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Taxonomic resolution is a determinant of biodiversity effects in arbuscular mycorrhizal fungal communities

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Summary

1. Arbuscular mycorrhizal fungi (AMF) are key regulators of ecosystem processes, yet how their biodiversity works in ecosystems remains poorly understood.

2. We documented the extent to which taxonomic resolution influenced the effect of biodiversity of AMF taxa on plant performance (growth, nutrient uptake and stress tolerance) in a meta-analysis of 902 articles.

3. We found that the effect of biodiversity of AMF taxa depended on taxonomic resolution. Plant performance was positively promoted by AMF family richness, while no effect was found for fungal species richness. In addition, negative effect was found between AMF phylogenetic diversity and plant growth. This pattern can be explained by functional conservatism within AMF families and functional differentiation among AMF families.

4. *Synthesis.* Conservation of AMF communities to maintain a full complement of ecosystem functions requires the presence of diverse families and not simply diverse species within a family. This finding may be of key importance for the function of ecosystems under various environmental perturbations to which AMF families may respond differently.

Key-words: arbuscular mycorrhiza, competition, diversity, ecosystem function, functional complementarity, niche, taxonomic level

Introduction

Biological diversity influences many ecosystem functions (Zavaleta *et al.* 2010). For example, some studies show that plant productivity increases with plant species richness (Hector *et al.* 1999; Tilman *et al.* 2001). This positive diversity effect is frequently explained by functional complementarity, the idea that different species occupy different niches and thus perform different functions. In some cases, functional complementarity may allow for a more complete use of available resources with increasing biodiversity (Yachi & Loreau 1999; Koide 2000; Hooper *et al.* 2005; Wagg *et al.* 2015). However, it is less well known whether functional complementarity can explain biodiversity effects in soil microbial communities (Wagg *et al.* 2011a).

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Soil microbial communities of various kinds play fundamental roles in nutrient cycling (Bonkowski & Roy 2005) and thus may be key regulators of ecosystem productivity and plant community composition (van der Heijden, Bardgett & Van Straalen 2008). Decomposer micro-organisms affect nutrient cycling primarily through mineralization and immobilization of nutrients. Mycorrhizal fungi may also both immobilize nutrients (Koide & Kabir 2001) and increase their uptake by plants (van der Heijden, Bardgett & Van Straalen 2008). For example, in nutrient-poor habitats, the arbuscular mycorrhizal fungi (AMF) may be responsible for 20% of nitrogen and 75% of phosphorus uptake for plants (van der Heijden, Bardgett & Van Straalen 2008). AMF provide several other functional benefits for plants, including increased tolerance to abiotic stresses (e.g. drought, heavy metals and salt) and enhanced resistance to fungal pathogens, nematodes and herbivores (Borowicz 2001; Smith & Read 2008; Veresoglou & Rillig 2012).

Arbuscular mycorrhizal fungi communities exhibit a great deal of functional diversity among species, which may contribute to ecosystem productivity (Jansa, Mozafar & Frossard

2005; Wagg *et al.* 2011a). For example, different AMF isolates may possess distinct functional traits; some are better at protecting their hosts from pathogens while others are better at improving phosphorus uptake. The combination of these AMF isolates in a single community may result in greater enhancement of plant productivity (Maherali & Klironomos 2007). Moreover, because distinct AMF communities associate with different plant species (Vandenkoornhuyse *et al.* 2003), high AMF diversity may facilitate recruitment of dissimilar plant species into the community (Vandenkoornhuyse *et al.* 2003; Montesinos-Navarro *et al.* 2012). Increased AMF species richness may also reduce competitive inequality among plant species, maintaining a stable level of plant productivity even under fluctuating soil conditions (Wagg *et al.* 2011b). In addition, the existence of divergent phenologies suggests that a greater diversity of AMF species will increase the probability that at least one taxon is functioning at any given time (Pringle & Bever 2002). Thus, ecosystem productivity and stability may actually increase with increasing AMF species richness.

The beneficial effects of increasing diversity of AMF on individual or community-wide plant productivity can potentially be explained by functional complementarity of the fungi (Maherali & Klironomos 2007). In terms of P uptake, for example, previous experiments have shown differences in spatial P exploitation among different AMF isolates (Smith, Jakobsen & Smith 2000). The functional complementarity hypothesis was subsequently proposed to explain mycorrhizal diversity effects on individual plant and community productivity (Koide 2000), and direct evidence of such was obtained in an experiment with wild leek (*Allium ampeloprasum* L.) in which the plant acquired more P with two AMF species than with either species alone (Jansa, Smith & Smith 2008) [but see (Reynolds *et al.* 2006; Vogelsang, Reynolds & Bever 2006; Gosling, Jones & Bending 2016)].

While distinct taxa of AMF may clearly be functionally complementary, the relationship between AMF taxonomic diversity and functional complementarity is likely to be dependent on the level of taxonomic resolution (Maherali & Klironomos 2007). Increasing the number of isolates of a particular species, or the number of species of a given genus, may have some impact on function. However, more functional variation may occur by increasing the number of genera or families (van der Heijden, Scheublin & Brader 2004). Indeed, some studies suggest that the most significant functional variation among the AMF exists among families (Hart & Reader 2002; Maherali & Klironomos 2007). Functional trait conservatism among AMF isolates at the family level may thus be more likely to reduce competition, promote coexistence and enhance ecosystem functioning (Maherali & Klironomos 2007; Powell *et al.* 2009).

