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Research

The effects of arbuscular mycorrhizal fungal species and taxonomic groups on stressed and unstressed plants: a global meta-analysis

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Summary

- The great majority of plants gain access to soil nutrients and enhance their performance under stressful conditions through symbiosis with arbuscular mycorrhizal fungi (AMF). The benefits that AMF confer vary among species and taxonomic groups. However, a comparative analysis of the different benefits among AMF has not yet been performed.
- We conducted a global meta-analysis of recent studies testing the benefits of individual AMF species and main taxonomic groups in terms of plant performance (growth and nutrition). Separately, we examined AMF benefits to plants facing biotic (pathogens, parasites, and herbivores) and abiotic (drought, salinity, and heavy metals) stress.
- AMF had stronger positive effects on phosphorus nutrition than on plant growth and nitrogen nutrition and the effects on the growth of plants facing biotic and abiotic stresses were similarly positive. While the AMF taxonomic groups showed positive effects on plant performance either with or without stress, Diversisporales were the most beneficial to plants without stress and Gigasporales to plants facing biotic stress.
- Our results provide a comprehensive analysis of the benefits of different AMF species and taxonomic groups on plant performance and useful insights for their management and use as bio-inoculants for agriculture and restoration.

Introduction

The challenges that plants face to survive, acquire nutrients, grow, and reproduce, either in natural or agricultural ecosystems, have been widely studied (e.g. Chapin, 1980; Chapin *et al.*, 1986, 1993). One of the main plant strategies to overcome environmental challenges is to engage in symbioses with rhizospheric microorganisms (e.g. Martin *et al.*, 2017; Meena *et al.*, 2017). Among these microorganisms, arbuscular mycorrhizal fungi (AMF), Glomeromycotina (Spatafora *et al.*, 2016), are the most widespread plant root symbionts (Tedersoo *et al.*, 2020). In this symbiosis, fungal extra-radical hyphae acquire nutrients (mainly phosphorus (P) and nitrogen (N)) from the soil, while the intra-radical hyphae penetrate root cells and provide these nutrients to the plant in exchange for hexoses and lipids (Smith & Read, 2008; Lanfranco *et al.*, 2018). Plants also receive a range of other benefits from AMF when they face biotic or abiotic stresses, to which they are constantly exposed and that negatively impact their development (Delavaux *et al.*, 2017). Biotic stress is caused by other organisms such as insects, microbial pathogens, nematodes, and/or other plants (e.g. Bonaventure, 2018; Horvath *et al.*, 2018; Marro *et al.*, 2018; Shine *et al.*, 2019). Meanwhile, the most studied abiotic stressors are drought, salinity, extreme temperatures, nutrient deficiency or heavy metals (Da Silva *et al.*, 2011; Gupta *et al.*, 2013; Parihar *et al.*, 2015; Salehi-Lisar & Bakhshayeshan-Agdam, 2016; Mathur & Jajoo, 2020). In presence of stress, plants can profit from nutritional benefits from mycorrhizal fungi (e.g. Püschel *et al.*, 2021), but also from nonnutritional benefits, which are not related to their improved mineral nutrition (Delavaux *et al.*, 2017). For example, some AMF species increase antioxidative enzyme activity under oxidative stress (Malicka *et al.*, 2021) or maintain ionic homeostasis in saline soils (Evelin *et al.*, 2019).

It is well known that the benefits provided by arbuscular mycorrhiza depend on the fungal species involved as partners (e.g. Van der Heijden *et al.*, 1998; Klironomos *et al.*, 2004; Jansa *et al.*, 2008). Specific benefits provided by AMF species have been attributed to certain fungal functional traits such as growth rate, the relative proportion of extra-radical and intra-radical mycelium, and regenerative strategies (Newsham *et al.*, 1995; Hart & Reader, 2002; Maherali & Klironomos, 2007; Chagnon *et al.*, 2013). These traits were shown to be phylogenetically

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conserved and to differ among three main taxonomic families (Gigasporaceae, Glomeraceae, and Acaulosporaceae) (Hart & Reader, 2002; De La Providencia *et al.*, 2005; Powell *et al.*, 2009; Koch *et al.*, 2017). However, the type and magnitude of benefits provided to plant hosts were shown to be phylogenetically conserved in one study (Powell *et al.*, 2009), but not in another (Koch *et al.*, 2017). While the evidence supporting these ideas is still scarce, the taxonomic definitions of AMF genera and higher-level taxa (families, orders) of several originally tested AMF species have been re-defined (Oehl *et al.*, 2011; Redecker *et al.*, 2013).

Despite the long-lasting research of testing the effects of single AMF isolates on plant growth, there is a lack of a comprehensive analysis of the AMF species effects on plant performance either with or without stress (e.g. Koide & Mosse, 2004). Moreover, the differential effects of AMF species on plants growing under biotic and abiotic stressors have received little attention. Given the worldwide distribution of many AMF species (Davison *et al.*, 2015), identifying differential benefits of AMF species and/or taxonomic groups could be a useful source of knowledge for further practical applications.

In this study, we conducted a global meta-analysis of recent studies, published between 2009 and 2019, to test the following hypotheses: (1) AMF positively affect plants in terms of performance either with or without stress; (2) AMF taxonomic groups differentially benefit plants in terms of performance with and without stress. According to the framework proposed by Chagnon *et al.* (2013), we expected higher nutritional benefits from Gigasporales on plants without stress, higher benefits from Glomerales to plants facing biotic stress and from Diversisporales to plants facing abiotic stress; (3) the most efficient AMF species in nutritional terms will be those that are most efficient in promoting plant growth. We also assessed which are the most beneficial AMF species and whether the effects of AMF are consistent among cultivable and wild plants and plant families.

