# Effects of arbuscular mycorrhizal fungi on root foraging and competitive ability depend on soil phosphorus distribution: Evidence from two pairs of invasive and native plants

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## Abstract

Besides uptake of nutrients by roots, plants can acquire nutrients through arbuscular mycorrhizal fungi (AMF). AMF play a crucial role in plant growth and competition. However, few studies have investigated the effects of AMF on root-foraging and competition between invasive and native species in response to heterogeneous nutrients. Two pairs of invasive and native plants of the Asteraceae family were selected to create a common garden experiment involving three factors (heterogeneous vs. homogeneous phosphorus (P), with vs. without AMF, and monoculture vs. mixture). The results showed that AMF significantly reduced the foraging scale of the invasive species, *Bidens pilosa*,and decreased the precision of the invasive species, *Praxelis clematidea*, and the native species, *Emilia sonchifolia*. In monoculture, AMF significantly decreased the total biomass of the two invasive species under heterogeneous P rather than homogeneous P, which was confirmed by N and P uptake. In mixture, heterogeneity significantly decreased the tolerance competitive ability of *B. pilosa*but increased that of *P. clematidea*. In the homogeneous P, AMF significantly decreased the suppression ability of *B. pilosa,* while in the heterogeneous P, AMF decreased that of *P. clematidea*. Heterogeneous P with AMF increased the suppression ability of *B. pilosa* but decreased that of *P. clematidea*. The interactive effects of AMF and soil P distribution on root foraging and nutrient uptake and competition differ among the four species and show invasive-native pair differences. These findings provide valuable insights into the interactive effects and highlight the context dependency of these interactions.


## Introduction

Soil nutrients are often spatially heterogeneous (Jackson and Caldwell 1993; Gross et al. 1995). This is particularly true for phosphate because of its low solubility and diffusivity (Hinsinger, 2001; Felderer et al., 2013). Plants can selectively place their roots in nutrient-rich patches, which can lead to a higher acquisition of nutrients and better performance in heterogeneous environments (Hodge, 2004; Cahill and McNickle, 2011). Plants respond to variations in nutrient distribution by adjusting their root investment, morphology, and physiology to improve their root foraging abilities (Jackson et al., 1990; Kembel and Cahill, 2005; Wang et al., 2022). Morphological plasticity enables plants to enhance their acquisition of essential resources by generating different resource-acquiring structures in response to different environmental conditions, which is referred to as root foraging ability (de Kroon and Hutchings, 1995; Fransen, 1999; Fransen et al., 1999a, 1999b). The root foraging scale (development of the root system) and precision (ability to proliferate more roots within nutrient-rich patches) are often used to reflect root foraging behaviour (Campbell et al., 1991; Kembel and Cahill, 2005). Besides the direct uptake of nutrients by roots, plants can acquire nutrients through the aid of arbuscular mycorrhizal fungi (AMF), and host plants and fungal symbionts benefit from the reciprocal exchange of mineral and organic resources (Smith et al., 2011; Bennett and Groten, 2022). Owing to the smaller diameter of hyphae and lower metabolic cost of hyphal growth, AMF may be more flexible in response to nutrient patches than roots (Hodge, 2006). Mycorrhizal fungi have been reported to have a strong influence on root proliferation and root function (Cui and Caldwell, 1996; Cheng et al., 2016; Gao et al., 2021), and therefore, change root foraging and plant nutrient uptake strategies (Felderer et al., 2013; Chippano et al., 2021). However, AMF colonization is not always beneficial for plants, as mycorrhizal associations vary from mutualism to parasitism, depending on the host species, soil fertility, and other environmental conditions (Klironomos, 2003; Shah et al., 2009). Therefore, it is essential to consider root foraging and AMF to better understand nutrient uptake under heterogeneous conditions.

Many studies have shown that AMF significantly influence plant competition (West, 1996; Stanescu and Maherali, 2017; Sun et al., 2022). AMF can interconnect plant root systems through common mycorrhizal networks (CMNs) of hyphae, which can influence mineral nutrient uptake by roots between interconnected individuals and, accordingly, affect competition (Weremijewicz and Janos, 2013; Lin et al., 2015). In nature, plants are exposed to heterogeneity of nutrients and neighbouring plants. When competing for underground resources with neighbours, plants alter the spatial distribution of their roots and foraging abilities (Cahill et al., 2010; Colom and Baucom, 2020; Garlick et al., 2021). At the same time, root foraging ability can influence the competitive ability of plants (Rajaniemi, 2007), and more effective root-foraging behaviour confers higher competitive ability in heterogeneous environments (Fransen et al., 2001). Resource competition has long been considered a major mechanism determining the success of invasive species (Levine et al., 2003). Studies have shown that exotic invasive plants exhibit greater root-foraging capacities than non-invasive species (Keser et al., 2014, 2015). Furthermore, AMF can form novel symbioses with exotic invasive plants and play a crucial role in their growth and competitive abilities (Callaway et al., 2001; Pringle et al., 2009; Menzel et al., 2017; Aslani et al., 2019; Chen et al., 2020; Sun et al., 2022). However, few studies have investigated the effects of AMF on root-foraging, and their interactive effects on competition between native and invasive species in response to heterogeneous nutrients.

The specific questions evaluated were as follows: (i) What are the effects of AMF on the scale and precision of root foraging? and (ii) How do AMF influence competition between invasive and native plants in both homogeneous and heterogeneous nutrient conditions? In this study, two invasive and two coexisting native species that form symbiotic associations with AMF were selected. The two invasive species were *Bidens pilosa* var. *radiata* (also called *Bidens alba* or *Bidens pilosa* L.) and *Praxelis clematidea*, widely distributed in South China, and the two native species were *Emilia sonchifolia* and *Eupatorium chinense*. As our previous study has shown that the studied two exotic invasive plants had a larger foraging scale, and the selected two native plants had higher precision (Chen et al., 2018), we predicted that AMF could reduce the root foraging scale of the invasive species while reduce the root foraging precision of the native species. In general, exotic invasive plants exhibit a higher growth rate than native plants, and their higher growth rates allow them to 'discover' and exploit nutrient patches faster, leading to a stronger competitive ability of invasive plants (Van Kleunen et al., 2010; Gioria and Osborne, 2014). Moreover, AMF in CMNs can increase competitive ability by preferentially allocating mineral nutrients to faster-growth or larger host plants (Weremijewicz et al., 2016). Therefore, we hypothesised that in monoculture (without competition), AMF could decrease the growth of invasive plants in heterogeneous P, while in competition AMF could improve the nutrient uptake and competitive ability of invasive species in heterogeneous P.