In this study, we conducted meta-analyses with data from 902 articles to compare the effects of AMF richness at species and family levels on plant performance and to test for variation among AMF families in aspects of mycorrhizal function. We predicted that (i) higher AMF family richness would be more positively associated with host plant growth promotion than AMF species richness and (ii) different AMF families would be observed to be superior for different metrics of mycorrhizal function. We conducted two sets of meta-analyses to test these predictions: one in which we analysed the effects of AMF species and family richness as well as phylogenetic diversity on plant growth response to AMF inoculation, and a different suite of analyses in which we tested for systematic variation in various mycorrhizal functions among three dominant AMF families.

Materials and methods

LITERATURE SEARCH

In order to obtain a comprehensive data set, we compiled published articles in the following three ways. First, we searched journal articles on 10 May 2012 in Web of Science (http://apps.webofknowledge.com/) and Google Scholar (http://scholar.google.com.hk) using the search terms: 'biomass AND (*Glomus* OR *Acaulospora* OR *Gigaspora* OR *Scutellospora* OR *Diversispora* OR *Paraglomus* OR *Archaeospora* OR *Entrophospora*)'. Secondly, we searched Web of Science with the original searching terms for existing meta-analyses, including Borowicz (2001), Koricheva, Gange & Jones (2009), Hoeksema *et al.* (2010) and Veresoglou & Rillig (2012), without restriction of publication year. Thirdly, Chinese papers were collected by searching the CNKI data base (http://www.cnki.net/) with the key terms 'mycorrhiza* AND biomass'. These searches yielded 4325 articles.

ARTICLE AND TRIAL INCLUSION CRITERIA

Inclusion of articles in our meta-analyses required satisfaction of the following criteria: (i) the article must have included at least one trial in which there were both control and experimental treatments. The control treatment was defined as plants grown in the absence of AMF, and the experimental treatment was defined as plants inoculated with AMF. (ii) The identity of all AMF isolates must have been known to species. (iii) Studies with fungicide treatments were excluded, because fungicides (e.g. benomyl) can reduce mycorrhizal colonization but not eliminate it. (iv) Data must have existed for biomass, P or N content (g plant^{-1}) in shoots, or for some assessment of growth or reproduction of nematodes or fungal pathogens (reduced effects indicating increased resistance in mycorrhizal plants) (Borowicz 2001). In all, 902 publications satisfied these criteria (Appendix S1 in Supporting Information).

Individual trials from the 902 publications were included in our analyses using the following criteria: (i) for experiments conducted along environmental gradients, data were included only from either end of the gradient. (ii) For multiple AMF species–plant species combinations in a single experiment, data were included for each combination (Hoeksema *et al.*2010). (iii) For a given AMF species–plant species pair in a time series, the data from the final time point were only included. (iv) For a given AMF species–plant species pair grown at different sites, each site was treated as an independent trial and included separately. (v) For factorial experiments with AMF and other beneficial microbes (i.e. rhizobia or *Pseudomonas* spp.), trials were only included from treatments that did not include interactions with those microbes. Trials from different studies (articles) were considered to be independent.

DATA EXTRACTION AND VARIABLE CONSTRUCTION

We extracted means, standard deviations (SD) or standard errors (SE), and sample sizes (N) for shoot or total biomass, N and P contents, and growth and reproduction variables of nematodes and fungal pathogens (data sets available on Dryad; Yang *et al.* 2016a). Graphed data were digitized with GetData (http://getdata-graph-digitizer.com/). When SDs were missing, we estimated them with the method of van Groenigen, Osenberg & Hungate (2011): we first calculated the average coefficient of variation (CV) within each data set and then approximated the standard deviation by multiplying the reported mean by the average CV and then squared it. We also collected data on research group identity, experimental duration, substrate type and fertility, and host plant types. We defined research group identity according to the corresponding author of the source articles. Substrate type was categorized as either soil, sand or soil–sand mixture. The fertility of the substrate was approximated according to the proportion of sand in the substrate. The fertility of the substrate was roughly characterized using the proportion of soil (from 0 to 1) as an index. The types of host plants were defined as grasses, forbs, non-woody legumes, woody legumes and non-legume trees as in Yang *et al.* (2016a).

In total, our data set included 104 AMF species in six families, and AMF family was defined according to *Index Fungorum* (http://www.indexfungorum.org/names/names.asp; 20 June 2012).

We also examined the effects of phylogenetic diversity (PD) of AMF communities on plant growth. PD was defined as the sum of total phylogenetic branch length for all taxa in one community (Faith 1992). Here, we first extracted the representative SSU rDNA sequence from GenBank for each AMF species when it was available. If not available for some AMF species, we utilized the available SSU rDNA sequences in the same genera as an approximation. We then aligned all the DNA sequences in Clustal X (Drummond *et al.* 2010) and constructed a maximum-likelihood phylogenetic tree using 'GTRCAT' model with 1000 bootstrap replications in RAXML v 7.0 (Stamatakis 2006). PD was calculated for each sample with the 'pd' command in the *picante* 1.6-2 package.