Materials and Methods

Literature search

The literature search was performed using SCOPUS during May 2019 with the sequence of words as follow: arbuscular AND mycorrhiza AND (phosphorus OR nitrogen OR biomass OR growth) OR (herbivory OR pathogen OR parasite OR stress). We had full access to SCOPUS via the Universidad Nacional de Córdoba, Argentina. The titles, abstracts and key words of the detected articles were checked. The review followed the Preferred Reporting Items for Meta-Analyses (PRISMA) guidelines (Moher *et al.*, 2009; Supporting Information Fig. S1). The search included articles published between January 2009 and May 2019 under glasshouse (96.9%) as well as field conditions (3.1%). The search included the following areas: 'agricultural and biological sciences', 'environmental sciences', 'biochemistry, genetics and molecular biology', 'microbiology', 'multidisciplinary', 'chemistry' and 'earth and planetary sciences'. Before the final literature search, several preliminary tests were carried out using different words, sequences, and disciplinary areas. Considering the number and relevance of the articles retrieved, we selected the earlier-mentioned criteria. This search yielded a total of 3597 articles that were analyzed for the inclusion to the meta-analysis. For a study to be selected, it had to report data on nonmycorrhizal plants vs mycorrhizal plants inoculated with a single AMF species. In addition, articles had to indicate the standard deviation or standard error and the number of replicates per treatment. Articles written in languages different from English, or those without the detailed information and necessary data for the analysis, were excluded. In order to avoid any confounding effects, we also excluded studies where the inoculation of AMF was combined with other microorganisms such as *Rhizobium* and/or additives such as fertilizers. From the remaining studies, we selected the most common response variables used in the literature to assess AMF effects on their host plants: shoot, root and/or total biomass, and P and N nutrition of nonmycorrhizal and mycorrhizal plants without any intentionally imposed stress (subsequently termed 'performance'). For studies that examined the effects of AMF on plants under experimentally imposed stress such as drought, heavy-metal presence, salinity or biotic stresses we extracted information of the plant biomass (shoot/root/total) of nonmycorrhizal and mycorrhizal plants (subsequently termed 'performance under stress') (Table S1). These studies included mycorrhizal and nonmycorrhizal plants under imposed stress but not all of them evaluated the effects of AMF on plants without stress. Therefore, we analyzed a subset of studies that included mycorrhizal and nonmycorrhizal plants with and without stress to precisely compare the effect size of AMF on plant performance under regular conditions with the effect size of AMF on plant performance under stress. We used GetData Graph Digitizer v.2.22 freeware digitizing software to extract data from figures (GetData Graph Digitizer v.2.22). The resulting data set comprised 418 articles, with a total of 3240 effect size measures, calculated as detailed in the data analysis section (multiple data were obtained from most studies).

Taxonomic grouping

The functional classification of species is a useful approach to simplify biotic complexity in order to disentangle the dynamics of communities and ecosystems, without necessarily knowing the identity of the species that compose them (Díaz & Cabido, 2001; Lavorel *et al.*, 2007). A functional group includes a set of organisms within a trophic guild (i.e. plants, mammals, and wood decay fungi), either monophyletic or polyphyletic, that share attributes that make them similar in their responses to the environment and/or their effects on other trophic guilds and/or ecosystem processes (Díaz & Cabido, 2001). Within this framework, our meta-analysis focused on the effects of AMF taxonomic groups on plant hosts since previous studies suggested that the glomeromycotan traits are relevant to their symbiotic functioning, such as the amount of extraradical hyphal production, the intensity of root colonization, among others, are phylogenetically conserved (Chagnon *et al.*, 2013; Weber *et al.*, 2019, and references cited therein).

The subphylum Glomeromycotina comprises > 300 described morphospecies distributed in 12 families and 43 genera

(Schüßler & Walker, 2010). As in Säle *et al.* (2021), to test the link between AMF taxonomy and mycorrhizal functioning, we followed Oehl *et al.* (2011) for clade names. They distinguished three main taxonomic groups: Glomerales, Diversisporales, and Gigasporales, and two small basal groups: Archaesporales and Paraglomerales, that are included here as a fourth group called 'basal lineages' (Table S2). For species names we followed Mycobank (www.mycobank.org).

Data analysis

To measure the effects sizes of AMF species and taxonomic groups on plant performance we used the *escalc* function from R package METAFOR (Viechtbauer & Cheung, 2010) to calculate the standardized mean difference (SMD) (i.e. Hedges), a useful effect size when comparing two experimental groups (i.e. treatment vs control). We calculated the mean effect size and 95% confidence interval (CI) for each outcome associated with AMF effects. A positive Hedges value indicates positive effects of AMF on their host performance, while a negative value indicates the opposite. We considered a mean effect size to be significant when the CI range did not include zero (Borenstein, 2009).

We used multivariate meta-analysis mixed effect models to test whether overall AMF effects on plants showed differences across studies. In addition, we examined whether the AMF effects on plant performance depended on host family and/or their use by humans (i.e. cultivated vs wild plants). Mixed-effect models allow the specification of fixed effects and of random terms. To avoid the nonindependence of the data we included the study identifier (ID), the experiment ID nested within study ID and host ID as random terms in order to contemplate and control the random variation of several outcomes from a single study, treatment or host identity (Tuck *et al.*, 2014; Ramírez-Viga *et al.*, 2018; Primieri *et al.*, 2022). Moderator levels with three or fewer outcomes (i.e. effect sizes) and/or coming from only one article were excluded from analyses in order to avoid small sample sizes (Borenstein, 2009). In the context of meta-analysis, a moderator variable is a systematic difference across studies that could explain the variation in the magnitude and direction of the response variables of interest (Steel & Kammeyer-Mueller, 2002).

Heterogeneity of effect sizes was assessed through Cochran's Q statistics which indicates the presence or absence of heterogeneity across studies (Borenstein, 2009). Specifically, the Q_E test accounts for residual heterogeneity and the Q_M (i.e. omnibus test) accounts for heterogeneity explained by moderators included in the model. The significance of moderators was evaluated through P-values (≤ 0.05) obtained from Q_M statistics. All the models were fitted with the *rma.mv* function of the METAFOR package (Viechtbauer & Cheung, 2010).

In order to evaluate the relationship between the effect sizes of a single inoculum of AMF species on plant growth and plant nutrition, we performed correlative tests with the *cor.test* function from the stats package.

Publication bias was assessed graphically with funnel plots of the SMD vs a sample size-based precision estimate such as $1/\sqrt{n}$. We chose this estimate because SMD plotted against the standard error is susceptible to distortion, leading to overestimation of the existence and extent of publication bias (Zwetsloot *et al.*, 2017). In addition, we tested publication bias statistically using Rosenberg's fail-safe number (fsn), which indicates the number of studies that need to be included in order to revert a significant result into a nonsignificant one (Rosenberg, 2005). A fail-safe number is considered robust if it is five times higher than the number of studies plus 10 (Rosenthal, 1991). All the analyses were conducted in an R environment (R Development Core Team, 2021).

