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LETTER

Arbuscular mycorrhizal fungi benefit plants in response to major global change factors

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Abstract

Land plants play a key role in global carbon cycling, but the potential role of arbuscular mycorrhizal fungi (AMF) in the responses of a wide range of plant species to global change factors (GCFs) remains limited. Based on 1100 paired observations from 181 plant species, we conducted a meta-analysis to test the role of AMF in plant responses to four GCFs: drought, warming, nitrogen (N) addition and elevated CO_2. We show that AMF significantly ameliorate the negative effects of drought on plant performance. The GCFs N addition and elevated CO_2 significantly enhance the performance of AM plants but not of non-inoculated plants. AM plants show better performance than their non-inoculated counterparts under warming, although neither of them showed a significant response to this GCF. These results suggest that AMF benefit plants in response to GCFs. Our study highlights the importance of AMF in enhancing plant performance under ongoing global change.

KEYWORDS

arbuscular mycorrhizal fungi, drought, elevated CO_2, global change, meta-analysis, nitrogen addition, plant performance, warming

INTRODUCTION

Global environmental change is affecting terrestrial plant growth (Reich et al., 2022; Yang et al., 2021). Plants have evolved various strategies to cope with these challenges, one of which is to form symbiotic associations (up to 80% of terrestrial plant species) with arbuscular mycorrhizal fungi (AMF) (Martin et al., 2017). AMF delivers various benefits to their host plants, for example, nutrient uptake, stress tolerance, herbivore defence and disease resistance, in exchange for sugar and lipids (Lanfranco et al., 2018). Given that plants not only govern the carbon (C) flux from the atmosphere into terrestrial ecosystems (e.g. photosynthesis) but also serve as one of the terrestrial C reservoirs (e.g. plant biomass), they play an important role in global C cycling and C-climate feedbacks (Houghton et al., 2009). As such, understanding and predicting the role of AMF in plant responses to global change factors (GCFs) is critically necessary because their responses can in turn feed back to exacerbate or ameliorate global change and thus the future trajectory of climate change (Malhi et al., 2020).

As the four most important GCFs, for example, drought, warming, nitrogen (N) deposition and elevated atmospheric CO_2 levels (elevated CO_2), their ecological consequences are intensifying (IPCC, 2021). AMF are expected to improve the drought tolerance of their host plants by facilitating water and nutrient uptake, regulating physiological processes and modifying soil-water relations (Augé, 2001; Li et al., 2019; Yooyongwech et al., 2013). Warming has been shown to affect the metabolism and nutrient exchange in AM-plant symbionts, and thus the plant performance (Hawkes et al., 2008; Kivlin et al., 2013). N enrichment may affect plant growth by altering the interaction between AMF and host plants, for example, from mutualism to parasitism (Johnson et al., 2010). Elevated CO_2 would increase the dependency of plants on AM symbionts due to the increasing nutrient demand for plant growth (Johnson, 2010; Terrer et al., 2018). Although a large number of studies over the past decades have explored the functioning of AM symbionts under the influence of GCFs (Gosling et al., 2016; Kivlin et al., 2013; Marro et al., 2022; Zhou et al., 2019), results are highly variable, spanning from positive to neutral to negative effects. Therefore, the field has not reached a generally accepted quantitative understanding of the role of AMF in plant responses to GCFs, which requires a more comprehensive analysis.

Another goal in mycorrhizal research is to understand how AMF diversity determines symbiotic functioning (Powell & Rillig, 2018). Although most studies of AMF diversity are constrained by species richness (Powell & Rillig, 2018), a recent meta-analysis did not find positive effects of AMF species richness on plant performance (Yang et al., 2017). In fact, specific benefits provided by AM symbionts, to some extent, can be attributed to certain fungal functional traits (Chagnon et al., 2013; Maherali & Klironomos, 2007). Given that these traits are thought to be phylogenetically conserved at the fungal family level (Koch et al., 2017; Powell et al., 2009), host plants might respond more significantly to AMF diversity at the family level than at the species level (Crossay et al., 2019; Yang et al., 2017). However, it is still unclear whether these findings can explain the variation of symbiotic function in host plants under GCFs, which hampers our ability to understand how AM symbionts and their diversity would influence plant responses in the context of ongoing global change.

While many studies have addressed the role of AMF in plant response to GCFs, these are commonly case studies involving only a single pair of plants inoculated with AMF and their non-inoculated counterparts, and thus the results cannot be generalized. Therefore, a top priority now is a comprehensive analysis to test patterns found in case studies for a wide range of plant species. Meta-analysis offers an opportunity to achieve this goal (Powell & Rillig, 2018). Although one study took this approach 10 years ago, it primarily focused on the differences among fungal symbiont groups and did not further identify the key moderators of the role of AM symbionts in plant responses (Kivlin et al., 2013). Importantly, the phylogeny of tested species can significantly change the outcomes of a meta-analysis (Chamberlain et al., 2012), and hence phylogenetic relatedness among tested species should be incorporated in any meta-analysis involving multiple species. Here, we compiled a dataset regarding the responses of plants inoculated with AMF and their non-inoculated counterparts to four GCFs, drought, warming, N addition and elevated CO_2, from 360 publications on 181 plant species. Our dataset builds on three times the number of papers compared to previous analysis (included 190% more papers; Figure S1). On the basis of this dataset, we conducted a phylogenetically controlled meta-analysis to address the following questions: (i) What role do AMF play in plant responses to GCFs? (ii) Does the role of AMF depend on their richness at different taxonomic resolutions (e.g. species and family levels)? Answering these questions will advance our understanding of the role of AM symbionts in plant responses to ongoing global environmental change (Powell & Rillig, 2018).