# Materials and methods

*2.1 Study site and seed collection*

The experiment was conducted in the glasshouse of the Ecological Research Station in Haizhu Wetland National Park, Guangzhou (23°04'38"N, 113°18'9"E), where the climate is subtropical monsoon.

Seeds were collected from 3–5 wild populations on Xiaoguwei Island, Guangzhou, Guangdong Province, South China. Each species' seeds were thoroughly mixed for later use.

*2.2 Soil collection and preparation*

The soil was collected from the Zengcheng district of Guangzhou (23°05'–23°37'N, 113°32'–114°00'E). Vermiculite and soil were air-dried, sieved through a 2 mm sieve, and sterilised using $^{60}Co$ gamma-irradiation at 10kGy. After sterilisation, the soil, sand, and vermiculite were mixed at a volume ratio of 4:1:5 and the pots were filled. The nutrient concentration of the soil mixture was quite low, with a total carbon (C) of 1.69 ± 0.03 g $kg^{-1}$, total nitrogen (N) of 0.74 ± 0.02 g $kg^{-1}$, and total phosphorus (P) of 0.58 ± 0.02 g $kg^{-1}$ dry soil.

*2.3 Experimental design*

We employed a completely randomised three-factor design with 24 treatments of soil P spatial distribution (homogeneous and heterogeneous), AMF (*G. mosseae* inoculation, without *G. mosseae* inoculation), and six planting treatments (four species monocultures, two mixtures of invasive and native species *B. pilosa* and *E. sonchifolia, P. clematidea* and *E. chinense*) (Fig. 1). Each treatment was repeated five times.

Homogeneous and heterogeneous P were created by adding an aqueous solution of $Ca(H_2PO_4)_2{\cdot}H_2O$ with equal total P added to all treatments. Rectangular pots (26, 15, and 12 cm in length, width, and height, respectively) were used, and half of them were divided into three sections (7+12+7 cm = 26 cm) to maintain the same P content as in the homogeneous treatments. In the homogeneous treatment, the P concentration was 20 mg $kg^{-1}$ soil throughout the pot. For the heterogeneous treatment, the pots were divided into three sections using thin plastic plates. Plants were planted in the middle of all the pots, where the P concentration was maintained at 20 mg $kg^{-1}$ soil. The left and right sides of the heterogeneous pots were supplied with P-poor and P-rich patches, respectively, as shown in Fig. 1. The P concentration was maintained at 10 mg $kg^{-1}$ P in the P-poor section and 100 mg $kg^{-1}$ P in the P-rich section. The homogeneous and heterogeneous treatments had the same total P content. Simultaneously, 50 mL of Hoagland nutrient solution without P was added to each pot every two weeks to reduce the limitations of other nutrients.

Before P treatment, the pots were inoculated with AMF. *Glomus mosseae,* which is symbiotic with most plants, was used for AMF inoculation. It was propagated symbiotically with white clover (*Trifolium repens*) in sterilized sand and vermiculite for two months in a greenhouse. After propagation, we cut the above ground of white clover and removed the roots. Then, the sand and vermiculite were mixed thoroughly as inoculum. The spore density of the inoculum was 100 spores $g^{-1}$. Each pot was filled with sterilized soil, sand,

and vermiculite mixed at a volume ratio of 4:1:5. For inoculation treatments, each pot contained 76 g of the inoculum at a depth of 3 cm in the soil. For the control treatments (without inoculation), the same weight of sand and vermiculite without *G. mosseae* were added in pot.

After soil P and AMF treatments, the seedlings were transplanted into pots. Seeds were sterilised with 0.5% potassium permanganate, and rinsed with pure water for 10 min. They were then placed in Petri plates with double layers of wet filter paper for germination in a growth chamber at 22 ± 1 °C and under 12 h of light and 12 h of darkness and then planted on a sterilised nursey tray after the emergence of the cotyledons. Seedlings of uniform size were chosen for transplantation into the centre of the pots. For the monoculture, one individual of each species was planted in each pot, while for the mixture, one individual each of native and invasive plants were planted in each pot. After two weeks, we created the P treatment again as the first time and then removed the inserted plastic plates between the sections of the heterogeneous pots after the locations of the plastic plates were marked (to separate them for collecting roots in each section).

The pots were rotated weekly to eliminate any potential effects of spatial heterogeneity in light and temperature in the glasshouse. All pots were watered every 2–3 days or as needed.

*2.4 Harvest and measurements*

Plants were harvested 80 days after transplantation. The shoot biomass was cut and dried at 60 °C for 72 h. For homogeneous treatments, roots were gently washed free of soil under running water through a sieve. For the heterogeneous treatments, soil samples and roots were collected from the three sections separately (according to the marked locations of the sections), and the roots were gently washed free of soil under running water through a sieve. The root length of each plant was analysed using the LA-S root analysis system (Wseen Inc., Hangzhou, China) after soaking the whole root system in water to calculate the root length density. Then, the roots were dried at 60 °C for 72 h and weighed. In addition, the AMF colonization rates of each species were measured. The results of AMF colonization rate are shown in supplementary information (Table S1).

Shoots were ground and digested with $H_2O_2/H_2SO_4$ (conc.) to measure the concentrations of N and P using the Kjeldahl and vanadate-molybdate-yellow colorimetry methods. The concentrations of N and P are shown in supplementary information (Fig. S2). Shoot total N and P uptake were calculated as N and P concentration multiplied by shoot biomass of each species (Reynolds et al., 2005; Meisner et al., 2011).

Foraging scale and precision were analysed to assess the root distribution of the four species in the monoculture. The foraging scale was presented as the total root biomass of the plants (Bliss et al., 2002), and foraging precision was measured in terms of root biomass according to Campbell et al. (1991), as follows:

$$\text{Precision} = (\text{Root-S}_{\text{rich}} - \text{Root-S}_{\text{poor}}) / \text{Root-S}_{\text{total}}$$

where $S_{rich}$ and $S_{poor}$ indicate P-rich and P-poor sections, respectively. $S_{total}$ indicates total biomass of root in each pot.

The total biomass of the four species was used to calculate the tolerance and suppression capacity of the invasive species *B. pilosa* and *P. clematidea* under heterogeneous and AMF treatments using the relative interaction intensity (RII) index of tolerance and suppression. The tolerance and suppression RII represent the ability of invasive plants to tolerate competition with native plants and suppress native plants, respectively (Fletcher et al., 2016). In this study, we calculated the tolerance and suppression RII of each invasive plant competing with its native neighbour as follows (Chen et al., 2020):

$$\text{Tolerance RII} = (\text{Biomass}_{\text{Invasive-mix}} - \text{Biomass}_{\text{Invasive-mono}}) / (\text{Biomass}_{\text{Invasive-mix}} + \text{Biomass}_{\text{Invasive-mono}})$$

$$\text{Suppression RII} = -(\text{Biomass}_{\text{Native-mix}} - \text{Biomass}_{\text{Native-mono}}) / (\text{Biomass}_{\text{Native-mix}} + \text{Biomass}_{\text{Native-mono}})$$

Higher tolerance RII and suppression RII reflect a stronger competitive ability of invasive plants.

