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Responses of arbuscular mycorrhizal fungi to nitrogen addition: A meta-analysis

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Abstract

Arbuscular mycorrhizal (AM) fungi play important roles in carbon (C), nitrogen (N) and phosphorus (P) cycling of terrestrial ecosystems. The impact of increasing N deposition on AM fungi will inevitably affect ecosystem processes. However, generalizable patterns of how N deposition affects AM fungi remains poorly understood. Here we conducted a global-scale meta-analysis from 94 publications and 101 sites to investigate the responses of AM fungi to N addition, including abundance in both intraradical (host roots) and extra-radical portion (soil), richness and diversity. We also explored the mechanisms of N addition affecting AM fungi by the trait-based guilds method. Results showed that N addition significantly decreased AM fungal overall abundance (−8.0%). However, the response of abundance in intra-radical portion was not consistent with that in extra-radical portion: root colonization decreased (−11.6%) significantly, whereas extra-radical hyphae length density did not change significantly. Different AM fungal guilds showed different responses to N addition: both the abundance (spore density) and relative abundance of the rhizophilic guild decreased significantly under N addition (−29.8% and −12.0%, respectively), while the abundance and relative abundance of the edaphophilic guild had insignificant response to N addition. Such inconsistent responses of rhizophilic and edaphophilic guilds were mainly moderated by the change of soil pH and the response of root biomass, respectively. Moreover, N addition had an insignificant negative effect on AM fungal richness and diversity, which was strongly related with the relative availability of soil P (i.e. soil available N/P ratio). Collectively, this meta-analysis highlights that considering trait-based AM fungal guilds, soil P availability and host plant C allocation can greatly improve our understanding of the nuanced dynamics of AM fungal communities under increasing N deposition.

KEYWORDS
abundance, arbuscular mycorrhizal fungi, nitrogen addition, phosphorus availability, richness and diversity, soil acidification

1 | INTRODUCTION

Arbuscular mycorrhizal (AM) fungi are widespread and ancient root-associated microorganisms (Davison et al., 2015; Lu & Hedin, 2019). They can form mycorrhizal symbiosis with plants and thus affect many important ecosystem processes (van der Heijden et al., 2015). The well-established function for AM fungi is to improve their host uptake of soil phosphorus (P) in exchange for plant carbon (C; Marschner & Dell, 1994). In addition, they can increase crop yield (Zhang et al., 2019), regulate plant diversity

(Bever et al., 2010; Yang et al., 2014) and microbial communities (Poosakkannu et al., 2017; Jing et al., 2018), and change soil structure (Rillig & Mummey, 2006).

Over the past several decades, human-induced nitrogen (N) deposition is increasing dramatically (Penuelas et al., 2013), and is predicted to continuously increase in the future (Galloway et al., 2008; Lamarque et al., 2005). N deposition is considered to be a severe threat to terrestrial ecosystems (Smith et al., 1999) because it has many negative effects on ecosystem structure and function, such as reducing the diversity of plants (Bobbink et al., 2010) and soil microbes (Kearns et al., 2016). Specifically, N deposition would increase soil N availability and result in soil acidification (Stevens et al., 2018; Tian & Niu, 2015), both of which can affect AM fungal communities and thereby alter their interactions with the abiotic environment and plant hosts (Lilleskov et al., 2019). Considering the widespread distribution and multiple ecological functions of AM fungi (Smith & Read, 2008), the effects of N deposition on AM fungal communities will inevitably affect global C and nutrient cycles, plant communities, other soil microbiota and many ecosystem processes (Cotton, 2018).

Although N deposition is different from N addition experiments in multiple ways, N addition experiments are useful in revealing mechanisms (Lilleskov et al., 2019). Currently, a great number of N addition experiments have been conducted to investigate the effects of N deposition on AM fungi. However, there is no consensus on how AM fungal communities respond to N deposition. Many studies found that N addition decreased the abundance, richness and diversity of AM fungi (Antoninka et al., 2011; Egerton-Warburton & Allen, 2000; Williams et al., 2017), whereas many others also found positive effects (Jefwa et al., 2006; Porras-Alfaro et al., 2007; Zheng et al., 2014) or no effects (Eom et al., 1999; Mueller & Bohannan, 2015; van Diepen et al., 2011). These discrepancies in the effects of N addition on AM fungal communities might be due to the differences in soil resource availability (N and P), host plants (composition and diversity) and experimental variables (the form, amount and duration of N addition). These disparities do not give us a clear understanding on how N deposition affects AM fungal communities. Filling up this critical knowledge gap will help predict the ecological consequences of changes in AM fungal communities under global change scenarios.

Several previous meta-analyses related to N addition effects on mycorrhizal fungi or soil microbes showed that N addition significantly decreased AM fungal abundance (Treseder, 2004; Zhang et al., 2018; Zhou et al., 2017). However, Treseder (2004) included only 17 observations and the other two studies did not focus on AM fungi. AM fungal abundance was represented by phospholipid fatty acid (PLFA) in those latter two studies. Actually, PLFA is not so good to represent AM fungal biomass in soil because there is a strong background by bacterial-derived PLFA 16:1ω5 (Olsson, 1999), and neutral lipid fatty acid (NLFA) is considered better to represent AM fungal biomass in soil (Drijber & Jeske, 2019). Moreover, the responses of other indices of AM fungal communities such as richness and diversity were not included in previous studies.

More importantly, previous studies also ignored AM fungal characteristics that differ from other soil microbes. AM fungi have intra- and extra-radical structures. However, it should be noted that different AM fungi may have contrasting life-history strategies: some fungal taxa can colonize roots heavily with less extra-radical hyphae and these AM fungi can be classified into the rhizophilic guild, while others may allocate more biomass to extra-radical hyphae and these fungi can be classified into the edaphophilic guild (Maherali & Klironomos, 2007; Sikes et al., 2010; Weber et al., 2019). These two AM fungal guilds may perform different functions: the rhizophilic guild appears to play a role in plant pathogen protection and the edaphophilic guild is considered to increase plant nutrient uptake (Weber et al., 2019). Thus, N addition may affect AM fungal abundance in root and soil in different ways. In addition, the relative availability of soil P might strongly affect the response of AM fungi, as AM fungi are obligate biotrophs and they acquire C by offering hosts soil P (Marschner & Dell, 1994). As predicted by theoretical models (Johnson, 2010; Lilleskov et al., 2019), in P-rich systems, with increasing soil N, plants should decrease dependency on their associated AM fungi to acquire soil P and then decrease C allocation to AM fungi. However, in P-poor systems, N addition-induced P limitation would stimulate plant C allocation to AM fungi and increase dependency on AM fungi to acquire limited soil P. Therefore, under N addition, host plants may shift the C allocation to AM fungi and then affect AM fungal responses (Janssens et al., 2010; Johnson et al., 2013). Considering those unique characteristics that AM fungi have, it is necessary to synthesize all available data to reveal an unambiguous and generalizable pattern of the responses of AM fungal communities and identify major factors strongly associated with their responses under N addition at a larger scale.

