

# Biogeographical patterns of arbuscular mycorrhizal fungi diversity in China's grasslands

TENG Jialing<sup>1,2</sup>, TIAN Jing<sup>3,1</sup>, \*YU Guirui<sup>1,2</sup>

1. Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, CAS, Beijing 100101, China;
2. College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China;
3. College of Resources and Environmental Sciences; Key Laboratory of Plant-Soil Interactions, Ministry of Education, China Agricultural University, Beijing 100193, China

**Abstract:** Arbuscular mycorrhizal fungi (AMF) are universally mutualistic symbionts that colonize the fine roots of most vascular plants. However, the biogeographical patterns and driving factors of AMF diversity of plant roots in grasslands are not well investigated. In this study, we used high-throughput sequencing techniques and bioinformatics to evaluate the AMF richness of 333 individual plant roots in 21 natural grassland ecosystems in northern China, including the Loess Plateau (LP), the Mongolian Plateau (MP), and the Tibetan Plateau (TP). The AMF richness showed a significant parabolic trend with increasing longitude. In regional situations, the AMF richness in the grasslands of the MP ( $60.4 \pm 1.47$ ) was significantly higher than those of the LP ( $46.4 \pm 1.43$ ) and TP ( $44.3 \pm 1.64$ ). Plant traits (including plant families, genera, and functional groups) explained the most variation in the AMF richness across China's grasslands, followed by energy and water; soil properties had the least effects. The results showed the biogeographical patterns of the AMF richness and the underlying dominant factors, providing synthetic data compilation and analyses in the AMF diversity in China's grasslands.

**Keywords:** arbuscular mycorrhizal fungi; biogeography; grassland ecosystems; northern China

## 1 Introduction

Arbuscular mycorrhiza are the mutualistic symbionts formed by plant fine roots infected by Glomeromycota fungi, which are presented in more than 80% of land plants (Chaudhary *et al.*, 2008; Bueno *et al.*, 2017; Botnen *et al.*, 2019). Arbuscular mycorrhizal fungi (AMF) promote nutrient foraging and absorption in the host plants, and the plants allocate photosynthate to the fungi for survival and development (Gavito *et al.*, 2003; Hawkes *et al.*, 2008). In addition, AMF enhance the resilience of plants and maintain ecosystem stability to some extent (Brundrett *et al.*, 2002; Mariotte *et al.*, 2013; Smith *et al.*, 2015). As an important link

**Received:** 2020-11-10 **Accepted:** 2021-03-10

**Foundation:** National Key R&D Program of China, No.2017YFA0604803; National Natural Science Foundation of China, No.31770560

**Author:** Teng Jialing (1992–), PhD, specialized in microbial ecology. E-mail: [tengjl92@gmail.com](mailto:tengjl92@gmail.com)

**\*Corresponding author:** Yu Guirui, Professor, E-mail: [yugr@igsnr.ac.cn](mailto:yugr@igsnr.ac.cn)

between aboveground vegetation and belowground microbes, knowledge regarding the biogeographical patterns of the AMF diversity and the variation mechanisms is crucial to understand the function of AMF and interactions with plants under the background of global climate change (Botnen *et al.*, 2019; Ceulemans *et al.*, 2019; Xu *et al.*, 2020). The biogeographical distribution patterns of species diversity and their mechanisms are one of the core aspects in ecology and biogeography (Wang *et al.*, 2009; Yin *et al.*, 2010; Chu *et al.*, 2020). Compared with macroorganisms, the geographical distribution patterns and mechanisms underlying microbes are not well investigated because of the limitations in quantificational and visualization tools (Crisp, 2001; Decaëns, 2010; Allen *et al.*, 2020; Chu *et al.*, 2020).