To examine the influence of inoculation with different AMF families on mycorrhizal functioning, we defined the following types of mycorrhizal functioning: nutrient uptake (P and N contents in shoots), plant growth performance (biomass) under abiotic (drought, heavy metals, salt) and biotic (nematode and fungal pathogens) stresses, and the inhibition of growth performance for nematodes and fungal pathogens with AMF inoculation. Plant performance under stress was used to assess stress tolerance. Although previous studies have summarized the mycorrhizal effects under stress conditions (Veresoglou & Rillig 2012; Jayne & Quigley 2014), they mainly focused on the effects of AMF species identity and could not be used to determine whether the extent to which plant performance enhancement by AMF was dependent on diversity of AMF taxa. Nematode performance was assessed by the number of galls or eggs per gram of root, or population density of per volume of soil. Pathogen performance was assessed by the frequency of plant tissue necrosis or vascular discoloration.

META-ANALYSIS

As a metric of plant response to mycorrhizal colonization, we used the natural log of the response ratio (ln RR) as the 'effect size' (Hedges, Gurevitch & Curtis 1999). For each variable, ln RR was calculated as the natural log ratio of its value in the experimental treatment (X_e) and control treatment (X_c) (eqn 1).

$$\ln RR = \ln\left(\frac{X_e}{X_c}\right) = \ln(X_e) - \ln(X_c) \quad \text{eqn 1}$$

The variance of ln RR was estimated with the following formula:

$$v = \frac{{S_e}^2}{N_e * X_e} + \frac{{S_c}^2}{N_c * X_c} \quad \text{eqn 2}$$

Here, S_e and S_c represent the standard deviations of experimental and control treatments, respectively. N_e and N_c refer to the sampling size of experimental and control groups, respectively. ln RR and its variance were calculated in METAWIN 2.0 (Rosenberg, Adams & Gurevitch 2000).

One of the presumptions of meta-analysis is that trials are independent of each other (Gurevitch & Hedges 1993). However, as with other meta-analytical studies, in some cases, two or more trials were extracted from a single article or from different articles by the same research group and so might not be independent (Yang *et al.* 2015). Plant identity or functional type is also an important potential influence on mycorrhiza–plant relationships that could drive non-independence among studies (Klironomos 2003; Yang *et al.* 2016a). In addition, experimental design (e.g. duration, substrate type or fertility) might also affect AMF functioning and species interactions (Knegt *et al.* 2014). We therefore conducted mixed-effects meta-analyses with several random factors to account for non-independence among trials due to those factors, as detailed below. All analyses were performed in the statistical software R 3.1.3 (R Core Team, 2013).

INFLUENCE OF AMF TAXONOMIC RICHNESS ON PLANT BIOMASS

To compare the effects of AMF biodiversity on plant biomass, we constructed a global model with main effects of fungal species richness (SR), fungal family richness (FR) and phylogenetic diversity (PD) together (Model 1); three reduced models with only two moderators: FR + SR (Model 2), FR + PD (Model 3) and SR + PD (Model 4), as well as three other reduced models with only one moderator: FR (Model 5), SR (Model 6) and PD (Model 7). The effect of AMF family richness will be assessed by Model 1, Model 2, Model 3 and Model 5. In these analyses, the effect size, ln RR, was calculated using the response of plant biomass to AMF inoculation. All these models were constructed by the respective fixed-effect moderators and random factors of trial, research group identity, experimental duration, plant type, substrate type and fertility with the *rma.mv*() function in 'metafor' package version 1.9-4 (Viechtbauer 2010). The effects of random factors were estimated with the variance components in the models. The performance of models was evaluated with AIC values (lowest being best).

INFLUENCE OF AMF FAMILIES ON MYCORRHIZAL FUNCTIONING

For comparing the nine types of mycorrhizal functioning among different AMF families, we constructed mixed-effects models with fungal family as a fixed-effect moderator and with trial, article and plant identity as random factors. In two of these analyses, testing how nutrient uptake by plants is affected by inoculation with AMF families, the effect size, ln RR, was calculated using plant nutrient content (N or P) response to AMF inoculation. In five of these analyses, each

testing how plant growth performance (biomass) is influenced by inoculation with AMF families under a different abiotic (drought, heavy metals, salt) or biotic (nematode and fungal pathogens) stress, the effect size, ln RR, was calculated using plant biomass response to AMF inoculation. In the other two of these analyses, testing how nematode or fungal pathogens on plants are influenced by inoculation with AMF families, the effect size, ln RR, was calculated using nematode or fungal performance response to AMF inoculation. *Post hoc* comparisons under all of these analyses were conducted by changing the reference level among AMF families and then refitting the models. Results were presented with mean effect size (ln RR) ± SE.

