

Arbuscular mycorrhizal fungal effects on plant competition and community structure

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Summary

1. Arbuscular mycorrhizal fungi (AMF) mediate plant interspecific competition and community structure. However, the magnitude and direction of AMF effects and underlying mechanisms are not clear. Here, we synthesized the results of 304 studies to evaluate how AMF affect plant competition and community structure and which abiotic and biotic conditions in experimental design modify these AMF effects.

2. The magnitude and direction of AMF effects on plant competitive ability (in terms of competitive response) differed markedly among plant functional groups. When AMF inoculum was added, competitive ability was strongly enhanced in N-fixing forbs and was significantly suppressed in C₃ grasses, whereas no effect was observed in C₄ grasses, non-N-fixing forbs and woody species. Furthermore, AMF inoculation increased competitive ability of perennial species when their competitors were annual species.

3. AMF inoculation differentially influenced separate aspects of plant community structure and species composition. AMF inoculation significantly increased plant diversity but had no effects on plant productivity. Response of dominant plant species to AMF inoculation was the determining factor in explaining variations in how and to what degree plant diversity was influenced by AMF inoculation. When dominant species derived strong benefits from AMF, their dominance level was increased by AMF inoculation, which consequently decreased plant diversity. We did not find stronger AMF effects on plant diversity and productivity when greater numbers of AMF species were used in the inoculation.

4. Synthesis. Despite large variations in AMF effects among studies, a unifying mechanism was observed that the mycorrhizal responsiveness (differences in plant growth between AMF and non-AMF colonization treatments) of target and neighbouring plant species can determine AMF effects on the competitive outcome among plant species, which in turn influenced plant species diversity and community composition. Given that plant traits, soil nutrient conditions and probably mycorrhizal fungal traits are all factors determining the degree of mycorrhizal response of plant species, future studies should explicitly consider each of these factors in experimental design to better understand AMF effects on plant coexistence, plant community dynamics and ecosystem processes.

Key-words: competitive response, dominant species, plant diversity, plant functional group, plant productivity, plant–soil (below-ground) interactions, root traits

Introduction

Understanding factors influencing plant community structure is a central topic in plant ecology. Various mechanisms have been used to explain species coexistence and community

structure including negative intraspecific interactions, competition–colonization trade-offs, competition–antagonist avoidance trade-offs and neutral models (Chesson 2000; Hubbell 2006; Bever *et al.* 2010). Recently, the role of arbuscular mycorrhizal fungi (AMF) in structuring plant communities has received increasing attention in empirical studies, conceptual models and systematic analyses (Hart, Reader & Klironomos 2003; Urcelay & Díaz 2003; Klironomos *et al.* 2011).

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In these previous studies, AMF have been shown to influence interspecific plant competition (Danieli-Silva *et al.* 2010; Wagg *et al.* 2011b; Mariotte *et al.* 2013). One mechanism controlling AMF effects on interspecific competition is the varying degree of benefit that AMF provide to different plant species (Hartnett *et al.* 1993; Urcelay & Díaz 2003). These variations in mycorrhizal responses (differences in plant growth performance between AMF and non-AMF colonization treatments) among plant species lead to the concept of the 'mutualism–parasitism continuum', which can occur in both obligate and facultative mycorrhizal plants (Johnson, Graham & Smith 1997). This continuum concept was corroborated by a meta-analysis by Hoeksema *et al.* (2010), which found that plant species of different functional groups responded differently to AMF inoculation.

Different mycorrhizal responses may be due to differences in plant traits among different plant functional groups (Hetrick, Wilson & Todd 1990) as plant traits can influence the degree to which plant species rely on AMF for nutrient acquisition from the soil (Brundrett 2002). For example, compared with C₄ grasses, C₃ grasses often have more fibrous (i.e. thinner), highly branched root systems with a lower dependency on AMF for nutrient uptake (Hetrick, Wilson & Todd 1990; Wilson & Hartnett 1998); thus, C₃ species may not respond strongly to changes in AMF inoculation. In contrast, the thicker roots common to many C₄ grasses are often more reliant on AMF to explore soil and acquire nutrients. Therefore, the suppression of AMF colonization could be expected to reduce competitive ability of C₄ grasses when competitors were C₃ grasses (Hartnett *et al.* 1993; Hetrick *et al.* 1994). Additionally, given the high phosphorus (P) requirements for nitrogen (N) fixation, N-fixing forbs are thought to have a high AMF dependency for absorbing P and thus AMF may be expected to increase the competitive ability of N-fixing forbs (Wagg *et al.* 2011b). Together, the different mycorrhizal responses among plant species may determine how AMF affect plant interspecific competition.

Considering that plant species differ in their mycorrhizal responses, it has been suggested that AMF may influence plant diversity and community structure (vander Heijden *et al.* 1998; Vogelsang, Reynolds & Bever 2006). A conceptual model by Urcelay & Díaz (2003) suggests that the AMF effects on plant diversity can be explained by the relative mycorrhizal response of dominant vs. subordinate plants. If mycorrhizal response of dominants is high, AMF should enhance competitive ability of dominants, leading to a decrease in plant diversity (Hartnett & Wilson 1999). By manipulating AMF inoculation and P conditions, Vogelsang, Reynolds & Bever (2006) found that variation in the mycorrhizal response of dominant species to AMF colonization partially explained changes in plant diversity. Conversely, if the subordinates are highly mycotrophic, AMF inoculation may increase plant diversity by enhancing competitive ability of subordinates (van der Heijden *et al.* 1998).

