RESEARCH ARTICLE

Plant community and soil properties drive arbuscular mycorrhizal fungal diversity: A case study in tropical forests

Jing Zhang^{1,2}, Changxin Quan^{1,3}, Lingling Ma^{1,3}, Guowei Chu¹, Zhanfeng Liu^{1,2,4}, Xuli Tang^{1,4,*}

1 Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China

2 Southern Marine Science and Engineering Guangdong Laboratory (Guangzhou), Guangzhou 511458, China

3 College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China

4 Center for Plant Ecology, Core Botanical Gardens, Chinese Academy of Sciences, Guangzhou, 510650, China

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ABSTRACT

The mutual interdependence of plants and arbuscular mycorrhizal fungi (AMF) is important in carbon and mineral nutrient exchange. However, an understanding of how AMF community assemblies vary in different forests and the underlying factors regulating AMF diversity in native tropical forests is largely unknown. We explored the AMF community assembly and the underlying factors regulating AMF diversity in a young (YF) and an old-growth forest (OF) in a tropical area. The results showed that a total of 53 AMF phylogroups (virtual taxa, VTs) were detected, 38 ± 1 in the OF and 34 ± 1 in the YF through high-throughput sequencing of 18S rDNA, and AMF community composition was significantly different between the two forests. A structural equation model showed that the forest traits indirectly influenced AMF diversity via the plant community, soil properties and microbes, which explained 44.2% of the total observed variation in AMF diversity. Plant diversity and biomass were the strongest predictors of AMF diversity, indicating that AMF diversity was dominantly regulated by biotic factors at our study sites. Our study indicated that forest community traits have a predictable effect on the AMF community; plant community traits and soil properties are particularly important for determining AMF diversity in tropical forests.

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1 Introduction

Arbuscular mycorrhizal fungi (AMF) are important ecological components of soils, forming symbioses with about 80% of vascular plants in terrestrial ecosystems (Smith and Read, 2008; Gao et al., 2019). AMF exhibit crucial roles in ecosystem: they are related with plant diversity (Grime et al., 1987; van der Heijden et al., 1998), maintain or increase ecosystem net primary production (van der Heijden et al.,

1998; Vogelsang et al., 2006) and improve soil structure (Wright and Upadhyaya, 1998; Wilson et al., 2009). The extent to which these mentioned above is determined by the AMF community composition (van der Heijden et al., 1998; Lovelock and Ewel, 2005). For example, higher AMF diversity is associated with higher plant diversity, biomass and nutrient uptake (van der Heijden et al., 1998). Specific AMF taxa appear to show different ecological functions. For example, Glomeraceae is expected to confer pathogen protection to plants (Powell et al., 2009), while Gigasporaceae and Scutellosporaceae are of special benefit for phosphorus (P) uptake (Treseder, 2005) and Acaulosporaceae is competitive in low-P soil (Dodd et al., 2000). Knowledge of AMF

* Corresponding author

E-mail address: xltang@sbcg.ac.cn (X. Tang)

community composition is therefore vital for understanding the functions of AMF in ecosystems.

Estimation of AMF community composition has traditionally been performed by counting identified AMF spores, but molecular methods and high-throughput sequencing technology are now more frequently used (Redecker et al., 2013). Approximately 250 AMF species have been identified worldwide on the basis of spore morphology, while the number of AMF species that may be identified via molecular techniques is expected to exceed 1500 (Börstler et al., 2006; Kivlin et al., 2011), although the number of morphological species is different with molecular techniques. Global sampling showed that the number of AMF phylogroups (virtual taxa, VTs) was 341 (Öpik et al., 2013), and this database is the most commonly used in AMF studies (<https://maarjam.botany.ut.ee/>). However, most of the studies related to AMF diversity have been conducted in grasslands (Sun et al., 2013; Hiiesalu et al., 2014), farmlands (Bainard et al., 2015; Wang et al., 2015) and pot culture experiments (Joner, 2000; Wang et al., 2008), and less information is available for tropical forests, especially native tropical forests with a rich plant composition (Rodríguez-Echeverría et al., 2017). A recent study found distinct difference in the microbial community composition in forests and pasture, but no significant difference of the microbial community in forests of different ages (Flores-Renteria et al., 2020). Sheldrake et al. (2017) identified 72 operational taxonomic units (OTUs) in a long-term litter removal experiment in a tropical forest in Panama, while 147 OTUs were identified in different vegetation types (grasslands, savannas, dry forests and miombo) in a dry tropical area in Africa (Rodríguez-Echeverría et al., 2017). Hence, more information about AMF diversity in tropical regions is needed, especially in native forests.