Results

The meta-analysis included articles from countries all over the world (Fig. S2). The majority of the studies were performed in Asia (208; 46.3%), mainly in China, followed by Europe (133; 29.5%) and Americas (87; 19.4%), which were mainly represented by Germany and the USA, respectively. The lowest proportions were from Oceania (15; 3.3%) and Africa (6; 1.3%).

Overall, the inoculation with AMF had significant positive effects on plant performance (Fig. 1a) and these effects were maintained under stress conditions (Fig. 1b). Considering the subset of studies that included mycorrhizal/nonmycorrhizal treatments and stress/no-stress treatments we observed that the positive effect size of AMF on the performance of unstressed plants did not differ from those grown with stress (Fig. S3).

In particular, the association with AMF increased plant biomass as well as P and N nutrition (Fig. 1a). The effect size of AMF inoculation was highest for P, followed by plant biomass and by N (Q_M = 37.9; $P = 0.0001$; Fig. 1a). The effects of AMF on the biomass of plants facing biotic and abiotic stresses were similar between both types of stresses (Q_M = 0.09, $P = 0.77$, Fig. S4). When we considered each of the four most represented stresses separately (i.e. drought, heavy metals, salinity, and biotic stress) we also observed significantly positive effects without significant differences between them (Q_M = 0.37, $P = 0.94$; Fig. 1b).

AMF species effects on plant performance with and without stress

A total of 25 AMF species were recovered for the meta-analysis of single AMF inoculum effects on plant biomass. Among them, 18 AMF species significantly enhanced plant biomass. *Scutellospora calospora*, *Diversispora versiformis* and *Acaulospora laevis* showed the highest effect sizes, albeit did not significantly differ from the remainder species. None of the AMF species showed negative effects (Fig. 2a). Regarding the effects of AMF species on P nutrition, 22 species were recovered. Fourteen had positive effects on P nutrition without significant differences among them, while the remaining nine did not differ from zero (Fig. 2b). Among the 10 species recovered for N nutrition, only four showed positive effects. *Diversispora spurca* had the greatest effect but with only two records (Fig. 2c). The three most-represented AMF species in the performance trials were *Funneliformis mosseae*, *Rhizophagus intraradices* and *Rhizophagus irregularis*.

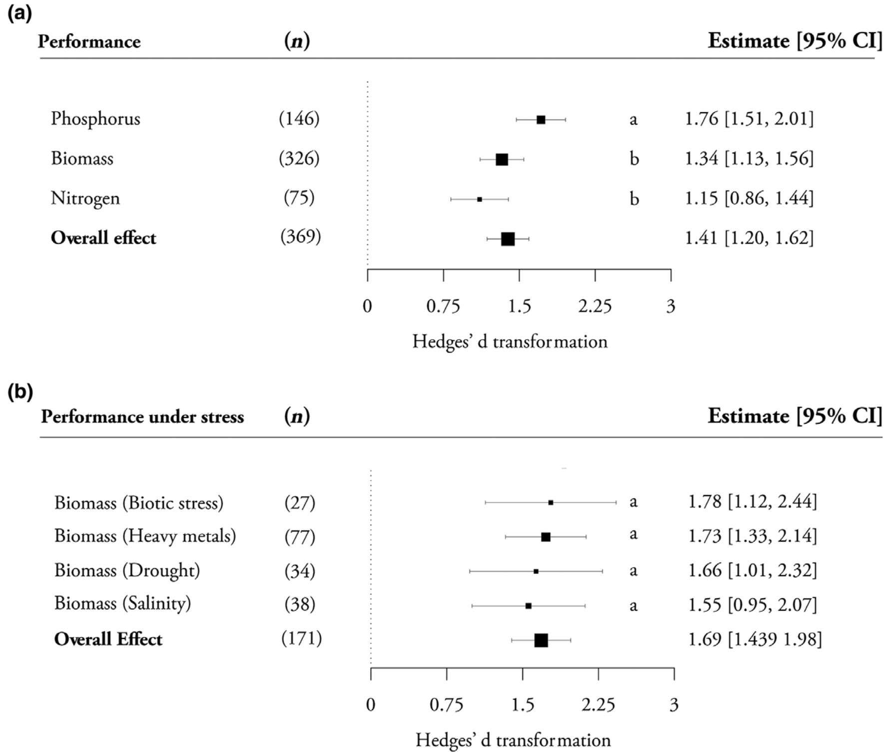

Fig. 1 Mean effect sizes and 95% confidence intervals (CIs) for (a) performance (i.e. phosphorus, biomass, nitrogen and overall effect) and (b) performance under stress (i.e. biomass of plants under drought, heavy metals, biotic stress, salinity and overall effect) used to estimate the effect of arbuscular mycorrhizal fungi (AMF) on their hosts. The order of the factors in the figure is based on the effect size. Number of articles (*n*) for each category is shown in parentheses. The size of each square represents the number of articles in relation to the overall mean calculation. Dotted line shows Hedges = 0. When the CI does not include zero, the effect size is statistically significant. Different letters indicate significant differences based on model output.

The effects of single AMF species on their host plants under drought conditions were recovered for only five species; among them, *F. mosseae, R. intraradices* and *D. versiformis* showed positive effect sizes (Fig. 3a). Eleven out of 14 AMF species promoted higher biomass under heavy metal stress (Fig. 3b). Among them, *Septoglomus deserticola* displayed the highest effect size, but with only two records (Fig. 3b). Most of the eight studied AMF species effectively promoted growth under salinity stress, except for *Claroideoglomus etunicatum* and *Gigaspora margarita* (Fig. 3c). In turn, *G. margarita* and *Rhizophagus fasciculatus* showed the highest positive effect on plants facing biotic stress, while *R. intraradices* and *R. irregularis* had no effect under this type of stress (Fig. 3d). Congruently with plant performance, the most represented AMF species in the experiments with imposed stress were *F. mosseae*, *R. intraradices* and *R. irregularis* (Fig. 3).