MATERIALS AND METHODS

Data collection

We searched Web of Science (WoS, http://apps.webofknowledge.com/) and China Knowledge Resource Integrated Databases (CNKI, www.cnki.net/) in May 2023, with the following keyword combinations for topic search: ("arbuscular mycorrhizal fung*" OR "AM fung*" OR "AMF" OR "AM symbiosis") AND ("warming" OR "elevated temperature" OR "climate change" OR "free-air carbon dioxide enrichment" OR "free-air CO_2 enrichment" OR "elevated CO_2" OR "elevated atmospheric CO_2" OR "eCO_2" OR "drought" OR "water deficit" OR "nitrogen fertilization" OR "nitrogen addition" OR "nitrogen deposition" OR "nitrogen application" OR "nitrogen enrichment") AND ("plant growth" OR "plant biomass" OR "nitrogen uptake" OR "phosphorus uptake" OR "nutrient uptake" OR "water uptake" OR "water transfer" OR "pathogen resistance" OR "pathogen protection" OR "chemical defen*" OR "herbivore defen*" OR "osmotic adjustment" OR "stomatal regulation" OR "physiological processes" OR "root length" OR "photosynthe*"). In the WoS, databases used for our search included the WoS Core Collection, Current Contents Connect, KCI-Korean Journal Database, MEDLINE and SciELO Citation Index. We also checked the reference lists of relevant meta-analyses to obtain target articles (Alberton et al., 2005; Duarte & Maherali, 2022; Kivlin et al., 2013; Marro et al., 2022). To avoid bias, the following criteria were used to screen studies: (1) Inoculated and non-inoculated groups must be the same except for the factor of AMF inoculation. (2) Inoculation of AMF in combination with other microorganisms that were not controlled for was excluded in our selection to avoid any confounding effects. (3) Studies in which the non-mycorrhizal group was created by fungicides (e.g. benomyl) were excluded since fungal inhibitors would also eliminate other fungal groups, such as pathogens (i.e. there are non-target effects). (4) The experimental soils had to be sterilized; if the soil condition was unknown in a study, we further checked the mycorrhizal colonization of plant roots in non-inoculated groups, and only studies with colonization rates below 0.5% were included in our dataset; if both soil condition and mycorrhizal colonization were unknown in a paper, then this paper was excluded from our selection. (5) Control and GCF treatment had to be established for both the inoculated and non-inoculated groups. (6) The study had to report data on plant (both inoculated with AMF and non-inoculated groups) responses to at least one of the four GCFs. (7) The means of target variables and sample sizes had to be reported or could be derived from the article. (8) Experimental details had to be provided, for example, the names of plant species. In this study, we preferentially selected plant biomass to assess its response to GCFs, as these data were reported in the majority of studies. If a study did not report biomass data, then we chose nutrient uptake (e.g. N and phosphorus[P]), root or shoot length or net photosynthetic rate as a surrogate of plant performance. It should be noted that only the data on total nutrient uptake rather than tissue nutrient concentrations were included, given the potential influence of the "dilution effect". To be included in this dataset, therefore, a study had to report at least one of the above-mentioned variables of plant performance. The procedure for article selection followed the PRISMA guidelines (Figure S2). Finally, a total of 360 publications (284 for drought, 23 for warming, 19 for N addition and 43 for elevated CO_2) were included in this meta-analysis (Figure 1a). For each study, we extracted means, sample size and standard deviation (SD) or standard error (SE) or 95% confidence interval (CI) if reported. Unspecified error bars were considered to be SE. If a study reported data for multiple time points and manipulations, we only collected data from the last time point and the highest level of a factor. If results were presented graphically in a study, the software WebPlotDigitizer 4.1 (https://automeris.io/WebPlotDigitizer/) was used to digitize the data.

Moderators

Given that the identity of both host plants and AMF species likely affects the outcomes of plant-AMF symbiosis (Hoeksema et al., 2010), we captured the identity of plant species and inoculated AMF species for each study. For the Latin names and taxonomic information of plant and AMF species, we followed World Flora Online (www.worldfloraonline.org) and Mycobank (www.mycobank.org), respectively. Because the diversity effect of AMF depends on its taxonomic resolution (Yang et al., 2017), we recorded the AMF richness at both the species and family levels for the inoculated group based on the original publications. We also collected experimental and environmental factors, for example, soil organic matter (SOM), soil pH, greenhouse temperature and treatment intensity (Figure S3).

Effect size and variance

In this study, the natural log response ratio (lnRR), a metric widely used in meta-analysis (Hedges et al., 1999), was used to evaluate the effect sizes of GCFs on plant performance:

$$\ln\mathrm{RR} = \ln\left(\mathrm{X_T}/\mathrm{X_C}\right) = \ln\mathrm{X_T} - \ln\mathrm{X_C} \tag{1}$$

where X_C and X_T are the arithmetic mean values of plant performance in the control and GCFs treatments, respectively. A positive value of lnRR indicates that GCFs promote plant growth, while a negative value indicates the opposite. The variance (v) for each lnRR was calculated as:

$$v = \frac{\mathrm{SD}_T^2}{N_T X_T^2} + \frac{\mathrm{SD}_C^2}{N_C X_C^2} \tag{2}$$

where SD_C and SD_T are the SD in the control and GCFs treatments, respectively; N_C and N_T are the sample size in the control and GCFs treatments, respectively. If a study reported SE, then the corresponding SD was calculated as:

$$\mathrm{SD} = \mathrm{SE} \times \sqrt{n} \tag{3}$$

where n is the sample size. If only a 95% CI was given in a study, the SD was computed as:

$$\mathrm{SD} = \left(\mathrm{CI_u} - \mathrm{CI_l}\right)\sqrt{n}/2\mathrm{Z}_{\alpha/2}. \tag{4}$$

where $\mathrm{CI_u}$ and $\mathrm{CI_l}$ are the upper and lower limits of the 95% CI, respectively. $Z_{\alpha/2}$ represents the Z score for a given level of significance (e.g. 1.96 at α=0.05). If both shoot and root biomass were reported in a study, then their sum was considered as the total biomass. The corresponding SD values were calculated following the method of error propagation (Lorber 1986):

$$\mathrm{SD_{sum}} = \sqrt{SD_a^2 + SD_b^2} \tag{5}$$

where $\mathrm{SD_{sum}}$ is the new SD for the sum values, with $\mathrm{SD_a}$ and $\mathrm{SD_b}$ as the values of each fraction of plant biomass. In the cases that did not report SD, SE or 95% CI in our dataset, the *Bracken1992* approach was used to impute missing SD using the R package *metagear* (Lajeunesse, 2016).

Data analysis

All statistical analyses were performed in R (R Development Core Team, 2019), and these analyses were conducted for each of the different components of GCFs (e.g. drought, warming, N addition and elevated CO_2) separately. First, to test whether the plants, on average, respond positively or negatively to GCFs regardless of their mycorrhizal status (e.g. inoculated AMF or not),