AMF community composition is thought to be influenced by a series of biotic and/or abiotic factors (Moora, 2014; Chaudhary et al., 2016; Rodríguez-Echeverría et al., 2017). Different vegetation types are believed to harbor different AMF communities (Kivlin et al., 2011) because of diverse host preferences among AMF species (Husband et al., 2002; Gosling et al., 2013). AMF community composition also changes with plant growth and plant community (Chaudhary et al., 2016; Wang et al., 2018) and bacterial dynamics (Pivato et al., 2009; Mahanta et al., 2018). In addition, abiotic factors affect AMF diversity, for example, litter removal (Sheldrake et al., 2017), nitrogen (N) and P addition (Jiang et al., 2018; Sheldrake et al., 2018; Zhao et al., 2018) and legacies of land use (Negrete-Yankelevich et al., 2020) because different AMF species have different nutrient acquisition abilities (Cozzolino et al., 2016). Mathematical models have been used to discriminate the most important factors influencing AMF composition. Soil properties such as soil pH, nitrate, organic matter and available phosphorus concentration were proven to relate to the composition of microbial community with different land cover but originated from tropical rain forest (Flores-Renteria et al., 2020). Studies also found the composition of AMF community also related to soil properties,

for example, precipitation and soil moisture are the most important determinants of AMF communities (Veresoglou et al., 2013), soil texture was the strongest predictor of the AMF community composition in an ecotone between pastures and agricultural fields (Xiang et al., 2014), and AMF diversity in forest ecosystems is mainly driven by different habitat types with latitude changes (Veresoglou et al., 2019). However, it is unclear whether soil properties have a direct effect on AMF or if they influence plant traits that in turn influence the AMF community composition in tropical forests.

Given the scarcity of AMF data from tropical native ecosystems, two different well-studied native tropical forests were selected to investigate the AMF composition and to analyze how AMF diversity was related to a number of different biotic and abiotic factors. A previous study indicated a larger belowground carbon flux in an old forest (OF, 60% of the total carbon fixed) than in a young forest (YF, 45%, Tang et al., 2011). Higher plant diversity and biomass (Peng and Wang, 1983; Tang et al., 2011) and more severe P deficiency have been observed (Huang et al., 2013) in OF than in YF. According to the functional equilibrium model (Johnson, 2010), we hypothesized that AMF diversity would be higher in OF than in YF, since the carbon (C) allocated to AMF can be expected to be proportional to the C allocated belowground (Hawkes et al., 2008), and P deficiency generally leads to higher AMF diversity (Khade et al., 2010). We also attempted to explain AMF diversity variation using the measured abiotic factors, combined with plant traits and microbe-related factors, to ascertain the most important drivers of AMF community assembly. The results will provide novel insight into the AMF community composition and the driving factors of the AMF community in natural tropical forests.