AMF taxonomic groups effects on plant performance with and without stress

The effects of AMF taxonomic groups on plant performance were positive and those of Diversisporales were higher than the others (Q_M = 14.12; P = 0.002; Fig. 4a). Under imposed stresses the effects were also positive but without significant differences between the taxonomic groups (Q_M = 1.43; P = 0.69; Fig. 4b). Under biotic stress, the AMF effects were significantly positive for Gigasporales, Glomerales and Diversisporales, with Gigasporales displaying significantly higher effect size than the other two groups (Q_M = 24.12, P < 0.0001, Fig. 5a). In turn, the four taxonomic groups did not significantly differ in their effects under abiotic stress (Q_M = 0.82, P = 0.85, Fig. 5b). No studies regarding the effects of basal groups on biotic stress were recovered.

Correlations of AMF effect sizes on plant performance

The AMF species' effect sizes on plant biomass positively correlated with those on P nutrition (r = 0.54, P = 0.008; Fig. 6) but not with N nutrition (r = 0.49, P = 0.49; Fig. S5a). The AMF effects on N and P nutrition were not correlated either (r=0.24, P = 0.51; Fig. S5b).

AMF effects on the performance (with and without stress) of cultivated vs wild plants and across plant families

The AMF taxonomic groups equally affected the performance of cultivated and wild plants under regular conditions and under imposed stress (Fig. S6). The analysis that combined the effects of AMF taxonomic groups on the most abundant plant families (i.e. Poaceae, Fabaceae, Asteraceae, and Solanaceae) showed that Gigasporales and Diversiporales had higher positive effects on plant performance of Poaceae than Glomerales and the basal lineages, which did not significantly differ from zero (Fig. S7a). In turn, Glomerales had higher positive effects on Fabaceae than Gigasporales, while Diversisporales showed an intermediate effect size (Fig. S7b). Glomerales also positively affected Asteraceae (Fig. S7c) and Solanaceae (Fig. S7d) while the effect of Diversiporales did not differ from zero. Diversisporales, however, was represented by three and two observations respectively, and the other two taxonomic groups were not recovered for these plant families at all. Under stress conditions, Gigasporales, Glomerales, and Diversisporales positively affected plant performance of Fabaceae (Fig. S8a) and Gigasporales (represented by only two observations) had a significantly higher effect size than the others. In turn, Glomerales positively affected Solanaceae (Fig. S8b)

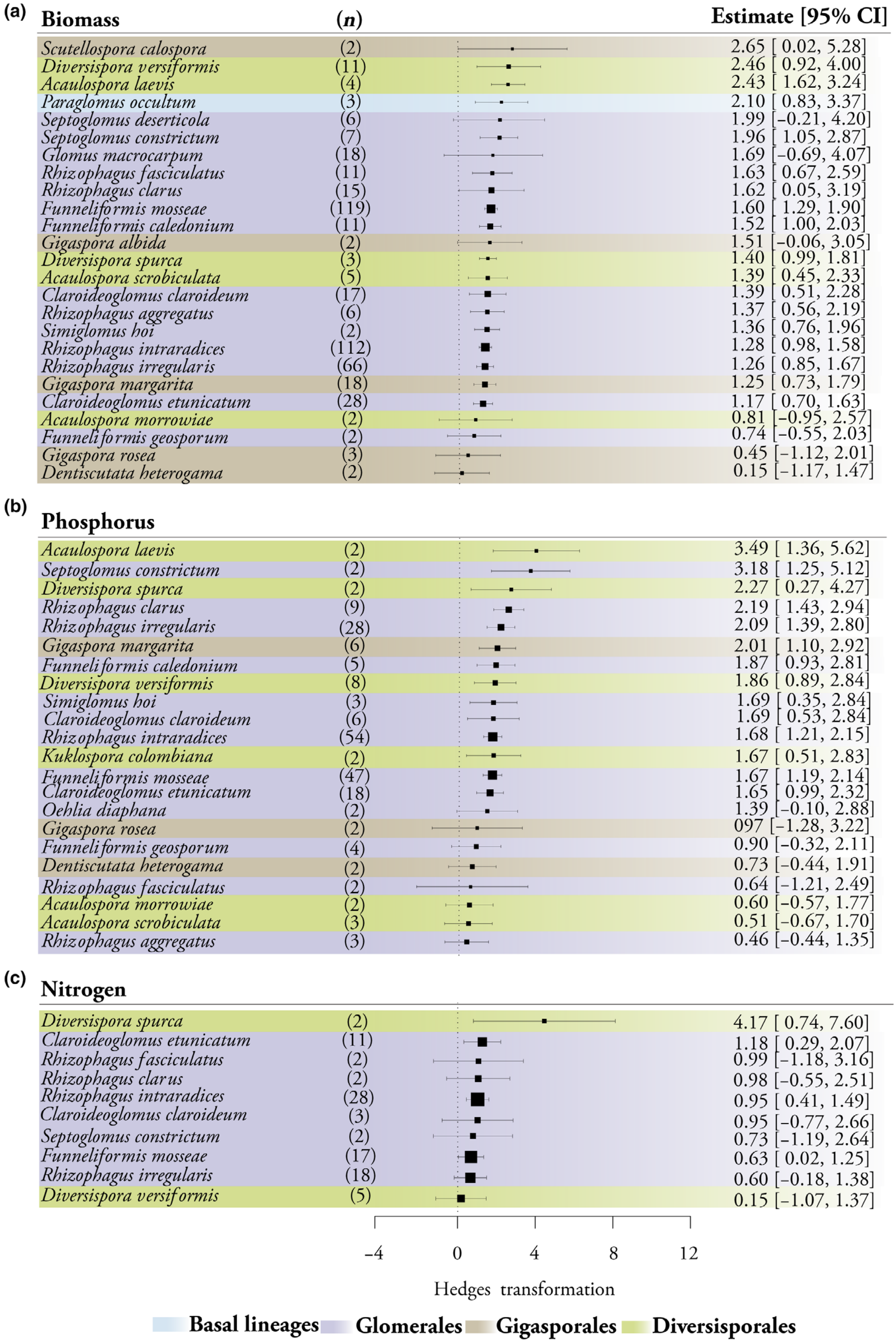

Fig. 2 Mean effect sizes and 95% confidence intervals (CIs) for different arbuscular mycorrhizal fungi (AMF) species used in monospecific inoculum to estimate the effect of arbuscular mycorrhizal fungi on plant performance considering (a) biomass, (b) phosphorus, and (c) nitrogen. The order of the species in the figure is based on the effect size. Number of articles for each category are shown in parentheses. The size of each square indicates the number of studies in relation to the overall mean calculation. Dotted line shows Hedges = 0. When the CI does not include zero, the effect size is statistically significant.