In addition, the mycorrhizal growth response (MGR) was calculated. More detailed descriptions of MGR calculation are presented in supplementary information. The results of MGR are shown in Table S2 and Fig. S1.

*2.5 Statistical Analyses*

All data were analysed using R v4.1.3 (R Core Team, 2022). A two-way ANOVA was used to analyse the effects of AMF and species on the scale of root foraging and the precision of monocultured plants. It was also used to analyse the effects of heterogeneity treatment and AMF inoculation on the total biomass and shoot N and P uptake of each species and to test the effects of heterogeneity and AMF inoculation on the competitive ability (tolerance and suppression of RII) of the two invasive species, *B. Pilosa* and *P. clematidea*. Post-hoc multiple comparisons were performed to determine the differences for each species using the least significant difference method, in which the *p* values were adjusted using the Bonferroni method. In addition, an independent t-test was used to test whether the effects of AMF inoculation differed with respect to total biomass, root foraging scale, and precision of each species. Before performing ANOVA, the normality of distributions and homogeneity of variance were tested, and some data were logarithmically transformed to meet these assumptions.

# Results

*3.1 Effects of AMF on root foraging scale and precision differ among the four species*

Plants respond to variations in nutrient distribution by adjusting their root distribution to improve their root foraging abilities. Root foraging scale refers to the total root biomass or RLD, and root foraging precision is calculated according to the different root biomass or RLD between nutrient-poor and -rich sections. Besides nutrient uptake by roots, most plants can take up soil nutrients through AMF symbiosis indirectly. What are the effects of AMF on the scale and precision of root foraging? As stated above, we predicted that AMF could reduce the root foraging scale of the invasive species and reduce the root foraging precision (ability to proliferate more roots within nutrient-rich patches) of the native species. The results of one pair of invasive and native species (*B. pilosa* and *E. sonchifolia*) consistent with our prediction, AMF inoculation reduced the root-foraging scale of the invasive species *B. pilosa* and the root-foraging precision of the native species *E. sonchifolia* (Fig. 2, Table 1). However, this is the case of another pair, AMF did not significantly reduce the root foraging scale but significantly reduced the foraging precision (root mass) of another invasive species *P. clematidea* (Fig. 2, Table 1).

*3.2 Effects of AMF and P distribution on plant biomass*

The total biomass of the two pairs of invasive and native plants in both monoculture and mixture were measured. In monoculture (without competition), soil heterogeneous P significantly improved the biomass of the four species except *E. chinense* relative to soil homogeneous P (Table 2, Fig. 3), while AMF significantly reduced the total biomass of the four species except *E. chinense* in soil heterogeneous P (Fig. 3). In mixture (with competition), heterogeneity increased the total biomass of all species, except *B. pilosa* with AMF and *E. chinense* without AMF inoculation, whereas AMF only significantly increased the total biomass of *E. chinense* in the heterogeneous treatment (Fig. 3). The above results indicate that soil heterogeneous P facilitate the growth of most species either with or without competition. To further understand the effects of AMF on plant biomass, we calculated the mycorrhizal growth response (MGR) of each species as the difference in total biomass of plants growing with AMF inoculation relative to those without AMF inoculation under the same treatment (Cavagnaro et al., 2003). Heterogeneity and competition had different effects on the MGR among the four species (Table S2, Fig. S1). Heterogeneity significantly decreased the MGR of the two invasive species but increased the MGR of the two native species in monoculture, whereas competition significantly increased the MGR of *E. sonchifolia* (in the homogeneous treatment) and *E. chinense* (in the heterogeneous treatment) (Fig. S1).

*3.3 Effects of AMF on shoot total N and P uptake of the two pairs of invasive and native plants*

To understand the effects of AMF on N and P uptake of plants, the shoot N and P concentration of the two pairs of invasive and native plants in both monoculture and mixture were measured. Then, we calculated shoot N and P uptake as N and P concentration multiplied by shoot biomass of each species (according to the calculation by Reynolds et al., 2005; Meisner et al., 2011). Regarding N and P concentration, in the monoculture, AMF inoculation increased the shoot N concentration of the four species except *E. chinense* in either soil heterogeneous or homogeneous P, but they had less effects on shoot P concentration of all species (Table S3, Fig. S2). In the mixture, however, the effects of heterogeneous P and AMF inoculation on shoot N and P concentration were smaller or even disappeared compared with those in the monoculture (Table S3, Fig. S2). Regarding total N and P uptake, heterogeneous P and competition increased the shoot N and P uptake of *B. pilosa* and *P. clematidea* consisting with our prediction, while heterogeneous P increased but competition decreased the shoot N and P uptake of *E. sonchifolia* (Table 3, Fig. 4).

*3.4 Effects of AMF and P distribution on competitive interactions between invasive and native species*

The competitive ability of the two invasive species *B. pilosa* and *P. clematidea* compared to their native counterparts were calculated using the index of tolerance and suppression RII. As stated above, we predicted that heterogeneity and AMF could improve the competitive ability of invasive species. However, our results showed that the competitive abilities of the two invasive species exhibited different responses to heterogeneity and AMF (Table 4 and Fig. 5). The tolerance RII represent the ability of invasive plants to tolerate competition with native plants (calculated as the relative change of invasive species biomass between mono- and mix-culture). The results showed that heterogeneity significantly decreased the tolerance RII of *B. pilosa* but increased that of *P. clematidea* (Fig. 5a, 5c). In the heterogeneous P treatment, AMF significantly promoted the tolerance RII of *B. pilosa*, but it had no significant effects on the tolerance RII of *P. clematidea* in either homogenous or heterogeneous P treatment. The suppression RII represent the ability of invasive plants to suppress native plants (calculated as the relative change of native species biomass between mono- and mix-culture). The results showed that AMF significantly decreased the suppression RII of *B. pilosa* in the homogeneous P treatment but decreased that of *P. clematidea* in the heterogeneous treatment, whereas heterogeneous P with AMF inoculation increased the suppression RII of *B. pilosa* but decreased that of *P. clematidea* (Table 4, Fig. 5b, 5d). Overall, these results indicate that AMF strengthened the competitive ability of *B. pilosa* by promoting tolerance RII in heterogeneous P and suppression RII in homogeneous P. But AMF inhibited the competitive ability of another invasive species *P. clematidea* by decreasing suppression RII in homogeneous P rather than by affecting tolerance RII.