In this study, we conducted a global-scale meta-analysis to assess the effects of N addition on AM fungi. AM fungi have intra- and extra-radical structures, thus, to better assess the response of AM fungal abundance, we classified AM fungal families into different guilds by patterns of biomass allocation to intra-radical portions (those in roots) and extra-radical portions (those in soil) referring to Weber et al. (2019; Table S1). We hypothesized that (a) N addition would affect different AM fungal guilds in different ways and then cause different changes in the fungal abundance in intra- and extra-radical portions and (b) the relative availability of soil P would affect the responses of AM fungal communities to N addition across sites.

2 | MATERIALS AND METHODS

2.1 | Data collection

Peer-reviewed journal articles that conducted N fertilization experiments and measured indices of AM fungal communities were searched using Web of Science and China National Knowledge Infrastructure (http://www.cnki.net) until March 2020. The search terms were '(arbuscular mycorrhizal fungi OR AM fungi OR AMF

OR AM symbiosis) AND (nitrogen addition OR nitrogen fertilization OR nitrogen deposition OR nitrogen application OR nitrogen enrichment)'. Studies included in this meta-analysis must meet the following criteria: (a) the manipulations of N addition in comparison with the control were conducted in the field, while greenhouse and laboratory-incubation studies were not included; (b) the study contained at least one of the target variables associated with AM fungi, including abundance in roots or soil, richness and diversity; (c) the mean, standard deviation (*SD*) and sample size (*n*) for the N addition treatment and the control could be obtained; (d) the studies only using inorganic N fertilizer as mimicking N deposition treatment were included, while compound fertilizer (containing other nutrients), organic manure and other fertilization treatments were not selected; and (e) if more than one publication evaluated the similar results from the same experiment, only data from the most recent paper were selected.

In total, 94 published papers were included (Table S2). For each study, we extracted main information on AM fungal communities, including abundance, richness and diversity. Measurements from different vegetation types, N addition levels or N fertilizer types within a single study were treated as independent observations. If a study elevated the effect of N addition under other different manipulation factors (multifactor experiment), the combined treatment versus ambient treatment (e.g. N addition plus warming vs. warming) were also recorded separately. However, for studies with combined N and P addition, considering the possible synergistic effect of N and P, this kind of treatment was not included. When a study included multiple sampling dates, we only included data from the peak growing season in natural ecosystems and the crop mature stage in agroecosystems. When a study included multiple soil layers, only data from the uppermost soil layer were selected. To extract the results presented in figures, we used the digitizing software GetData Graph Digitizer 2.25 (http://getdata-graph-digitizer.com).

Finally, our dataset included 259 observations for AM fungal abundance, 74 for richness and 61 for diversity. AM fungal abundance indicators included root colonization, extra-radical hyphae length density (EHL), spore density and soil NLFA. The richness meant the total number of species or taxa present, based on morphology (spore taxonomy) or genetics (OTU numbers). The diversity included taxonomic diversity (indicated by Shannon–Weiner index) and phylogenetic diversity (indicated by Faith's index). For richness, we grouped AM fungi into two portions: the extra-radical portion (those in soil) and the intra-radical portion (those in roots).

We further classified AM fungi into three guilds (Table S1) referring to Weber et al. (2019). The rhizophilic guild included three AM fungal families: Glomeraceae, Claroideoglomeraceae and Paraglomeraceae. The edaphophilic guild included Gigasporaceae and Diversisporaceae. Other families presented in the selected literatures such as Archaeosporaceae, Ambisporaceae and Acaulosporaceae belonged to the ancestral guild. If original studies showed AM fungi at genera or species level, we grouped these species and genera into their corresponding families by searching species names on Index Fungorum (http://www.indexfungorum.org/names) and referring to a checklist of AM fungi in the recent taxonomic system of Glomeromycota listed by Wang and Liu (2017). If a species name in a previous publication was not found in Index Fungorum or a species no longer belonged to Glomeromycota, we excluded them from our dataset. Some studies showed the proportional abundance of a taxon of AM fungi to total AM fungal taxonomies (based on total number of sequences or spore numbers) and others gave the absolute abundance of a taxon (represented by spore density). Considering that OTU numbers are not suitable to refer to abundance, we did not include those studies that used OTU numbers to calculate these two indexes. Then we grouped the proportional abundance into 'relative abundance' and the absolute abundance into 'abundance' for further analysis.

Moreover, soil chemical properties (pH, total and available N, total and available P, available N/P ratio, soil organic C and C/N ratio), biological variables (plant aboveground and belowground biomass, N and P concentration of plants, N/P ratio of plants, microbial biomass C and microbial biomass N), experimental variables (N fertilizer types, N addition levels and experimental durations), climatic factors (mean annual temperature and mean annual precipitation) and ecosystem types were also collected and recorded. Our data on a global scale mainly encompassed four types of terrestrial ecosystems, including forest, grassland, cropland and others. The locations of 101 study sites included in this meta-analysis are presented in Figure 1.

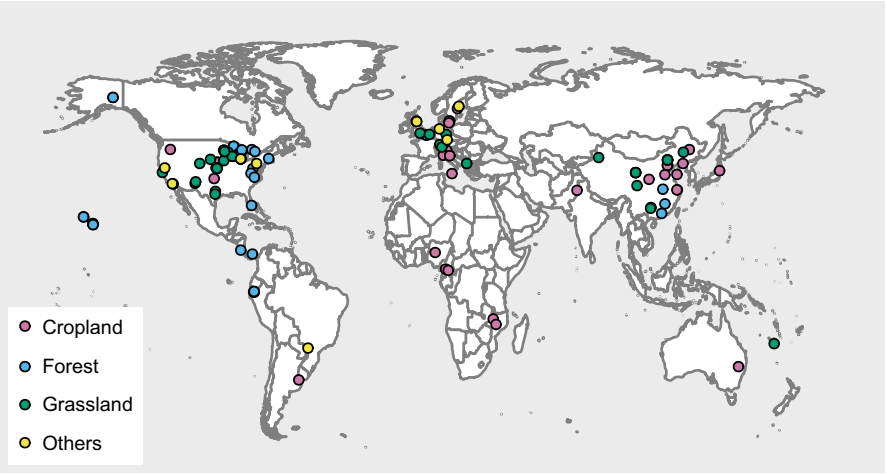

FIGURE 1 Global distribution of studies included in this meta-analysis (101 sites). Others includes experiments conducted in plantation, shrubland and unreported ecosystem types described in original case studies

