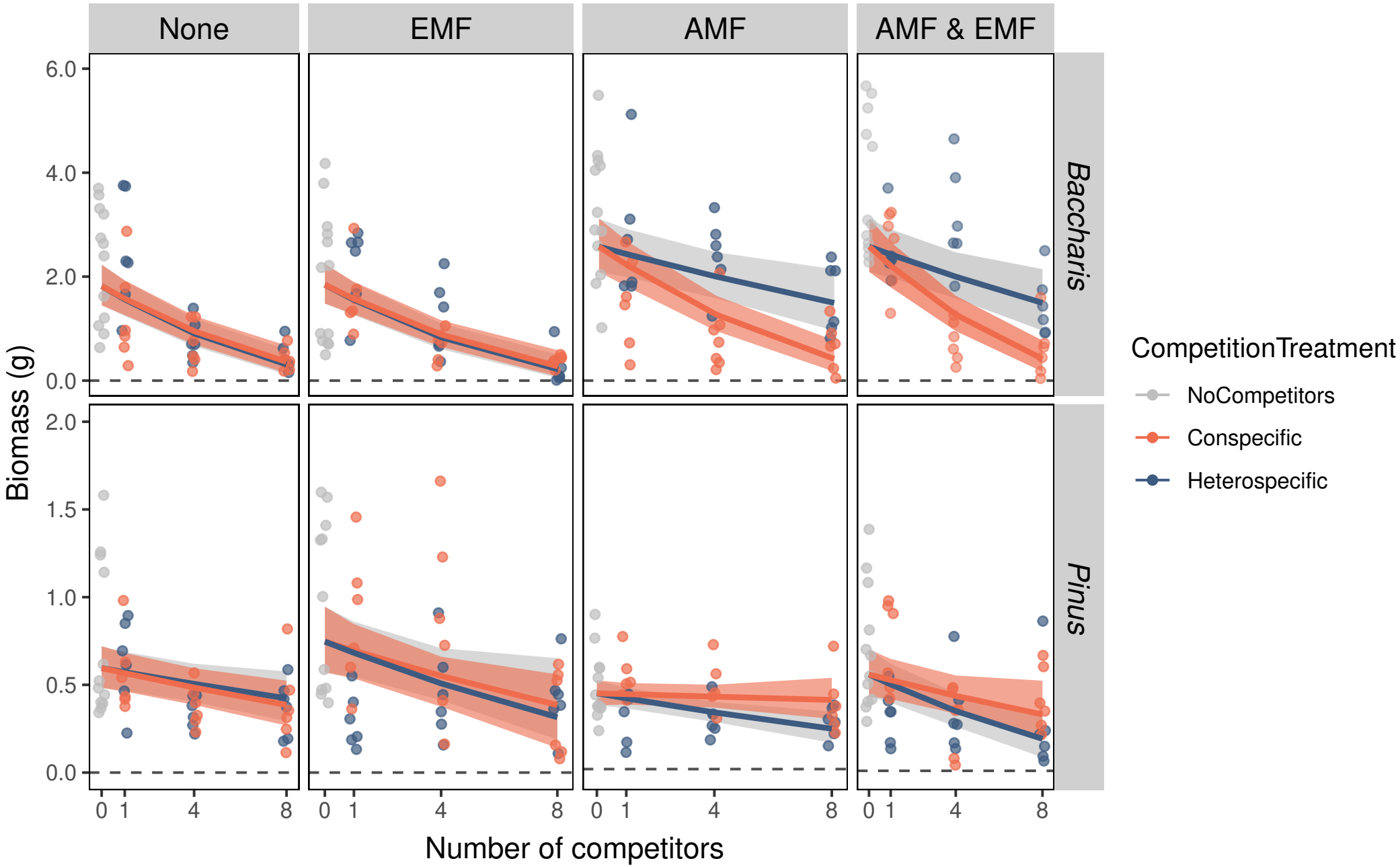


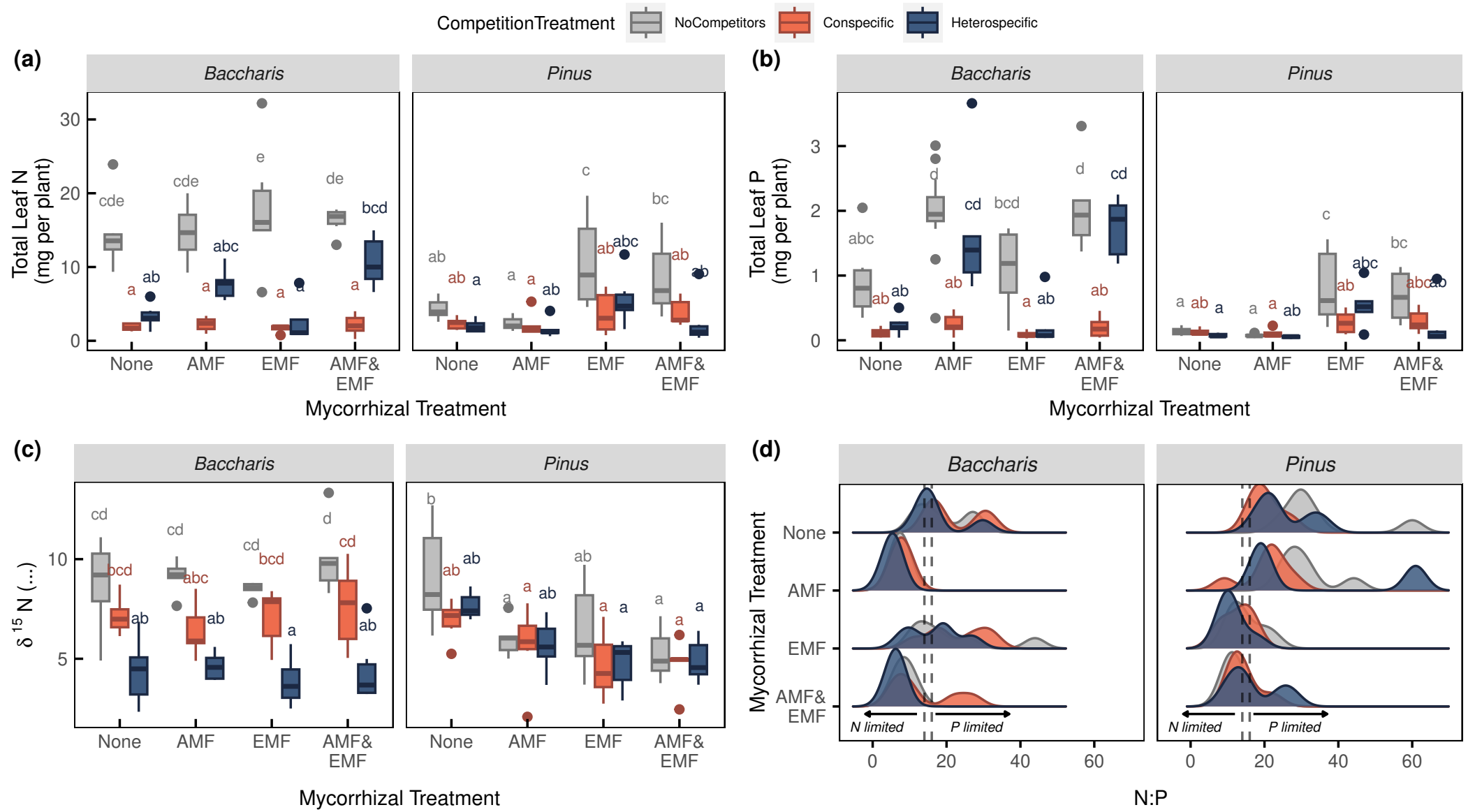
x

4 Mycorrhizal treatments




(a)
Baccharis
Pinus
Plant biomass (g)
6.0
4.0
2.0
1.5
1.0
0.5
a
ab
a
b
ab
a
b
ab
None
AMF
EMF
AMF&
EMF
Mycorrhizal Treatment
(b)
Total Leaf P (mg)
3
2
1
0
(c)
Total Leaf N (mg)
30
20
10
0
(d)
Mycorrhizal Treatment
None
AMF
EMF
AMF&
EMF
N limited
P limited
0
20
40
60
N:P


None
EMF
AMF
AMF & EMF
Baccharis
Pinus
Biomass (g)
6.0
4.0
2.0
0.0
2.0
1.5
1.0
0.5
0.0
0
1
4
8
Number of competitors
CompetitionTreatment
NoCompetitors
Conspecific
Heterospecific


CompetitionTreatment
NoCompetitors
Conspecific
Heterospecific
(a)
Baccharis
Pinus
Total Leaf N (mg per plant)
None
AMF
EMF
AMF& EMF
Mycorrhizal Treatment
(b)
Total Leaf P (mg per plant)
(c)
δ15 N (...)
(d)
Mycorrhizal Treatment
N limited
P limited
N:P