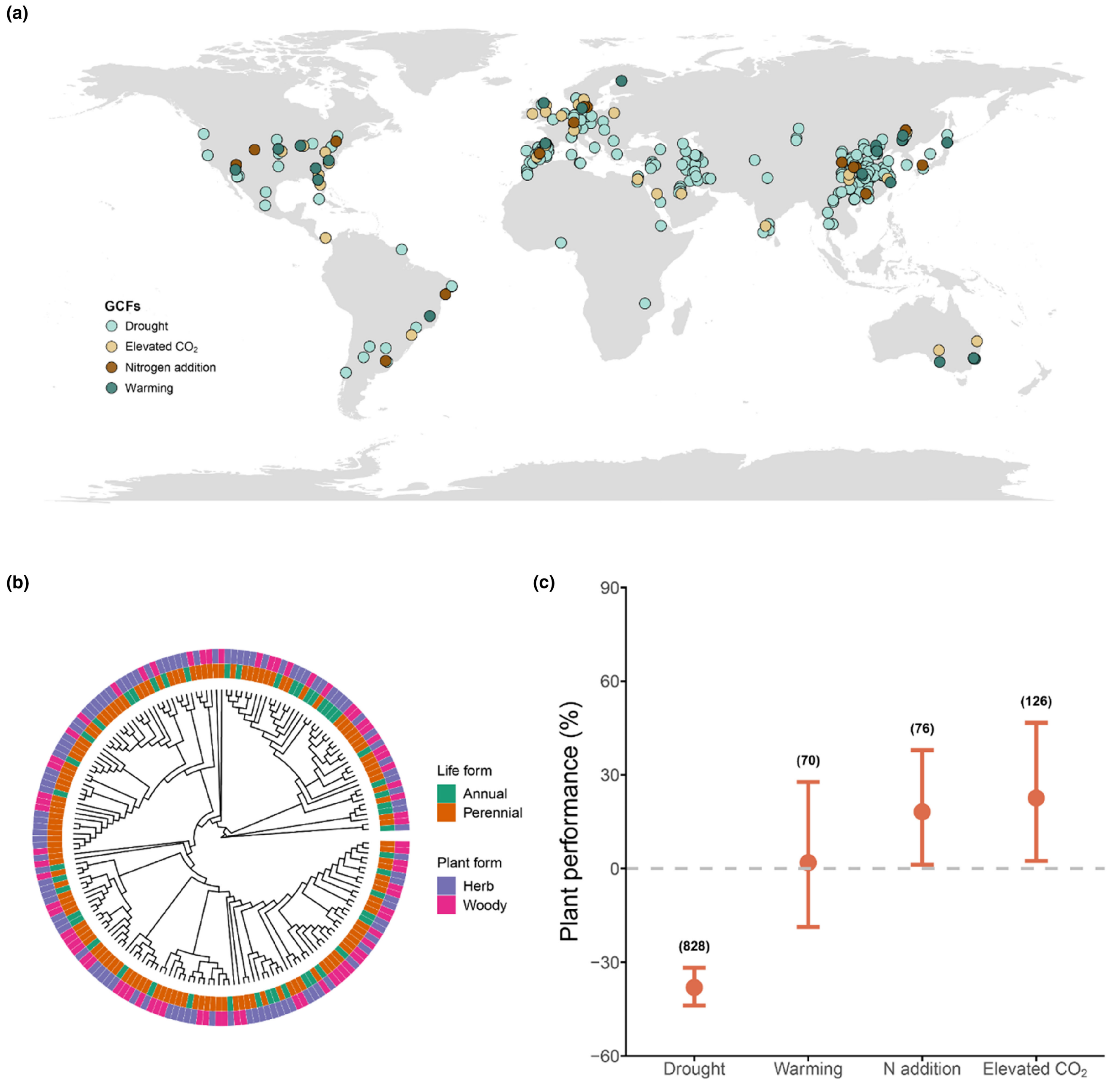

FIGURE 1 Site location of studies with global change factors (GCFs) included in this dataset (a), the phylogenetic tree of plant species incorporated in the meta-analysis (b) and plant performance (regardless of mycorrhizal status) in response to drought, warming, N addition and elevated CO_2 (c). Circles and error bars represent the mean effect size and 95% confidence intervals (CIs), respectively. If the 95% CIs do not overlap with zero, a significant effect of GCFs ($p<0.05$) was considered. Sample sizes are given in parentheses.

a mixed-effects model with a restricted maximum likelihood approach (REML) was used to calculate the weighted mean of lnRR ($\ln\overline{RR}$) via the R package *metafor* (Viechtbauer, 2010). Specifically, the $\ln\overline{RR}$ was calculated as:

$$\ln\overline{RR} = \sum_{i=1}^{m} w_i lnRR_i \Big/ \sum_{i=1}^{m} w_i \tag{6}$$

where m represents the number of comparisons in the group and $\ln RR_i$ is the effect size of the *i*th study. The weighing of the *i*th study (w_i) was computed as:

$$w_i = \frac{1}{v_i} \tag{7}$$

$$v_i = v + \tau^2 \tag{8}$$

where v_i represents the variance of study (i), v indicates the variance within study and τ^2 is the variance between studies. The $\ln\overline{RR}$ was considered significantly different from zero if the 95% CI around the mean did not overlap with zero. Given that some studies contributed more than one effect size, we ran a hierarchical meta-analysis to control for non-independence in this dataset. To deal with this, the *id* of the effect size nested in the *study* was treated as a random factor in the mixed-effect model. Because the research group of origin of a study might bias the results of meta-analysis (Moulin & Amaral, 2020), we constructed author networks using the R package *bibliometrix* (Aria & Cuccurullo, 2017). The author clusters were finally implemented in the mixed-effect model to control for this kind of non-independency of data. In addition, to control for the potential non-independence of effect sizes from plant species with shared evolutionary history (Figure 1b), the phylogenetic relatedness among the tested plant species was also incorporated in the mixed-effect model by including the variance–covariance matrix of species relatedness as an additional random factor. To obtain this matrix, we first constructed a phylogenetic tree for the tested plant species using the Open Tree of Life (OTL) database (Hinchliff et al., 2015) and the R package *rotl* (Michonneau et al., 2016). The phylogenetic tree was then transformed into an ultrametric tree through Grafen's method (Grafen, 1989) using the R package *ape* (Paradis et al., 2004). Finally, a variance–covariance matrix was calculated from the ultrametric tree, representing phylogenetic relatedness among plant species (Paradis et al., 2004). In addition, given that the differences in experimental and environmental conditions among studies might affect plant responses to GCFs, we also treated treatment intensity, greenhouse temperature, SOM and soil pH as random terms in the mixed-effect model. To ease interpretation, the lnRR was back-transformed and expressed as a percentage change (%):

$$\text{Percentage change}\,(\%) = \left(e^{\ln\text{RR}} - 1\right) \times 100 \qquad (9)$$

Second, to test whether plants inoculated with AMF and their non-inoculated counterparts differed significantly in their responses to each of the different GCFs, we used the approach of pooled estimation in the mixed-effects model to calculate $\ln\overline{RR}$ and its corresponding 95% CIs for the moderator of mycorrhizal status (e.g. with vs. without AMF). In these models, the total heterogeneity of effect sizes can be partitioned into heterogeneity explained by moderators included in the model (Q_M) and residual heterogeneity (Q_E). We used the Q_M statistics to evaluate the significance of this moderator (Koricheva et al., 2013).

In order to examine whether the role of AMF in plant responses to GCFs depended on AMF richness at different taxonomic resolutions (e.g. species and family levels) and AMF identity, we used the above models to calculate $\ln\overline{RR}$ and its 95% CIs for the moderator, and the Q_M test was adopted to evaluate the differences among these moderator levels. Moderator levels with a sample of size <3 ($n<3$) were excluded from our analyses in order to avoid small sample sizes. In this meta-analysis, AMF richness was divided into two subgroups: single and mixed AMF species. Similarly, AMF richness at the family level was grouped by single AMF family and mixed AMF families.

Finally, given the bias against publishing negative results, we first used a funnel plot to examine this possibility, and the asymmetry of the funnel plot was tested by Egger's regression test (Egger et al., 1997). If asymmetry was detected, the Rosenberg fail-safe number was used to further determine whether the unpublished articles would influence our conclusions (Rosenberg, 2005). We also tested the robustness of our results by conducting *leave-one-out* analysis using the *leave1out* function. The quality of this meta-analysis was checked according to the checklist of quality criteria (Table S1) proposed by Koricheva and Gurevitch (2014).

RESULTS

Effects of AMF on plant responses to GCFs

Based on 1100 pairs of observations of plant performance from 181 plant species (Figure 1), we tested the potential role of AMF in plant responses to GCFs. When not considering the mycorrhizal status of a plant species (e.g. inoculated with AMF or not), drought significantly decreased plant performance by 38.1% (95% CI, −43.8 to −31.7%; $p<0.001$), while the opposite trend was observed for N addition (mean, 18.2%; 95% CI, 1.2 to 37.9%; $p=0.03$) and elevated CO_2 (mean, 22.6%; 95% CI, 2.4 to 46.7%; $p<0.001$; Figure 1c). However, we found no significant effect of warming on plant performance on the basis of this dataset ($p=0.87$; Figure 1c). To test the potential role of AMF in plant responses to GCFs, we treated the mycorrhizal status of plants (inoculated with AMF vs. non-inoculated ones) as a moderator in these mixed-effect models. Results showed that plants associating with AMF tended to have a significantly weaker negative response to drought than non-inoculated plants ($p<0.001$; Figure 2). Similarly, warming, N addition and elevated CO_2 resulted in stronger increases in plant performance for plants inoculated with AMF than for non-inoculated ones ($p=0.03$, 0.02 and 0.02, respectively; Figure 2).