2.2 | Data analysis

The meta-analysis method we used followed that of Hedges et al. (1999) and Luo et al. (2006). The responses of AM fungal communities to N addition were assessed by the response ratio (RR):

$$RR = \ln\left(\frac{X_N}{X_C}\right) = \ln(X_N) - \ln(X_C), \quad (1)$$

where X_N and X_C are the mean values of a given variable in the N treatment and the control groups, respectively. Soil pH change (ΔpH) resulted from N addition was calculated as $pH_{nitrogen} - pH_{control}$ (Tian & Niu, 2015). The variance (v) of each RR was calculated as:

$$v = \frac{S_N^2}{n_N X_N^2} + \frac{S_C^2}{n_C X_C^2}, \quad (2)$$

where n_N and n_C are the sample sizes; and S_N and S_C are the standard deviations of means in the N treatment and control groups, respectively. Most included studies reported standard errors (*SE*), and they were transformed to *SD* according to the equation:

$$SD = SE\sqrt{n}, \quad (3)$$

where n is the sample size. In several studies that neither *SD* nor *SE* was given, we assigned the *SD* as 1/10 of the corresponding mean (Luo et al., 2006; Zhou et al., 2017).

We chose the mixed-effects model to calculate the weighted response ratio (RR_{++}) and 95% confidence interval (CI) using the *rma.mv* function in the '*metafor*' package (Viechtbauer, 2010). The 'site' was included as random factor because some studies included multiple cases of N addition manipulations (e.g. multiple N addition rates and N fertilizer forms) or AM fungal taxa, which would contribute more than one effect size (van Groenigen et al., 2017). If the 95% CI values did not overlap zero, the effect of N addition was considered significant ($p < .05$). For AM fungal guilds (including their relative abundance and abundance), we calculated the response ratio of a particular fungal taxon or OTU and then got their RR_{++} (representing the response of AM fungal guilds) using mixed-effects model. To test whether the responses differed among different groups, we performed between-group heterogeneity tests (Q_B tests). When Q_B values were significant ($p < .05$), the responses among groups were different (Liu et al., 2016). For a better explanation, the weighted response ratio and its corresponding 95% CI were transformed back to the percentage change calculated by the formula: $(e^{RR_{++}} - 1) \times 100\%$.

To identify the relative importance of environmental variables in influencing the responses of AM fungi to N addition, a weighted random-forest analysis was carried out (Han & Zhu, 2020; Terrer et al., 2019). While variables of host plants (e.g. plant species richness, root/shoot biomass ratio and plant N/P stoichiometry) are important for controlling the responses of AM fungi to N addition, they were unfortunately not reported in most original studies in our dataset. Thus, in the random-forest analysis, we chose a number of plant (root biomass), edaphic, environmental and experimental variables that are available. The linear regression model was used to determine the relationship between response ratios of AM fungal abundance, richness or diversity and predictor variables. Publication bias of AM fungal variables was tested using Kendall's tau rank correlation and Spearman's rank correlation (Dieleman & Janssens, 2011). When the correlation was non-significant ($p > .05$), it meant no publication bias. All statistical analyses were conducted by R 3.6.1.

3 | RESULTS

3.1 | Effects of N addition on AM fungal communities

Across all studies and measuring methods, N addition significantly decreased the abundance (−8.0%) of AM fungi, but had insignificant (negative) effect on the richness (−7.1%) and diversity (−1.7%) of AM fungi (Figure 2a). In terms of abundance, N addition significantly decreased root colonization (−11.6%) and NLFA (−31.9%), but did not significantly change EHL and spore density. For richness, the reduction of intra-radical portion in root (−10.0%) under N addition was higher than that of extra-radical portion in soil (−6.2%), but both responses were not significant. For diversity, N addition had minor effects on both taxonomic diversity (−1.4%) and phylogenetic diversity (−3.0%), and the difference between them was not significant.

There were insignificant heterogeneities in the responses of AM fungal abundance and diversity to N addition among ecosystem types (Figure 2b). For richness, the responses had a significant heterogeneity among ecosystem types ($p < .001$), and only the response in cropland was significantly negative (−27.6%). We further tested the variations of N addition effects on four indicators of AM fungal abundance. Only the response of EHL varied significantly among ecosystem types (Figure S2).

3.2 | Effects of N addition on AM fungal guilds

The effects of N addition varied among trait-based AM fungal guilds (Figure 3a). For example, N addition significantly decreased both relative abundance (−12.0%) and abundance (−29.8%) of the rhizophilic guild, and had a significant overall negative effect on the rhizophilic guild (−18.2%). However, N addition did not significantly affect the edaphophilic guild (7.3%), in terms of both relative abundance and abundance. Moreover, N addition had non-significant negative effect on the ancestral guild (−30.4%), and significantly decreased its abundance (−50.3%), but not relative abundance.

The effects of N addition on AM fungal families also varied among different guilds. Given no difference in the results of