Other variables may also modify AMF effects on plant interspecific competition and community structure including abiotic soil conditions, especially P availability, and AMF

species identity and diversity (Collins & Foster 2009; Wagg *et al.* 2011b; Birhane *et al.* 2014). Collins & Foster (2009) found that positive effects of AMF on plant diversity and productivity declined with increasing soil P availability. Additionally, different species of AMF may have distinct colonization strategies and functional roles in nutrient uptake and pathogen protection (Maherali & Klironomos 2007). Indeed, it has been found that AMF species identity and diversity can influence AMF effects on plant interspecific competition and community structure (Vogelsang, Reynolds & Bever 2006; Wagg *et al.* 2011b). Therefore, to fully understand the magnitude and direction of AMF effects on plant interspecific competition and community structure, systematic tests examining each of these factors are needed.

Here, we performed a meta-analysis to assess AMF effects on interspecific competition, plant diversity and productivity. Using this quantitative method, we aimed to answer the following questions:

- 1 Do the effects of AMF on interspecific competition depend on plant characteristics such as plant functional group, life history and mycorrhizal status, because plant species that differ in these characteristics also vary in their responsiveness to mycorrhizal colonization?
- 2 Is the mycorrhizal response of dominant species a good predictor of AMF effects on plant diversity, since AMF may influence competitive ability of the dominant species which then affect the growth of subordinate species and overall plant diversity?
- 3 Do AMF effects on plant competition, plant diversity and productivity depend on experimental conditions (i.e. AMF inoculum complexity, soil nutrient availability), given that mycorrhizal response and the cost-benefit balance of plant species depend on these experimental conditions?

Materials and methods

IDENTIFICATION AND SELECTION OF STUDIES

To develop a comprehensive data base, we searched Web of Science for published papers and ProQuest for unpublished dissertations using the following themes: (*plant interaction* OR *plant competition* OR *plant diversity* OR *plant community* OR *productivity*) AND (*arbuscular mycorrhizal fungi* OR *mycorrhizal fungi* OR *endomycorrhizal fungi*). References of review articles in this research field (e.g. Hart, Reader & Klironomos 2003; Urcelay & Díaz 2003; Klironomos *et al.* 2011) were also used to find further studies which were not covered by the above searches.

To determine AMF effects on plant competition, we selected experiments reporting the factorial effects of interspecific competition and AMF inoculation on target species biomass. Previous reports usually reported competitive responses of the same target species with different neighbour species. In these cases, different target and neighbour species combinations were each categorized as a different study. To analyse AMF effects on the competition of plant species with different mycorrhizal status, we included three reports which investigated competition between genotypes of AM hosts and AM-defective mutant hosts of the same plant species. For AMF-mediated effects on plant community composition and productivity, we selected studies

reporting AMF effects on any of the following: plant species evenness, plant species richness, plant diversity and plant productivity, under AMF colonization and non-AMF colonized conditions. In the present study, field studies that applied fungicides to reduce AMF colonization were regarded as non-AMF-inoculated controls, although controls (non-AMF-inoculated treatment) were not completely AMF free. In cases where articles contained multiple combinations of plant community with different AMF species and community, we treated each combination as a separate study, although not all studies were statistically independent.

For the present study, in cases where response variables (e.g. plant biomass; species diversity; plant productivity) were measured repeatedly through time, we only used data from the last measurement in each study. When additional treatments existed, such as fertilization, increased CO₂ and adjustments in soil fauna, only the ambient (control) treatment was used in this analysis. Furthermore, we only included studies that reported the mean, sample size and standard deviation (or provided sufficient information to calculate standard deviation).

DATA EXTRACTION

For each study of AMF effects on interspecific competition that met the above criteria, we extracted the whole-plant biomass or shoot biomass (when the whole-plant biomass was not reported) of target species with and without AMF inoculation in the presence or absence of interspecific competition. When necessary, we digitized graphs using the GETDATA software (Moscow, Russia) to obtain this information. We also collected data regarding plant traits (plant functional group, life history, provenance and mycorrhizal status of target and neighbour species), experimental design and AMF inoculum complexity as well as treatments of non-AMF inoculation (Table 1) which might influence AMF effects on interspecific competition.