Sensitivity analyses were conducted in the following ways (Koricheva & Gurevitch 2014; Pellegrino *et al.* 2015): first, a single trial was randomly selected from each article that had supplied multiple trials and the mean effect size and 95% CIs from this reduced data set were recalculated. By bootstrapping using 999 iterations, 95% CIs were constructed. If effect sizes were not significantly different from that of the full data set, we were satisfied that our conclusions were robust. Secondly, publication bias (Rosenberg, Adams & Gurevitch 2000) was explored with Spearman rank-order and Kendall's Tau correlations. Both methods estimate the publication bias using the correlation between standardized effect size of raw data and sample size. No significant correlations suggest no-publication bias. Thirdly, we calculated fail-safe numbers (Pellegrino *et al.* 2015), the number of non-significant, unpublished or missing trials that would be needed to be added to the data set in order to change the results of the meta-analysis from significance to non-significance. These analyses were conducted in METAWIN 2.0 (Rosenberg, Adams & Gurevitch 2000).

Table 1. Meta-regressions of mycorrhizal growth response of plants to different AMF diversity

Model		Estimate	*Z* value	*P* value	AIC
Model 1	Intercept	0.346	3.984	**<0.001**	7718.936
	FR	0.356	5.488	**<0.001**	
	SR	−0.047	−1.004	0.315	
	PD	−0.398	−1.684	0.092	
Model 2	Intercept	0.337	3.893	**<0.001**	7719.771
	FR	0.359	5.538	**<0.001**	
	SR	−0.115	−5.042	**<0.001**	
Model 3	Intercept	0.364	4.267	**<0.001**	7717.943
	FR	0.330	5.548	**<0.001**	
	PD	−0.605	−5.221	**<0.001**	
Model 4	Intercept	0.586	7.107	**<0.001**	7746.984
	SR	0.055	1.274	0.203	
	PD	−0.432	−1.822	0.069	
Model 5	Intercept	0.465	5.644	**<0.001**	7743.067
	FR	0.109	2.604	**0.009**	
Model 6	Intercept	0.577	6.972	**<0.001**	7748.299
	SR	−0.019	−1.261	0.207	
Model 7	Intercept	0.588	7.101	**<0.001**	7746.628
	PD	−0.148	−1.812	0.070	

FR, family richness; SR, species richness; PD, phylogenetic diversity. Model 1 is a global model combined with FR, SR and PD; Model 2 a reduced model with FR and SR; Model 3 with FR and PD; Model 4 with SR and PD; Model 5 with FR; Model 6 with SR, and Model 7 with PD.
Significant effect ($P < 0.01$) was shown in bold.

Results

INFLUENCE OF AMF TAXONOMIC RICHNESS ON PLANT GROWTH

Based on AIC values, Model 3 (FR + PD) was the best (Table 1) and suggested that plant growth response increased with the number of AMF families ($Z = 5.488$, $P < 0.001$) while decreased with AMF phylogenetic diversity ($Z = -5.221$, $P < 0.001$). In contrast, Model 1 (containing FR, PD and SR) indicated that no significant relationship existed between plant growth response and AMF species richness ($Z = -1.004$, $P = 0.315$). Comparison between Model 1 and Model 2 (FR + SR) showed that the addition of PD into the model shifted the negative effect of SR to no effect on plant growth, but did not affect the effect of FR. Comparison between Model 1 and Model 3 showed that the inclusion of SR into the model changed the effect of PD from negative to neutral. Comparison between Model 1 and Model 4 (SR + PD) showed that the inclusion of FR into the model did not affect the effects of SR and PD on plant growth (Table 1). Considered together, these results suggest that the effect of FR is independent of SR and PD, but SR and PD are closely related to each other.

INFLUENCE OF AMF FAMILIES ON MYCORRHIZAL FUNCTIONING

Arbuscular mycorrhizal fungi family identity significantly affected the response of host plant P uptake to mycorrhizal inoculation, mycorrhizal growth response of plants under heavy metal stress and the fungal pathogen performance when co-inoculated with AMF (Table 2; $Q_M = 13.44$, d.f. = 3, $P = 0.004$ for P uptake; $Q_M = 24.995$, d.f. = 3, $P < 0.001$ for heavy metal stress; $Q_M = 9.462$, d.f. = 3, $P = 0.009$ for fungal pathogen inhibition). P uptake response was significantly increased by 110.64%, 98.97% and 158.57%, while plant growth response under heavy metal stress was significantly increased by 48.74%, 299.88% and 53.73% under inoculation with Claroideoglomeraceae, Gigasporaceae and Glomeraceae, respectively. Plant growth response under drought stress was marginally significantly increased by 43.05%, 38.13% and 63.56% ($Q_M = 5.174$, d.f. = 3, $P = 0.075$), while the performance of fungal pathogens was inhibited by 55.16%, 39.83% and 58.27% when co-inoculated with these three AMF families, respectively. Thus, Glomeraceae had the most positive effect on P uptake and fungal pathogen inhibition, while Gigasporaceae showed better performance in assistance host plants tolerating heavy metal stress (Table 2). No significant variation among Claroideoglomeraceae, Gigasporaceae and Glomeraceae was found for N uptake, salt tolerance, plant growth under nematode and fungal pathogen attacks, as well as the performance of nematode inhibition ($P > 0.05$).