2 Materials and methods

2.1 Site description

This study was carried out in the Dinghushan Biosphere Reserve (DBR, 23°10'N, 112°32'E) in southern China (Fig. 1). The DBR, covering an area of 1200 ha, was established to protect undisturbed natural monsoon evergreen broad-leaved forests in the 1950s. The DBR has a typical tropical monsoon climate, with mean annual precipitation of 1927 mm, nearly 80% of which falls in the hot-wet season (April–October), while the remaining 20% falls in the cool-dry season (October–March). The annual mean temperature in this area is 22.3°C. The DBR bedrock is classified as Devonian sandstone and shale (He et al., 1982; Wu et al., 1982). The soil is classified as lateritic red earth (oxisol), with a pH lower than 4 in the top 10 cm (Appendix A). More information about this study site can be found in Zhang et al. (2017).

Two forest types, a young forest (YF) and an old-growth forest (OF), were selected for this study. The OF has been well protected from human disturbance for more than 400 years, while the YF is the result of reforestation after a clear cut in the 1950s (Shen et al., 2001). The OF and YF experience the

Fig. 1 Location of our study sites (panel A) and pictures of the young (YF) and the old-growth forest (OF).

same climate and environmental changes, as these two sites are only 1 km apart.

The YF is located in the periphery of the DBR. *Pinus massoniana* Lamb. was planted at this site in the 1950s. Broad-leaved tree species, including *Cratoxylum cochinchinense* (Lour.) Bl., *Mallotus paniculatus* (Lam.) Müll. Arg., and *Evodia lepta* (Spreng.) Merr. then appeared gradually. The YF with dense understory plants is dominated by *Dicranopteris pedata* (Houtt.) Nakaike. The OF represents zonal vegetation type with a complex community structure. *Castanopsis chinensis* (Spreng.) Hance, *Gironniera subaequalis* Planch., *Schima superba* Gardner et Champ., *Syzygium acuminatissimum* (Blume) DC. and *Syzygium rehderianum* Merr. et L. M. Perry. dominate the upper canopy. *Aidia canthioides* (Champ. ex Benth.) Masam, *Psychotria rubra* (Lour.) Poir. and *Blastus cochinchinensis* Lour. dominate the understory, and *Cryptocarya concinna* Hance, *Machilus chinensis* (Champ. ex Benth.) Hemsl. and *Lophatherum gracile* Brongn., dominate the herbaceous layer. Arbuscular mycorrhizae are the major mycorrhizal symbionts in both the YF and the OF with more than 70% of the plants are AMF hosts in these forests (Zheng et al., 2013).

2.2 Field sampling

Twelve 10 m × 10 m plots were randomly arranged in each forest for soil sampling in July 2015. A composite topsoil (0–10 cm depth) sample was collected in each plot using a five-spot pattern with a 2.5 cm diameter auger. Each soil sample was thoroughly mixed and divided into two subsamples. One subsample (approximately 100 g) was stored at –80°C in a freezer until DNA extraction, analyses of phospholipid fatty acids (PLFAs) and acid phosphatase activity (APA) (analyzed within 15 days). Another subsample (approximately 300 g) was air-dried for the measurement of physicochemical soil

properties. Soil properties, including pH, the soil organic carbon (SOC) content, and soil nitrogen (Appendix A), were analyzed with the methods described in Liu et al. (1996). For the measurement of PLFAs and APA, the method of Bossio and Scow (1998) and Schneider et al. (2000) was followed, respectively.

All trees with diameter at breast height (DBH) > 1 cm or > 1.3 m in height were investigated in each plot. The species and DBH of each AMF tree (Niu, 1990; Zheng et al., 2013) were recorded in all plots when soil samples were collected. The corresponding biomass of each plot was calculated as described by Wen et al. (1997).

2.3 Molecular identification of AMF

Soil DNA was isolated from 0.5 g of thoroughly mixed soil, employing the Powersoil DNA Isolation kit (Mo Bio Laboratories, Carlsbad, CA, USA). The DNA was then diluted to 10–20 ng µL^{–1} with double-distilled H₂O for nested PCR, after the integrity of the DNA was tested. Two pairs of primers were selected to amplify the partial small subunit (SSU) rRNA gene fragment: the universal eukaryotic NS1/NS4 primers (White et al., 1990) and the AMF-specific AMV4.5NF/AMDGR primers (Lumini et al., 2010). The AMV4.5NF/AMDGR primer pair was augmented with Illumina high-throughput sequencing adapters and a 12 bp barcode sequence for multiplexing, leading to the following constructs: AMV4.5NF: AACGCACGC-TAGCCCAAGCTCGTAGTTGAATTCG; and AMDGR: CCCAACTATCCCTATTAATCAT (the specific primers are indicated in boldface; the barcode is shown in italics; and the connected bases are underlined).

