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META-ANALYSIS

Global arbuscular mycorrhizal fungal diversity and abundance decreases with soil available phosphorus

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Abstract

Aim: Arbuscular mycorrhizal fungi (AMF) are widely distributed soil organisms that play critical roles in ecosystem functions. However, little is known about their global distribution and the underlying mechanisms. Here, we aimed to explore distribution pattern and key predictors of AMF diversity and abundance at the global scale.

Location: Global.

Time Period: 1987–2022.

Major Taxa Studied: Arbuscular mycorrhizal fungi.

Methods: We investigated the distribution pattern and key predictors of AMF diversity and abundance at the global scale by compiling 654 field studies.

Results: We found that cold climate zones had relatively low AMF diversity. At the ecosystem level, grassland tended to have higher AMF diversity and abundance. Soil available phosphorus (P) and latitude were the most important predictors of AMF diversity. AMF richness and Shannon index decreased with increasing soil available P and latitude. Soil available P and soil pH were the main predictors for global distribution of AMF abundance. AMF colonization rate and spore abundance declined with soil available P and increased with soil pH. Mean annual precipitation was also an important, positive correlate of spore abundance.

Main Conclusions: Our findings highlight soil available P as an important predictor affecting the distribution of AMF diversity and abundance, advancing our understanding of the mechanisms underlying the distribution patterns of mycorrhizal fungal diversity and abundance at the global scale.

KEYWORDS

abundance, arbuscular mycorrhizal fungi, biodiversity, distribution pattern, global analysis, soil available phosphorus

1 | INTRODUCTION

Mycorrhizae are widely recognized as key plant symbionts that sustain primary production, nutrient biogeochemical cycling and below- and above-ground biodiversity (Klironomos et al., 2011; Lee et al., 2013; Powell & Rillig, 2018; Rillig, 2004; van der Heijden et al., 2015; van der Heijden, Boller, et al., 1998). As the most widespread mycorrhizal fungal types, arbuscular mycorrhizal fungi (AMF) form mutualistic symbiosis associations with approximately 80% of terrestrial plant species (Smith & Read, 2008) and are present in almost all ecosystems (van der Heijden et al., 2015). In exchange for plant-assimilated carbon (C), symbiotic associations facilitate water and nutrient uptake for host plants (Smith & Read, 2008), alleviate plant abiotic stress (Chandrasekaran et al., 2014; Egerton-Warburton et al., 2007; Li et al., 2013; Pozo et al., 2015), improve pathogen resistance (Borowicz, 2001; Jung et al., 2012; Smith & Read, 2008), influence plant–plant interactions and plant community structures (Klironomos et al., 2011; Van Der Heijden et al., 2008; van der Heijden, Klironomos, et al., 1998; Vogelsang et al., 2006), and thus affect ecosystem maintenance and restoration. Although the primary importance of mycorrhizal fungi for multiple ecosystem functions has been widely studied, the global diversity and abundance distribution patterns of AMF remain largely unknown, in contrast to the well-studied diversity patterns of macroorganisms. Such information is critical for understanding the roles of AMF in ecosystem processes and predicting soil C and nutrient dynamics with a changing global environment.

AMF (Subphylum: Glomeromycotina) are an ancient but species-poor group of root symbionts (Öpik et al., 2014; Öpik & Davison, 2016; Spatafora et al., 2016). Because many AMF species are unculturable, at present, the identification of AMF taxa is primarily dependent on sequencing technology. The standardized methodologies for delineating AMF taxa and processing samples exist and are widely used (Hart et al., 2015; Pärtel et al., 2017), making it possible to study global diversity distribution patterns and underlying mechanisms. The provisioning of ecosystem functions by AMF likely depends on the abundance of AMF species (Li et al., 2015; Sheng et al., 2022). AMF can form extensive fungal hyphae that run parallel to the endodermis inside the cortical root cells (van der Heijden et al., 2015). Vegetative structures play importance roles in the nutrient exchange of AMF symbiosis where extra-radical hyphae can access nutrients (mainly phosphorus (P) and inorganic nitrogen (N)) from soil and intra-radical hyphae form the interface for the exchange of these nutrients and host plant photosynthates (Fellbaum et al., 2012; Smith & Read, 2008; Talbot et al., 2008). In addition, AMF can form dormant asexual spores. The AMF spores were important propagules for AMF colonization and dispersal, which represent an important survival strategy under adverse environmental conditions (Aguilar-Trigueros et al., 2019; Chagnon et al., 2013). Many previous studies have focused on distribution patterns of biodiversity with less emphasis on the patterns of abundance at the global scale. Whether AMF diversity and abundance have different global distribution patterns and key predictors remain unclear.