Water and energy are important determinants of large-scale biodiversity patterns (Hawkins *et al.*, 2003). Most studies showed that contemporary water, energy, and soil properties were the main factors affecting the spatial distribution of microorganisms (Drenovsky *et al.*, 2010; Heino *et al.*, 2014; Andrew *et al.*, 2018; Chu *et al.*, 2020). Precipitation and temperature directly affect the AMF diversity (Bueno *et al.*, 2017; Ceulemans *et al.*, 2019; Duffy *et al.*, 2019). Precipitation influences the AMF diversity mainly through changes in the soil moisture, evapotranspiration rate, and plant productivity (Nielsen *et al.*, 2010; Zhou *et al.*, 2018). Temperature directly affects colonization, development, and geographical distribution of the AMF richness (Hawkes *et al.*, 2008; Duffy *et al.*, 2019). In addition, the same species would select different survival and development strategies at varied temperatures: adopt a conservative strategy to store energy in vesicles at lower temperatures and aggressive strategies to generate more extraradical mycelia to obtain nutrients at a higher temperature. Therefore, temperature extremes may have been an underrated factor in previous research. Soil properties are mostly studied to analyze the shaping of the AMF community and richness. Soil structure, organic carbon, pH, and nitrogen and phosphorus nutrition (Gavito *et al.*, 2003) cause fine adjustments in the AMF richness and distribution.

AMF occupy a dual niche of both soil and plant roots (Vályi *et al.*, 2016), and besides abiotic factors, there are direct effects from plants. As a symbiont, AMF require photosynthetic products from host plants for survival and development, and host plants allocate photosynthates to various AMF according to selection mechanisms (van der Heijden *et al.*, 2015). Therefore, compared with other microbes, the geographical distribution of AMF is tightly linked to the characteristics of host plants to a certain extent (Davison *et al.*, 2015; Andrew *et al.*, 2018). Plant distribution is determined by water and energy conditions at a large scale. However, knowledge about the joint effects of climate, soil, and plant traits on the AMF richness is limited.

Grassland accounts for approximately more than 40% of the land area in China and is typically fragile ecological regions and sensitive to global changes (Mu *et al.*, 2013; Zhang *et al.*, 2014; Dai *et al.*, 2016; Jiao *et al.*, 2017; Yuan *et al.*, 2017; Wang *et al.*, 2018). AMF is an essential link between aboveground vegetation and belowground microbes. Temperate grassland is one of the regions with high AMF colonization intensity (Öpik *et al.*, 2006). The spatial distribution of AMF and the variation mechanisms are crucial for understanding the function of AMF and their interactions with plants in the context of global climate changes (Steidinger *et al.*, 2020). In this study, we investigated AMF richness in plant roots across 21 natural grassland ecosystems in northern China, including the Loess Plateau (LP), the Mongolian Plateau (MP), and the Tibetan Plateau (TP). Based on the measured data, we analyzed

the biogeographic patterns of the AMF richness and investigated: 1) the longitudinal patterns of variation in the AMF richness in different areas, and 2) the primary factors controlling longitudinal variation.

## 2 Materials and methods

### 2.1 Study sites and sampling

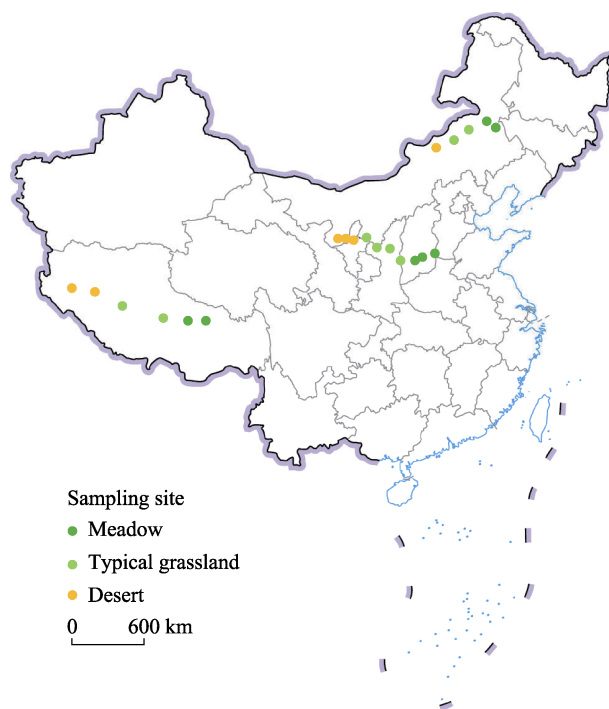
The study area included the Loess Plateau (LP), the Mongolian Plateau (MP), and the Tibetan Plateau (TP) (Figure 1). The sampling sites in the LP were at latitudes from 35.99°N to 37.46°N and longitudes from 104.44°E to 113.36°E and had mean annual temperatures (MAT) of 5.22–11.85 °C and mean annual precipitation (MAP) of 180–493 mm. The sampling sites in the MP were at latitudes from 44.01°N to 45.10°N and longitudes from 114.89°E to 121.04°E and had MAT of 1.08–6.65 °C and MAP of 228–393 mm. The sampling sites in the TP were at latitudes from 31.54°N to 32.41°N and longitudes from 81.23°E to 93.53°E and had MAT of –2.98 to 0.575 °C and MAP of 75–593 mm.