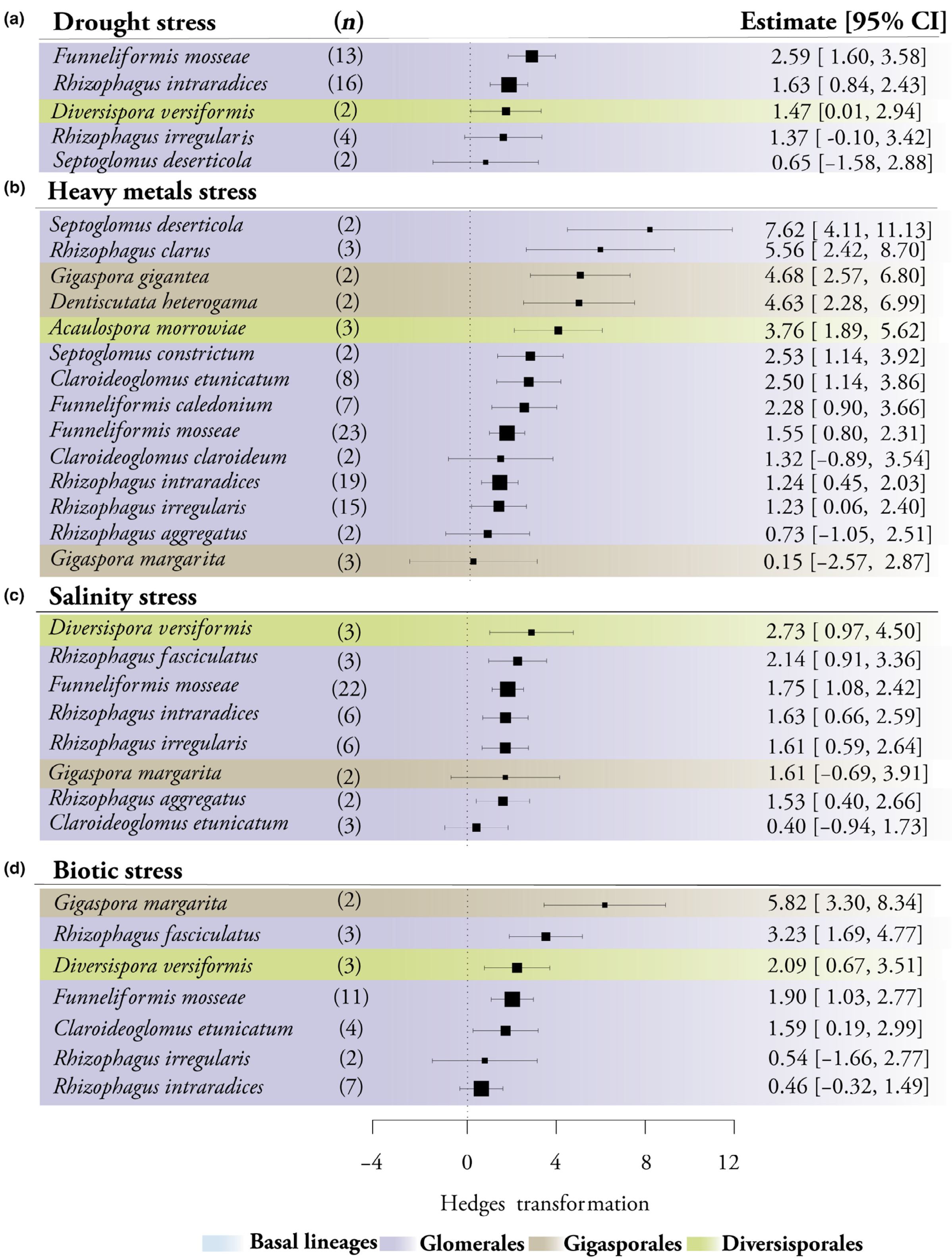

Fig. 3 Mean effect sizes and 95% confidence intervals (CIs) for different arbuscular mycorrhizal fungi (AMF) species used in monospecific inoculum to estimate the effect of arbuscular mycorrhizal fungi on plant performance under (a) drought, (b) heavy metal, (c) salinity, and (d) biotic stresses. The order of the species in the figure is based on the effect size. Number of articles for each category are shown in parentheses. The size of each square represents the number of articles in relation to the overall mean calculation. Dotted line shows Hedges = 0. When the CI intervals does not include zero, the effect size is statistically significant.

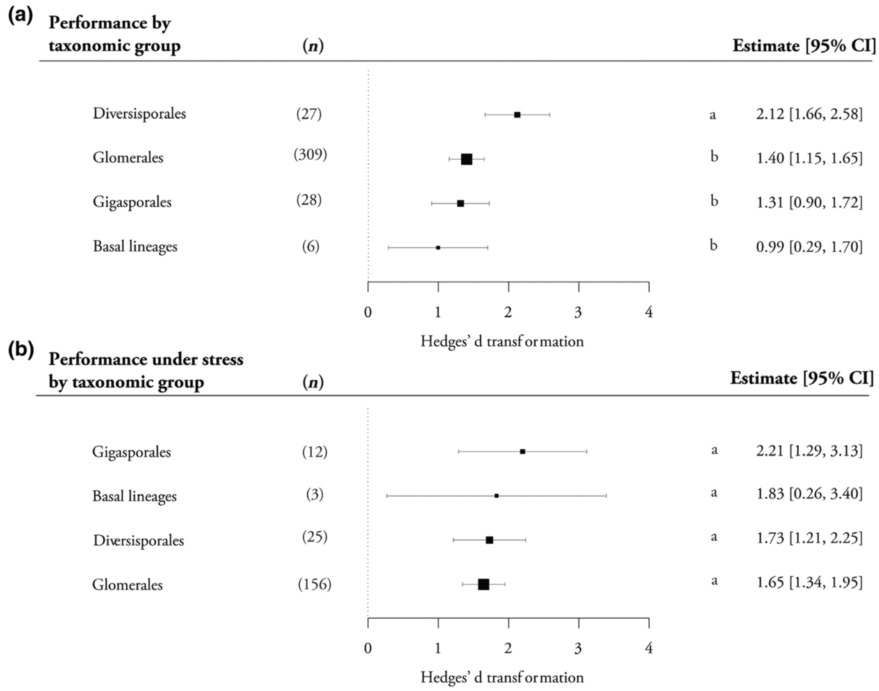

Fig. 4 Mean effect sizes and 95% confidence intervals (CIs) of arbuscular mycorrhizal fungi taxonomic group (i.e. basal lineages, Gigasporales, Glomerales and Diversisporales) for plant (a) performance and (b) performance under stress. Sample sizes (*n*) for each category are shown in parentheses. The taxonomic groups are ordered according to their effect size. The size of each square represents the number of articles in relation to the overall mean calculation. Dotted line shows Hedges = 0. When the CI does not include zero, the effect sizes are statistically significant. Different letters indicate significant differences based on model output.