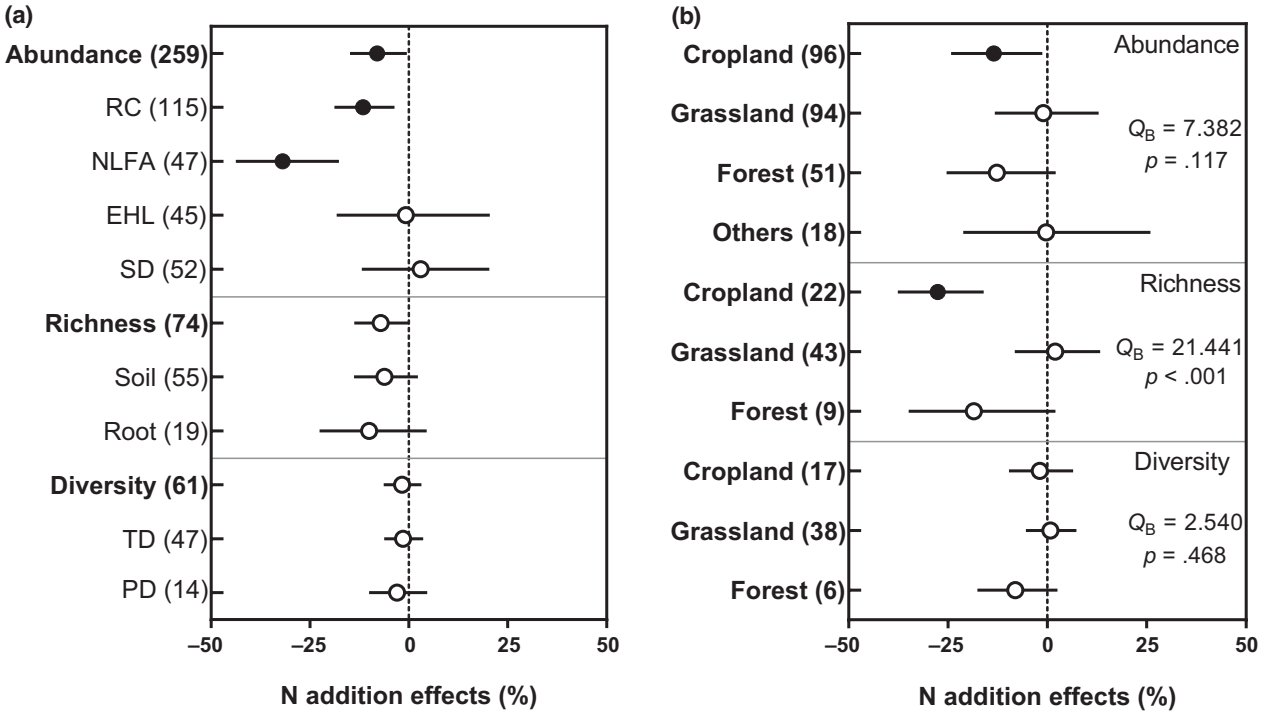

FIGURE 2 Effects of nitrogen addition on AM fungal abundance, richness and diversity (a) across all ecosystem types and (b) in different ecosystem types. EHL, extra-radical hyphal length density; NLFA, neutral lipid fatty acid; PD, phylogenetic diversity; RC, root colonization; SD, spore density; TD, taxonomic diversity. Others (ecosystem type) include experiments conducted in plantation, shrubland and unreported ecosystem types described in original case studies. Errors are 95% confidence intervals (CIs) of the weighted percentage change. Solid and open points represent significant (95% CIs not overlapping with zero) and non-significant effect sizes, respectively. Numbers in parentheses represent the sample size of observations

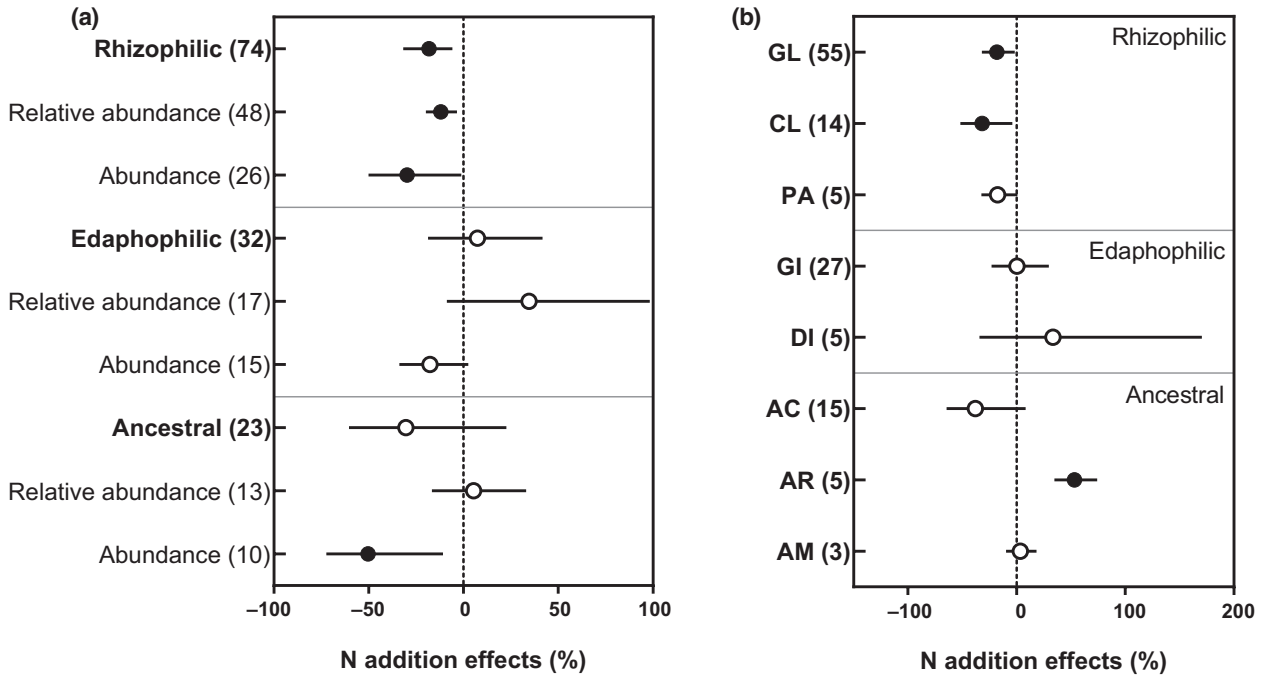

FIGURE 3 Effects of nitrogen addition on (a) AM fungal guilds and (b) AM fungal families in different guilds. Relative abundance represents the proportional abundance of the AM fungal guild, while abundance represents the absolute abundance of the AM fungal guild. AC, Acaulosporaceae; AM, Ambisporaceae; AR, Archaeosporaceae; CL, Claroideoglomeraceae; DI, Diversisporaceae; GI, Gigasporaceae; GL, Glomeraceae; PA, Paraglomeraceae. The errors are 95% confidence intervals (CIs) of the percentage change. Solid and open points represent significant (95% CIs not overlapping with zero) and non-significant effect sizes, respectively. Numbers in parentheses represent sample sizes of observations

relative abundance and abundance for most families, we showed both results together as overall abundance for each family here (Figure 3b). We found that N addition significantly decreased the overall abundance of Glomeraceae and Claroideoglomeraceae by 18.2% and 31.8%, respectively, but did not significantly change the overall abundance of the families in the edaphophilic guild. For AM fungal family in the ancestral guild, only the overall abundance of Archaeosporaceae significantly increased (Figure 3b). Notably, there were no significant publication biases for the responses of AM fungal communities and guilds to N addition (Table S3).

3.3 | Factors influencing the responses of AM fungi

Our results showed that N addition significantly changed soil and plant properties (Figure S3). N addition led to soil acidification (−6.7% or 0.39 units of pH). Moreover, N addition significantly increased soil total N (6.3%), available N (47.9%), ammonium N (44.7%), nitrate N (105.5%), available N/P ratio (58.5%), plant N/P ratio (21.6%) and plant aboveground biomass (26.4%). However, N addition did not significantly change plant belowground biomass.