Effects of AMF richness and identity on plant responses to GCFs

Our subset analysis found no significant effects of AMF richness on plant performance at either the species (e.g. single AMF species vs. mixed AMF species; Figure 3a) or family levels (e.g. single AMF family vs. mixed AMF families; Figure 3b), except for the positive effects of mixed AMF families on plant performance under elevated CO_2 ($p=0.04$). We used a subset of studies involving plants inoculated with single AMF species to test whether the identity of AMF species would differently

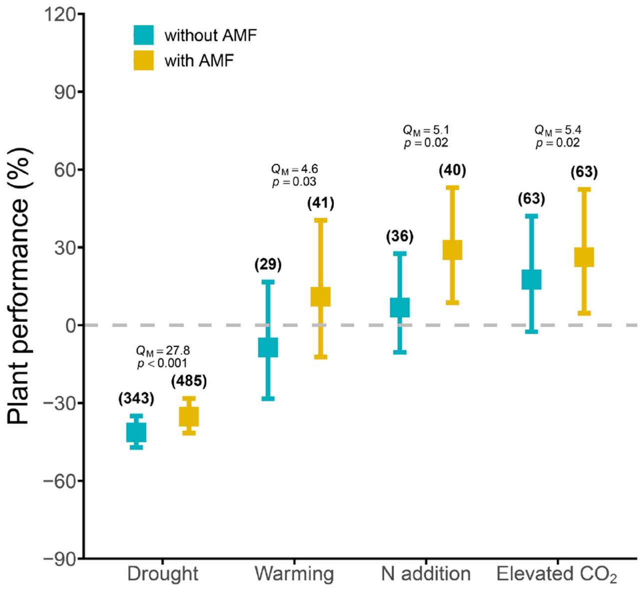

FIGURE 2 Meta-analysis of the effects of global change factors (drought, warming, N addition and elevated CO_2) on the performance of plants inoculated with AMF (with AMF) vs. non-inoculated plants (without AMF). Squares and error bars represent the mean effect size and 95% confidence intervals (CIs), respectively. The numbers above the CIs indicate the sample size.

affect plant performance in response to GCFs. Results of the Q_M test showed that AMF identity significantly affects plant performance in response to N addition ($p<0.001$ Figure 4). A total of 19 AMF species were included in the analysis of AMF identity effects on plant performance in responses to GCFs. Among them, *Funneliformis mosseae*, *Rhizophagus intraradices* and *Rhizophagus irregularis* were the three most studied AMF species (Figure 4).

Publications bias and sensitivity analysis

There was no evidence of publication bias for plant performance in responses to warming and N addition (Figure S4, Table S2; Egger's test: $p>0.05$). The funnel plots were asymmetrical for plants in response to drought and elevated CO_2 (Figure S4, Table S2; Egger's test: $p<0.05$), but the Rosenberg fail-safe numbers were much larger than 5 k + 10 for both GCFs (Table S2). These results suggest that publication bias is unlikely to be an issue for the interpretation of our results. In addition, we found that our findings are unlikely to be driven by a single influential study (Figure S5).

DISCUSSION

Our meta-analysis here included 190% more papers (Figure S1) than the last analysis on this topic from 10 years ago (Kivlin et al., 2013) and could identify the role of AMF richness at different taxonomic resolutions (e.g. fungal species and family level). We could also identify patterns in plant responses to GCFs as a consequence of better data availability, the inclusion of moderators and the use of phylogenetically informed methods.

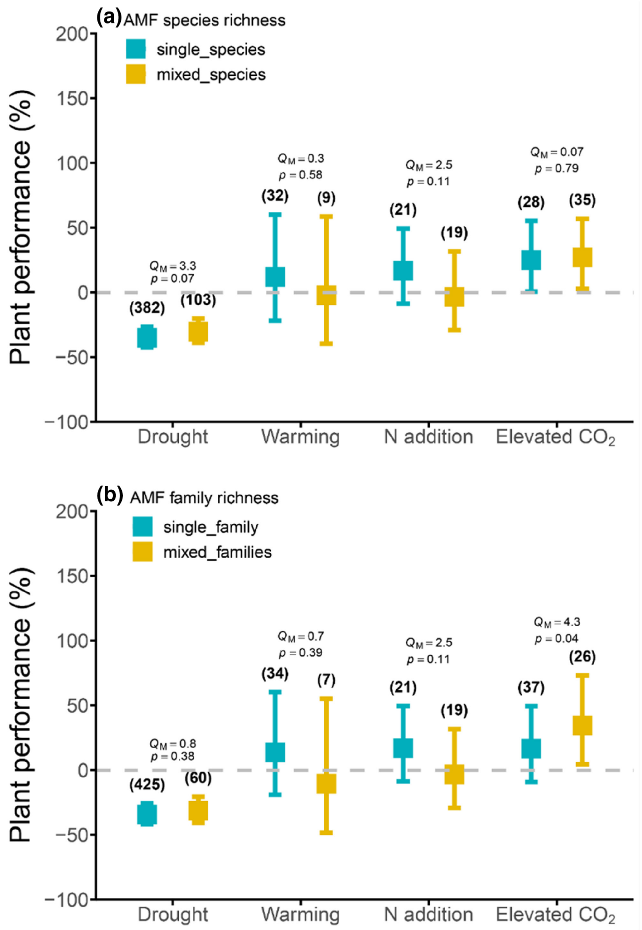

FIGURE 3 Plants responses to global change factors (drought, warming, N addition and elevated CO_2) under different AMF species richness (a; single AMF species and mixed AMF species) and family-level richness (b; single family and mixed families). Means and 95% confidence intervals (CIs) are given. The numbers above the CIs indicate the sample size.

Mycorrhizal plants outperform their non-inoculated counterparts in responses to GCFs

Consistent with most of the individual case studies and meta-analyses (Jayne & Quigley, 2014; Kivlin et al., 2013), our analysis showed that AMF significantly ameliorate the negative effect of drought on plant performance in comparison with their non-inoculated counterparts. AMF can not only facilitate water and nutrient uptake to mitigate the negative effect of drought on plants but also improve the drought tolerance of their host plants through increased osmotic adjustment (Kubikova