For studies of AMF-mediated plant community structure and productivity, we extracted data regarding plant diversity (Shannon's or Simpson's diversity index) or its two components: species evenness (relative abundance of each species to the total biomass of a plant community) and richness (number of species in a plant community), and productivity. In addition, studies that recorded whole-plant cover were included as surrogate index of biomass when plant biomass was not reported. Three categorical variables (AMF inoculum complexity, non-AMF inoculation treatment and experimental location; Table 1)

Table 1. Categorical variables obtained from each study case

Categorical variables	Categories
Plant traits (targets and neighbours)	
Plant functional groups	C ₃ grasses, C ₄ grasses, N-fixing forbs, non-N-fixing forbs, woody species
Life history	Annual, perennial
Provenance	Native, invasive
Mycorrhizal status	Obligately mycorrhizal (OM), facultatively mycorrhizal (FM), non-mycorrhizal (NM)
Experimental conditions	
Experimental design	Additive, substitutive
AMF inoculum complexity	Soil inoculum, mixture, single
Non-AMF inoculation treatment	Benomyl application, autoclaving
Experimental location	Greenhouse, field

and one continuous variable (dominant species response to AMF inoculation) were selected. In the present study, a dominant species was defined as the species with the maximum biomass in a plant community of control treatment (non-AMF inoculated) at the last sampling period. We also divided dominant species into different functional groups (Table 1). Dominant species response to AMF inoculation was calculated by the equation: [(inoculated – uninoculated)/uninoculated] (Seifert, Bever & Maron 2009).

A total of eight categorical variables were selected (Table 1) and their descriptions are shown in the Appendix S1 (Supporting Information). All the categorical variables listed in Table 1 were assigned following the description of the papers used in our analyses. When the neighbours were mixtures of species, we did not consider the traits of neighbours. If plant traits of target and neighbour species were not described in papers, their traits were determined by searching the Plant Database (<http://plants.usda.gov/java/>), The Euro + Med Plant-Base (<http://ww2.bgbm.org/EuroPlusMed/query.asp>) and eFloras (<http://www.efloras.org>).

DATA ANALYSIS

Effect size of plant species response to AMF inoculation was calculated as the natural log response ratio of inoculated to non-inoculated plant biomass when there was no neighbour species. Mean effect sizes and 95% confidence intervals (CIs) were calculated using random-effect models. Between-group heterogeneity (Q_b) of the random-effect models was used to analyse whether categorical variables had different effects on plant species response to AMF inoculation.

Competitive response of target species was calculated by the equation: $\bar{X}_{pres}/\bar{X}_{abs}$, where \bar{X}_{pres} and \bar{X}_{abs} denoted mean plant biomass of target species in the presence (\bar{X}_{pres}) or absence (\bar{X}_{abs}) of neighbour species. A species with a high value of competitive response means that it has a high competitive ability (Niu & Wan 2008). Effect size was calculated as the natural log of the competitive response [i.e. $\ln(\bar{X}_{pres}/\bar{X}_{abs})$]. Negative and positive values of effect size indicated that target species responded negatively and positively to neighbours, respectively. Using random-effect models, we calculated mean effect sizes in each of experimental groups (AMF inoculation) and control groups (non-AMF inoculation) for the entire data set and its subsets (Hector *et al.* 2011). Subsets were gathered by dividing the entire data set by the categorical variables described in Table 1. To determine AMF effects on interspecific competition, we used the methods described by He, Bertness & Altieri (2013). Specifically, we used between-group heterogeneity (Q_b) of the random-effect models to determine whether the effect sizes differed significantly between inoculated and non-inoculated groups across the entire data set and its subsets. In Q_b analysis, Q statistic < 0.05 was accepted as statistically significant.

To better understand AMF effects on plant community and productivity, effect size was calculated as natural log response ratio of AMF-inoculated to non-AMF-inoculated plant communities. We also calculated mean effect sizes and 95% CIs using random-effect models as described above. Due to the low sample sizes of species richness and species evenness, we only analysed whether categorical variables had different effects on species diversity and productivity response to AMF inoculation by calculating between-group heterogeneity as described above. We then regressed effect size against continuous variable (dominant species response to AMF inoculation). P value of the slope < 0.05 was accepted as statistically significant.

We assessed publication bias using nonparametric rank correlation tests (Kendall's tau and Spearman's rho) for the analysis having at

least 25 samples within the data base (Rosenberg, Adams & Gurevitch 2000). This approach indicated the presence of publication bias when the significant correlation ($P < 0.05$) between standardized effects size and sample size was found. Above data base analyses were performed in METAWIN software version 2.0 (Rosenberg, Adams & Gurevitch 2000).

Where publication bias was detected, trim and fill method was used to estimate the number of studies needed to achieve symmetry in the funnel plot and calculate the trim and fill-corrected effect size (Viechtbauer 2010). The trim and fill procedure was conducted using the METAFOR package (Viechtbauer 2010) in R v3.1.2.

Results

SUMMARY OF DATA BASE

Overall, 304 studies met our criteria from 68 papers (63 published papers and 5 Graduate Theses; Appendix S2 and S3). The mean effect size and 95% CIs of each analysis are shown in supplemental materials (Tables S1 and S2 in Supporting Information).

AMF EFFECTS ON INTERSPECIFIC COMPETITION IN RELATION TO PLANT CHARACTERISTICS

For plant species grown alone without a competitive neighbour, AMF significantly increased plant biomass (95% CIs: 0.15 to 0.27, $N = 142$; Fig. 1). Plant species response to AMF inoculation, as measured by change in biomass, depended on plant functional group ($Q_b = 66.4$, $P < 0.01$), life history ($Q_b = 12.4$, $P < 0.01$) and mycorrhizal status ($Q_b = 8.5$, $P = 0.01$; Fig. 1). Plants of different provenance (i.e. native vs. invasive) did not show different response to AMF inoculation ($Q_b = 1.3$, $P = 0.25$; Fig. 1).