Sensitivity analyses suggested that our analyses were robust (Table 3). By comparing the mean effect sizes, we found no difference by randomly selecting one trial in each article in comparison with all the trials in each article. Except for the P and N uptake data sets as well as plant mycorrhizal growth response under nematode pressure, all other data sets showed

Table 2. Variations of plant response to different AMF families for nutrient uptake, stress tolerance and resistance

		Nutrient uptake		Abiotic stress			Biotic stress			
		P	N	Drought	Heavy metal	Salt	Nematode[1]	Nematode[2]	Pathogen[1]	Pathogen[2]
Family	Claroideoglomeraceae	0.75 ± 0.11^{b} (56;29;34)	0.38 ± 0.19^{a} (25;11;18)	0.39 ± 0.12^{ab} (18;9;8)	0.40 ± 0.11^{b} (25;9;8)	0.49 ± 0.14^{a} (10;5;5)	0.96 ± 0.21^{a} (6;6;6)	-0.70 ± 0.31^{a} (6;6;6)	0.37 ± 0.13^{a} (9;7;8)	-0.80 ± 0.19^{ab} (13;10;12)
	Gigasporaceae	0.69 ± 0.12^{b} (46;21;26)	0.54 ± 0.27^{a} (20;5;18)	0.32 ± 0.11^{b} (13;3;5)	1.39 ± 0.20^{a} (4; 1;1)	0.46 ± 0.18^{a} (4;3;3)	0.83 ± 0.18^{ab} (17;12;9)	-0.44 ± 0.25^{a} (10;9;6)	0.41 ± 0.10^{a} (17;7;9)	-0.51 ± 0.17^{a} (18;8;10)
	Glomeraceae	0.95 ± 0.08^{a} (389;121;103)	0.64 ± 0.09^{a} (158;53;73)	0.49 ± 0.07^{a} (156;52;42)	0.43 ± 0.06^{b} (249;64;36)	0.67 ± 0.09^{a} (241;57;56)	0.56 ± 0.10^{b} (102;51;34)	-0.74 ± 0.13^{a} (98;49;33)	0.55 ± 0.07^{a} (130;53;38)	-0.87 ± 0.13^{b} (169;62;44)
Model statistic	Q_M	13.44	1.71	5.17	25.00	4.19	4.23	1.44	4.27	9.46
	P	<0.01	0.43	0.08	<0.01	0.12	0.12	0.50	0.12	<0.01

Data were presented as ln RR ± SE.
The number in the parentheses represents (# trial; #study; #host).
Different letters within the same column indicate significant differences in variable means among fungal families ($P < 0.05$).
Nematode[1] represents plant growth response to mycorrhiza under nematode attacks.
Nematode[2] represents nematode performance with mycorrhiza inoculation.
Pathogen[1] represents plant growth response to mycorrhiza under fungal pathogen infestation.
Pathogen[2] represents fungal pathogen performance with mycorrhiza inoculation.

no-publication bias. All data sets showed much greater Rosenberg's fail-safe number than $5N + 10$, suggesting that even if there was slight publication bias, it would likely not affect our conclusions.

Discussion

Positive fungal diversity–host growth relationships may be attributed to a high degree of functional complementarity among fungal species (Maherali & Klironomos 2007; Jansa, Smith & Smith 2008). There are still a very limited number of individual studies with which we can compare the effects of monocultures and polycultures of AMF on the same host species. However, a large number of studies do exist in which various host plants are inoculated with varying numbers of AMF taxa. By using meta-analysis across a large number of such studies, the average response of all host plant species to variation in AMF diversity indicated that greater levels of taxonomic diversity did result in greater benefit to the host. However, the diversity effects were primarily due to AMF family richness rather than AMF species richness or phylogenetic diversity (Fig. 1; Table 1). Our analyses of variation in symbiotic function suggest that phylogenetic trait conservatism exists within AMF families, which supports the hypothesis that complementarity of function in different AMF families contributes most to the positive relationship between AMF diversity and plant productivity.

RELATIONSHIPS BETWEEN PLANT GROWTH RESPONSE AND AMF RICHNESS

Overall, we found a positive effect of AMF family richness but no significant effect of AMF species richness on plant growth response (Fig. 1; Table 1). Although species richness and family richness are not inherently orthogonal, our analyses suggested that fungal family richness behaved independently of fungal species richness in plant growth performance by comparing the global model with reduced models (Table 1). There are at least four processes that help explain the taxonomy-dependent pattern of AMF biodiversity effects on host plant growth.