## Discussion

In general, soil nutrients are distributed in a heterogeneous or patchy manner. Plants respond to soil nutrient heterogeneity by adjusting root morphology and physiological plasticity to improve their foraging ability (Jackson et al., 1990; Hodge, 2004; Kembel and Cahill, 2005), and soil nutrient heterogeneity often promotes the growth of invasive plants because they take advantage of the heterogeneous nutrients (James et al., 2009; Zhou et al., 2011; Wang et al., 2017; Liang et al., 2020). The results of the pair of invasive–native species (*B. pilosa* vs. *E. sonchifolia*) are consistent with our prediction that AMF reduced the root-foraging scale of the invasive species and reduced the foraging precision of native species, but another pair (*P. clematidea* vs. *E. chinense*) is not the case that AMF reduced the foraging precision of the invasive species *P. clematidea*. In addition, AMF inoculation eliminated the foraging advantage of the two invasive species *B. pilosa* (advantage of scale) and *P. clematidea* (advantage of precision) over the native species (Fig. 2). Heterogeneity and AMF exerted different effects on the competitive ability of the two invasive species compared to their native counterparts (Fig. 5). On the other hand, competition altered the effects of AMF on plant growth, and these effects were dependent on P distribution (Fig. 5).

The effects of AMF on host plants range from mutualism to parasitism, with variations in soil nutrient availability (Johnson et al., 1997; van Der Heijden et al., 1998; Bennett and Groten, 2022). Our previous study showed that AMF facilitated the growth of *B. pilosa* under low P nutrient status, but inhibited its growth under high P nutrient status (Chen et al., 2020). Our monoculture results showed that AMF generally exhibited negative effects on plant growth, and these effects were species-specific and dependent on the soil P distribution (Fig. 2). The total biomass of the two invasive species, *B. pilosa* and *P. clematidea,* was significantly decreased by AMF under heterogeneous treatment rather than homogeneous treatment (Fig. 2), whereas heterogeneity decreased their MGR and shifted the positive effects of AMF to negative effects on the growth of *B. pilosa* (Table S2, Fig. S1). Negative or parasitic effects of AMF on host plants often occur when the net cost of symbiosis exceeds the net benefits. The parasitic effects of AMF are generally characterised by low nutrient delivery and/or high C demand by the fungus (Bennett and Groten, 2022). This was confirmed by our monoculture results, which showed that AMF significantly reduced the uptake of N and P from the shoots of *E. sonchifolia* under homogeneous treatment, and reduced the uptake of N and P from the shoots of *B. pilosa* and *P. clematidea* under heterogeneous treatment (Fig. 4). In general, plants can proliferate their roots or mycorrhizal hyphae to explore and acquire resources from nutrient-rich soil patches (Hodge, 2006), and some invasive plants differ in root-foraging traits (scale and precision) from those of native species (Rajaniemi and Reynolds, 2004; Drenovsky et al., 2008; Chen et al., 2018). Our previous study found that two exotic invasive plants (*B. pilosa* and *Mikania micrantha*) had a larger foraging scale, whereas two native plants (*Vernonia cinerea* and *Paederia scandens*) had higher precision (Chen et al., 2018). Given that the metabolic cost of hyphal growth is much lower owing to its smaller diameter, AMF may be more flexible in responding to soil nutrient patches than to roots (Hodge, 2006). Furthermore, when large numbers of roots and mycorrhizal fungal hyphae are close together, the mycorrhizal roots likely compete for limited soil nutrients (e.g., N and P), indicating a trade-off between root foraging and AMF (Felderer et al., 2013). However, little is known about the effects of AMF on root foraging in invasive and native species. Our results showed that AMF reduced the root-foraging scale and precision of the host plants. AMF decreased the root foraging scale of *B. pilosa* and decreasing root foraging precision of *P.*

*clematidea*, respectively (Fig. 2). This indicates that there is a trade-off between root foraging traits and AMF inoculation (i.e., foraging scale versus AMF for *B. pilosa* and foraging precision versus AMF for *E. sonchifolia* and *P. clematidea*). The decrease in the precision of root foraging in *E. sonchifolia* and *P. clematidea* caused by AMF is supported by previous studies showing that inoculation with AMF inhibits the preferential allocation of roots in P-rich patches (Cui and Caldwell, 1996; Felderer et al., 2013).

Competition has long been considered a major mechanism determining the success of some invasive species (Levine et al., 2003). Soil nutrient heterogeneity and AMF can influence the competitive ability and expansion of invasive plants (Zhang et al., 2017, 2018; Luo et al., 2021). Some studies have shown that AMF promote the competitive ability of invasive plants with native plants (Zhang et al., 2018; Dong et al., 2021), while others have found that AMF reduces the ability of invasive plants to compete with native plants (Luo et al., 2021). However, the interactive effects of nutrient heterogeneity and AMF on the competition between invasive and native plants remain unclear. We found that competition significantly increased the MGR of *E. sonchifolia* in the homogeneous treatment, and *E. chinense* in the heterogeneous treatment (Table S2, Fig. S1). To understand the response of competitive ability to AMF and P heterogeneity, we calculated the tolerance RII and suppression RII of the two invasive plants compared to their native counterparts. Our results showed that the effects of AMF on the competitive ability differed between the two invasive species and are dependent of P (homogenous vs heterogeneous) distribution (Table 4, Fig. 5). Under heterogeneous conditions, AMF increased the competitive tolerance of *B. pilosa* but had no significant effects in the homogeneous P treatment, resulting a significant heterogeneity AMF interaction on tolerance RII of *B. pilosa.* The results indicated that heterogeneity induced a stronger AMF effect on tolerance rather than on the suppression of *B. pilosa* (Fig. 5), which is consistent with the finding that strong competitors can select tolerance to competition more than the ability to suppress neighbours (Fletcher et al., 2016; Golivets and Wallin, 2018). However, this was not the case for another invasive species, *P. clematidea.* AMF had no significant effects on the tolerance RII of *P. clematidea* in either homogenous or heterogeneous P treatment, while heterogeneity induced a negative AMF effect on competitive suppression. Interestingly, similar to the competitive suppression of *P. clematidea* in the heterogeneous treatment, AMF decreased the suppression of *B. pilosa* in the homogeneous treatment group. This is consistent with results showing that the invasive species *Centaurea solstitialis* (yellow star thistle) was more strongly suppressed by the established native bunchgrass *Stipa pulchra* in the presence and absence of AMF (Waller et al., 2016). These results highlight the role of AMF in plant competition is dependent of P distribution.