The weighted random-forest analysis showed that the most important moderator of the effect of N addition on both richness and diversity of AM fungi was the background (i.e. the control treatment) soil available N/P ratio (Figure 4a,b). Response ratios of both richness and diversity had a positive relationship with the background soil available N/P ratio ($p < .001$; Figure 4c,d). The second most important moderator was the change of soil pH for richness and the response ratio of soil available N for diversity (Figure 4a,b). Specifically, the response ratio of richness increased significantly with the change of pH (ΔpH), and the response ratio of diversity decreased significantly with the response ratio of soil available N (Figure S4).

Importantly, response ratios of the abundance of two main AM fungal guilds were significantly affected by different factors (Figure 5). The most important moderator was the change of soil pH for the rhizophilic guild (Figure 5a) and the response ratio of belowground biomass for the edaphophilic guild (Figure 5b). Correspondingly, linear regression analysis showed significant positive correlation between the response ratio of AM fungal abundance and the change of pH (Figure 6a) and the response ratio of belowground biomass (Figure 6f). Specifically, response ratios of root colonization and NLFA had significant positive relationships with the change of pH (Figure 6b,c), and response ratios of root colonization and EHL had significant negative relationships with the response ratio of belowground biomass (Figure 6g,i). Additionally, linear regression analysis indicated other factors influencing the responses of AM fungal abundance, richness and diversity, but with less importance (Table S4). Notably, N fertilizer forms did not significantly affect the responses of AM fungal abundance, richness and diversity to N addition (Figure S5).

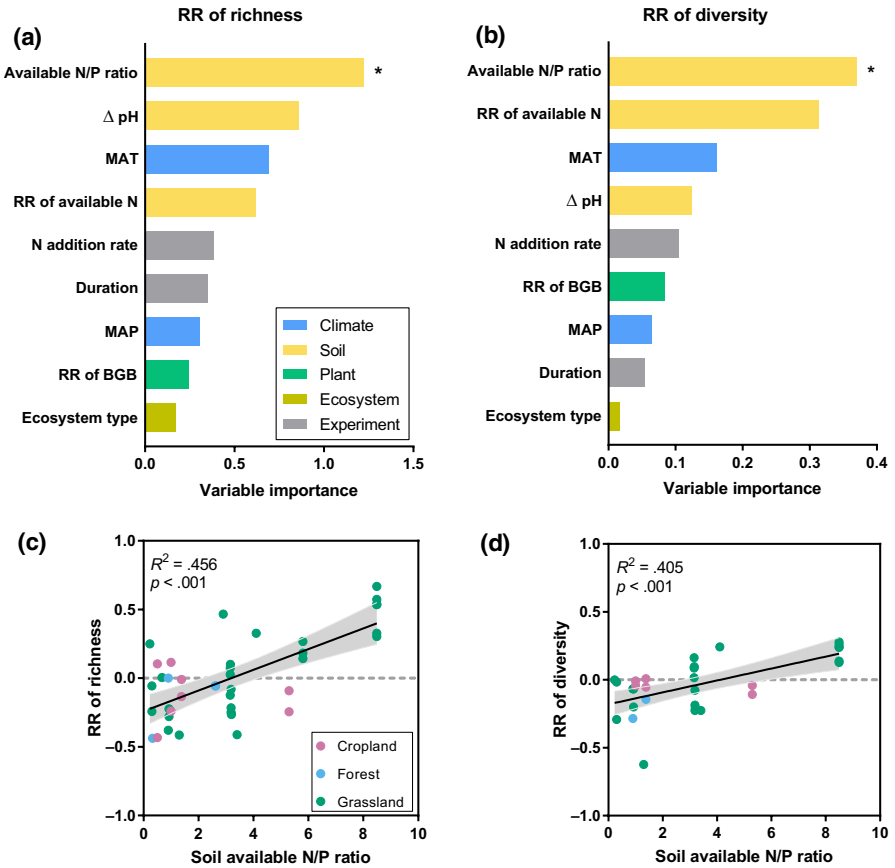

FIGURE 4 (a and b) Variable importance of moderators for the responses of AM fungal richness and diversity to N addition. The importance values are derived from a weighted random-forest analysis including variables as moderators in the model. The asterisks (*) indicate significant ($p < .05$) moderators. (c and d) Relationships between response ratios (RR) of AM fungal richness and diversity under N addition and background (the control treatment) soil available N/P ratio. ΔpH, change of pH; BGB, belowground biomass; Duration, experimental duration; MAP, mean annual precipitation; MAT, mean annual temperature. The colours of circles indicate ecosystem types. Grey area represents the 95% confidence interval

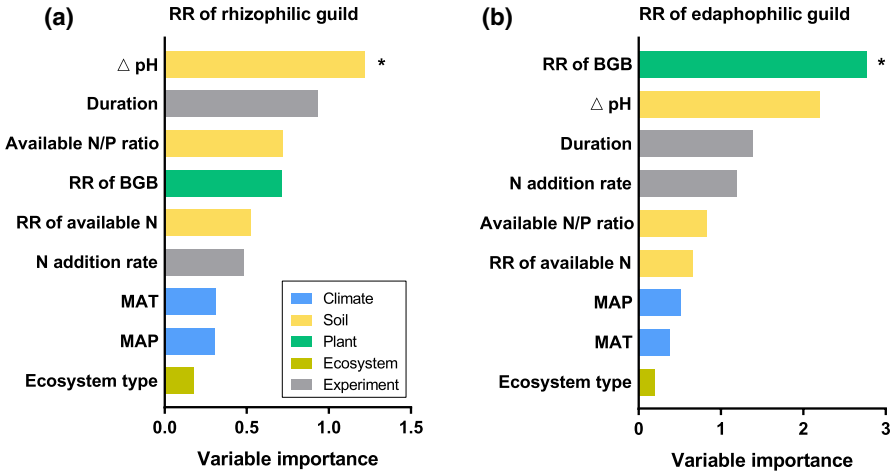

FIGURE 5 Variable importance of moderators for the responses of the abundance of (a) rhizophilic and (b) edaphophilic AM fungal guilds to N addition. The importance values are derived from a weighted random-forest analysis including variables as moderators in the model. The asterisks (*) indicate significant ($p < .05$) moderators. ΔpH, change of pH; BGB, belowground biomass; Duration, experimental duration; MAP, mean annual precipitation; MAT, mean annual temperature; RR, response ratio