Field sampling was carried in July 2018 at the peak of the growing seasons. The dominant arbuscular mycorrhizal plant species that appeared within a 1-km radius circle were surveyed and identified at each site in natural grassland communities. Three randomly selected individuals of each plant species were collected by removing the soil and other materials adhering to the roots. The fresh fine roots were cut off using sterile scissors and stored in centrifuge tubes in an ice box. Overall, 333 individuals belonging to 41 genera in 17 families were sampled from 21 sites (including meadow, typical grassland, and desert). Further, the topsoil (0–10 cm) was randomly sampled (with eight replicates at each site) to evaluate the physical and chemical properties.

### 2.2 Environmental variables

The temperature, precipitation, and wind-speed values pertaining to the 1970–2000 period were collected from the WorldClimate data platform (<https://www.worldclim.org/>). Dryness index (DI) was computed using the following formula:  $DI = MAP/(MAT + 10)$  (Martonne, 1926). Solar radiation data were obtained from Liu *et al.* (2017) and Tang *et al.* (2017). Potential evapotranspiration data were obtained from the CGIAR-CSI database (<https://cgiarcsi.community/>).

Soil organic carbon (SOC) and nitrogen were determined using an el-



**Figure 1** Geographic locations of sampling sites

emental analyzer (Vario MAX CN, Elementar, Germany). The 150-mg soil samples were soaked in a solution of 10 ml of  $\text{HNO}_3$  overnight and boiled for digestion in a microwave digestion system (Mars X press Microwave Digestion System, CEM Corporation, NC, Matthews, USA). The cooled solutions were adjusted to 15 ml and determined concentration of carbon and nitrogen using an elemental analyzer. Soil total phosphorus (STP) and available phosphorus (SAP) were determined using an inductively coupled plasma-optical emission spectrometry (ICP-OES, Optima 5300 DV, USA). The 0.05-g soil samples were soaked in a solution of 6 ml of  $\text{HNO}_3$  and 3 ml of HF overnight, then the solutions were boiled for digestion (Mars X press Microwave Digestion System, CEM Corporation, NC, Matthews, USA) and removed the acid by 0.5 ml of  $\text{HClO}_4$ . The cooled solutions were adjusted to 15 ml for the concentration of P. The soil pH and oxidation reduction potential (ORP) were determined using a multiparameter conductivity/pH tester (MYRON L, Ultrameter II TM, USA) in a 1:2.5 soil-to-water ratio.

All environmental variables in the analysis are shown in Table 1.