Previous studies suggest that AMF diversity and abundance are affected by a suite of abiotic and biotic factors, including climatic factors (e.g. temperature and precipitation), soil properties (e.g. soil pH, soil available N, soil available P and soil available N:soil available P) and above-ground plant properties (e.g. host plant species, plant community composition and plant species richness) (Albornoz et al., 2022; Ceulemans et al., 2019; Davison et al., 2020; De Beenhouwer et al., 2015; Johnson et al., 2003; Öpik et al., 2006; Soudzilovskaia et al., 2015; Van Geel et al., 2017; Xu et al., 2016). Of the dozens of abiotic and biotic factors that can influence mycorrhizal fungal diversity and abundance, soil nutrients have undoubtedly received more attention. From a resource economy perspective, the availability of soil-derived nutrients is a key factor affecting the symbiotic C for P trade, mycorrhizal cost and benefits, and diversity and abundance of mycorrhizal fungi (Johnson, 2010; Johnson et al., 2015). In addition, many studies have also explored the relationship between plants and AMF (Davison et al., 2020; Hiiesalu et al., 2014; Rasmussen et al., 2022). The biotic filtering hypothesis states that host plants select compatible mycorrhizal fungi (HilleRisLambers et al., 2012). The diversity of AMF and plants is highly correlated (Landis et al., 2004; Xu et al., 2016). Although these studies have improved our understanding of factors affecting mycorrhizal fungal diversity and abundance, the relative contributions or the effects of these factors are inconsistent among studies. For example, both negative (Borriello et al., 2012; Ceulemans et al., 2019; De Beenhouwer et al., 2015; Rozek et al., 2019; Verbruggen et al., 2012) and no effects (Moora et al., 2014; Zhang et al., 2020; Zhang et al., 2021) of soil available P on AMF diversity and abundance have been reported. Indeed, our knowledge about these relationships is based on site-level experiments, while determinants of mycorrhizal fungal diversity and abundance at local scales may differ from those at larger scales (Allison & Goldberg, 2002; van der Linde et al., 2018). Therefore, although previous studies have undoubtedly contributed to identifying the main drivers affecting mycorrhizal fungal diversity and abundance at local scales, their limitations do not allow these insights to be extrapolated to global scales.

To fill knowledge gaps in global patterns and main predictors for AMF diversity and abundance, we compiled a dataset from 654 field studies of AMF diversity and abundance. In this study, we aim to address the following questions: (a) what are the global patterns of AMF diversity and abundance, (b) do the distribution patterns differ between diversity and abundance of AMF and (c) what are the main predictors of the distribution patterns of AMF diversity and abundance at the global scale?

2 | MATERIALS AND METHODS

2.1 | Data collection

To investigate the global distribution of AMF diversity and abundance, we systematically searched the published literature up to July 2022. Published papers were searched using the ISI Web of Science, Google

Scholar and the China National Knowledge Infrastructure (CNKI, for articles published in Chinese) with the search term of 'arbuscular mycorrhizal fungi'. All selected papers met the following criteria in this analysis: (a) at least one AMF metric, including AMF alpha-diversity (Shannon index or species richness) and AMF abundance (total colonization rate or spore abundance) was reported, (b) high-throughput sequencing techniques were used for AMF diversity identification, and sequences that did not reach the rarefaction curve plateau were excluded, (c) only field experiments were included, (d) when the paper contained results from multiple soil sampling depths, we collected data from the surface layer (top 30 cm), (e) only data from control (no-manipulates) plots were included in manipulative experiments, and (f) when the paper reported the interannual variation or seasonal variation in AMF diversity and abundance, the mean value of interannual or seasonal variation was calculated to provide a single data point.

The literature search and selection yielded 654 field studies (Figure S1), from which we compiled a dataset of 1322 observations of AMF richness, 906 observations of Shannon index, 1428 observations of total colonization rate (%) and 1461 observations of spore abundance (per g dry soil) (Figure 1; Appendix S1). For each study, we extracted the mean values, standard deviation and number of replicates of AMF metric. AMF diversity and abundance were the mean of sample measures. AMF spore abundance was transformed to number per g dry soil. Information for data sources and data are shown in Appendix S1 and S3.

In addition to AMF diversity and abundance, we also collected the geographical coordinates (latitude and longitude), altitude, climatic variables [mean annual temperature (MAT) and mean annual precipitation (MAP)], ecosystem types (agro-ecosystem, desert, forest, grassland, shrubland and wetland), sampling soil depth, sample types (soil, root, and a mixture of soil and root) and soil properties (soil pH, soil nitrate content, soil ammonium content, soil available N content, soil available P content and soil available N:soil available P) from the papers or their cited papers or the papers at the same experiment site. Raw data were extracted from figures and retrieved directly from the text and tables. When data were presented in graphs, we obtained numerical data using GetData Graph Digitizer 2.24 (http://getdata-graph-digitizer.com/). If the soil available N content was not provided in study, we calculated it by the sum of the soil nitrate content and soil ammonium content (Dai et al., 2018). For papers that did not report geographical locations (latitude and longitude) and altitude, we obtained it from Google Earth (https://www.google.com/earth/). If studies did not provide the information on climatic factors (MAT and MAP), we obtained this information from the global climate database at http://www.world clim.org/ according to latitude and longitude.

Climate zones were divided into tropical, temperate and cold zones based on latitude (tropical ≤ 23°26′, 23°26′ < temperate ≤ 60° and cold > 60°). Ecosystems were partitioned into agro-ecosystem, desert, grassland, forest, shrubland and wetland. According to the collected soil sampling depth, we categorized sampling depths into four types (0–10, 0–20, 0–30 cm and other). Other included experiments that did not report soil sampling depth in the original study. Samples used to determine AMF richness and Shannon index included soil, root and the mixture of soil and root.