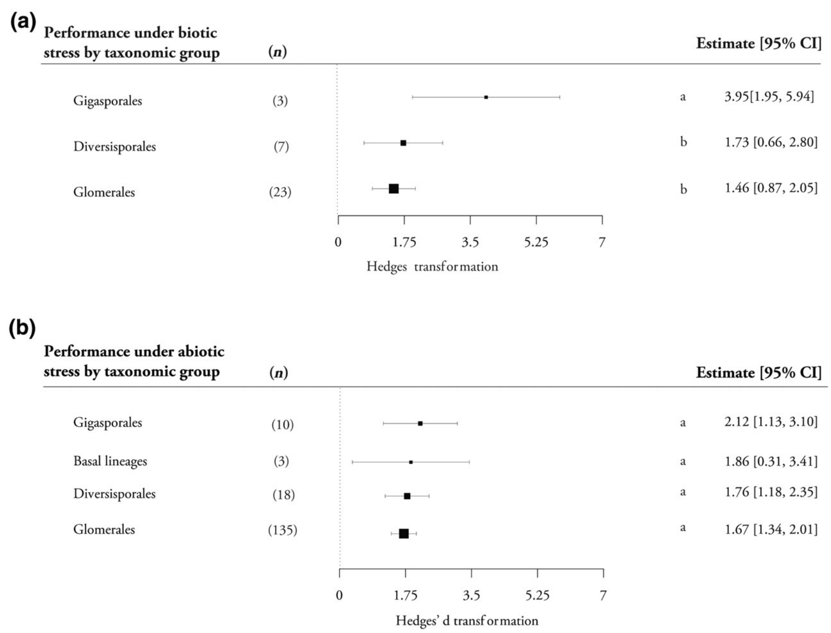

Fig. 5 Mean effect sizes and 95% confidence intervals (CIs) of arbuscular mycorrhizal fungi taxonomic group (i.e. basal lineages, Gigasporales, Glomerales and Diversisporales) for (a) biotic stress and (b) abiotic stress. Sample sizes (*n*) for each category are shown in parentheses. The order of the species in the figure is based on the effect size. The size of each square represents the number of articles in relation to the overall mean calculation. Dotted line shows Hedges = 0. When the CI does not include zero, the effect size is statistically significant. Different letters among taxonomic groups indicate significant differences among them based on model output.

while the effect of Diversisporales (two observations only) did not significantly differ from zero. No studies were recovered for the other plant families.

Publication bias

No significant publication biases were detected. Funnel plots of effect sizes vs inverse sample size did not show any significant skewness for plant performance data (Fig. S9). In addition, the obtained fail-safe numbers (fsn) indicated that a high number of studies would have to be included to revert significant effect sizes into nonsignificant ones for both data-sets: plant 'performance under stress' data (Rosenberg fsn = 549 627; average effect size = 1.13; $P < 0.0001$) and plant 'performance' data (Rosenberg fsn = 1262 590; average effect size = 0.59; $P < 0.0001$).

Discussion

Effects of AMF on plant performance

The beneficial effects of AMF on plant performance are widely documented in the literature (e.g. Hoeksema *et al.*, 2010; Delavaux *et al.*, 2017). Our meta-analysis reinforces some of the previous observations and trends but challenges others. Our

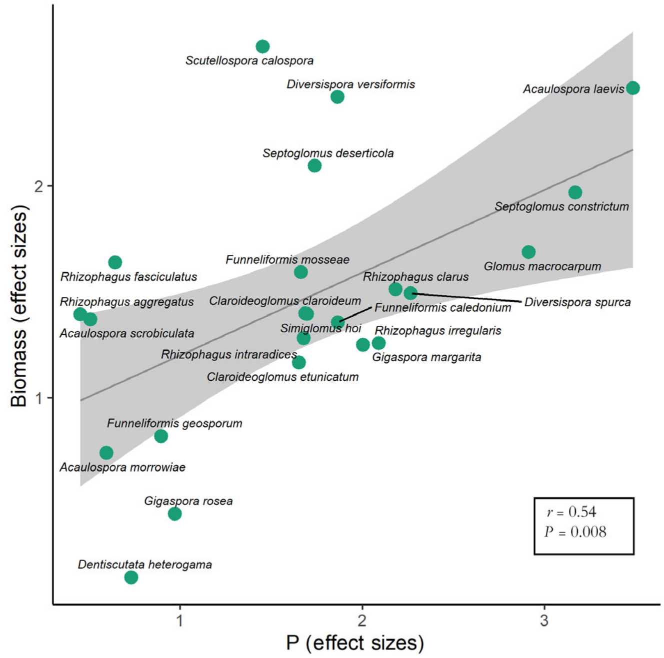

Fig. 6 Correlation between the effect sizes of plant biomass and plant phosphorus (P) nutrition. The gray shaded area represents the 95% of confidence interval.

results show which AMF species and taxonomic groups confer more benefits on plant growth and nutrition and on plant growth under biotic and abiotic stress conditions. While there are more than twice as many studies on performance under regular conditions (i.e. without imposed stress) than under stress, we found that the positive effects of AMF on plant performance were equally important under both circumstances. Despite the overall more positive effects of AMF under stressing conditions than in regular ones, the lack of differences in the subset of studies that specifically compared plants with and without stress, suggests that the beneficial effects of AMF to stressed plants do not exceed those conferred to plants in unstressed conditions, where primarily nutritive benefits are assumed (see later).