**Table 1** List of environmental factors

		Variables	Abbreviation	Unit
Climate	Energy	Mean annual temperature	MAT	$^{\circ}\text{C}$
		Mean temperature of coldest month	MTCM	$^{\circ}\text{C}$
		Mean temperature of warmest month	MTWM	$^{\circ}\text{C}$
		Annual total radiation	Rd	$\text{MJ m}^{-2}\text{yr}^{-1}$
		Maximum monthly radiation	$\text{Rd}_{\max}$	$\text{MJ m}^{-2}\text{day}^{-1}$
		Minimum monthly radiation	$\text{Rd}_{\min}$	$\text{MJ m}^{-2}\text{day}^{-1}$
		Minimum photosynthetically active radiation	$\text{PAR}_{\min}$	$\text{mol m}^{-2}\text{day}^{-1}$
		Maximum photosynthetically active radiation	$\text{PAR}_{\max}$	$\text{mol m}^{-2}\text{day}^{-1}$
		Potential evapotranspiration	$\text{ET}_0$	$\text{mm yr}^{-1}$
	Water	Mean annual precipitation	MAP	mm
		Precipitation of the driest month	PDM	mm
		Precipitation of the wettest month	PWM	mm
	Other	Maximum monthly wind speed	$\text{Wind}_{\max}$	$\text{m s}^{-1}$
		Dryness index		
Soil		Organic carbon	SOC	%
		Carbon-Nitrogen ratio	CN	/
		Total phosphorus	STP	$\text{mg kg}^{-1}$
		Available phosphorus	SAP	$\text{mg kg}^{-1}$
		$\text{NO}_3^-$	/	$\text{mg kg}^{-1}$
		$\text{NH}_4^+$	/	$\text{mg kg}^{-1}$
		pH	/	/
		Oxidation reduction potential	ORP	mv

### 2.3 Molecular analysis

DNA was extracted from 70 mg freeze-dried roots using a PowerSoil kit (MOBIO Laboratories, USA) according to the manufacturer's instructions. Primers GeoA2/AML2 (first PCR,

targeting the SSU region) (Schwarzott and Schüßler, 2001; Lee *et al.*, 2008) and NS31/AMDGR (second PCR) (Simon *et al.*, 1992; Sato *et al.*, 2005) were used for amplification. After PCR and purification, a DNA library was constructed and run on a MiSeq Illumina platform at Biobit Biotech Inc., Chengdu, China.

Sequencing data were analyzed using FLASH (V1.2.7), Qiime (V1.9.0), and Usearch (v8.0) software. The number of operational taxonomic units (OTUs) was obtained using Qiime (V 1.9.0); each OTU had > 97% sequence similarity. A randomly selected subset of 408 sequences per sample was used in the subsequent analysis. Richness (observed species, indicating phylotype richness) was calculated and analyzed using Qiime (V 1.9.0).

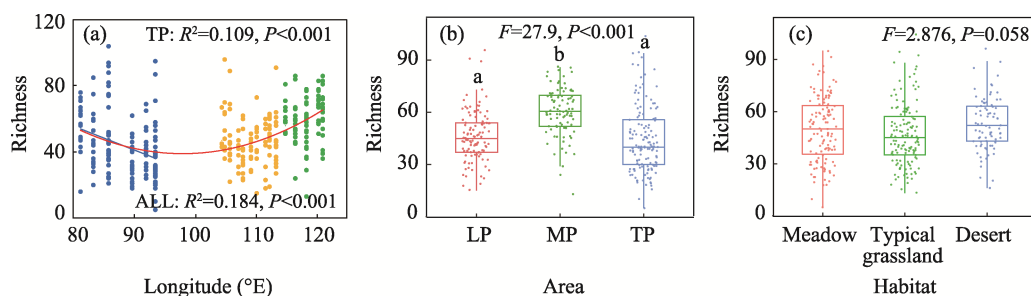
## 2.4 Data analysis

A one-way analysis of variance (ANOVA) with least significant difference (LSD) post-hoc testing was used to test the significance of the effects of the study area, habitats, and plant traits on the AMF richness. Relationships between the AMF richness and environmental factors were determined using Pearson correlation analysis, and linear or square regression analysis was used to select the best fitting model with the highest  $R^2$  value. Variation partitioning analysis (VPA) was used to assess the effects of climate, soil, and plant factors on the AMF richness. Because of the high autocorrelation between environmental variables, only one variable was chosen from among the variables with significant correlations to avoid collinearity. All analyses were conducted using *R* software (version 3.6.3, R Development Core Team).