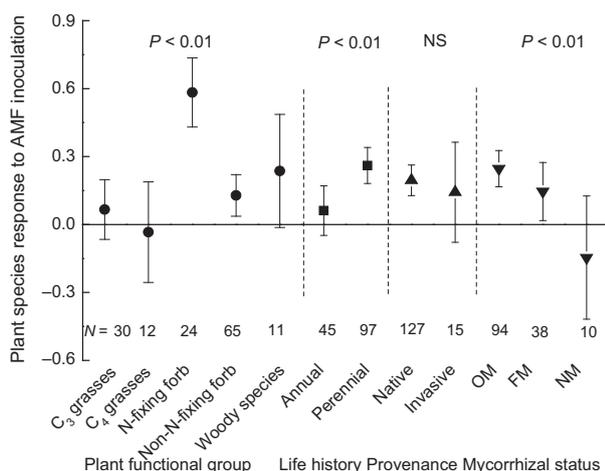


Fig. 1. Plant species response to AMF inoculation for the levels of categorical variables 'plant functional group', 'life history', 'provenance' and 'mycorrhizal status'. Symbols are means (closed circles) \pm 95% confidence intervals (error bars). Differences among different levels of each categorical variable were analysed by between-group heterogeneity of random-effect model size calculations. OM, obligately mycorrhizal; FM, facultatively mycorrhizal; NM, non-mycorrhizal. NS meaning no significance.

Across the entire data set, AMF had no significant effect on competitive response of target species ($P = 0.56$, $N = 170$). P values of Kendall's tau and Spearman's rho were 0.48 and 0.54, respectively, indicating that there was no publication bias.

Among different plant functional groups, AMF significantly decreased competitive response (ratio of target species biomass when there is no interspecific competition to that in the presence of interspecific competition) of C_3 grasses from 0.98 to 0.73 (Fig. 2a). Competitive response of N-fixing forbs was significantly increased from 0.32 to 0.60 by AMF inoculation (Fig. 2a). AMF did not significantly change competitive response of C_4 grasses, non-N-fixing forbs and woody species (Fig. 2a). When functional groups were different between target species and neighbours (e.g. when target species was a C_3 grass, the neighbours were not C_3 grasses), the results of AMF effects on competitive response of different functional groups were not changed (Fig. S1 in Supporting Information).

For mycorrhizal status, AMF inoculation significantly decreased competitive response of non-mycotrophic species from 1.22 to 0.90 and had no significant effects on competitive response of obligate and facilitative mycotrophic species (Fig. 2b). When mycorrhizal status was different between target species and neighbours, the results of AMF effects on competitive response of target species were not changed (Fig. S1). For life histories, when the life history of target and neighbour species was specified (i.e. Annual/Annual, Annual/Perennial, Perennial/Annual and Perennial/Perennial), we found that growth of target species was significantly reduced by interspecific competition (Fig. 3a). Moreover, AMF

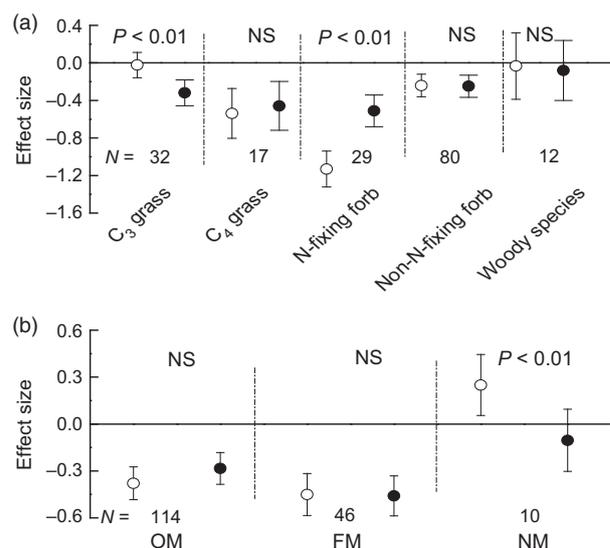


Fig. 2. Competitive response of target species in non-inoculated groups (open circles) and inoculated groups (filled circles) classified by functional groups (a) and mycorrhizal statuses (b) of target species. Shown are mean effect sizes (circles) and 95% confidence intervals (error bars). Differences between non-inoculated and inoculated groups were analysed by between-group heterogeneity of random-effect model size calculations. OM, obligately mycorrhizal; FM, facultatively mycorrhizal; NM, non-mycorrhizal. NS meaning no significance.