It has been well documented that CMNs connect neighbours and exchange resources (e.g., C, N, and P) between plants (Barto et al., 2012; Wipf et al., 2019), and influence plant inter-competition by transferring nutrient between the competitors (Weremijewicz et al., 2016). Thus, we guess soil P distribution may influence nutrient transfer between the competing invasive and native species. To understand the possible role of CMNs in N and P uptake in different P distribution, we compared the results in the mixture (with competition) in heterogeneous P with homogeneous P. We found that heterogeneity shifted the positive effects of AMF in N and P uptake of the native species *E. sonchifolia* into negative effects compared to homogeneity. On the contrary, heterogeneity shifted the negative effects of AMF in shoot P uptake of its competitor *B. pilosa* into positive effects. It seems that *B. pilosa* probably derived P via CMN to benefit from AMF, but its neighbour, *E. sonchifolia* contributed biomass for AMF to pay for the cost. However, this was not the case for another native–invasive pair (*E. chinense* and *P. clematidea*), where heterogeneity shifted the negative effects of AMF in N and P uptake of the native species *E. chinens* into positive effects, but the effects are converse to its competitor the invasive species *P. clematidea*. These results imply that the native species *E. chinense* probably derived N and P via CMN to benefit from AMF, but its neighbour, *P. clematidea* contributed biomass for AMF to pay for the cost. These results imply that the effects of nutrient heterogeneity, AMF, and competition on plant growth and nutrient uptake show invasive-native pair differences, and are dependent on which plant species was the donor or receiver.

Notably, different species of AMF have different functions (Reynolds et al., 2005), and the effects of AMF on invasive plants range from positive to negative depending on the host plant and fungal species (Aslani et al., 2019). Further studies are needed to explore the effects of different AMF species on the competition between native and invasive plants and to explain the role of AMF in the success of plant invasion in a heterogeneous environment.

## Conclusions

Our results showed that in the monoculture, soil heterogeneous P significantly facilitated the growth of all four species except *E. chinense* compared to homogeneous P regardless of AMF inoculation, while AMF inoculation reduced the growth of all four species except *E. chinense* in heterogeneous P rather than in homogeneous P. In the mixture (with competition), AMF inoculation increased the

tolerance RII of *B. pilosa* in the heterogeneous P but decreased the suppression of RII of *B. pilosa* in the homogeneous P. Heterogeneity induced a negative AMF effect on competitive suppression of *P. clematidea.* Furthermore, competition altered the effects of AMF on plant growth and nutrient uptake; these effects were pairs-specific and dependent on the distribution of P. Competition eliminated the heterogeneity-induced negative effects of AMF on *B. pilosa* growth. These findings provide valuable insights into the interactive effects of AMF and soil nutrient distribution on plant growth and competition and highlight the context dependency of these interactions.

# Declarations


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### Data availability

Data are available on FigShare (https://figshare.com/s/1c3652bdf851e502f19c).

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# Tables

**Table 1** Two-way ANOVA for the effects of AMF inoculation and species on root foraging scale and precision of monoculture plants. Species refers to the identity of the species being planted. Statistically significant values are in bold ($p < 0.05$). RLD indicates root length density.

| | Foraging scale (mass) | | | Foraging Scale (RLD) | | Foraging precision (mass) | | | Foraging precision (RLD) | |
|---|---|---|---|---|---|---|---|---|---|---|
| Treatments | *df* | *F* | *p* | *F* | *p* | *df* | *F* | *p* | *F* | *p* |
| AMF | 1 | **10.404** | **0.003** | **10.159** | **0.004** | 1 | **13.003** | **0.001** | 3.361 | 0.080 |
| Species | 3 | **38.766** | **<0.001** | **23.333** | **<0.001** | 2[#] | **17.37** | **<0.001** | **15.102** | **<0.001** |
| AMF × S | 1 | **7.507** | **<0.001** | 2.664 | 0.067 | 1 | **6.962** | **0.004** | 0.778 | 0.471 |

[#] The foraging precision of *E. chinense* cannot be determined since its roots do not spread in P-rich soil. Therefore, we measured the root foraging precision of three species, but without *E. chinense*.

**Table 2** Two-way ANOVA analysis for the effects of heterogeneity and AMF inoculation on total biomass of plants in monoculture and mixture. Statistically significant values are in bold ($p < 0.05$).

| Species | | | *B. pilosa* | | *E. sonchifolia* | | *P. clematidea* | | *E. chinense* | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Treatments | *df* | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* |
| Monoculture | Heterogeneity | 1 | **101.618** | **<0.001** | **49.267** | **<0.001** | **29.776** | **<0.001** | 1.194 | 0.300 |
| | AMF | 1 | **17.059** | **<0.001** | **22.846** | **<0.001** | 0.540 | 0.473 | 0.770 | 0.401 |
| | H × AMF | 1 | **19.668** | **<0.001** | 1.862 | 0.191 | **7.375** | **0.015** | 0.450 | 0.518 |
| Mixed culture | Heterogeneity | 1 | **28.154** | **<0.001** | **41.721** | **<0.001** | **146.027** | **<0.001** | **16.907** | **0.002** |
| | AMF | 1 | 0.012 | 0.916 | 0.014 | 0.907 | 0.327 | 0.575 | **5.986** | **0.032** |
| | H × AMF | 1 | 3.673 | 0.070 | 3.914 | 0.065 | 3.121 | 0.096 | **9.843** | **0.009** |

**Table 3** Two-way ANOVA analysis for the effects of heterogeneity and AMF inoculation on shoot N and P uptake in monoculture and mixture. Statistically significant values are in bold ($p < 0.05$).

| Species | | | *B. pilosa* | | *E. sonchifolia* | | *P. clematidea* | | *E. chinense* | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Treatments | *df* | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* |
| N uptake in monoculture | Heterogeneity | 1 | **101.618** | **<0.001** | **49.267** | **<0.001** | **29.776** | **<0.001** | 1.194 | 0.300 |
| | AMF | 1 | **17.059** | **<0.001** | **22.846** | **<0.001** | 0.540 | 0.473 | 0.770 | 0.401 |
| | H × AMF | 1 | **19.668** | **<0.001** | 1.862 | 0.191 | **7.375** | **0.015** | 0.450 | 0.518 |
| P uptake in monoculture | Heterogeneity | 1 | **28.154** | **<0.001** | **41.721** | **<0.001** | **146.027** | **<0.001** | **16.907** | **0.002** |
| | AMF | 1 | 0.012 | 0.916 | 0.014 | 0.907 | 0.327 | 0.575 | **5.986** | **0.032** |
| | H × AMF | 1 | 3.673 | 0.070 | 3.914 | 0.065 | 3.121 | 0.096 | **9.843** | **0.009** |
| N uptake in mixture | Heterogeneity | 1 | **19.401** | **<0.001** | **17.452** | **<0.001** | **11.386** | **0.003** | **68.261** | **<0.001** |
| | AMF | 1 | 1.905 | 0.186 | 0.646 | 0.433 | 0.641 | 0.432 | **49.456** | **<0.001** |
| | H × AMF | 1 | 1.888 | 0.188 | ***3.237*** | ***0.091#*** | 0.196 | 0.662 | **27.906** | **0.003** |
| P uptake in mixture | Heterogeneity | 1 | **13.931** | **0.002** | **28.7474** | **<0.001** | **7.079** | **0.014** | 3.254 | 0.131 |
| | AMF | 1 | 0.116 | 0.738 | 2.116 | 0.165 | 0.028 | 0.867 | 1.531 | 0.271 |
| | H × AMF | 1 | 1.687 | 0.212 | 2.629 | 0.125 | 0.477 | 0.497 | 0.502 | 0.510 |