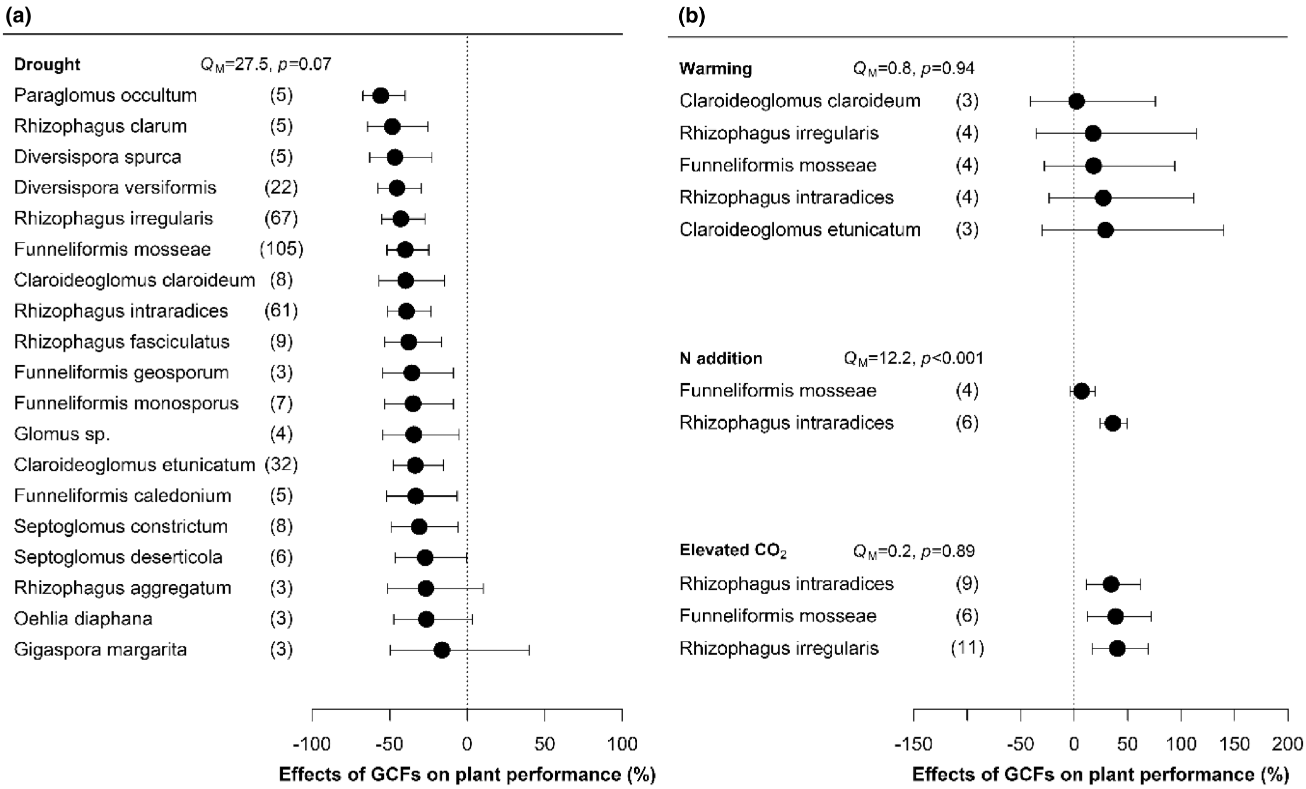

FIGURE 4 Meta-analysis of the effects of global change factors (drought, warming, N addition and elevated CO_2) on the performance of host plants inoculated with different AMF species. Circles and error bars represent mean effect size and 95% confidence intervals, respectively. Sample sizes are given in parentheses.

et al., 2001; Yooyongwech et al., 2013) and stomatal regulation (Duan et al., 1996). In addition, AMF can modify soil properties (e.g. soil structure and soil water relations), affecting plant access to water (Augé, 2001). AMF have even been shown to alleviate drought stress in plants by up-regulating antioxidant systems (Li et al., 2019).

Although warming had little effect on plant performance overall, mycorrhizal plants benefit more from such conditions than non-inoculated plants. It is generally assumed that the metabolism of both plants and fungi should be stimulated by warming conditions, leading to an increase in growth (Kivlin et al., 2013). In symbiotic associations, increased metabolism can also lead to higher rates of nutrient transfer to and C transfer from the host plants (Hawkes et al., 2008). Nevertheless, AM symbiosis is expected to provide greater net benefit to the host plants in warmer climates (Kivlin et al., 2013). In addition, warming is often concurrent with decreasing soil moisture. Therefore, the symbiosis may also be expected to improve the drought resistance of host plants when warming creates drier conditions, resulting in a better performance of host plants.

In general, N enrichment can alleviate N limitation in plants and thus stimulate plant growth, which is further corroborated by this meta-analysis. However, the role of AMF in plant responses to N addition differs between studies. N addition may shift the interaction between AMF and host plants from mutualism to parasitism, producing context-dependent responses to N addition (Hoeksema et al., 2010; Johnson et al., 2010). The mechanism driving these changes is likely that plants would reduce C allocation to their AM symbionts when they can acquire N from soils directly, for example, under N enrichment (Johnson et al., 1997). In contrast to previous findings (Hoeksema et al., 2010; Kivlin et al., 2013), our results showed that N addition significantly increased the performance of plants inoculated with AMF relative to non-inoculated plants. According to the trade balance model, the outcomes of plant–AMF symbiosis are not only determined by the relative availability of N but also P (Johnson, 2010). A large body of evidence has demonstrated that N enrichment can increase the plant leaf N:P ratio and further cause P limitation (Gusewell, 2004; Mei et al., 2019; Zhan et al., 2017). Under such conditions, AMF symbionts are thought to play an important role in maintaining the homoeostasis of N:P stoichiometry for host plants by decreasing the plant N:P ratio, for example, by stimulating phosphate mobilization (Zhang et al., 2018, 2022) and facilitating plant P uptake (Mei et al., 2019). These results are consistent with the predictions of the functional equilibrium model that N-induced P limitation would enhance mutualism in AMF–plant symbiosis (Johnson, 2010).

We found that AMF allow their host plants to benefit more from elevated CO_2 compared with non-inoculated plants. Elevated CO_2 frequently has a positive effect on plant performance (Drigo et al., 2010; Reich et al., 2006; Shi et al., 2021), resulting in an increased transfer of photosynthate belowground (Drigo et al., 2010), which might be the cause for the improvement of AMF symbionts (Terrer et al., 2018). Meanwhile, stimulation of plant growth will increase plant demand for soil resources, for example, N and P, to maintain growth (Johnson, 2010). Due to the important role of AMF in the acquisition of nutrients for host plants, the functional equilibrium model predicts that CO_2 enrichment would boost the mutualism in AMF–plant symbiosis (Johnson, 2010; Terrer et al., 2018). Given that elevated CO_2-induced stimulation of plant growth would be progressively constrained by nutrient limitation in soils over time (Luo et al., 2004; Reich et al., 2006; Terrer et al., 2019), it is reasonable to assume that elevated CO_2 will increase the dependency of plants on AM symbionts. Further, the signalling cascade that plants employ to increase mycorrhization in response to CO_2 enrichment has also been reported in a recent study (Zhou et al., 2019), providing biochemical evidence underpinning this response. Our results suggest that AM symbionts are likely to play an increasingly important role in the growth of terrestrial plants, given that these plants have to contend with conditions of continuously increasing CO_2 and decreasing P availability in the future (Hause, 2019).

In summary, we show that AMF can enhance plant performance in the context of GCFs, but the mechanisms driving these changes differ between GCFs. Therefore, understanding these mechanisms is critical to improving our knowledge of how AMF affect plant responses to GCFs. Nevertheless, the interactions between these GCFs are difficult to predict here, as few studies have tested the potential role of AMF in plant responses to multiple GCFs simultaneously. It is well known that soil harbours a rich AMF community, which results in a diverse range of functional traits that enable them to help plants in response to various environmental stress conditions (Chagnon et al., 2013; Chaudhary et al., 2022). As such, we believe that AMF still have the potential to enhance plant performance under the simultaneous occurrence of multiple GCFs, given the diverse functions exhibited by AMF.