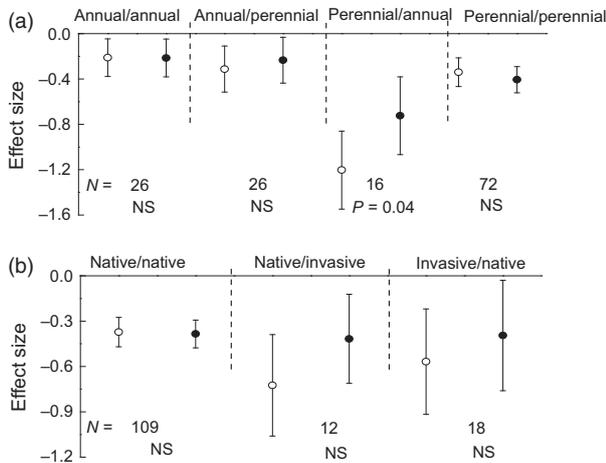


Fig. 3. Competitive response of target species in non-inoculated groups (open circles) and inoculated groups (filled circles) classified by target/neighbour life history (a) and provenance (b). Shown are mean effect sizes (circles) and 95% confidence intervals (error bars). Differences between non-inoculated and inoculated groups were analysed by between-group heterogeneity of random-effect model size calculations. NS meaning no significance.

significantly increased competitive response of perennial from 0.30 to 0.48 when the competing species was an annual species (Fig. 3a). Among the different studies related to provenance of targets and neighbours (i.e. Native/Native, Native/Invasive and Invasive/Native; there was no study of Invasive/Invasive), AMF inoculation did not significantly change competitive response of target species (Fig. 3b).

AMF EFFECTS ON PLANT DIVERSITY AND PRODUCTIVITY

Across the entire data base, AMF inoculation significantly increased species evenness (95% CIs: 0.02–0.21, $N = 15$) and plant diversity (as measured by Shannon's or Simpson's diversity index; 95% CIs: 0.06–0.18, $N = 42$) with no significant effect on species richness (95% CIs: –0.07 to 0.20, $N = 17$; Fig. 4). For the analysis of plant diversity, P values of Kendall's tau and Spearman's rho analyses were 0.06 and 0.07, respectively, indicating that there was no publication bias. Additionally, AMF had no significant effects on plant productivity (95% CIs: –0.007 to 0.03, $N = 60$). However, Kendall's tau and Spearman's rho for the correlation were –0.18 ($P = 0.04$) and –0.26 ($P = 0.04$) indicating the presence of publication bias. The trim and fill method estimated that theoretically there should be six missing studies on the left side of funnel plot. When these six 'studies' were added, AMF inoculation was expected to significantly decrease plant productivity (95% CIs: –0.04 to –0.003, $N = 66$).

MYCORRHIZAL RESPONSES OF DOMINANT SPECIES AFFECTING AMF EFFECTS ON PLANT DIVERSITY

Dominant species response to AMF inoculation was an important factor in explaining variation in effect sizes of species richness ($Q_b = 16.1$, $P < 0.01$; Fig. 5a), evenness

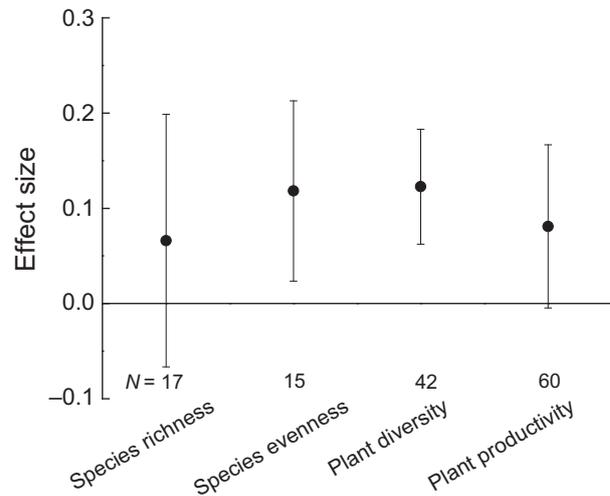


Fig. 4. Effect size of species richness, evenness, diversity and productivity response to arbuscular mycorrhizal fungi inoculation calculated by random-effect model. Symbols are means (closed circles) \pm 95% confidence intervals (error bars). Analyses were considered significant when 95% confidence intervals did not overlap zero.

($Q_b = 4.3$, $P = 0.04$; Fig. 5b) and plant diversity ($Q_b = 8.4$, $P < 0.01$; Fig. 5c). There was no relationship between dominant species response to AMF inoculation and effect sizes of productivity ($Q_b = 1.2$, $P = 0.28$; Fig. 5d).

EXPERIMENTAL CONDITIONS AFFECTING AMF EFFECTS

AMF inoculation did not have significant effects on the competitive response of target species across different AMF inoculum complexity, experimental design and sterilization treatment (Fig. S2). AMF effects on plant diversity depended on experimental location (i.e. greenhouse or field) ($Q_b = 14.7$, $P < 0.01$) and AMF inoculum complexity ($Q_b = 24.8$, $P < 0.01$). In particular, AMF significantly increased plant diversity only when experiments were conducted in a greenhouse (Fig. 6a). However, the identity of experimental location ($Q_b = 3.3$, $P = 0.07$) and AMF inoculum complexity ($Q_b = 3.5$, $P = 0.89$) were not significant in explaining variation in effect sizes of plant productivity (Fig. 6b). The type of sterilization treatment was significant in explaining variation in effect sizes of both plant diversity ($Q_b = 18.0$, $P < 0.01$) and plant productivity ($Q_b = 5.7$, $P = 0.02$). In particular, AMF inoculation significantly increased plant diversity and plant productivity only when the method of autoclaving was used in control treatments (Fig. 6a,b).