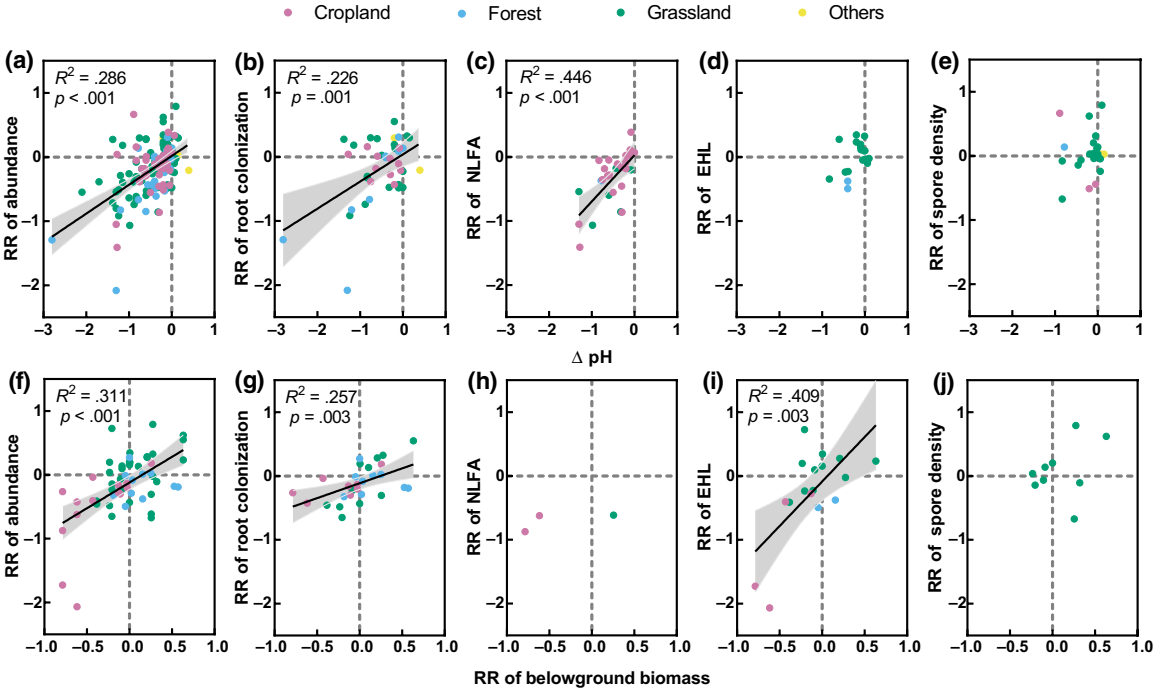

FIGURE 6 Relationships between response ratios (RR) of (a,f) AM fungal overall abundance and four specific indicators (b,g) root colonization, (c,h) NLFA, (d,i) EHL and (e,j) spore density under N addition and changes of environmental variables under N addition, including (a–e) change of pH (ΔpH) and (f–j) RR of belowground biomass. Each point on the figure represents a different observation. EHL, extra-radical hyphal length density; NLFA, neutral lipid fatty acid. Others (ecosystem type) include experiments conducted in plantation, shrubland and unreported ecosystem types described in original case studies. Grey area represents the 95% confidence interval. Only significant linear relations ($p < .05$) are drawn with regression lines

4 | DISCUSSION

Through a global scale (101 sites) quantitative synthesis based on 94 studies, we found a comprehensive response pattern of AM fungi to N addition. Our results showed that N addition had a significant negative effect on AM fungal abundance, especially on root colonization and NLFA, but had non-significant effects on AM fungal richness and diversity. The non-significant responses of AM fungal richness and diversity could be due to the moderating influence of initial soil N/P ratio as well as the fact that the different guilds are behaving differently. The responses of two main AM fungal guilds (rhizophilic and edaphophilic) were strongly predicted by different factors resulting in different responses of AM fungal abundance in root and soil. Collectively, these novel findings provide experimental evidence for theoretical models (e.g. the functional equilibrium model proposed by Johnson, 2010) and are valuable for mechanistic understanding of the responses of AM fungi to elevated N availability.

4.1 | N addition effects on AM fungal abundance

We found that N addition had a significant negative effect on AM fungal overall abundance (Figure 2a). This finding is consistent with

that of earlier meta-analyses (Treseder, 2004; Zhang et al., 2018; Zhou et al., 2017). Unlike previous results, we included four indicators of AM fungal abundance: root colonization representing AM fungal biomass in host roots, NLFA representing living AM fungi in soil and extra-radical hyphal length density and spore density in soil. We found that not all of these indicators significantly decreased after N addition (Figure 2a). We hypothesized that N addition affected AM fungal abundance in roots and soil in different ways. Therefore, we grouped AM fungi into different guilds based on their biomass allocation patterns (Weber et al., 2019). Glomeraceae is the main family in rhizophilic guild and Gigasporaceae is the main family in edaphophilic guild. Here, we found that N addition had a strong negative effect on the overall abundance of Glomeraceae, but a minor effect on that of Gigasporaceae (Figure 3b). Previous reviews proposed that the abundance of Gigasporaceae would decline and that of Glomeraceae would be favoured with increasing N (Cotton, 2018; Lilleskov et al., 2019; Treseder et al., 2018), which was opposite to our finding at a global scale. The conclusion of these reviews was based on the theory that the dependence of host plants on nutrient uptake from AM fungi in Gigasporaceae decreased as nutrient availability increased (Sikes et al., 2010; Weber et al., 2019), and Glomeraceae seemed to be able to persist or thrive under high N (Lilleskov et al., 2019). However, these reviews (Cotton, 2018; Lilleskov et al., 2019; Treseder et al., 2018) ignored the decrease in soil pH caused by N addition. Soil acidification had a negative effect on AM fungi. Specifically, acidification can reduce colonization, spore production and extra-radical hyphal growth (Figure 6b,c; Clark, 1997; Daniels & Trappe, 1980; van Aarle et al., 2002). Furthermore, although edaphophilic AM fungi are considered to be nitrophobic (Treseder et al., 2018), our results showed that the effect of pH change (soil acidification) on the edaphophilic guild was more important than the effect of increased available N (Figure 5b). Moreover, the change of pH can affect the availability of soil P which is an important soil resource (Penn & Camberato, 2019). Edaphophilic AM fungi can improve P uptake of host plants (Weber et al., 2019). Thus, the regulation of host plants (via C allocation shift) induced by relative soil P availability could be very important for the response of edaphophilic AM fungi to N addition (Johnson et al., 2015).

Various responses of edaphophilic guild to N addition across sites may cause the response of EHL to be insignificant overall (Figure 2a) and vary greatly among different ecosystems (Figure S2), as extra-radical hyphae are generally considered a trait of AM fungi to forage P from soil (Lilleskov et al., 2019; Weber et al., 2019). Moreover, as NLFA is found in large amounts in AM fungal spores (Olsson, 1999), it can represent both rhizophilic and edaphophilic active fungal biomass in soil. In other words, NLFA data are comprised of different fatty acids. The primary fatty acid that is used as a signature of AMF is 16:1ω5 which is a very good indicator of the biomass of Glomeraceae and Acaulosporaceae, but a poor indicator of Gigasporaceae. The fatty acids 18:1ω5 or ω9 and 20:1ω9 or 20:4 fatty acids tend to be better for the Gigasporaceae (Graham et al., 1995). However, most studies in our dataset just used 16:1ω5 to represent AM fungi. Therefore, NLFA data in the present study are mainly for the rhizophilic guild but not the edaphophilic guild. This may result in the congruence between the responses of rhizophilic guild and NLFA (Figures 2a and 3a). The insensitive response of spore density might relate with the stable ability of sporulation under different N conditions and the high tolerance of fungal spores to changes in the environment (Sýkorová et al., 2007).