**Table 4** Two-way ANOVA for the effects of soil phosphorus heterogeneity, AMF inoculation on tolerance and suppression competitive ability of *B. Pilosa* and *P. clematidea*. Statistically significant values are in bold ($p < 0.05$).

| ıments | | *B. pilosa* | | | | *P. clematidea* | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Tolerance RII | | Suppression RII | | Tolerance RII | | Suppression RII | |
| | *df* | *F* | *p* | *F* | *p* | *F* | *p* | *F* | *p* |
| rogeneity | 1 | **149.788** | **<0.001** | 0.062 | 0.807 | **59.008** | **<0.001** | **21.198** | **0.001** |
| AMF | 1 | **8.874** | **0.009** | **5.527** | **0.032** | 0.054 | 0.819 | **11.153** | **0.009** |
| × AMF | 1 | **11.869** | **0.003** | **6.319** | **0.023** | 0.202 | 0.659 | **6.190** | **0.035** |

# Figures

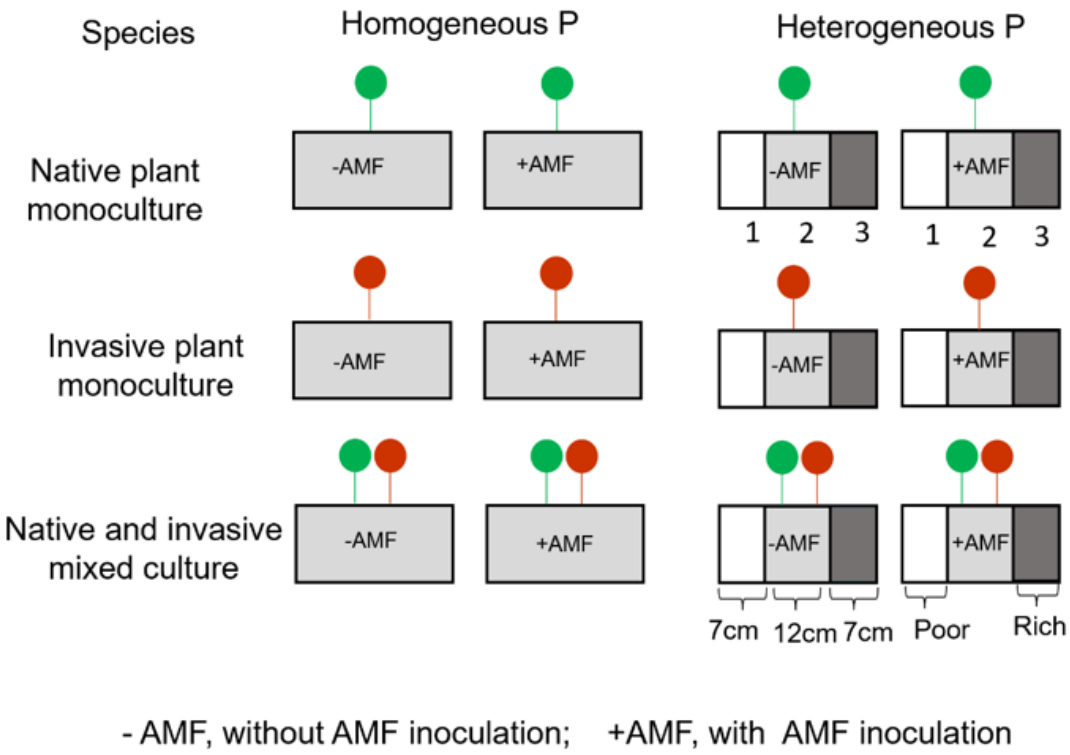



**Figure 1**

Schematic representation of the experimental design. Each species was grown alone and in competition with its counterpart under homogeneous and heterogeneous conditions. The pots of heterogeneous phosphorus treatment were divided into three sections (1, 2 and 3). Section 1 (7 cm) was phosphorus-poor, and Section 3 (7 cm) was phosphorus-rich. Gray represents homogeneous soil; dark shading represents phosphorus-rich soil; and white represents phosphorus poor soil. Total nutrient availability was similar between treatments. Each treatment was replicated 5 times.