## 3 Results

### 3.1 Biogeographical patterns in AMF richness

The AMF richness showed a significant parabolic trend with increasing longitude ( $R^2 = 0.184$ ,  $P < 0.001$ , Figure 2a). However, in the regional situations, only the AMF richness of the TP showed an obvious trend with longitude ( $R^2 = 0.109$ ,  $P < 0.001$ ) (Figure 2a). The AMF richness was considerably different in different areas ( $F = 27.9$ ,  $P < 0.001$ ) (Figure 2b). The richness on the MP ( $60.4 \pm 1.47$ ) was significantly higher than that on the LP ( $46.4 \pm 1.43$ ) and TP ( $44.3 \pm 1.64$ ). However, there was no significant difference in the richness of different habitats ( $F = 2.88$ ,  $P = 0.058$ ) (Figure 2c).



**Figure 2** Longitudinal trends in arbuscular mycorrhizal fungi (AMF) richness (a) and AMF richness in different (b) areas and (c) habitats. Solid line represents model-predicted values of richness at a range of longitudes. Different letters indicate significant difference in richness between two groups.



**Table 2** Correlation coefficients and significance between arbuscular mycorrhizal fungi (AMF) richness and environmental variables

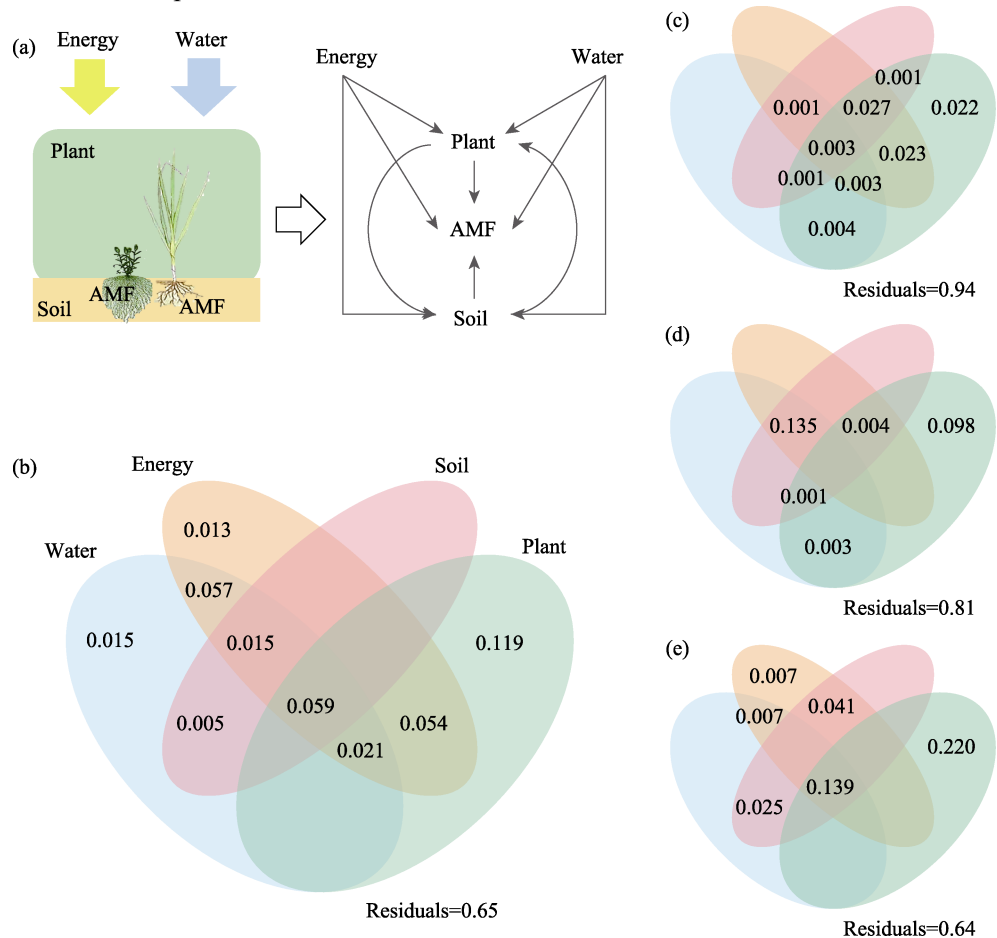