First, competitive exclusion could reduce fungal community species richness during the course of the various experiments. Gosling, Jones & Bending (2016) argued that competition between AMF combined with host/fungus preference and the priority effects of colonization could result in the realized fungal diversity being lower than that the diversity of the inoculum. Unfortunately, most researchers did not track the species composition of the AMF community during their experiments. This may have been a particular problem for closely related species for which there is a high degree of niche overlap (Webb *et al.* 2002). In our data set, species in the Glomeraceae accounted for a large proportion in the high AMF species group (i.e. >3 species). Such closely related AMF species might have caused intensive competition resulting in competitive exclusion (Thonar *et al.* 2014). Thus, it is possible for

Table 3. Sensitivity analysis of different data sets used in this study

Data sets	Full vs. reduced (±95% CI)	Rs (*P* value)	Tau (*P* value)	5*N* + 10 (Fail-safe number)
Biomass	0.58 (±0.02) vs. 0.57 (±0.04)	0.01 (0.65)	0.01 (0.63)	19 095 (77 895 689)
P uptake	1.01 (±0.06) vs. 0.89 (±0.13)	−0.09 (**0.04**)	0.07 (**0.02**)	2525 (6 925 396.4)
N uptake	0.51 (±0.10) vs. 0.63 (±0.17)	0.17 (**0.02**)	0.14 (**0.00**)	1025 (348 009.2)
Drought	0.53 (±0.05) vs. 0.49 (±0.10)	−0.04 (0.59)	−0.02 (0.66)	940 (329 235.6)
Heavy metal	0.42 (±0. 04) vs. 0.44 (±0.09)	0.08 (0.19)	0.05 (0.19)	1480 (577 182.1)
Salt	0.63 (±0. 07) vs. 0.56 (±0.56)	0.05 (0.41)	0.04 (0.39)	1285 (763 806.0)
Nematode[1]	0.57 (±0.07) vs. 0.55 (±0.09)	0.19 (**0.04**)	0.15 (**0.02**)	635 (40 149.1)
Nematode[2]	−0.68 (±0.11) vs. −0.66 (±0.14)	0.13 (0.16)	0.07 (0.24)	575 (62 916.8)
Fungal pathogen[1]	0.46 (±0.06) vs. 0.46 (±0.09)	0.08 (0.31)	0.05 (0.35)	790 (60 936.3)
Fungal pathogen[2]	−0.79 (±0.35) −0.99 (±0.55)	−0.17 (0.02)	−0.09 (0.06)	1010 (310 084.9)

N represents the total sampling number.
Nematode[1] represents plant growth response to mycorrhiza under nematode attacks.
Nematode[2] represents nematode performance with mycorrhiza inoculation.
Fungal pathogen[1] represents plant growth response to mycorrhiza under fungal pathogen infestation.
Fungal pathogen[2] represents fungal pathogen performance with mycorrhiza inoculation.
'Full' represents the full data set without any data entry removing.
'Reduced' represents the data set only includes data entry randomly selected from one article.
Rs is the coefficients of Spearman rank-order correlation analysis between sample size and the standardized effect size.
Tau is the coefficients of Kendall's Tau correlation analysis between sample size and the standardized effect size.
Significant effect ($P < 0.05$) was shown in bold.

relatively rich communities to become less so over time. In one study, <40% of species were retained after 1 year (Maherali & Klironomos 2007).

Also, functional trade-offs may occur between AMF competitive ability and host growth promotion (Bennett & Bever 2009). Thus, in an assemblage comprising closely related taxa, AMF species may allocate resources to increase competitive ability (i.e. increased hyphal growth, sporulation, root colonization). Bever *et al.* (2009) found that competition between mycorrhizal fungi strongly increased the cost of mutualism borne by the plant. Thus, it is possible that little benefit is provided to hosts by an AMF community comprising intensely competing species.

In addition, in AMF communities of high species richness, some AMF species are undoubtedly at least partially functionally redundant (Gosling, Jones & Bending 2016). This can be evidenced by previous findings that mycorrhizal functioning is phylogenetically conserved (Maherali & Klironomos 2007; Powell *et al.* 2009). Some other AMF species might not provide any benefits to the host. Hosts may discriminate against non-beneficial fungal partners (Kiers *et al.* 2011), but Hart *et al.* (2013) reported that less beneficial fungi could exist within a diverse community of mycorrhizal fungi if there is no ability for the host to discriminate against it. Thus, less beneficial fungi could contribute to AMF species richness without providing any benefit to the host.

Finally, in dealing with the unpredictable environments, that is, inconstant soil moisture, nutrient availability or pathogen pressure under the natural conditions, plants might evolutionarily employ a bet-hedging strategy by hosting multiple AMF taxa on a single-root system, even if some do not provide an immediate benefit (Lekberg & Koide 2014). However, our data were extracted from glasshouse trials, in which it cannot show that long-term geometric fitness is maximized at the expense of short-term fitness in a single year where it would have been optimal to select the single best fungus. Thus, the benefits of a bet-hedging strategy would not necessarily be evident under glasshouse conditions, although under more naturally variable conditions, bet-hedging may prove to be valuable.

In theory, PD will be greater for a community comprising a given number of species distributed among different families than distributed within a given family, and thus, the biodiversity effects should be consistent between PD and family richness. However, our results showed that the biodiversity effect of PD was closely correlated with SR, but not with FR (Table 1). This pattern was likely determined by the nature of the available data sets. For the studies with multiple species, most trials were inoculated solely with Glomeraceae species. These 'low family richness but high species richness' treatments would get high PD but without showing high-functional differentiation among species, thus possibly decoupling PD and functional diversity. Thus, the closely related species in the AMF communities with higher PD might experience intense competition, functional redundancy or bet-hedging, as suggested in the above discussion. These potential processes might exert negative effects on plant growth (Table 1; Fig. 1b).