Discussion

We synthesized 304 studies to analyse the magnitude and direction of AMF effects on interspecific plant competition and community structure by considering the differences in plant traits and other abiotic and biotic factors. Our results showed that plant functional group was an important predictor of AMF effects on interspecific competition with the

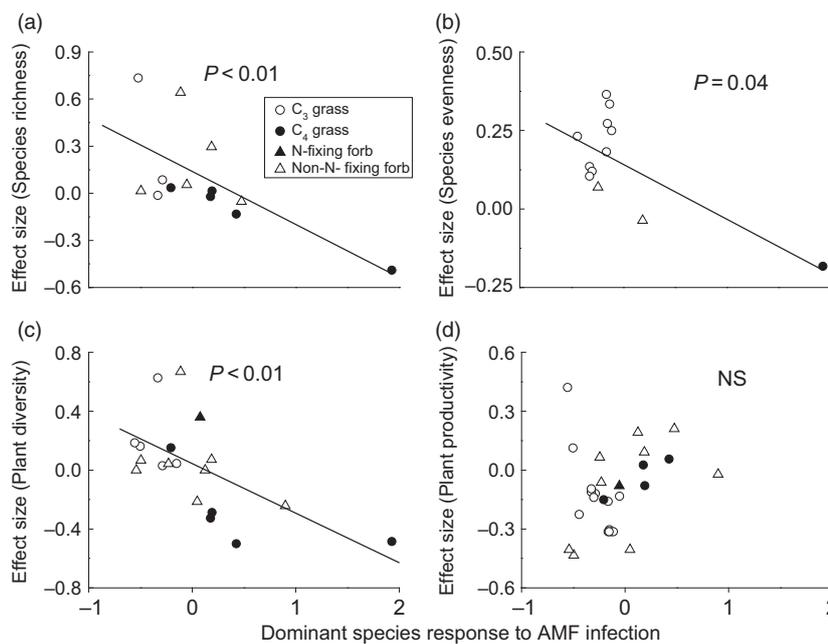


Fig. 5. Relationship between mean effect size and dominant species response to AMF inoculation for species richness (a), species evenness (b), plant diversity (c) and productivity (d). Dominant species with different functional groups were shown with different symbols. NS meaning no significance.

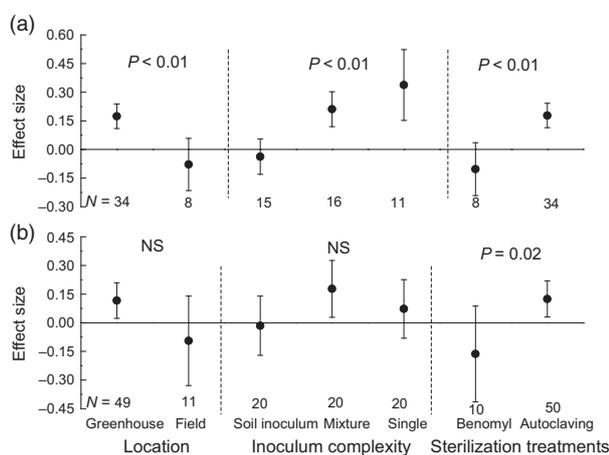


Fig. 6. Effect size of species diversity (a) and productivity (b) response to arbuscular mycorrhizal fungi inoculation classified by experimental location, inoculum complexity and sterilization treatment. Shown were mean effect sizes (circles) and 95% confidence intervals (error bars). Between-group heterogeneity of random-effect model was used to test whether effect sizes were consistent under different experimental conditions. NS meaning no significance.

mycorrhizal response of target species largely determining AMF effects on their competitive ability. Additionally, the mycorrhizal response of dominant plant species strongly influenced the magnitude and direction of AMF effects on overall plant diversity. Apart from plant characteristics, abiotic and biotic factors can also influence plant mycorrhizal response and then mediate plant community structure.

PLANT CHARACTERISTICS INFLUENCING AMF EFFECTS ON INTERSPECIFIC COMPETITION

Our meta-analysis showed that AMF effects on interspecific competition were dependent on plant functional type.

Competitive ability of C_3 grasses was significantly decreased by AMF inoculation (i.e. AMF significantly decreased competitive response of C_3 grasses; Fig. 2a). This may be because C_3 grasses often have fibrous and highly branched root systems with rapid nutrient uptake rates by virtue of the high root surface area (Hetrick, Wilson & Todd 1990; Wilson & Hartnett 1998) and are less dependent on AMF. As a result, C_3 grasses often show little positive and even negative responses to AMF inoculation (Hetrick, Wilson & Todd 1990; Wilson & Hartnett 1998; Fig. 1). Accordingly, it is not surprising that AMF inoculation decreases the competitive ability of C_3 grasses, because their competitors may derive more benefit from AMF inoculation (Hartnett *et al.* 1993; Hetrick *et al.* 1994).