2.2 | Statistical analysis

We tested the normality of the data distribution using the function 'Shapiro test' in R software (version 3.6.2) (R Core Team, 2019).

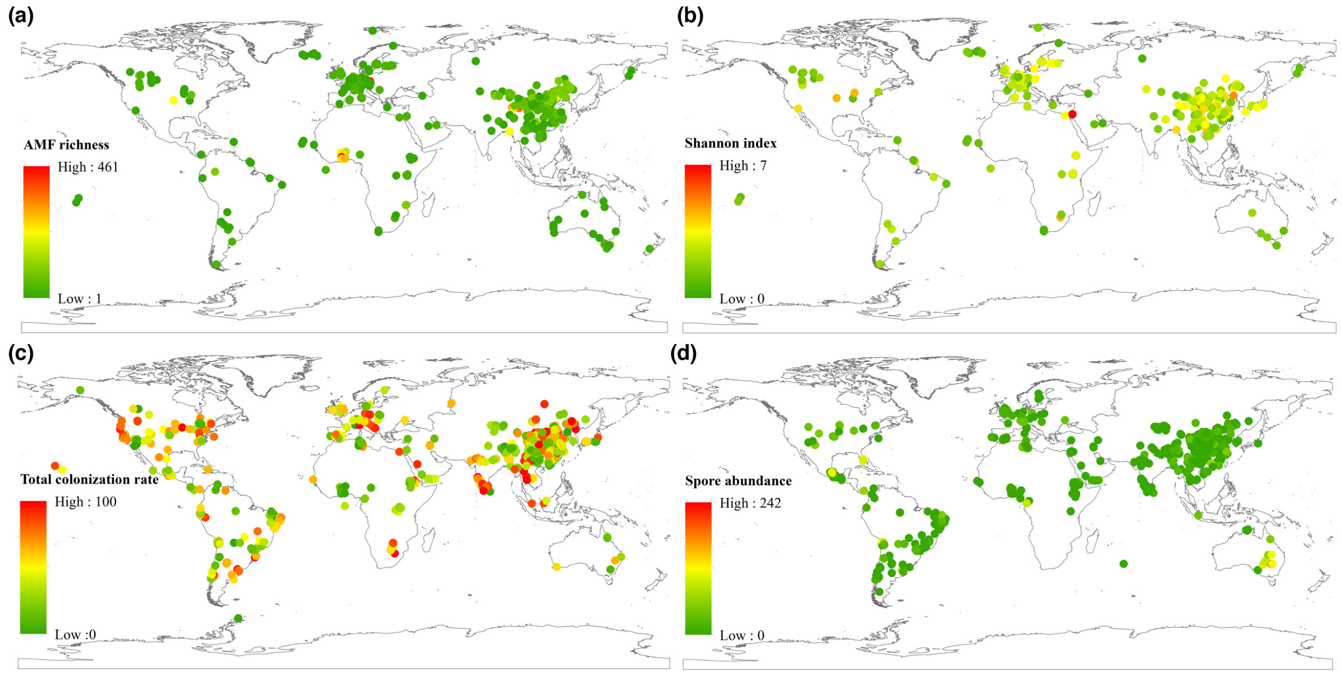

FIGURE 1 Global distribution of study sites from which data were collected in this analysis. Global distribution of data points of arbuscular mycorrhizal fungi (AMF) richness (a), Shannon index (b), total colonization rate (c) and spore abundance (d).

Variables were log-transformed when necessary for statistical analysis. To explore global distribution patterns of AMF diversity and abundance, we performed a linear mixed-effect model for a comparison of AMF diversity and abundance among climate zones and ecosystem types as follows:

$$Y = \beta_0 + \beta_1 \times X + \pi_{\text{site}} + \varepsilon \qquad (1)$$

where Y is AMF diversity and abundance, X is climate zones or ecosystem types, β_n are estimated coefficients, π_{site} is the random effect factor of 'site' that considers the potential temporal and spatial autocorrelation of repeated measures and method autocorrelation from the same study, and ε is the sampling error. Groups with small numbers of observations (≤5) were removed in these analyses (Zhou et al., 2020). We applied linear mixed-effect models using restricted maximum likelihood estimation with the '*lme4*' package in R software (version 3.6.2) (Bates et al., 2015). We used the number of replicates (the sample size corresponding to each mycorrhizal diversity and abundance attribute reported in original studies) for weighting (Wan et al., 2021).

To further account for the potential impact of soil sampling depth and sample types, we analysed their effect on AMF diversity and abundance using linear mixed-effect models. We found that AMF diversity varied significantly among soil sampling depths and sample types, and AMF abundance varied significantly among soil sampling depths (Table S1, Figures S2 and S3). Therefore, we added soil sampling depth and sample type as additional random factors (Table S2). However, we found that estimates of fixed effects were consistently similar between models without (Model 1) or with (Model 2) these methods as additional random factors (Table S2). Therefore, for simplicity, we report results using 'site' as the only random factor.