The higher positive effect on P than N nutrition is in line with a general consensus on the greater importance of AMF for plant P nutrition (e.g. Clark & Zeto, 2000; Smith *et al.*, 2015). Access to nutrients, particularly P, can increase plant biomass (Lekberg & Koide, 2005). Although no causal relationship should be attributed to the correlation analysis, in our study, the most beneficial AMF species in terms of P nutrition were also the most beneficial in terms of biomass production.

The effects of AMF on plant responses to biotic and abiotic stresses may conflate improved nutrition (e.g. Chandrasekaran *et al.*, 2014) with a range of physiological mechanisms such as the activation of plant defense system against pathogens and parasites (Azcón-Aguilar & Barea, 1997), decrease in proline accumulation under drought (Augé, 2001), and production of osmoregulation compounds against salinity impact (Porcel *et al.*, 2012; Chandrasekaran *et al.*, 2014). Interestingly, the magnitude of the effects did not differ between biotic and abiotic stresses, although it varied considerably among AMF species and, to a lesser degree, among the taxonomic groups. Further studies are needed to assess the relative contribution of mechanisms other than nutrition to the positive effects of AMF under stressful conditions.

Comparison among AMF species

Despite the overall positive effects of AMF, our study reveals that not all the effect sizes of AMF species on host performance differ from zero, though no significant negative effects were found. The order of the species in the ranks differed among growth, P and N nutrition, and between nonstress and stress, suggesting that a species that is efficient at providing one benefit may not be efficient for another. These results also suggest that the mechanisms involved in the benefits under stress could go beyond mere nutrition (Delavaux *et al.*, 2017). AMF that rank distinctly high under stressful conditions, such as *G. margarita*, are suspected to trigger nonnutritional mechanisms.

Some of the species that stood out in two types of benefits were *Acaulospora laevis* and *Septoglomus constrictum* that ranked high for P nutrition and biomass. In turn, *D. spurca* was the best considering P and N nutrition. However, the CIs for the effect sizes were wide in these three species due to the low number of studies recovered from the literature. In these cases, a greater number of studies are needed to be sure about the symbiotic performance of these species.

Funneliformis mosseae, *R. intraradices*, and *R. irregularis* were the three most studied species, including most types of benefits but with moderate effect sizes. This is probably because they are generalist species, easily cultured, and considered to be ruderals (e.g. Chagnon *et al.*, 2013). Other meta-analyses have also shown that species in Glomerales are the most studied for some types of stress (Chandrasekaran *et al.*, 2014; Jayne & Quigley, 2014). While Jayne & Quigley (2014) found no differences among the six AMF species studied for plant growth under drought, Chandrasekaran *et al.* (2014) reported that *R. fasciculatus* promoted the highest effect size under salt stress among three Glomerales species studied. In our study, *R. fasciculatus* ranked second in growth promotion under salt stress, although there were no differences between species. The fact that the three most studied species mentioned earlier showed moderate effects is relevant since much of our knowledge about the functioning of mycorrhizae is based on them; this may indicate that our idea about the importance of AMF in plant performance may change if studies that test the effects of species belonging to other lineages increase.

The mechanisms by which some AMF species perform better than others have been seldom studied, albeit certain studies provide some cues. For example, the good symbiotic performance (i.e. benefits provided to the plants) of *G. margarita* under biotic stress conditions could be explained by the endosymbiotic bacteria that this fungus carries. The bacteria affect fungal metabolism by promoting sporulation, ATP production, and detoxifying mechanisms against oxygen-reactive species (Salvioli *et al.*, 2016; Vannini *et al.*, 2016). Resistance to fungal pathogens by alleviation of oxidative stress is one of the benefits provided by AMF symbiosis (e.g. Wu *et al.*, 2021). Other efforts aimed to disentangle the genetic basis of intra-specific trait variability of *R.*

irregularis (Chen *et al*., 2018; Serghi *et al*., 2021) that may have consequences for the symbiotic functions of the fungus. For example, it has been shown that the proportion and speed of spore germination are higher in homokaryons, while the hyphal network structure is more complex in dikaryons (Serghi *et al*., 2021). In any case, the physiological mechanisms underlying the differences between AMF species is an aspect of Glomeromycotan biology that requires further study. On this, it has been proposed that some fungal traits could explain the differential effects of AMF species or functional groups on plants (e.g. Chagnon *et al*., 2013), but this was not supported by our data (see later).

Comparison between AMF taxonomic groups

In contrast to the findings of Maherali & Klironomos (2007) and the framework proposed by Chagnon *et al.* (2013), our global analysis did not reveal higher nutritional benefits by Gigasporales in comparison to the other groups. Instead, we observed that all the four taxonomic groups showed positive effect sizes and that the effect size of Diversisporales was higher than the others. This suggests that although AMF taxonomic groups generally differ in their developmental traits (Hart & Reader, 2002; De La Providencia *et al*., 2005; Voets *et al*., 2006; Maherali & Klironomos, 2007), these differences do not consistently translate into nutritional or growth benefits (Koch *et al*., 2017).

It is widely accepted that the evolution of symbiosis with AMF has allowed plants to access limited soil resources, primarily P, and to protect themselves from abiotic stressors (Strullu-Derrien *et al*., 2018). Our findings suggest that these primary functions are maintained among all the taxonomic lineages. Nonetheless, the outcome of mycorrhizal symbiosis varies among different plant–fungus combinations and depends on environmental conditions (e.g. van der Heijden *et al*., 1998; Antunes *et al*., 2011). For example, in a recent comparison of several AMF species belonging to different lineages, it was shown that two species (i.e. *Archaeospora europaea* and *Paraglomus laccatum*) belonging to basal lineages did not provide nutritional benefits to leek (Säle *et al*., 2021). Our meta-analysis showed overall positive effects of basal lineages on plant performance, although in Poaceae they did not differ from zero. These findings show that certain plant–fungus combinations may display different behavior than the general trends observed here (see Fig. S6).

The highest positive effect size of Gigasporales under biotic stress contrasts with previous studies which found that Glomerales provided greater protection against root antagonists, such as pathogenic fungi and oomycetes (Sikes *et al*., 2009). These discrepancies also suggest that the outcome of the symbiosis between certain plant–fungus combinations may stand apart from general trends. However, we cannot discard that the differences may be attributable to the number of studies and the inclusion of aboveground and belowground antagonists in our analyses. It is worth mentioning that we analyzed several studies for Glomerales (23), while only a few were recovered for Diversiporales (seven) and Gigasporales (three). Interestingly, Gigasporales showed a low effect size on plant performance in Fabaceae under regular conditions but the highest under stressful conditions, supporting the idea that this AMF lineage may trigger specific mechanisms other than nutrition in face of stress.