VARIATION AMONG AMF FAMILIES IN MYCORRHIZAL FUNCTION

Our analyses of nine types of symbiotic functioning showed that all three fungal families frequently exhibited significant positive effects on their hosts, but that substantial variation was found among AMF families, and that the same family was not superior for in every function. For example, Glomeraceae was the best in promoting plant P uptake and plant

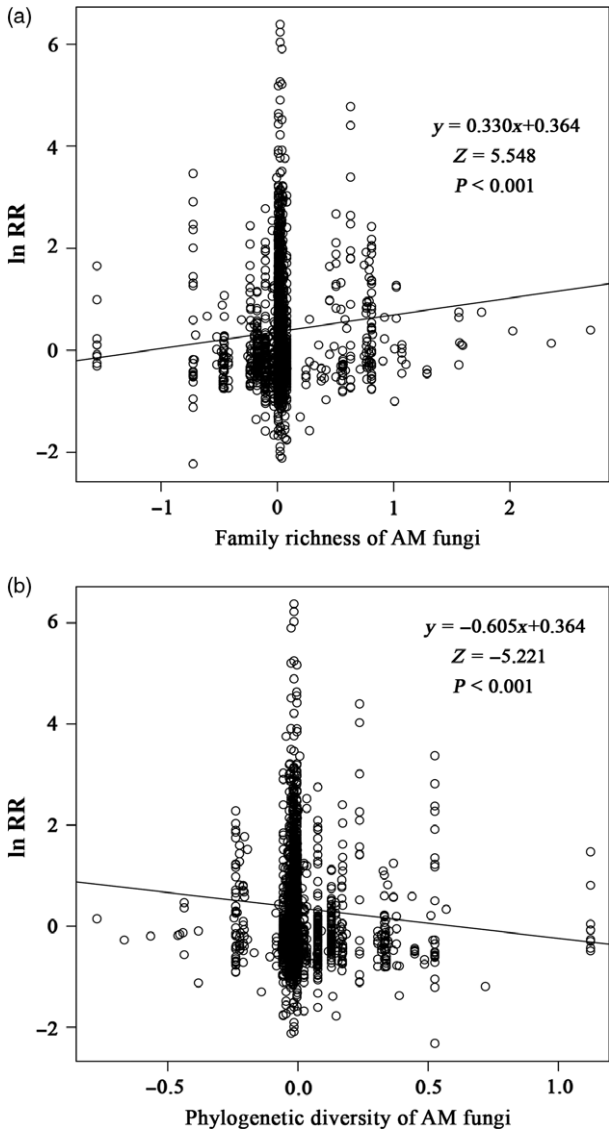

Fig. 1. The relationships between mycorrhizal growth response of plants and (a) fungal family richness and (b) phylogenetic diversity. Scatterplots represent partial regression plots of parameter estimates from the best model, Model 3, which contained main effects of both family richness and phylogenetic distance.

growth under drought stress, as well as in inhibiting fungal pathogens (Table 2). In contrast, Gigasporaceae was the best promoter of plant growth under heavy metal stress and Claroideoglomeraceae was the best for promoting plant growth under nematode stress (Table 2). These results provide some support for the idea of phylogenetic niche differentiation among the AMF families (Maherali & Klironomos 2007; Powell *et al.* 2009).

A number of key traits differ among AMF families and may help explain their differing functions. Some studies have indicated that members of the Gigasporaceae possess large external hyphal networks, have potential to exploit a greater soil volume and exhibit better nutrient transfer efficiency to their hosts than members of the Glomeraceae (e.g. Hart & Reader 2002; Maherali & Klironomos 2007). However, other studies suggest that nutrients are mainly concentrated in the intraradical hyphae of Gigasporaceae, with reduced transfer to the host compared with Glomeraceae (Smith, Smith & Jakobsen 2003; Gosling, Jones & Bending 2016). This inconsistency may be caused by the short duration of the pot experiments. Gigasporaceae are expected to deliver P in a nonlinear fashion with time, owing to their P-storing activities in auxiliary cells before spore production (Declerck *et al.* 2004). Thus, it is reasonable to detect the lower ability to transfer P by Gigasporaceae in the brief pot studies. Under drought stress, the faster initial colonization of roots by Glomeraceae compared to other AMF families might be important as activators of genes responsible for drought tolerance, such as aquaporins, proline and ABA (Ruiz-Lozano, Porcel & Aroca 2006; Aroca *et al.* 2008). Gigasporaceae may promote heavy metal stress tolerance better than other AMF families because of its extensive hyphal network which could help to chelate more metal ions and reduce their transportation into plant tissues (Chen & Zhao 2007). However, some caution should be exercised in this regard because our data were extracted from a single article for the Gigasporaceae group.

Our results suggest that niche conservatism within families and niche diversity among families could drive AMF community assembly. We predict, for example, that in most situations there should be selection for a diversity of AMF families by host plants. This would both reduce competition between AM species (Mayfield & Levine 2010) and increase benefit to the host. Host benefit would increase because of the trade-off between AMF competitive ability and host benefits (Bennett & Bever 2009), and because of functional complementarity among species in different families (Maherali & Klironomos 2007).