We analysed the effects of environmental variables (latitude, altitude, MAT, MAP, soil pH, soil available N, soil available P and soil available N:soil available P ratio) on AMF diversity and abundance. Absolute latitude was used in multiple regression models. The random forest analysis can handle overfitting and multicollinearity and is an effective machine-learning method (Xu et al., 2018). First, we used a random forest algorithm to evaluate the relative importance of all predictor factors and methods on AMF diversity and abundance. The increase in node purity was used to evaluate the importance of each driving factor where higher index values indicate greater variable importance in the regression (Kuhn et al., 2008). The number of trees that were used in the random forest analysis was set as 500. The random forest analysis was performed with the '*randomForest*' package in R software (version 3.6.2) (Liaw & Wiener, 2002). As their importance was very low, we concluded that soil sampling depth and sample type does not have an important influence on AMF diversity and abundance (Figure S4).

We next used multiple regression models to assess the combined effects of the eight predictors on AMF diversity and abundance. The variance inflation factor (VIF) was calculated to test collinearity among the predictors; predictors were excluded when VIF was greater than five (Elrys et al., 2022). The variable was excluded if its VIF exceeded five (Table S3), and this step was repeated until all variables had a VIF of less than five (Gao et al., 2022). All continuous predictors were standardized before analyses using a Z-score transformation to interpret parameter estimates on a comparable scale. We performed the linear mixed-effect model with 'site' as the random effect and the number of replications as 'weight'. Linear mixed-effect analysis used maximum likelihood estimation with the '*lme4*' package in R software (version 3.6.2) (Bates et al., 2015). To evaluate whether our model estimates could be affected by spatial autocorrelation, we employed Moran's I test using the '*ape*' package R software (version 3.6.2) (Paradis & Schliep, 2019). Except for total colonization rate, the residuals of our models for AMF richness, Shannon index and spore abundance were significantly autocorrelated at $\alpha = 0.05$ (Table S4). In addition, we further analysed whether spatial autocorrelation affected our estimates. According to Hisano et al. (2019), we include spatial coordinates (latitude and longitude) in our models using the '*spaMM*' package in R software (version 3.6.2) (Rousset et al., 2018). We found that the models both with and without spatial structure yielded quantitatively similar parameter estimates of significant predictors (Table S5), which indicated that our models were not biased.

Finally, we performed a model selection analysis to calculate the relative importance of controlling factors on AMF diversity and abundance (Calcagno & de Mazancourt, 2010; Terrer et al., 2016). Model selection was based on Akaike information criterion corrected. We implemented model selection analyses using the '*glmulti*' package (Calcagno & de Mazancourt, 2010) in R software (version 3.6.2) (R Core Team, 2019). The relative importance value of each predictor for AMF diversity and abundance was computed as the sum of Akaike weights for models including this predictor. These values can be regarded as the overall support for each predictor across all models. A cut-off of 0.8 was set to differentiate between essential and nonessential predictors (Terrer et al., 2016). All statistical analyses were performed in R software (version 3.6.2) (R Core Team, 2019).

3 | RESULTS

3.1 | Global patterns of AMF diversity and abundance among climate zones and ecosystem types

At the global scale, AMF diversity varied significantly among climate zones (Table 1). Although the observations in cold zone were limited, the cold zone tended to consistently have the lowest AMF richness and Shannon index (Figure 2a,b). However, no significant differences in AMF abundance were found among climate zones (Table 1, Figure 2c,d). There was a larger variation in ecosystem-level AMF diversity and abundance (Table 1, Figure 3). Grassland had significantly higher AMF richness than agro-ecosystem, forest and desert (Figure 3a). The Shannon index in grassland was higher than that in forest and desert (Figure 3b). For AMF abundance, we found that grassland and desert exhibited high total colonization rates (Figure 3c). Spore abundance in grassland and shrubland were

TABLE 1 Results of linear mixed models for a comparison of arbuscular mycorrhizal fungi (AMF) diversity and abundance among climate zones and ecosystems.

	AMF richness		Shannon index		Total colonization rate		Spore abundance	
	df	*F,p*	df	*F,p*	df	*F,p*	df	*F,p*
Climate zones	2	10.58***	2	15.38***	2	2.22	1	1.48
Ecosystems	4	11.21***	4	4.07**	5	7.39***	5	13.18***

Note: The linear mixed model is described in Equation 1. Asterisk indicates significant differences. $^{**}p<0.01$; $^{***}p<0.001$.