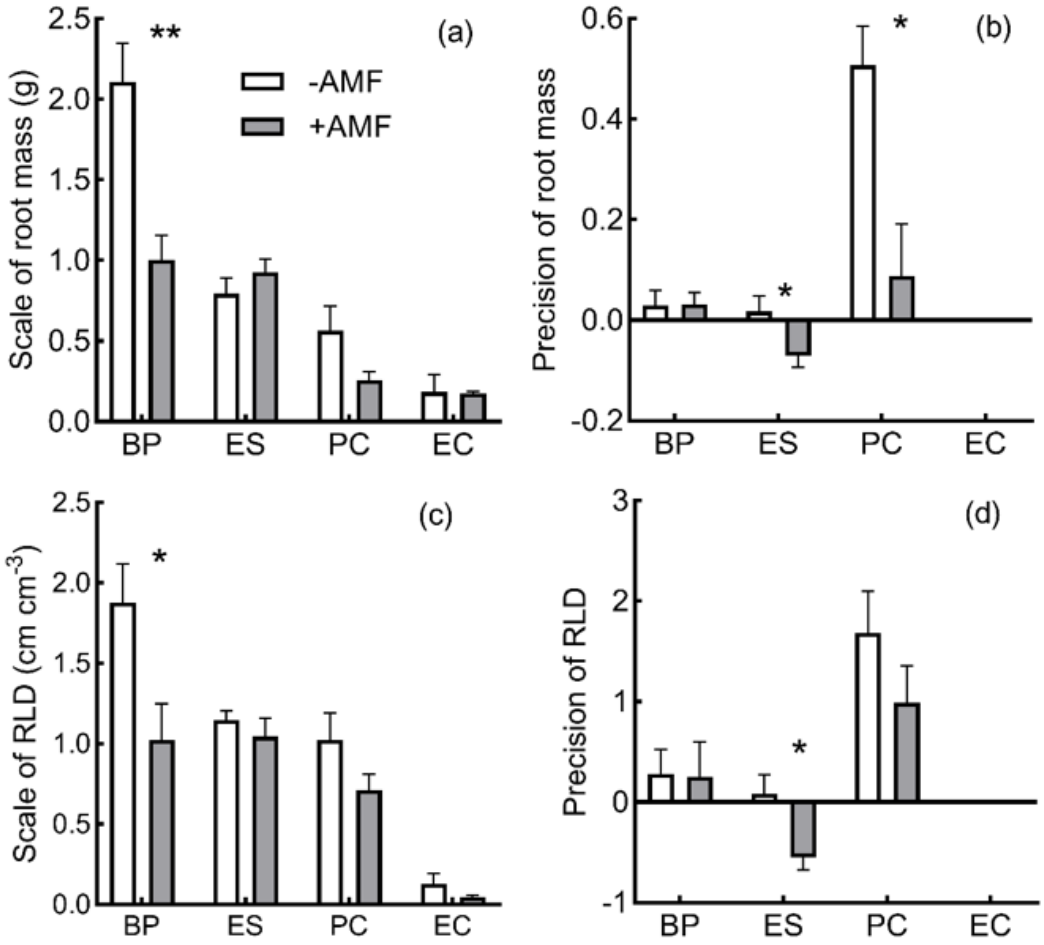
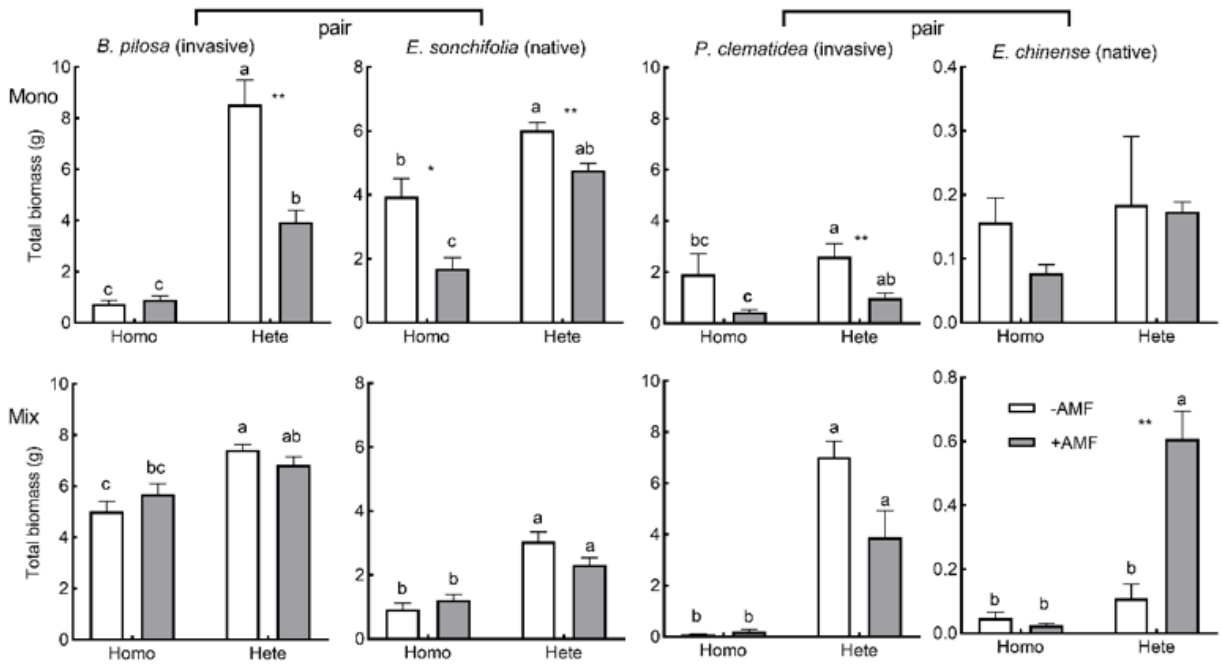