Significant AMF effect on competitive ability also occurred in N-fixing forbs with AMF inoculation leading to the increased competitive ability of N-fixing forbs (Fig. 2a). N-fixing forbs are commonly associated with two groups of beneficial organisms, that is AMF and rhizobia, which can have synergistic effects on plant biomass production (Larimer, Clay & Bever 2014). Therefore, N-fixing forbs may show high mycorrhizal response and AMF inoculation may significantly improve the competitive ability of N-fixing forbs (Scheublin, Van Logtestijn & van der Heijden 2007; Wagg *et al.* 2011b). However, inconsistent with our results (Fig. 1), Hoeksema *et al.* (2010) found that N-fixing forbs exhibited lower mycorrhizal response than other functional groups. This low mycorrhizal response may be due to many of the studies used in their synthesis originating from P-rich soil (Hoeksema *et al.* 2010). Considering high carbon cost of AM and rhizobial symbionts, AMF inoculation may play negligible roles in P uptake in soils with high P availability, resulting in negative effects on the growth performance of N-fixing forbs (Larimer, Clay & Bever 2014). Clearly, there is an interaction between plant functional type and soil nutrient conditions in regulating the direction of plant mycorrhizal response.

Given the generally coarse root systems and high mycorrhizal response of C₄ grasses, this functional group is predicted to increase their competitive ability after mycorrhizal inoculation (Hartnett *et al.* 1993; Hetrick *et al.* 1994; Wilson & Hartnett 1998). However, no significant AMF effects were observed in the competitive ability of C₄ grasses (Fig. 2a). This lack of AMF effect may be because all studies involving C₄ grasses in our analysis came from greenhouse experiments with low light levels. Indeed, our results were consistent with another meta-analysis conducted by Hoeksema *et al.* (2010) which found that C₄ grasses showed a lower mycorrhizal response in greenhouse than in the field. The lower light levels in greenhouse settings compared to field experiments may influence carbon allocation patterns and suppress AMF function due to the high light requirement of C₄ grasses (Hoeksema *et al.* 2010). Still, the speculation that lighting conditions affect AMF effects on competitive response of C₄ grasses needs to be further validated.

For life-history groups, AMF inoculation significantly increased competitive ability of perennials when competitors were annuals (Fig. 3a). Compared with perennial species, annual species may have higher specific root length and lower tissue density (Roumet, Urcelay & Díaz 2006); thus, the annuals may have lower mycorrhizal response (Brundrett 2002; Fig. 1). Wilson & Hartnett (1998) found that compared with perennial species, annual species usually showed neutral response to mycorrhizal colonization. When mycorrhizal colonization is reduced or inhibited, annual species with high specific root length and rapid nutrient acquisition may show stronger competitive ability to reduce growth of their competitors than perennial species (Fig. 3a). Therefore, the competitive effects of annual species on perennial species should decrease with AMF colonization.

AMF EFFECTS ON PLANT DIVERSITY AND PRODUCTIVITY

Our study showed that AMF significantly increased species evenness and diversity (as measured by Shannon's and Simpson's diversity indices) with no significant effects on species richness (Fig. 4). Thus, AMF may influence plant diversity mainly by changing the performance of the existing species, rather than altering the composition of the species in plant community (though this needs to be further tested in future studies). Our results also clearly demonstrated that AMF effects on community structure depended largely on the mycorrhizal responses of dominant species (Fig. 5a–c), verifying the theoretical model proposed by van der Heijden (2002). When mycorrhizal response of the dominant species was high, AMF inoculation increased the competitive ability of the most dominant species, which may increase competitive suppression of subordinate species and eventually decrease plant diversity. This was consistent with a study in C₄ grass dominated tallgrass prairie where AMF inoculation decreased plant diversity (Hartnett & Wilson 1999). Conversely, when C₃ grasses were dominant, their competitive ability might be reduced in the presence of AMF inoculation,

which then might relieve subordinate species from competitive suppression, leading to increased plant diversity (van der Heijden *et al.* 1998).

Despite the observation that AMF inoculation significantly increased plant diversity, our meta-analysis showed that, on the whole, AMF had no significant effects on plant productivity (Fig. 4). This non-significant effect may be partly due to the presence of publication bias. When trim and fill method was conducted, AMF inoculation was found to negatively affect community productivity. These neutral or negative effects of AMF on community productivity may be explained by the hypothesis that plant communities may not benefit from AMF when plant diversity is high (Klironomos *et al.* 2000). Given that plant species have distinct nutrient absorption strategies, soil nutrients are used more effectively under higher plant diversity, which may lead to a reduction in amount of nutrients available for uptake by the extraradical AMF hyphae (McKane *et al.* 2002). Finally, different experimental conditions may also play a role in determining the perceived influence of AMF on plant communities and productivity.