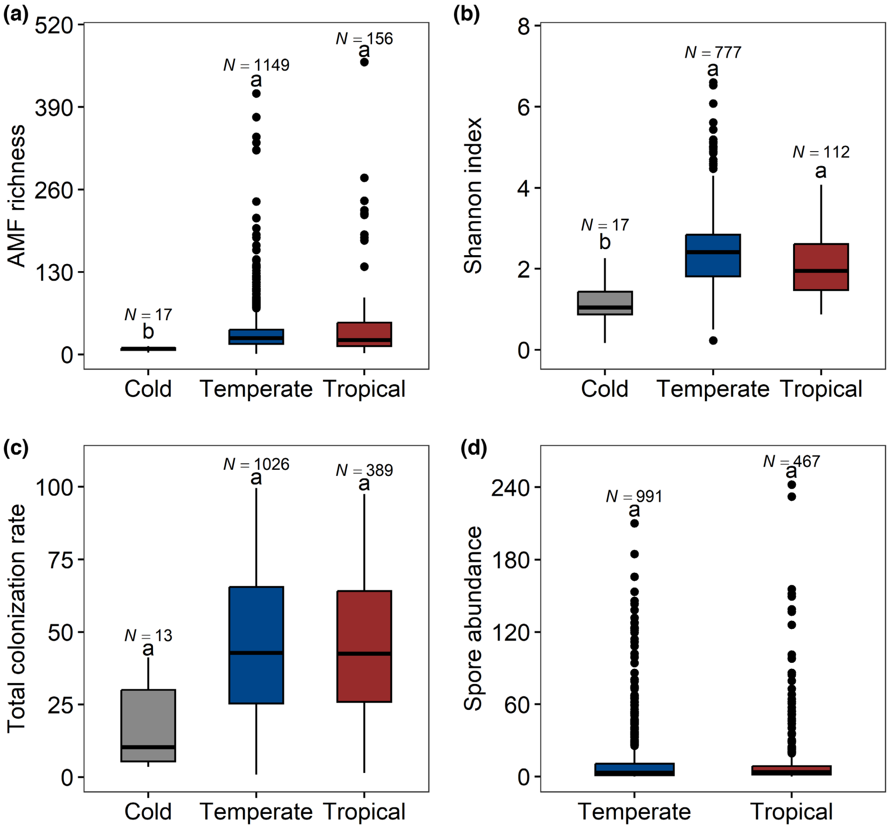

FIGURE 2 Comparison of arbuscular mycorrhizal fungi (AMF) richness (a), Shannon index (b), total colonization rate (c) and spore abundance (d) among climate zones. Values for boxplots are medians, with 75% of observations in the boxes, and whiskers below and above the boxes indicating the 5th and 95th percentiles. Different letters above boxes indicate significant differences at $p<0.05$. *N* is the number of observations.

higher than in agro-ecosystem (Figure 3d). In general, grassland displayed higher AMF diversity and abundance.

3.2 | Factors controlling AMF diversity and abundance variation

AMF richness and Shannon index significantly decreased with increasing soil available P (all $p<0.01$, Table 2) and latitude (all $p<0.01$, Table 2) at a global scale. The model selection analysis further showed that soil available P and latitude were the most important predictors explaining variation in AMF richness and Shannon index (Figure 4a,b).

The model selection analysis revealed that AMF total colonization rate was predominantly affected by soil available P and soil pH at the global scale (Figure 4c). Consistent with the AMF diversity, total colonization rate decreased with increasing soil available P ($p<0.001$, Table 2). Total colonization rate was positively correlated with soil pH (Table 2, Table S5). For spore abundance, MAP, soil pH and soil available P were the most important factors that reached the threshold value (0.8) of the summed Akaike weights (Figure 4d). Spore abundance increased significantly with increasing MAP ($p<0.001$, Table 2) and soil pH ($p=0.02$, Table 2). Additionally, spore abundance marginally decreased with increasing soil available P ($p=0.08$, Table 2).

4 | DISCUSSION

4.1 | Global patterns of AMF diversity and abundance

We found that AMF diversity varied significantly among climate zones. In comparison to the others, cold zones had lower AMF diversity. The low number and abundance of AMF host plants and C allocation of host plants to symbiosis in cold zones affect the formation