Effects of AMF diversity on plant performance in response to GCFs

Our meta-analysis showed that inoculating plants with more than one AMF species was not more efficient than single-species inoculation in improving the performance of host plants in response to GCFs. A possible explanation for this finding is interspecific competition, especially for those species within a family, which would limit the synergistic effects of AMF species on plant performance (Crossay et al., 2019; Gosling et al., 2016; Powell et al., 2009; Yang et al., 2017). Given that functional traits of AMF are phylogenetically conserved at the family level (Koch et al., 2017; Powell et al., 2009), positive effects of increasing family richness of AMF on plant performance can be expected (Crossay et al., 2019; Maherali & Klironomos, 2007). However, we only found a significant effect of increasing AMF family richness on plant performance in response to elevated CO_2, suggesting that the effect of AMF family richness on plant performance is environment-specific (Crossay et al., 2019;Gosling et al., 2016; Horsch et al., 2023). For example, inoculation with multiple AMF species from different families did induce more beneficial effects on plant performance only when the host plant was exposed to multiple abiotic stress factors (Gosling et al., 2016; Horsch et al., 2023) rather than to a single one (Crossay et al., 2019). When plants are exposed to a single stress factor, they may preferentially allocate resources to AMF taxa that best help mitigate the negative effects of that factor on their performance, such that factors can over-select for a specific set of AM fungal traits (Kivlin et al., 2011; Vályi et al., 2016), potentially indicating reduced importance of AMF family richness for plant performance (Crossay et al., 2019). Therefore, the positive effects of AMF richness on plant performance at the family level may only reach their maximum potential in the context of multiple factors, for example, complex natural environmental conditions (Crossay et al., 2019; Gosling et al., 2016). Despite this, it is still reasonable to assume that AMF diversity plays a critical role in plant responses to ongoing global change, especially in future scenarios where multiple GCFs are occurring simultaneously (Gosling et al., 2016; Horsch et al., 2023).

Effects of AMF identity on plant performance in response to GCFs

We showed that symbiont functions in plant responses to GCFs were associated with AMF identity. In fact, the difference among AMF species in terms of their ability to promote plant growth has been frequently reported (Jansa et al., 2008; Marro et al., 2022; Sale et al., 2021). Much of this difference can be attributed to differences in C and nutrient exchange between plants and specific AMF taxa, for example, taxa from certain AMF lineages (*Paraglomeraceae* and *Acaulosporaceae*) seem to provide only a limited amount of nutrients to their host plants (Sale et al., 2021). Another possible explanation is the difference in stress tolerance and ability of AMF species to protect plant hosts against stress (Gosling et al., 2016; Millar & Bennett, 2016; Parvin et al., 2020). Although the species specificity of forming symbiosis between plants and AMF is relatively low (Smith & Read, 2008), the response to such AM symbionts is highly species-specific (Chagnon et al., 2013). Therefore, the fitness consequences for both plants and AMF depend on the identities of both partners (Chagnon et al., 2013). One of these diverse traits of AMF may benefit certain aspects of the performance of plant hosts the most in a given situation (e.g. GCFs). In our dataset, however, most of the tested AMF species were constrained to *Glomeraceae* to GCFs warming, N addition and elevated CO_2, which hampers our ability to test these mechanisms at a broader level.

Data limitations and implications for future research

While this study provides important insights into the role of AMF in plant responses to GCFs, several limitations still exist. These limitations, in turn, point to future research directions. First, most of the studies compiled into our dataset focused primarily on individual plant responses, and thus the extrapolation of these findings to natural communities is subject to many uncertainties. Although the impact of AM symbionts might extend beyond individual plants, for example, the known effects of the symbiont on plant community dynamics (Rudgers et al., 2012), more studies on the effects of AMF on plant communities in response to GCFs are needed. Second, given the possibilities of competitive exclusion between AMF species, preference of both AMF and host plant and priority effects of AMF colonization, the realized diversity of AMF species in the roots of plant hosts may be lower than that in the inoculum (Gosling et al., 2016). Unfortunately, the species composition of the AMF community in the roots of tested plants was not measured in most studies. This may be an important issue, especially for those closely related species with potentially highly overlapping niches (Webb et al., 2002). Third, the inoculated AMF species compiled in our dataset were biased towards species belonging to *Glomeraceae*, especially for the GCFs warming, N addition and elevated CO_2. Therefore, we strongly recommend the integration of more AMF species from other families in future studies. Fourth, although most of the studies in our dataset added microbial suspensions without fungal spores in the control and inoculated groups to simulate microbial–fungal interactions in natural systems, this still differs to some extent from the actual situation. Finally, there is growing evidence that we are currently in a situation where multiple GCFs occur simultaneously (Rillig et al., 2019), however, almost all studies included in this meta-analysis have mainly focused on individual GCF. Moreover, the number of GCFs has been shown to significantly affect soil functioning (Rillig et al., 2019) and plant community dynamics (Speißer et al., 2022), and even has the potential to regulate soil microbial diversity effects on soil functions (Yang et al., 2022). Given this, we call for more studies to test the potential role of AMF in plant responses in the context of the simultaneous occurrence of multiple GCFs. By doing so, we may provide a more complete picture in which the role of AMF in plant responses to ongoing global environmental change can be better understood and predicted.

CONCLUSIONS

Our meta-analysis showed that AMF significantly ameliorate the negative effects of drought on plant performance and that mycorrhizal plants benefit more from conditions of warming, N addition and elevated CO_2 than non-inoculated plants. This is the first meta-analysis to reveal an important role of AMF in plant responses to several GCFs. These results suggest that AMF are beneficial for their host plant in response to several GCFs, which would feed back to regulate ongoing global change. Our study provides important insights into the role of AMF in the responses of a wide range of plant species to GCFs, highlighting the continued importance of proper stewardship of this key mutualism by means of restoration, conservation and proper management.

AUTHOR CONTRIBUTIONS

B.T. conceived the idea. B.T., J.M. and M.R. designed this study. B.T. and J.M. collected data. B.T., J.M. and A.L. performed the meta-analysis. B.T. wrote the first draft of the manuscript, and all authors contributed substantially to the revisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data and R code that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.24138822.

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REFERENCES

Alberton, O., Kuyper, T.W. & Gorissen, A. (2005) Taking mycocentrism seriously: mycorrhizal fungal and plant responses to elevated CO_2. *New Phytologist*, 167, 859–868.

Aria, M. & Cuccurullo, C. (2017) Bibliometrix: an R-tool for comprehensive science mapping analysis. *Journal of Informetrics*, 11, 959–975.

Augé, R.M. (2001) Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza*, 11, 3–42.

Chagnon, P.L., Bradley, R.L., Maherali, H. & Klironomos, J.N. (2013) A trait-based framework to understand life history of mycorrhizal fungi. *Trends in Plant Science*, 18, 484–491.