	Variables	ALL	LP	MP	TP
Energy	MAT	0.052	0.074	<b>0.245*</b>	−0.118
	MTCM	<b>−0.190**</b>	0.036	<b>0.265*</b>	<b>−0.188*</b>
	MTWM	<b>0.216**</b>	0.079	0.191	0.048
	Rd	<b>−0.155**</b>	−0.063	−0.181	<b>0.299**</b>
	Rd <sub>max</sub>	0.022	−0.052	−0.123	<b>0.383**</b>
	Rd <sub>min</sub>	<b>−0.298**</b>	−0.093	0.13	0.01
	PAR <sub>max</sub>	−0.069	−0.069	−0.207	<b>0.341**</b>
	PAR <sub>min</sub>	<b>−0.297**</b>	−0.099	−0.015	−0.052
	ET <sub>0</sub>	<b>0.196**</b>	<b>0.241*</b>	<b>0.245*</b>	<b>0.189*</b>
Water	MAP	<b>−0.213**</b>	−0.094	0.16	<b>−0.352**</b>
	PDM	<b>−0.203**</b>	0	−0.201	0.003
	PWM	−0.076	−0.039	0.2	<b>−0.360**</b>
Other	Wind <sub>max</sub>	<b>0.255**</b>	<b>0.200*</b>	−0.011	<b>0.244**</b>
	DI	<b>−0.257**</b>	−0.183	<b>−0.242*</b>	<b>−0.211*</b>
Soil	SOC	<b>−0.160**</b>	−0.027	0.128	<b>−0.225**</b>
	CN	−0.056	−0.016	0.012	<b>0.244**</b>
	STP	<b>−0.239**</b>	−0.121	−0.003	−0.076
	SAP	0.052	0.101	<b>−0.344**</b>	−0.157
	NH <sub>4</sub> <sup>+</sup>	<b>−0.203**</b>	−0.173	−0.1	<b>−0.172*</b>
	NO <sub>3</sub> <sup>−</sup>	−0.033	−0.145	−0.147	−0.156
	pH	<b>0.116*</b>	−0.007	<b>0.253*</b>	<b>0.266**</b>
	ORP	<b>−0.211**</b>	−0.099	−0.015	−0.052