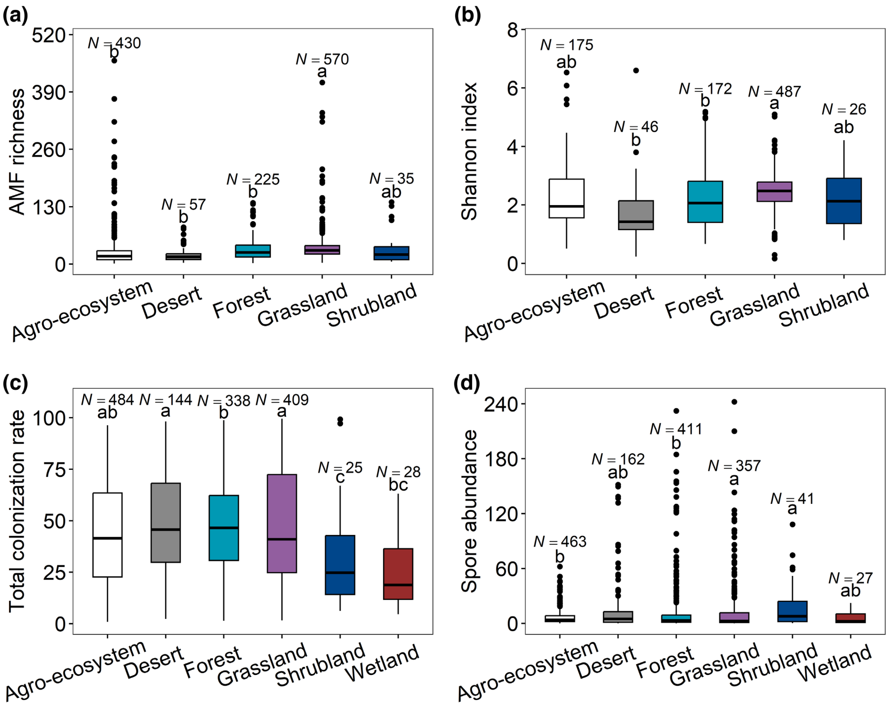

FIGURE 3 Comparison of arbuscular mycorrhizal fungi (AMF) richness (a), Shannon index (b), total colonization rate (c) and spore abundance (d) among ecosystems. Values for boxplots are medians, with 75% of observations in the boxes, and whiskers below and above the boxes indicating the 5th and 95th percentiles. Different letters above boxes indicate significant differences at $p < 0.05$. *N* is the number of observations.

of mycorrhizal symbiosis (Barbosa et al., 2017; Barceló et al., 2019; Bueno et al., 2017; Gardes & Dahlberg, 1996; Olsson et al., 2004; Timling et al., 2012). Veresoglou et al. (2019) proposed that irradiance constraints in cold zones contribute to a reduction in mycorrhizal responsiveness, and the reduced mycorrhizal responsiveness further induces a decline in AMF species. In addition, according to the metabolic theory, low temperature can affect soil productivity, microbial activity and ecological interactions (Brown et al., 2004; Tylianakis et al., 2008). Thus, extremely low temperatures in cold zones can restrict mycorrhizal physiological activities and inhibit mycorrhizal growth to develop and provide benefits to host plants (Barbosa et al., 2017; Barceló et al., 2019; Rillig et al., 2002). These may contribute to relatively low AMF diversity in cold zones. However, we lack sufficient data in cold zones to fully corroborate this conclusion. More mycorrhizal fungal data from future investigations are needed, especially in cold zones, to draw more firm relationships among differences in mycorrhizal fungal diversity and abundance with the biophysical features of climate zones.

At the global scale, AMF diversity and abundance showed similar patterns among ecosystems: grasslands tend to have high AMF diversity and abundance. This finding corroborates previous reports in which grasslands have higher AMF diversity and abundance (Davison et al., 2015; Öpik et al., 2006; Treseder & Cross, 2006; Voříšková et al., 2016; Xu, Li, et al., 2017). Several factors may be responsible for the high AMF diversity and abundance in grassland. First, relatively high plant diversity or a high proportion of AMF host plants in grassland can provide broad niches for more diverse AMF in grassland (Castillo et al., 2006; Xu, Li, et al., 2017). It is widely reported that mycorrhizal fungal diversity is positively correlated with plant diversity (Anderson et al., 1984; Hiiesalu et al., 2014; Ishida et al., 2007; Xu et al., 2016). The plant diversity hypothesis predicts that higher plant diversity can provide more soil microbial niches, making it more potentially for soil microbes to find an eligible host (Hooper et al., 2000; Waldrop et al., 2006). Thus, higher plant diversity leads to heterogeneity of the mycorrhizal environment (Caruso et al., 2012), which could support higher mycorrhizal fungal diversity. Second, the diversification of the majority of current AMF virtual taxa by phylogenetic analysis (Davison et al., 2015) coincides with the appearance and expansion of grassland (Parr et al., 2014; Pärtel et al., 2017; Strömberg, 2011; Strömberg et al., 2013). Developing grassland possibly created new and spatially very abundant habitat for AMF (Pärtel et al., 2017). In addition, the high density and large total abundance of host plant roots in grassland potentially host diverse AMF and high AMF abundance (Pärtel et al., 2017; Xu, Li, et al., 2017). Consequently, grassland appears be a favourable habitat for AMF (Davison et al., 2015).

4.2 | Predictors for the global variations of AMF diversity and abundance

At a global scale, AMF diversity declined with increasing latitude. This finding was consistent with previous reports based on systematic sampling of 67 sites around the world (Davison et al., 2015) and the current known pattern of AMF host plant abundance–latitude relationships (Barceló et al., 2019). The decline of AMF diversity with latitude can be partially explicated by the transition from ecosystems dominated by AMF host plants at low latitude to ectomycorrhizal and ericoid mycorrhizal host plants dominated ecosystems at high latitude (Barceló et al., 2019; Bueno et al., 2017; Smith & Read, 2008). The 'sun-worshipper' hypothesis proposed by Veresoglou et al. (2019) predicts that latitude affects AMF

TABLE 2 Coefficients of predictors based on weighted averages of the model coefficients across all models in multivariate regression model.