4.2 | N addition effects on AM fungal richness and diversity

Overall, N addition had a non-significant effect on AM fungal richness and diversity in this study (Figure 2a). We further found that the background soil available N/P ratio was strongly associated with the responses of AM fungal richness and diversity to N addition (Figure 4). This result was similar to that of a regional-scale research in European grasslands (Ceulemans et al., 2019), which found that soil available P had a significant negative relationship with AM fungal richness. Resource availability can control AM fungal diversity (Liu et al., 2015; Waldrop et al., 2006); thus, the great variation of soil resource availability (e.g. soil available N/P ratio, Figure 4c,d) on a global scale might affect the response of AM fungal richness and diversity to N addition.

It should be noted that the response of AM fungal richness to N addition was not consistent among different ecosystem types. N addition significantly decreased AM fungal richness only in cropland (Figure 2b). N fertilizer inputs are generally high and maintained for a longer period in cropland (Cotton, 2018; Liu et al., 2010). Negative effects of N addition on AM fungal richness increased with N addition rate and experimental duration (Table S4). Moreover, agroecosystems are relatively not limited by P because compound fertilizer (containing P) is widely applied to maintain soil fertility (Bakhshandeh et al., 2017; Ercoli et al., 2017; Wang et al., 2009). Therefore, in such P-rich agroecosystems, host plants would decrease dependency on AM fungi to acquire P from soil and reduce the amount of C allocated to belowground under N addition (Hoeksema et al., 2010; Johnson et al., 2013). That would intensify competition among AM fungal species for plant C. The edaphophilic AM fungi which have more extra-radical hyphae may be suppressed due to their high demand for C (Lilleskov et al., 2019).

However, the regulation of moderators on responses of AM fungal richness to N addition in grassland and forest was relatively complex. In addition to great variations of soil P availability in these two ecosystems, changes of plant species composition and richness induced by N addition would also affect AM fungal richness and diversity. For example, N addition could decrease plant species richness and cause local extinction of susceptible plant functional groups in grassland (Clark & Tilman, 2008; Stevens et al., 2004; Suding et al., 2005). Some studies showed positive relationships between AM fungal richness and plant species richness in grassland (Hiiesalu et al., 2014; Landis et al., 2004; Liu et al., 2012); thus, N addition could suppress both plant and AM fungal richness in grassland (Chen

et al., 2017). However, several studies in Tibetan alpine meadows (Jiang et al., 2018; Zheng et al., 2014) found that N addition caused lower plant richness but higher AM fungal richness, and changed the community composition of both plants and AM fungi. Unfortunately, most studies in our dataset did not report the change of plant species composition or richness after N addition; thus, we could not get enough data to quantitatively assess the effect of this factor on the responses of AM fungal richness and diversity to N addition. Given available data and literature results, we speculate that great variations of soil P availability and complex interactions between host plants and AM fungi may lead to highly variable (and not significant) responses of AM fungal richness and diversity to N addition in grassland and forest ecosystems (Figure 2b).

4.3 | Mechanisms of the N addition effects on AM fungi

Integrating our meta-analysis results (Figure 7) and existing theoretical models, we summarized potential mechanisms to explain how N addition affects AM fungal communities on a global scale. The previous viewpoint is that N addition leads to soil acidification and increases available N in soil, both of which have negative effects on AM fungi (Lilleskov et al., 2019). Our results also showed a significant positive relationship between the response ratio of AM fungal richness and the change of soil pH and a significant negative relationship between the response ratio of AM fungal diversity and that of soil available N (Figure S4). Moreover, the response of rhizophilic AM fungi seemed to be affected by the change of soil pH (Figure 5a). Rhizophilic AM fungi are considered to allocate more biomass into roots, so decreased rhizophilic fungal abundance (Figure 3a) likely results in decline of root colonization by AM fungi (Figure 2a). However, we found that soil available N/P ratio is an important factor to predict the responses of AM fungi (Figure 4). There may be a threshold of P limitation to determine AM fungal response (positive or negative) to N addition (Figure 7, inset). When soil P is not limited, there is little chance that N addition will have a positive effect on AM fungi, and there is a much greater chance that N addition will have a negative effect. When P is limited, there is an increasing chance that N addition will have a positive effect. Therefore, a great heterogeneity of soil P availability may result in these overall non-significant responses of