In reality, functional complementarity among mycorrhizal fungal taxa will do the host plant no good unless the fungal taxa can stably coexist on the same root system. Because all mycorrhizal fungi require the same resource from the host (carbohydrates), competitive exclusion is always possible, but its probability may be minimized by either temporal or spatial partitioning within the root system (Smith, Jakobsen & Smith 2000; Pringle & Bever 2002). For example, if members of the Glomeraceae were less competitive for carbohydrate than members of the Gigasporaceae, Glomeraceae might still stably occur on the root if they more rapidly colonized new root tips than Gigasporaceae (Cadotte *et al.* 2006; Calcagno *et al.* 2006). In that way there would be a spatial partitioning of a single root in which Glomeraceae occupied the newer portion of the root while Gigasporaceae occupied the older portion of the root.

SIGNIFICANCE, LIMITATIONS AND FUTURE RESEARCH

Our results do suggest that the taxonomic resolution at which one appreciates AMF diversity may have significant consequences for ecosystems. Greater AMF diversity at the family taxonomic scale can provide more host plant benefits, resulting in greater primary productivity. This finding could be of

great importance for the function of ecosystems if, for example, different AMF families respond differently to various environmental or anthropogenic disturbances.

Although our results put emphasis on AMF function at family level, it did not rule out the significance of functional variation at genotypic scale. On the contrary, we acknowledge that the genotypic variability might cause taxonomic overdispersion in the context of limiting similarity among different families for AMF. More importantly, AMF might express different diversity effects at family or genotypic levels, that is, the opposite effects of AMF diversity on plant growth within populations (Roger *et al.* 2013) or among families (Maherali & Klironomos 2007). After all, AMF family number is relatively small, and thus, genotypic differences at functional traits would seem to strengthen the robustness in function of AMF communities in responding to some extreme environments (Munkvold *et al.* 2004).

Yet, there are still some limitations for interpretation of our analyses. The primary limitation is that the studies from which we obtained data for this analysis in most cases fell short of replicating the diversity and complexity of natural systems. Data synthesis from these artificial environments might overstate or underestimate the real effects of AMF biodiversity. For example, in these controlled conditions, mycorrhizal helper bacteria or pathogenic microbes, both of which closely interact with AMF in natural systems and may alter host responses to AMF (Veresoglou & Rillig 2012; Mediavilla *et al.* 2016), might not be present in the experimental soils. In addition, most of our source experiments utilized very low AMF diversity of ≤5 species or ≤3 families, which is much lower than what is found in natural systems (Helgason *et al.* 1998; Lumini *et al.* 2010).

Therefore, we can suggest many fruitful areas in future research related to the study of the biodiversity effects in AMF communities. First, we need more individual studies in which plant productivity and other aspects of ecosystem function are determined for plants grown with varying numbers of AMF taxa. A larger set of such studies would facilitate within-studies meta-analysis, in which each effect size observation quantifies the effect of AMF diversity on plant response. Also, the impacts of AMF on their plant hosts are often context-dependent (Hoeksema *et al.* 2010). However, the underlying mechanisms that context dependency of symbiotic function among AMF taxa are still not well understood. For example, Gigasporaceae are often shown to be more effective in P uptake and transfer than Glomeraceae (Maherali & Klironomos 2007; Yang *et al.* 2015). But the opposite does exist (Smith, Smith & Jakobsen 2003; Nisha & Rajeshkumar 2010). Yet, the factors that govern variation in uptake and transfer efficiency have not been explicitly explored.

In addition, the role of AMF in host N nutrition is still a subject of debate (Hodge & Fitter 2010; Thirkell, Cameron & Hodge 2016). Our results show that inoculation of AMF can significantly increase plant N uptake (Table 2). Experimental evidence has also shown that some AMF taxa capture a significant amount of N from organic materials (Hodge, Campbell & Fitter 2001) and some are better than others (Cheng *et al.* 2012). However, a major uncertainty is whether AMF promote N uptake and the magnitude of AMF-mediated N acquisition in natural environments. Whether and how the diversity of AMF affects their host N nutrition remains virtually unexplored. Finally, our prediction that selection occurs for a diversity of families of AMF fungi on a single host plant should be tested in multiple situations. Some studies found that closely related AMF species may engage in competitive displacement (Maherali & Klironomos 2007; Thonar *et al.* 2014), but this is apparently not always true (Wubet *et al.* 2006; West *et al.* 2009). Because the expression of biodiversity effects requires the stable coexistence of AMF taxa, the mechanisms that promote coexistence of AMF taxa on a single-root system also require further study.

Conclusions

Our meta-analysis, based on 902 peer-review publications, provides evidence that fungal taxonomic resolution is a determinant of the biodiversity effects of AMF communities on host plant function. AMF family richness is a better predictor of host plant growth response than species richness and phylogenetic diversity. Our results highlight the potential importance of niche complementarity of soil biota in determining ecosystem function.

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Data accessibility

Data deposited in the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.4mv7h (Yang *et al.* 2016b).

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Supporting Information

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

Appendix S1. Source references.