Lastly, as can be seen from the previous paragraphs, a remarkable aspect of our analyses is that there are many studies for certain easily culturable ruderal species in Glomerales, while only a few studies are available for the remaining majority of AMF species. Given this, the data set is not sufficient to draw definitive conclusions about the symbiotic performance of the basal clades and further studies with Gigasporales and Diversisporales under stressful conditions are needed to confirm the observed patterns.

Implications for AMF management

Individual AMF isolates, or a mix of them, are increasingly used as bio-inoculants for remediation of contaminated soils (e.g. Solís-Ramos *et al*., 2021), restoration of degraded lands (Maltz & Treseder, 2015; Asmelash *et al*., 2016), and as biofertilizers for horticulture and crop production, though their production and application at large scales remain challenging (Berruti *et al*., 2016; Igiehon & Babalola, 2017). Interestingly, we did not find differences between cultivable and wild plants, so the general patterns observed here may apply both to the restoration of natural communities and crop production. However, most of the studies analyzed here are glasshouse experiments, so these suggestions remain to be tested in the field.

Our meta-analysis provides a ranking of AMF species according to their effects on plant performance with and without biotic and abiotic stress, which can be useful to select the most efficient species, considering the main constraints that the target plants face in a particular environment. Even though we recovered studies irrespective of plant species, both wild and cultivated, belonging to different plant life forms, it is remarkable that the most efficient AMF species found in this meta-analysis are not necessarily the most widely used as bio-inoculants (Basiru *et al*., 2021). For example, *Acaulospora laevis* was found here to be efficient both for P nutrition and biomass promotion, *D. spurca* for P and N nutrition, and *G. margarita* for growth under stress, though these species are hardly used as commercial bio-inoculants (Basiru *et al*., 2021). Anyway, this initial approach reveals that most of the species located at the extremes of the rankings have also been poorly studied, so further studies are necessary to confirm these trends.

The AMF species most widely used as bio-inoculants, such as *R. irregularis* and *F. mosseae*, showed moderately positive effects and were not among the most beneficial symbionts. Among the taxonomic groups, Glomerales predominate as commercial bio-inoculants and in patents related to agricultural technology, while Gigasporales, the most beneficial under biotic stress, are poorly represented as bio-inoculants (Basiru *et al*., 2021; Srivastava *et al*., 2021). These may be some of the reasons why the success of AMF as bio-inoculants is not always evident and their use has been called into question (Hart *et al*., 2017; Salomon *et al*., 2022).

Anthropogenic land-use and land-use changes, such as agricultural practices and ecological restoration, affect AMF communities (e.g. Helgason *et al*., 1998; Oehl *et al*., 2003; Cofré *et al*., 2017; Guzman *et al*., 2021; Medeiros *et al*., 2021). Some studies have shown that Gigasporales are sensitive to increased land-use intensity and/or disturbance, while Glomerales are more ruderal and remain mostly unaffected, or even increase in abundance under these conditions (e.g. Jansa *et al*., 2003; Longo *et al*., 2016; Cofré *et al*., 2017). Given the greatest benefits provided by Gigasporales under biotic stress, land-use strategies that have the least impact on this group would be desirable, particularly in agriculture.

Finally, it is worth highlighting that certain species within Acaulosporaceae, the main lineage of Diversisporales, show their niche optimum at lower temperature and pH values than the other groups (Jansa *et al*., 2014; Davison *et al*., 2021). Then, some AMF groups may show greater symbiotic efficiency under their optimal climatic or edaphic conditions than those present in controlled glasshouse studies. This type of knowledge may be highly relevant in the context of current global changes.

Conclusions

Our meta-analysis supports previous studies about AMF benefits to plant nutrition and growth but also highlights the positive effects of AMF under stress, showing no significant differences between stress types. However, the relative contribution of mechanisms other than nutrition to the positive effects of AMF in stressful conditions is still unclear. One of the main findings of this study is that many species, especially those outside of Glomerales, have been poorly studied, suggesting the need to target a phylogenetically broader range of AMF species in future studies of AMF role in plant performance. However, the results challenge previous ideas on functional differences between taxonomic groups for most of the benefits, as only a few differences in effect sizes among AMF taxonomic groups were observed. Also, the trends differ from previous assumptions. The general trends observed here were consistent between cultivable and wild plants but revealed some nuances when examined across plant families. Overall, the results of this study allow for a better comprehension of the AMF functioning in nature and could provide the basis for selecting species or groups of species as bio-inoculants for agriculture, remediation and soil restoration.

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Author contributions

NM, GG and CU planned and designed the research. NM, GG, FS, MC, SL, NC, VB and MB conducted literature search and data collection. GG analyzed data. NM, GG, MJ and CU wrote the first draft of the manuscript, all authors contributed to the final version. NM and GG contributed equally to this work.

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Data availability

Data will be made available from corresponding authors (NM and GG) on request.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Flow diagram.

Fig. S2 Global distribution of the articles used in the meta-analyses.

Fig. S3 Different stress levels (with and without) used to estimate the effect of arbuscular mycorrhizal fungi (AMF) on their hosts performance.

Fig. S4 Different stress attributes (abiotic and biotic) used to estimate the effect of arbuscular mycorrhizal fungi (AMF) on their hosts performance.

Fig. S5 Correlations among plant biomass, nitrogen and phosphorus.

Fig. S6 Effect of arbuscular mycorrhizal fungi taxonomic groups for cultivated and wild plants performance with and without stress.

Fig. S7 Effect of arbuscular mycorrhizal fungi taxonomic groups for the performance of Poaceae; Fabaceae; Asteraceae and Solanaceae.

Fig. S8 Effect of arbuscular mycorrhizal fungi taxonomic groups for the performance under stress of Fabaceae and Solanaceae.

Fig. S9 Funnel plots for plant performance and plant performance under stress.

Table S1 List of moderator variables considered in the meta-analysis for assessing the effects of arbuscular mycorrhizal fungi on plant hosts.

Table S2 Genera included within each taxonomic group considered in the present meta-analysis (adopted from Oehl *et al.*, 2011).

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