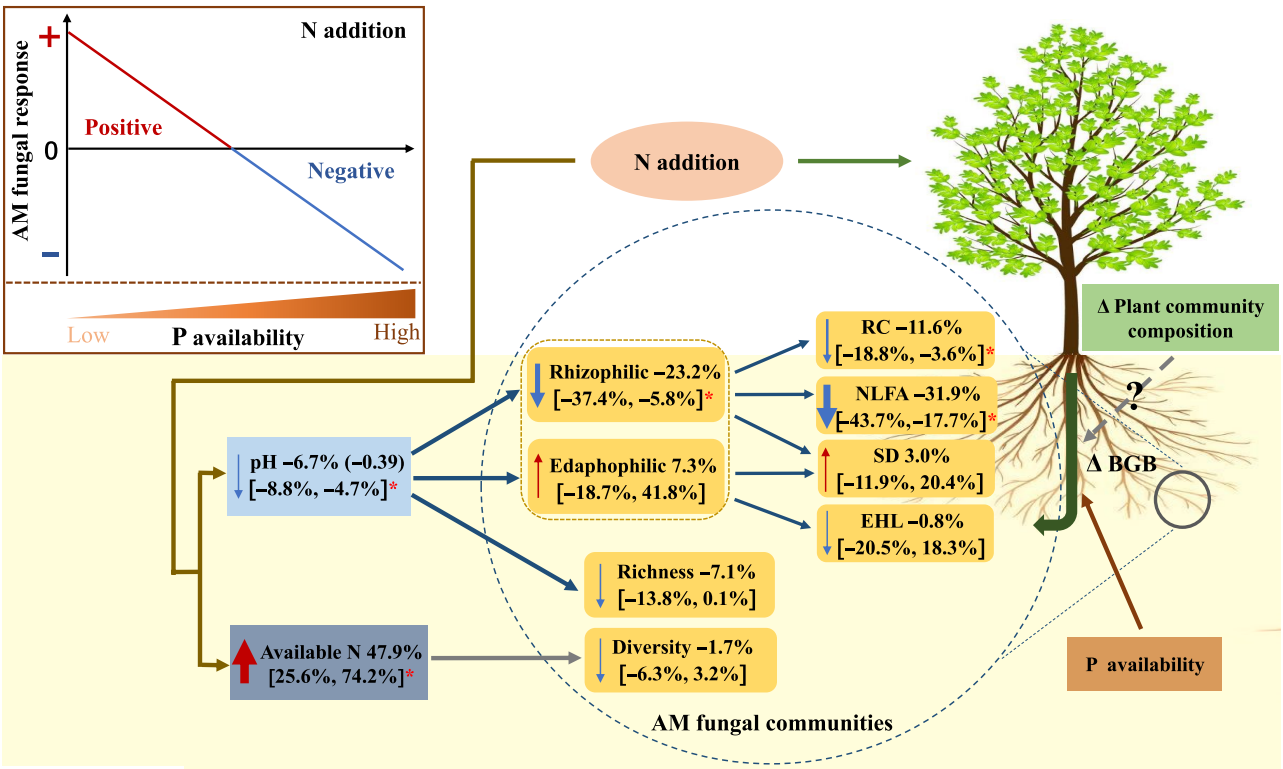

FIGURE 7 Schematic figure summarizing the relationships between N addition and AM fungal communities discovered in this study. Numbers in rectangles represent weighted percentage changes and their corresponding lower and upper 95% confidence intervals (CIs) in AM fungal communities (abundance, richness and diversity) or soil chemistry (pH and available N) after N addition. For pH, values in parentheses (−0.39) represent 0.39 units decrease in pH. ΔBGB, change of belowground biomass; EHL, extra-radical hyphal length (EHL) density; NLFA, neutral lipid fatty acid; RC, root colonization; SD, spore density. The red up and blue down arrows represent positive and negative responses, respectively. The red asterisks (*) indicate significant effects ($p < .05$). Dashed arrows mean that the mechanism (change in plant community composition) has been hypothesized in the literature but could not be tested (due to lack of enough data in original studies) in this global-scale meta-analysis. The illustration on the upper left shows specifically how soil P availability influences the response of AM fungi to N addition. AM fungal response here means richness, diversity or EHL

AM fungi (such as richness, diversity and EHL) to N addition. The threshold of P limitation can be explained by the C-P trade-off between host plants and AM fungi.

Different from other soil microbes, AM fungi are obligate biotrophs and almost all of their C sources come from host plants (Smith & Read, 2008). Therefore, N addition also had indirect effects on AM fungi through changing their hosts. Specifically, N addition can change the nutrition status of plants and then change plant C allocation to roots or associated AM fungi to maintain the balance of resources (Janssens et al., 2010; Johnson et al., 2013). AM fungi offer soil P to their hosts in exchange for plant C (Smith & Read, 2008). Therefore, C allocation shift induced by relative availability of soil P may control the response of AM fungi to N addition. Moreover, the change of plant community composition induced by N addition may also affect AM fungi directly or indirectly by changing plant C allocation to belowground (Antoninka et al., 2011). Overall, the impact of N addition on AM fungal community is jointly controlled by the initial soil P availability as well as N-induced changes in soil chemistry (pH and available N) and host plants (community composition and diversity).

4.4 | Implications and future research

Using meta-analysis technique, we quantitatively estimated the effects of N addition on AM fungal communities on a global scale (Figure 7). Our results showed that N addition strongly affected AM fungal communities, which may have important consequences for ecosystem functioning.

We found that the responses of AM fungal abundance, richness and diversity decreased with N addition rates and the response of AM fungal richness decreased with experimental duration (Table S4). These results implied that elevated N inputs for long term would cause more severe damage to AM fungi. Therefore, in high N-input systems such as cropland, proper N-input management is essential for maintaining the ecological function of AM fungi. The N addition rates in many experiments simulating atmospheric N deposition were much higher than the rates of natural N disposition (Figure S7), which might not be able to reveal the actual responses of AM fungi to N deposition. Actually, even low N deposition rates can do harm to AM fungal communities (Ceulemans et al., 2019). Therefore, further N fertilization experiments with realistic rates should be conducted to reveal actual mechanisms of the effects of N deposition on AM fungi.

In addition to focusing on N added (amount and duration [Table S4] but not form [Figure S5]), we should also pay attention to P availability in soil and C allocation from host plants (Figures 4 and 5b) to improve our mechanistic understanding of the N addition effects on AM fungi. The change of the availability of one of these three elements (C, N and P) can affect host plants and AM fungi acquiring the others (Miller et al., 2002). Therefore, resource stoichiometry is important for elucidating the structure and function of AM fungal communities across scales (Johnson, 2010). Changes of plant community composition due to N addition are also crucial to regulate the response of AM fungal community (Antoninka et al., 2011; Jiang et al., 2018; Zheng et al., 2014). However, most studies in our dataset did not report this factor. To untangle the complexity of the effects of N deposition on AM fungi, future studies need to pay more attention to the availability of soil P and the change of host plants (including aboveground community composition and belowground C allocation).

Furthermore, studies of AM fungi in response to N addition in tropical regions are very rare in our database (Figure 1). Given that most tropical ecosystems are thought to be P-limited (Turner et al., 2018; Vitousek et al., 2010) and most tropical plants are AM species (Smith & Read, 2008; Steidinger et al., 2019), AM fungi should play an essential role in plant nutrition and growth in tropical ecosystems. The response of AM fungi to N deposition could dramatically influence biodiversity and functioning of tropical ecosystems. Therefore, the response of AM fungi to N addition in tropical ecosystems deserves more attention in future work.

In summary, our comprehensive meta-analysis clearly reveals general patterns of the impact of N addition on AM fungal communities on a global scale. We also explicitly show the relationships between AM fungal responses and soil chemistry (change in pH and available N) and resource availability (soil P availability), host plant (belowground biomass), environmental and experimental variables. Specifically, N addition had a significantly negative relationship with AM fungal abundance (root colonization and NLFA), but not with AM fungal richness and diversity. Importantly, it is necessary to look more deeply into the moderating factors to understand the non-significant responses better. We found that the relative availability of soil P (soil available N/P ratio) was the most important predictor for the responses of AM fungal richness and diversity across sites, and the responses of two main AM fungal guilds (rhizophilic and edaphophilic) were strongly predicted by different factors resulting in different responses of AM fungal abundance in root and soil. Taken together, these novel results provide a mechanistic framework for understanding the dynamics of AM fungal communities under N enrichment, and contribute to developing theoretical models to better predict ecological functions of AM fungi under global change.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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