Predictors	Estimate	*p* value
AMF richness		
AP	−0.28	**<0.001**
Latitude	−0.32	**0.003**
pH	−0.08	0.27
Altitude	−0.08	0.42
MAP	−0.06	0.47
AN	0.02	0.59
MAT	0.02	0.79
AN:AP	0.01	0.71
Shannon index		
Latitude	−0.33	**<0.001**
AP	−0.25	**0.002**
Altitude	−0.15	0.17
pH	−0.03	0.61
MAP	−0.03	0.63
AN:AP	0.01	0.73
AN	0.0001	1.00
Total colonization rate		
AP	−4.85	**<0.001**
pH	4.36	**0.004**
Latitude	3.57	0.22
AN:AP	−1.74	0.27
MAT	2.37	0.40
Altitude	0.04	0.97
MAP	−0.54	0.66
AN	−0.02	0.97
Spore abundance		
MAP	16.12	**<0.001**
pH	3.25	**0.02**
AP	−2.08	0.08
MAT	−4.89	0.17
AN	−1.34	0.27
Latitude	3.06	0.34
Altitude	1.53	0.44
AN:AP	0.21	0.70

Note: Bold values indicate significant differences at $p<0.05$.

Abbreviations: AMF, arbuscular mycorrhizal fungi; AN, soil available N; AN:AP, soil available N:soil available P; AP, soil available P; MAP, mean annual precipitation; MAT, mean annual temperature.

responsiveness in plants through three complementary mechanisms: phenotypic responses, environmental filtering and eco-evolutionary processes. Changes in abiotic conditions may allow host plants to obtain more benefits from the symbiosis at low latitudes through phenotypic plasticity. Environmental filtering refers to the process of abiotic environment more favourable for symbioses close to the tropics that could further exclude species less dependent on AMF by competition. The process further results in plant communities that are more dependent on AMF at low latitudes. From the perspective of eco-evolutionary processes, because of a more limited pool of suitable AMF partners, AMF host plants at higher latitude encounter a less diverse pool of potential symbiotic partners (Davison et al., 2015). However, we found that the abundance of AMF did not decline with increasing latitude. The provisioning of ecosystem functions by AMF likely depends on the abundance of the AMF species. Although AMF diversity is lower at the sites with high latitude, AMF still maintains relatively high abundance owing to the dependence of host plants on AMF for nutrient acquisition and resistance to biotic and abiotic stresses.

The production of spores is part of the AMF life cycle and is highly dependent on environmental conditions, their physiological status and life strategy (de Mello et al., 2018; Smith & Read, 1997). We found that MAP was the best predictor of AMF spore abundance worldwide. Our finding of the positive effect of MAP on AMF spore abundance was consistent with previous reports (Escudero & Mendoza, 2005; He et al., 2016; Meddad-Hamza et al., 2017; Ortas & Coskan, 2016). Relatively low precipitation limits the net primary production of above-ground plants (Wiesmeier et al., 2019). Under this condition, limited C resources may be preferentially allocated to hyphae used to absorb and translocate limiting nutrients and water rather than stored in spores (Bai et al., 2009). Therefore, AMF sporulation will be higher in environments with more precipitation (Gai et al., 2006).

Our results showed that soil properties played important roles in the global variation of mycorrhizal fungal diversity and abundance. The results were consistent with those of many studies showing that mycorrhizal fungal diversity and abundance decrease with increasing soil available P at local (Abdedaiem et al., 2020; De Beenhouwer et al., 2015; van Geel et al., 2015) and large spatial scales (Ceulemans et al., 2019). Mycorrhizal plants have developed a direct pathway from the rhizosphere through their roots and mycorrhizal pathway for P absorption from soil (Smith et al., 2015). In soil with low available P content, more soil volume must be exploited for P absorption, and the cost of exploration by extensive and narrow external mycorrhizal hyphae are less than that expended by host plant roots (Raven et al., 2018; Smith & Smith, 2012). Under such conditions, plants tend to allocate more C to mycorrhizae for P absorption (Johnson, 2010; Johnson et al., 2010; Johnson et al., 2015). With increasing soil available P, direct uptake pathway by roots will cost less than uptake by mycorrhizae (Raven et al., 2018). Thus, host plants favour a direct root uptake pathway and decrease C allocation to mycorrhizae (Johnson, 2010), which may result in low mycorrhizal fungal diversity and abundance.

Soil pH is another important predictor of global AMF abundance. At the global scale, we found that soil pH is positively correlated to AMF abundance. Previous studies have shown that soil pH may have an important direct influence on AMF growth and performance (Coughlan et al., 2000; Siqueira et al., 1984; Wang et al., 1993). Similarly, Davison et al. (2021) recently found that pH was the most