Chamberlain, S.A., Hovick, S.M., Dibble, C.J., Rasmussen, N.L., Van Allen, B.G., Maitner, B.S. et al. (2012) Does phylogeny matter? Assessing the impact of phylogenetic information in ecological meta-analysis. *Ecology Letters*, 15, 627–636.

Chaudhary, V.B., Holland, E.P., Charman-Anderson, S., Guzman, A., Bell-Dereske, L., Cheeke, T.E. et al. (2022) What are mycorrhizal traits? *Trends in Ecology & Evolution*, 37, 573–581.

Crossay, T., Majorel, C., Redecker, D., Gensous, S., Medevielle, V., Durrieu, G. et al. (2019) Is a mixture of arbuscular mycorrhizal fungi better for plant growth than single-species inoculants? *Mycorrhiza*, 29, 325–339.

Drigo, B., Pijl, A.S., Duyts, H., Kielak, A., Gamper, H.A., Houtekamer, M.J. et al. (2010) Shifting carbon flow from roots into associated microbial communities in response to elevated atmospheric CO_2. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 10938–10942.

Duan, X.G., Neuman, D.S., Reiber, J.M., Green, C.D., Saxton, A.M. & Auge, R.M. (1996) Mycorrhizal influence on hydraulic and hormonal factors implicated in the control of stomatal conductance during drought. *Journal of Experimental Botany*, 47, 1541–1550.

Duarte, A.G. & Maherali, H. (2022) A meta-analysis of the effects of climate change on the mutualism between plants and arbuscular mycorrhizal fungi. *Ecology and Evolution*, 12, e8518.

Egger, M., Smith, G.D., Schneider, M. & Minder, C. (1997) Bias in meta-analysis detected by a simple, graphical test. *Bmj-British Medical Journal*, 315, 629–634.

Gosling, P., Jones, J. & Bending, G.D. (2016) Evidence for functional redundancy in arbuscular mycorrhizal fungi and implications for agroecosystem management. *Mycorrhiza*, 26, 77–83.

Grafen, A. (1989) The phylogenetic regression. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 326, 119–157.

Gusewell, S. (2004) N:P ratios in terrestrial plants: variation and functional significance. *New Phytologist*, 164, 243–266.

Hause, B. (2019) Elevated CO_2-induced improvement of mycorrhization – which players lie in-between? *New Phytologist*, 224, 5–7.

Hawkes, C.V., Hartley, I.P., Ineson, P. & Fitter, A.H. (2008) Soil temperature affects carbon allocation within arbuscular mycorrhizal networks and carbon transport from plant to fungus. *Global Change Biology*, 14, 1181–1190.

Hedges, L.V., Gurevitch, J. & Curtis, P.S. (1999) The meta-analysis of response ratios in experimental ecology. *Ecology*, 80, 1150–1156.

Hinchliff, C.E., Smith, S.A., Allman, J.F., Burleigh, J.G., Chaudhary, R., Coghill, L.M. et al. (2015) Synthesis of phylogeny and taxonomy into a comprehensive tree of life. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 12764–12769.

Hoeksema, J.D., Chaudhary, V.B., Gehring, C.A., Johnson, N.C., Karst, J., Koide, R.T. et al. (2010) A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecology Letters*, 13, 394–407.

Horsch, C.C.A., Antunes, P.M. & Kallenbach, C.M. (2023) Arbuscular mycorrhizal fungal communities with contrasting life-history traits influence host nutrient acquisition. *Mycorrhiza*, 33, 1–14.

Houghton, R.A., Hall, F. & Goetz, S.J. (2009) Importance of biomass in the global carbon cycle. *Journal of Geophysical Research-Biogeosciences*, 114, G00E03.

IPCC. (2021) *Climate change 2021: the physical science basis: contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change*. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.

Jansa, J., Smith, F.A. & Smith, S.E. (2008) Are there benefits of simultaneous root colonization by different arbuscular mycorrhizal fungi? *New Phytologist*, 177, 779–789.

Jayne, B. & Quigley, M. (2014) Influence of arbuscular mycorrhiza on growth and reproductive response of plants under water deficit: a meta-analysis. *Mycorrhiza*, 24, 109–119.

Johnson, N.C. (2010) Resource stoichiometry elucidates the structure and function of arbuscular mycorrhizas across scales. *New Phytologist*, 185, 631–647.

Johnson, N.C., Graham, J.H. & Smith, F.A. (1997) Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytologist*, 135, 575–586.

Johnson, N.C., Wilson, G.W.T., Bowker, M.A., Wilson, J.A. & Miller, R.M. (2010) Resource limitation is a driver of local adaptation in mycorrhizal symbioses. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 2093–2098.

Kivlin, S.N., Emery, S.M. & Rudgers, J.A. (2013) Fungal symbionts alter plant responses to global change. *American Journal of Botany*, 100, 1445–1457.

Kivlin, S.N., Hawkes, C.V. & Treseder, K.K. (2011) Global diversity and distribution of arbuscular mycorrhizal fungi. *Soil Biology & Biochemistry*, 43, 2294–2303.

Koch, A.M., Antunes, P.M., Maherali, H., Hart, M.M. & Klironomos, J.N. (2017) Evolutionary asymmetry in the arbuscular mycorrhizal symbiosis: conservatism in fungal morphology does not predict host plant growth. *New Phytologist*, 214, 1330–1337.

Koricheva, J. & Gurevitch, J. (2014) Uses and misuses of meta-analysis in plant ecology. *Journal of Ecology*, 102, 828–844.

Koricheva, J., Gurevitch, J. & Mengersen, K. (2013) *Handbook of meta-analysis in ecology and evolution*. Princeton, NJ: Princeton University Press.

Kubikova, E., Moore, J.L., Ownley, B.H., Mullen, M.D. & Auge, R.M. (2001) Mycorrhizal impact on osmotic adjustment in Ocimum basilicum during a lethal drying episode. *Journal of Plant Physiology*, 158, 1227–1230.

Lajeunesse, M.J. (2016) Facilitating systematic reviews, data extraction and meta-analysis with the metagear package for r. *Methods in Ecology and Evolution*, 7, 323–330.

Lanfranco, L., Fiorilli, V. & Gutjahr, C. (2018) Partner communication and role of nutrients in the arbuscular mycorrhizal symbiosis. *New Phytologist*, 220, 1031–1046.

Li, J.Q., Meng, B., Chai, H., Yang, X.C., Song, W.Z., Li, S.X. et al. (2019) Arbuscular mycorrhizal fungi alleviate drought stress in C_3 (Leymus chinensis) and C_4 (Hemarthria altissima) grasses via altering antioxidant enzyme activities and photosynthesis. *Frontiers in Plant Science*, 10, 499.

Lorber, A. (1986) Error propagation and figures of merit for quantification by solving matrix equations. *Analytical Chemistry*, 58(6), 1167–1172. https://doi.org/10.1021/ac00297a042

Luo, Y., Su, B., Currie, W.S., Dukes, J.S., Finzi, A.C., Hartwig, U. et al. (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *Bioscience*, 54, 731–739.

Maherali, H. & Klironomos, J.N. (2007) Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science*, 316, 1746–1748.

Malhi, Y., Franklin, J., Seddon, N., Solan, M., Turner, M.G., Field, C.B. et al. (2020) Climate change and ecosystems: threats, opportunities and solutions. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 375, 20190104.