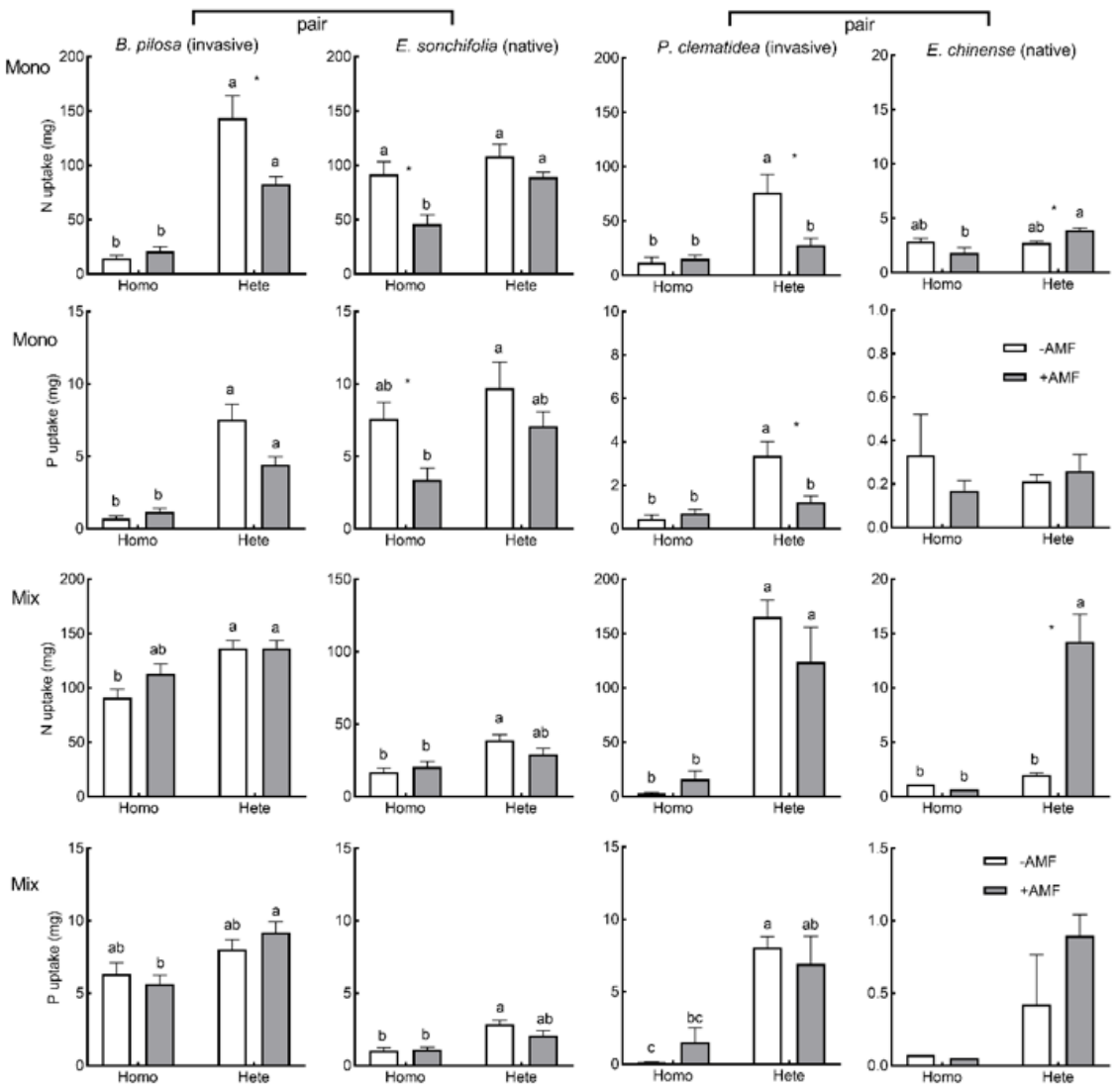

**Figure 2**

The effects of AMF and heterogeneity on root foraging scale in terms of root mass (a) and RLD (c) of the four species under monoculture, while on root foraging precision in terms of root mass (b) and RLD (d) of these species (except EC because its roots do not spread in phosphorus-rich soil) in monoculture. BP, *B. pilosa*; ES, *E. sonchifolia*; PC, *P. clematidea*; EC, *E. chinense*. Values are the means + 1 SE (n = 5). RLD, root length density. -AMF, without AMF inoculation; +AMF, AMF inoculation. Asterisks indicate significant difference between AMF and without AMF inoculation, where **: $0.001 < p < 0.01$, *: $0.01 < p < 0.05$. The two-way ANOVA analysis for the effects of AMF inoculation and species on root foraging scale and precision is shown in Table 1.




## Figure 3

The effects of heterogeneity and AMF inoculation on the total biomass of the four species in monoculture and mixture. Values are the means + 1 SE (n = 5). Homo, homogeneous phosphorus; hete, heterogeneous phosphorus. -AMF, without AMF inoculation; +AMF, AMF inoculation. Different letters represent significant differences in post hoc comparisons ($p < 0.05$). Asterisks indicate a significant difference between with AMF and without AMF inoculation, where **: $0.001 < p < 0.01$, *: $0.01 < p < 0.05$. The two-way ANOVA analysis for heterogeneity and AMF is shown in Table 2.




## Figure 4

The effects of AMF and heterogeneity on N and P uptake of the four species in monoculture and mixture. Values are the means + 1 SE (n = 5). Homo, homogeneous phosphorus; hete, heterogeneous phosphorus. -AMF, without AMF inoculation; +AMF, AMF inoculation. Different letters represent significant differences in post hoc comparisons ($p < 0.05$). Asterisks indicate a significant difference between with AMF and without AMF inoculation, where **: $0.001 < p < 0.01$, *: $0.01 < p < 0.05$. The two-way ANOVA analysis for heterogeneity and AMF is shown in Table 3.

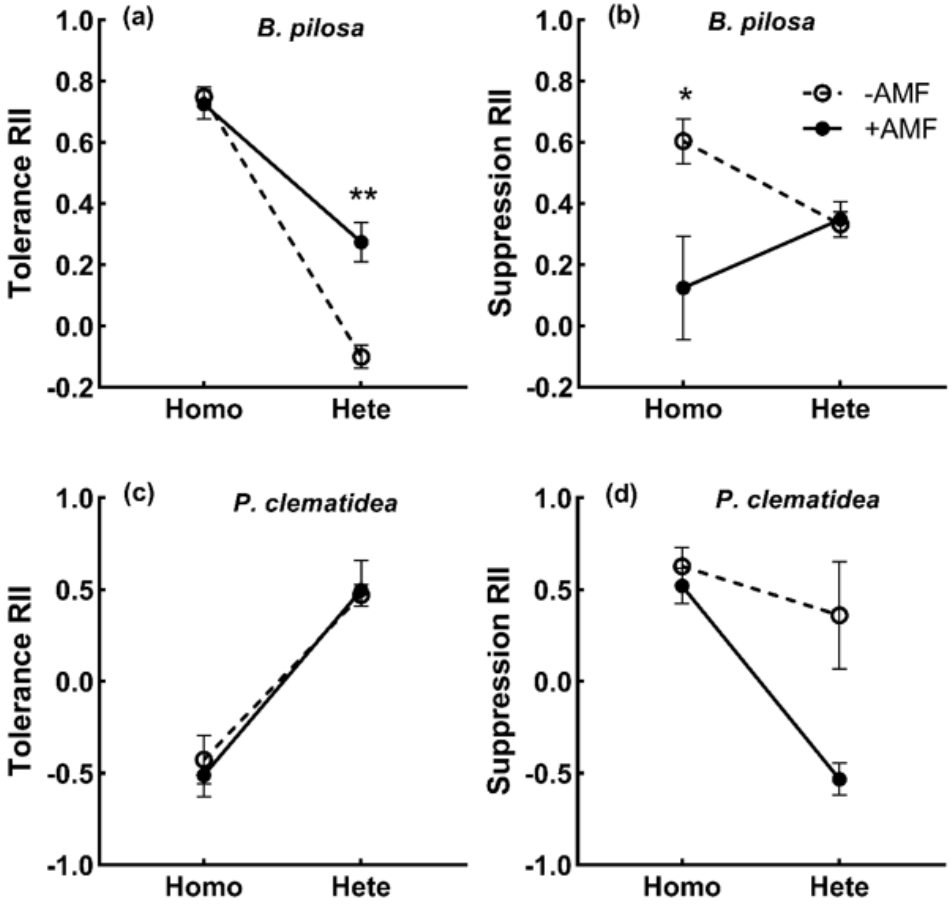



Figure 5

The effects of P heterogeneity and inter-competition on mycorrhizal growth responsiveness. Homo and Hete represent homogeneous and heterogeneous phosphorus, respectively. Values are the means + 1 SE (n = 5). Different letters represent significant differences in post hoc comparisons ($p < 0.05$). The effects of heterogeneity are significantly different with (*) at $p < 0.05$, and with (**) at $p < 0.01$ tested separately with independent t-test. The two-way ANOVA analysis for heterogeneity and AMF is shown in Table 4.

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Supplementarymaterial.docx