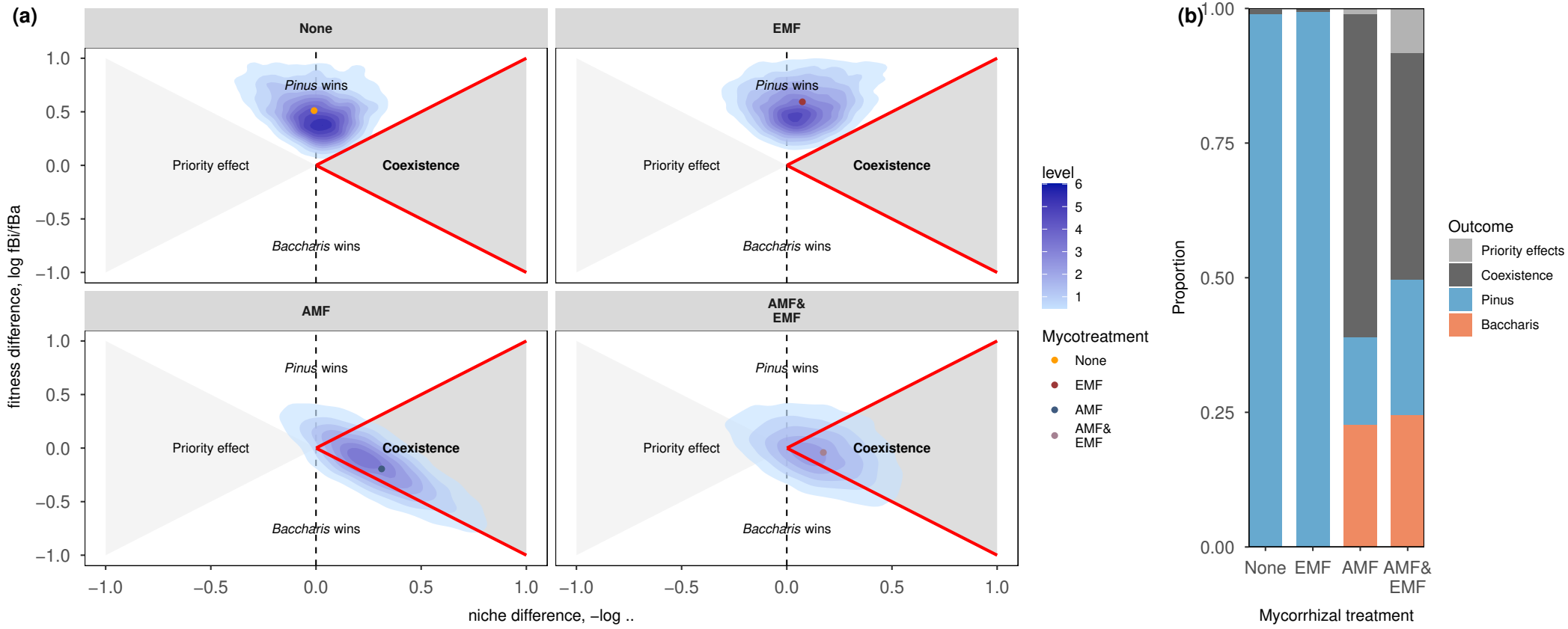

(a)
None
EMF
AMF
AMF&
EMF
Pinus wins
Baccharis wins
Priority effect
Coexistence
fitness difference, log fBi/fBa
niche difference, –log ..
level
Mycotreatment
None
EMF
AMF
AMF&
EMF
(b)
Proportion
Mycorrhizal treatment
Outcome
Priority effects
Coexistence
Pinus
Baccharis

Table 1. Modern coexistence theory interaction coefficients (α) and niche and fitness differences calculated from Ke and Wan (2020) based on n=8 competitors. (A) refers to *B. pilularis* and (B) refers to *P. muricata* where α_{AB} refers to the growth of *B. pilularis* growing in conspecific competition and where α_{AB} refers to the growth of *B. pilularis* growing in conspecific competition.

Mycorrhizal Treatment	α_{AB}	α_{AA}	α_{BB}	α_{BA}	Fitness Ratio	Niche Difference
None	-0.0994	-0.1022	-0.0591	-0.0619	1.6669	-0.0090
EMF	-0.1119	-0.1034	-0.0666	-0.0530	1.8097	0.0716
AMF&EMF	-0.0444	-0.0915	-0.0551	-0.0801	0.9597	0.1597
AMF	-0.0363	-0.0889	-0.0602	-0.0790	0.8234	0.2681