For the first PCR step, each reaction (20 µL volume) contained 0.75 units of *Ex Taq* DNA polymerase (TaKaRa, Dalian, China), 1 × *Ex Taq* loading buffer (TaKaR), 0.2 mmol L^{–1} dNTP mix, 0.2 µmol L^{–1} of each primer and

50 ng of template DNA (TaKaRa), and the following reaction conditions were applied: 94°C for 5 min, followed by 6 cycles at 94°C for 45 s, 51°C for 45 s, and 72°C for 1 min, with a final step of 72°C for 10 min. The first amplification product was diluted 10 times with dH₂O (1:10). For the second PCR step (30 µL volume), the same conditions were employed as in the first step, except that the amount of template DNA was 1 µL in this PCR procedure, and 30 PCR cycles were performed instead of 6. This procedure was repeated 3 times for each sample during the second round of PCR, and the products were subsequently mixed. All PCR amplifications were performed in a Bio-Rad T100 thermal cycler (Bio-Rad T100, Mississauga, ON, Canada). Subsequently, 2 µL of the PCR products was subjected to 1% agarose gel electrophoresis using DL2000 as the marker and then purified using the EZNATM Gel Extraction Kit (Omega, USA) after excising the bands. Each PCR product was mixed at equimolar concentrations and then subjected to sequencing on an Illumina HiSeq2500 platform.

2.4 Bioinformatics analysis

The bioinformatics analysis of the high throughput sequencing data was performed following the methods described by Vasar et al. (2017) and Öpik et al. (2013). Based on analysis of the quality of the Illumina high-throughput sequencing reads, reads showing significant degradation of the 3'-end sequence, a quality score lower than 20, adapter contamination or N-exceeding sequences were removed and excluded from further analysis by VSEARCH and USEARCH (v9.0.2132, Edgar et al., 2011) using the QIIME platform (Caporaso et al., 2010). Moreover, the barcode sequence was trimmed to a minimum length of 250 bp by VSEARCH (Caporaso et al., 2010). The data set was checked for chimeric sequences in reference database mode (the MaarjAM database, <https://maarjam.botany.ut.ee/>, Opik et al., 2010), and all potential chimeric sequences were removed before further analysis. The remaining sequences were assigned to virtual taxa (VTs) with the MaarjAM database as the reference database by BLAST v2.5 (Camacho et al., 2009) with the criteria of sequence similarity level $\geq 97\%$ and e-value $< 1e-60$ (Jiang et al., 2018). VTs less than 0.001% in the database were discarded.

AMF α diversity was represented by the Shannon–Wiener index (H' , Eq. (1)). The minimum number of sequencing reads among all samples was 8804; therefore, 8804 effective sequence reads ($n = 1000$ iterations) were randomly extracted from each sample to calculate the α diversity,

$$H' = -\sum [p_i \times \ln(p_i)] \quad (1)$$

($p_i = n_i/N$, where n_i is the number of individuals of VT i , and N is the total number of individuals across all VTs).

2.5 Nucleotide sequence accession numbers

All sequencing data analyzed in this study have been

deposited in the NCBI Sequence Read Archive (SRA) under accession numbers SRR6283070–SRR6283093.

2.6 Statistical analyses

All data were checked for a normal distribution and homogeneity of variance before statistical analysis, and data with a non-normal distribution were $\log(x + 1)$ transformed to ensure a normal distribution. To compare AMF diversity between the YF and OF, we ran an independent samples t test with SPSS 22.0 (SPSS Inc., Chicago, IL, USA).