EXPERIMENTAL CONDITIONS INFLUENCING OBSERVED AMF EFFECTS ON PLANT COMMUNITY

While AMF inoculum complexity and sterilization treatment did not alter AMF effects on plant competition (Fig. S2), they, along with the experimental location, did have significant effects on plant diversity (Fig. 6a). For the experimental location, AMF increased plant diversity in greenhouse experiments but had no significant effects on plant diversity in field experiments. Previous meta-analyses also have found that AMF effects on soil aggregate formation (Leifheit *et al.* 2014) and plant growth (Lekberg & Koide 2005) in the field were lower than expected when compared with greenhouse experiments. These differences between field and greenhouse experiments may be attributed to harsher environmental conditions in the field or the variations in methodologies used to reduce AMF colonization where field and greenhouse experiments mostly adopted benomyl addition and autoclaving, respectively (Lekberg & Koide 2005; Leifheit *et al.* 2014). For example, grazing pressure from fungivores in the field may represent a significant cost to AMF and their host plants, which can then reduce beneficial effects of AMF (Jonas *et al.* 2007). Apart from this, field plants may experience high grazing intensity from herbivores, leading to carbon limitation (Hartnett & Wilson 2002). When carbon limitation occurs, AMF inoculation may have detrimental rather than beneficial effects on their hosts (Johnson 2010). Additionally, using benomyl application to create a non-AMF treatment has also been found to inhibit soil pathogenic fungi infection (Newsham, Fitter & Watkinson 1994). Therefore, the side effect of benomyl addition on pathogenic fungi might lead to the underestimation of AMF effects, which was consistent with our finding that AMF had greater effects on plant diversity and productivity when autoclaving method was used to reduce AMF colonization (Fig. 6a,b).

High AMF species richness has been suggested to reduce competition among plant species and increase plant diversity

because of the different functional roles among AMF species (Maherali & Klironomos 2007). However, in our study, we found the opposite pattern as plant diversity decreased with more complex levels of AMF inoculum (soil inoculum vs. single and mixture AMF species). This phenomenon may be due to the lower competitive ability of beneficial AMF compared with the non-beneficial species in well-mixed fungal communities (Bever *et al.* 2009). In this case, the potential dominance of non-beneficial AMF species may reduce cost efficiency of their hosts and decrease beneficial effects of AMF. Another explanation may be that soil inoculum can have other soil biota including pathogens and fungivores mixed with AMF which may also influence AMF effects (Jonas *et al.* 2007).

LIMITATIONS AND FUTURE RESEARCH

Our study has several limitations which should be explored in future research. First, due to small sample sizes, we did not analyse all variables which might have important roles in affecting AMF effects including a number of soil biotic and abiotic factors (Collins & Foster 2009; Rillig *et al.* 2014). Secondly, AMF identity and diversity effects were not fully considered here and should be further investigated. Different AMF species may have different life-history strategies and functional roles in natural communities (Maherali & Klironomos 2007; Chagnon *et al.* 2013), which are often phylogenetically conserved (Powell *et al.* 2009). However, previous studies have mostly focused on the genus of *Glomus*, which may create a bias in evaluating AMF effects (Chagnon *et al.* 2013). Additionally, AMF diversity should be measured at the end as well as the beginning of the experiments, because actual AMF diversity may change over time due to competition among AMF species with similar strategies (Maherali & Klironomos 2007; Wagg *et al.* 2011a).

Finally, greenhouse experiments that investigated AMF effects, which dominated our analysis, are frequently limited to a single growing season, preventing the analysis of long-term AMF effects. AMF inoculation has been shown to increase the total length of anthesis and flower production, but reduce the levels of seed abortion, thus leads to high seed quantity (Lu & Koide 1994; Koide & Dickie 2002). Apart from seed quantity, AMF inoculation can also significantly enhance individual seed weight and P concentration (Lu & Koide 1994), increasing seedling vigour and survivorship (Koide & Dickie 2002). Furthermore, AMF can also benefit vegetative reproduction, and previous work has shown that the ramet growth rate of *Salvia azurea* is greater in the presence of AMF inoculum (Wilson *et al.* 2001). Therefore, long-term AMF influence on plant community may be profitable as an important area for future studies.

Conclusions

This meta-analysis of 304 studies analysed how AMF influenced plant competition and community structure and how these AMF effects changed with different abiotic and biotic

factors. Plant characteristics including functional groups and life histories were significant predictors of AMF effects on plant competitive responses. Within a multispecies community, the response of dominant species to AMF inoculation was an important predictor determining AMF effects on plant community structure. These findings support the hypothesis that mycorrhizal dependency of dominant plant species is the central determinant of how plant communities are mediated by AMF (van der Heijden 2002; Urcelay & Díaz 2003). To better understand AMF effects in more natural conditions, future research should consider all key factors regulating plant mycorrhizal response, including plant functional traits, soil nutrient conditions (e.g. N and P availability), identity and diversity of AMF, and other soil biota (e.g. earthworms and endophytes), to better understand AMF effects on plant community structure and function.

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Data accessibility

Data used in analyses have been uploaded as online Supporting Information.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Effect sizes of competitive response of target species at low and high AMF colonization.

Table S2. Effect sizes of plant diversity and productivity response to AMF inoculation.

Fig. S1. Competitive response of target species in non-inoculated groups and inoculated groups when plant functional types of neighbors were not the same as targets.

Fig. S2. Competitive response of target species in non-inoculated groups and inoculated groups under different experimental conditions.

Appendix S1. Categorical variables and their characteristics

Appendix S2. Data used in meta-analysis

Appendix S3. List of published papers and unpublished dissertations included in meta-analysis