TP, respectively (Figure 4). Plant traits played a more important role compared with climate and soil variability in determining the AMF richness across China's grasslands (Figure 4), followed by energy and water; soil had the least effects. However, the factors impacting the AMF richness varied between different areas in this study. Plant traits, energy, and soil played greater roles in affecting the AMF richness of the LP and the TP, whereas, energy, soil, and water contributed more to the MP. Moreover, interactions among these factors contributed to considerable explanations, and a single factor explained less variation besides plant traits.

#### 4 Discussion

This study provides a comprehensive documentation of the biogeographical patterns of the AMF richness in plant roots in grassland ecosystems in northern China. Studies have shown that the geographical distribution patterns and environmental drivers of belowground microbes are similar to those of aboveground plant communities (Prober *et al.*, 2015; Yang *et al.*, 2017). Climatic factors (primarily energy and water) control the distribution of terrestrial biodiversity (Wang *et al.*, 2009; Nielsen *et al.*, 2010), which is in agreement with our findings. The AMF richness of plant roots showed a geographical pattern that initially decreased

significantly and then increased along the longitude; this was mainly determined by the solar radiation and temperature.



**Figure 4** Effects of water, energy, soil, and plant factors on the arbuscular mycorrhizal fungi (AMF) richness patterns (a. Diagrams showing biotic and abiotic factors affecting AMF richness; b. Entire grasslands; c. Loess Plateau (LP); d. Mongolian Plateau (MP); e. Tibetan Plateau (TP))

In recent years, many emphases have been placed on the predominant role of energy in shaping geographical biodiversity patterns (Wang *et al.*, 2009; Pinel-Alloul *et al.*, 2013). Energy takes distinct forms, and both forms of energy may influence biodiversity through different mechanisms (Allen *et al.*, 2007; Wang *et al.*, 2009). The effects of energy on AMF richness arise from both habitat and resources. Solar radiation directly determines the habitat conditions of host plants and soil fungi. Furthermore, solar radiation is a fundamental resource for plants to produce photosynthates and allocate to roots for AMF. In this study, the AMF richness was mainly controlled by variations in  $Rd_{min}$  and decreased with increasing  $Rd_{min}$ , which may be attributed to intense radiation restricting survival and development of host plants and AMF. Previous research has shown that temperature is usually a main factor affecting the distribution of the AMF richness (Gai *et al.*, 2012; Davison *et al.*, 2015). Different AMF have their unique optimum temperature ranges, and extreme temperatures are unfavorable for colonization, multiplication, and spread; minimum, optimum, and lethal



temperatures are key parameters determining the AMF niche (Soudzilovskaia *et al.*, 2015).

As symbiotic microbes that depend on plants for energy, the AMF diversity must be significantly influenced by the host plant (Merckx *et al.*, 2017). Various studies have found that aboveground diversity, community structure, and productivity are determining factors of the AMF richness and community (Johnson *et al.*, 2004; De Deyn *et al.*, 2011; Merckx *et al.*, 2017) because plant photosynthetic products are a major source of AMF. Furthermore, host plants may allocate more energy to collaborators who provide more nutrients, and AMF may provide more nutrients for those who allocate more energy (Bever *et al.*, 2009; Kiers *et al.*, 2011; Fellbaum *et al.*, 2014). Therefore, functionally similar plant species may choose functionally similar AMF on the basis of this mutual benefit, and plant functional groups may be an important factor affecting AMF richness. Unexpectedly, we did not find a significant variation of AMF richness in different plant functional groups, although plant taxonomy significantly affected AMF richness. This may be due to the functional redundancy of AMF. Different groups of fungi can be substituted for each other in function; thus, changes in diversity had no obvious effects on function.

As microbes that occupy a dual ecological niche of soil and plant roots, AMF are closely related to soil properties. Krüger *et al.* (2015) recorded the AMF community variation in soils on a scale and in severe phosphorus deficiency conditions and found that strong environmental filtration is the main driver of AMF diversity and soil phosphorus availability is the most important soil variable. Phosphorus availability is the basic soil condition that affects mycorrhizal function (Smith *et al.*, 2008). Compared with soil nitrogen, soil phosphorus has stronger effects on AMF (Treseder, 2004; Twieg *et al.*, 2007; Dickie *et al.*, 2009). The results of this study showed that soil phosphorus was the dominant soil factor and negatively correlated with the AMF richness. In addition, soil pH was also an important factor affecting mycorrhizal colonization and spatial distribution; overall, AMF preferred alkaline soil. The grassland soil was prevalently weakly alkaline, and the soil pH in our study area was 6.6–8.4 and mostly > 7. Under suitable pH conditions, the AMF richness increased with increasing soil pH. In particular, the average soil pH was 8.1 on the Loess Plateau, where soil pH had no significant effects.

The climate, soil, and plant variables considered here provided only a partial explanation for the variations in the AMF richness along the environmental gradient, and more than half of the variation in the AMF richness remained unclear. This is most likely due to the influence of random factors such as dispersal limitation (Jenkins *et al.*, 2007; Kivlin, 2020) and ecological drift (Queloz *et al.*, 2011), and further analysis is needed.

## 5 Conclusions

This study provided a comprehensive documentation of the biogeographical patterns of the AMF richness in plant roots in China's grasslands and quantified the potential influencing factors. The AMF richness in plant roots initially decreased and then increased with increasing longitude in China. The AMF richness on the MP was significantly higher than that on the LP and the TP. Climate, soil, and plant variables jointly determined the AMF richness in China's grasslands. Plant traits played a more important role in determining the AMF richness, followed by energy and water; soil had the least effects. However, the generality of

these results, regarding the relative importance of climate, soil, and plant factors, may be further investigated by examining the effects of random factors to evaluate the biogeographical patterns of AMF more comprehensively.

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