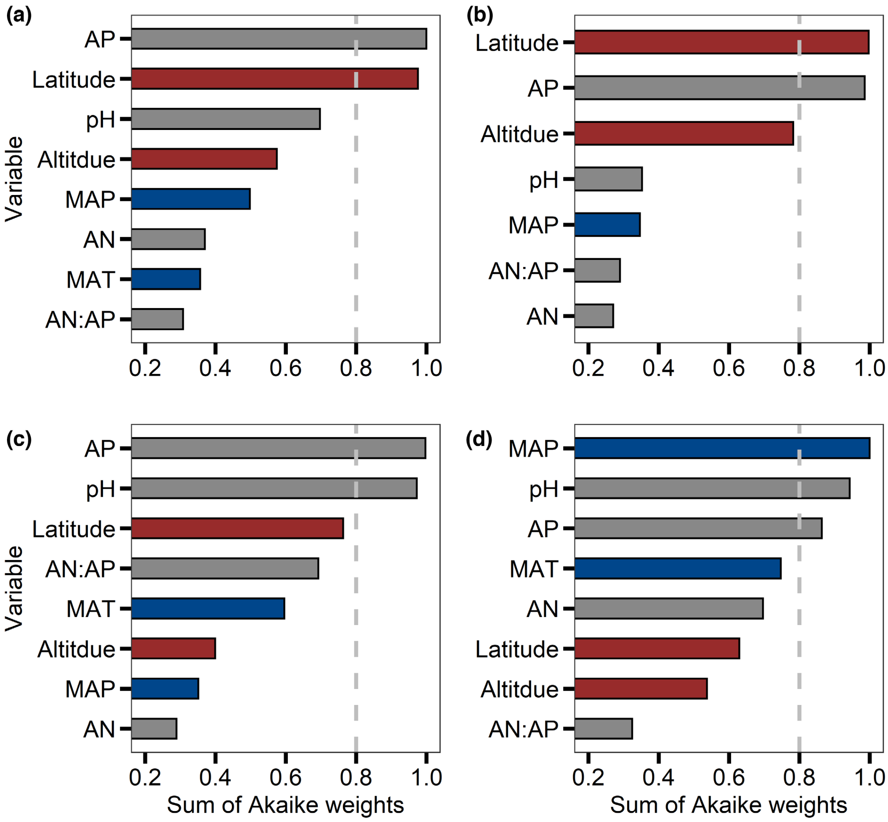

FIGURE 4 Model-averaged importance of predictors of arbuscular mycorrhizal fungi (AMF) richness (a), Shannon index (b), total colonization rate (c) and spore abundance (d). Importance is based on the sum of Akaike weights derived from model selection using Akaike's information criteria (AIC) corrected. A cut-off of 0.8 is set to differentiate between important and non-essential predictors. AN, soil available nitrogen; AN:AP, soil available nitrogen:soil available phosphorus; AP, soil available phosphorus; MAP, mean annual precipitation; MAT, mean annual temperature.

important abiotic driver of AMF distribution, and define the realized AMF niche space. Thus, it is possible that soil pH represents a strong structuring force of the mycorrhizal fungal niche space. Lower soil pH could impose a physiological constraint on AMF growth (Kohout et al., 2015; Xu, Chen, et al., 2017).

4.3 | Potential limitations

Some limitations need to be acknowledged in our study. First, the observations of AMF diversity and abundance were concentrated in the temperate zone, while data were limited in the cold zone. An uneven distribution of data points from each climate zone might lead to bias in the predicted global pattern. Therefore, more mycorrhizal fungal data in cold zones are needed. Second, AMF diversity varied significantly across soil sampling depths and sample types. Topsoil in the top 0–10 cm tended to have higher AMF diversity. Compared with root samples, soil samples have higher AMF diversity. Although our results were consistently similar between models without or with the methods to account for this variation, different study methods to measure AMF diversity and abundance still may lead to a slight bias in the global distribution of AMF diversity and abundance. Third, some predictors (e.g. soil pH, soil available N and soil available P) were not available in all studies and filling in missing values with global data leads to greater uncertainty. Other factors, such as host plant identity, plant diversity, plant community compositions and soil physical properties, can affect AMF diversity and abundance (Aliasgharzadeh et al., 2001; Fei et al., 2022; Hiiesalu et al., 2014; Neuenkamp et al., 2018; Xiang et al., 2014; Xu et al., 2016). However, most studies in our dataset did not report these factors. To accurately predict changes in mycorrhizal fungal diversity and abundance under future climatic scenarios, future studies need to pay more attention to below-ground soil available nutrients and above-ground plant community composition. Finally, it should be noted that biodiversity is expected to be a product of the simultaneous and potentially confounding effects of regional (evolutionary changes and historical dispersal) and local (dispersal in contemporary landscapes, biotic and abiotic filtering, and natural and anthropogenic disturbance) processes (Pärtel et al., 2017). Understanding the relative roles of multiple processes in shaping biodiversity patterns of AMF is an ongoing challenge.

5 | CONCLUSIONS

This study provided a comprehensive analysis of AMF diversity and abundance and its predictive factors at the global scale. We found that soil available P and latitude were the most important predictors of AMF diversity. Soil available P and pH were the main predictors of the global distribution of AMF abundance. At the global scale, AMF diversity decreased with increasing latitude while AMF abundance did not change with latitude. Consistently, we found that the diversity and abundance of AMF declined with soil available P. In addition, MAP was an important predictor of spore abundance and positively correlated with spore abundance. These findings were crucial for our understanding of the distribution patterns of AMF diversity and abundance at the global scale and the role of the mycorrhizal symbiosis in ecosystem functioning in the face of global change.

AUTHOR CONTRIBUTIONS

All authors contributed intellectual input and assistance to this study and manuscript preparation. Xia Xu conceived the idea and designed the study. Xiaocui Ma collected the data. Xiaocui Ma analysed the data with help from Xia Xu, Qinghong Geng, Yiqi Luo, Qian Li, Chenghui Ju and Yan Zhou. Xiaocui Ma and Xia Xu wrote the paper with input from all authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing financial interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

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BIOSKETCH

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SUPPORTING INFORMATION

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

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