Marro, N., Grilli, G., Soteras, F., Caccia, M., Longo, S., Cofre, N. et al. (2022) The effects of arbuscular mycorrhizal fungal species and taxonomic groups on stressed and unstressed plants: a global meta-analysis. *New Phytologist*, 235, 320–332.

Martin, F.M., Uroz, S. & Barker, D.G. (2017) Ancestral alliances: plant mutualistic symbioses with fungi and bacteria. *Science*, 356, eaad4501.

Mei, L.L., Yang, X., Zhang, S.Q., Zhang, T. & Guo, J.X. (2019) Arbuscular mycorrhizal fungi alleviate phosphorus limitation by reducing plant N:P ratios under warming and nitrogen addition in a temperate meadow ecosystem. *Science of the Total Environment*, 686, 1129–1139.

Michonneau, F., Brown, J.W. & Winter, D.J. (2016) Rotl: an R package to interact with the open tree of life data. *Methods in Ecology and Evolution*, 7, 1476–1481.

Millar, N.S. & Bennett, A.E. (2016) Stressed out symbiotes: hypotheses for the influence of abiotic stress on arbuscular mycorrhizal fungi. *Oecologia*, 182, 625–641.

Moulin, T.C. & Amaral, O.B. (2020) Using collaboration networks to identify authorship dependence in meta-analysis results. *Research Synthesis Methods*, 11, 655–668.

Paradis, E., Claude, J. & Strimmer, K. (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290.

Parvin, S., Van Geel, M., Yeasmin, T., Verbruggen, E. & Honnay, O. (2020) Effects of single and multiple species inocula of arbuscular mycorrhizal fungi on the salinity tolerance of a Bangladeshi rice (Oryza sativa L.) cultivar. *Mycorrhiza*, 30, 431–444.

Powell, J.R., Parrent, J.L., Hart, M.M., Klironomos, J.N., Rillig, M.C. & Maherali, H. (2009) Phylogenetic trait conservatism and the evolution of functional trade-offs in arbuscular mycorrhizal fungi. *Proceedings of the Royal Society B-Biological Sciences*, 276, 4237–4245.

Powell, J.R. & Rillig, M.C. (2018) Biodiversity of arbuscular mycorrhizal fungi and ecosystem function. *New Phytologist*, 220, 1059–1075.

R Development Core Team. (2019) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Reich, P.B., Bermudez, R., Montgomery, R.A., Rich, R.L., Rice, K.E., Hobbie, S.E. et al. (2022) Even modest climate change may lead to major transitions in boreal forests. *Nature*, 608, 540.

Reich, P.B., Hobbie, S.E., Lee, T., Ellsworth, D.S., West, J.B., Tilman, D. et al. (2006) Nitrogen limitation constrains sustainability of ecosystem response to CO_2. *Nature*, 440, 922–925.

Rillig, M.C., Ryo, M., Lehmann, A., Aguilar-Trigueros, C.A., Buchert, S., Wulf, A. et al. (2019) The role of multiple global change factors in driving soil functions and microbial biodiversity. *Science*, 366, 886–890.

Rosenberg, M.S. (2005) The file-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. *Evolution*, 59, 464–468.

Rudgers, J.A., Miller, T.E.X., Ziegler, S.M. & Craven, K.D. (2012) There are many ways to be a mutualist: Endophytic fungus reduces plant survival but increases population growth. *Ecology*, 93, 565–574.

Sale, V., Palenzuela, J., Azcon-Aguilar, C., Sanchez-Castro, I., da Silva, G.A., Seitz, B. et al. (2021) Ancient lineages of arbuscular mycorrhizal fungi provide little plant benefit. *Mycorrhiza*, 31, 559–576.

Shi, S., Luo, X., Dong, X., Qiu, Y., Xu, C. & He, X. (2021) Arbuscular mycorrhization enhances nitrogen, phosphorus and potassium accumulation in *Vicia faba* by modulating soil nutrient balance under elevated CO_2. *Journal of Fungi*, 7, 361.

Smith, S.E. & Read, D.J. (2008) *Mycorrhizal symbiosis*, 3rd edition. New York, NY: Academic Press.

Speißer, B., Wilschut, R.A. & Van Kleunen, M. (2022) Number of simultaneously acting global change factors affects composition, diversity and productivity of grassland plant communities. *Nature Communications*, 13, 7811.

Terrer, C., Jackson, R.B., Prentice, I.C., Keenan, T.F., Kaiser, C., Vicca, S. et al. (2019) Nitrogen and phosphorus constrain the CO_2 fertilization of global plant biomass. *Nature Climate Change*, 9, 684.

Terrer, C., Vicca, S., Stocker, B.D., Hungate, B.A., Phillips, R.P., Reich, P.B. et al. (2018) Ecosystem responses to elevated CO_2 governed by plant-soil interactions and the cost of nitrogen acquisition. *New Phytologist*, 217, 507–522.

Vályi, K., Mardhiah, U., Rillig, M.C. & Hempel, S. (2016) Community assembly and coexistence in communities of arbuscular mycorrhizal fungi. *ISME Journal*, 10, 2341–2351.

Viechtbauer, W. (2010) Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36, 1–48.

Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33, 475–505.

Yang, G.W., Roy, J., Veresoglou, S.D. & Rillig, M.C. (2021) Soil biodiversity enhances the persistence of legumes under climate change. *New Phytologist*, 229, 2945–2956.

Yang, G.W., Ryo, M., Roy, J., Lammel, D.R., Ballhausen, M.B., Jing, X. et al. (2022) Multiple anthropogenic pressures eliminate the effects of soil microbial diversity on ecosystem functions in experimental microcosms. *Nature Communications*, 13, 4260.

Yang, H., Zhang, Q., Koide, R.T., Hoeksema, J.D., Tang, J., Bian, X. et al. (2017) Taxonomic resolution is a determinant of biodiversity effects in arbuscular mycorrhizal fungal communities. *Journal of Ecology*, 105, 219–228.

Yooyongwech, S., Phaukinsang, N., Cha-um, S. & Supaibulwatana, K. (2013) Arbuscular mycorrhiza improved growth performance in Macadamia tetraphylla L. grown under water deficit stress involves soluble sugar and proline accumulation. *Plant Growth Regulation*, 69, 285–293.

Zhan, S.X., Wang, Y., Zhu, Z.C., Li, W.H. & Bai, Y.F. (2017) Nitrogen enrichment alters plant N: P stoichiometry and intensifies phosphorus limitation in a steppe ecosystem. *Environmental and Experimental Botany*, 134, 21–32.

Zhang, L., Shi, N., Fan, J.Q., Wang, F., George, T.S. & Feng, G. (2018) Arbuscular mycorrhizal fungi stimulate organic phosphate mobilization associated with changing bacterial community structure under field conditions. *Environmental Microbiology*, 20, 2639–2651.

Zhang, L., Zhou, J.C., George, T.S., Limpens, E. & Feng, G. (2022) Arbuscular mycorrhizal fungi conducting the hyphosphere bacterial orchestra. *Trends in Plant Science*, 27, 402–411.

Zhou, Y.H., Ge, S.B., Jin, L.J., Yao, K.Q., Wang, Y., Wu, X.D. et al. (2019) A novel CO_2-responsive systemic signaling pathway controlling plant mycorrhizal symbiosis. *New Phytologist*, 224, 106–116.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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