The relative abundance of AMF VTs in each sample was employed for the AMF community-related analysis. Dissimilarities in species composition of AMF communities between YF and OF were analyzed by nonmetric multidimensional scaling (NMDS), using R package “VEGAN” with the Bray–Curtis dissimilarity index (“metaMDS” function, Oksanen et al., 2016). The difference in AMF community composition between the YF and OF was analyzed by permutational multivariate analysis of variance (PERMANOVA) using PAST 3.0 software (<https://folk.uio.no/ohammer/past/>). The corresponding two-dimensional NMDS ordination plots (“enfit” function from R package “VEGAN”) was used to correlate AMF community composition with environmental factors.

A structural equation model (SEM) was applied to distinguish the direct and indirect influence of forest traits (YF or OF) on AMF diversity (α diversity, Shannon–Wiener index). We hypothesized that the vegetation community either directly or indirectly influences AMF diversity through the effects of soil nutrients and microbes (only the significant environmental index ($P < 0.05$) in the NMDS with environmental factor analysis was selected). The plant community index was one synthetic variable of the first principal component (PC1) for AMF tree diversity and biomass, explaining 87.8% of the total variability. The soil index was another synthetic variable derived from PC1 for soil moisture, available N, availability of P (available P/total P), soil organic carbon (SOC) and the pH value, explaining 75.50% of the variability. The microbe-related index was the PC1 component for APA and total PLFAs, explaining 87.4% of the total variability. The fitness of the model was evaluated based on the following criteria: $X^2/df < 2$, $P > 0.05$, root mean square error of approximation < 0.07 and goodness-of-fit index (GFI) > 0.9 (Hooper et al., 2008). SEM was conducted using the Amos 17.0 software program (Amos Development Corporation, Crawfordville, FL, USA); the theoretical model is shown in Fig. 5A.

3 Results

3.1 AMF diversity and community composition

A total of 966 456 SSU rRNA sequences obtained in this study on the basis of a 97% similarity level were assigned to 53 AMF VTs based on the MaarjAM database (Fig. 2). The number of

Fig. 2 Arbuscular mycorrhizal fungi (AMF) phylogroups (VTs) number (panel A) and AMF diversity (Shannon index, panel B) in the YF and OF in DBR. Data are shown as mean $\pm$ SD ($n = 12$). YF is young forest, and OF is old-growth forest, * represents significant difference between YF and OF at $P < 0.05$.

AMF VTs identified in the YF (35 ± 1) was significantly lower than that identified in the OF (38 ± 1) ($P < 0.05$, Fig. 2A). In total, 14 out of 53 AMF VTs were the dominant ($> 1\%$) VTs at these study sites, including VT24 (belonging to Acaulosporaceae), VT82 (belonging to Glomeraceae) and VT89 (belonging to Glomeraceae) etc. (Fig. 3). VT348 (belonging to Paraglomeraceae) was the richest species at our study sites accounting for $35.87 \pm 7.89\%$ of all AMF VTs. Among all the dominant VTs, VT124 (belonging to Glomeraceae), VT126 (belonging to Glomeraceae) and VT369 (belonging to Glomeraceae) differed significantly between the YF and the OF (Fig. 3).

Fig. 3 The relative richness of the dominant arbuscular mycorrhizal fungi phylogroups (VTs) ($> 1\%$) in the young forest (YF) and the old forest (OF). * and ** indicate that the VT percentage differed significantly at $P < 0.05$ and $P < 0.01$ respectively between the YF and OF ($n = 12$).

In general, all the obtained VTs were classified as 7 AMF families in our study forests. Glomeraceae and Paraglomeraceae were the dominant AMF families and accounted for

more than 95% of all the AMF (Table 1). The relative abundance of Gigasporaceae was significantly higher in the OF ($0.60 \pm 0.25\%$) than in the YF ($0.08 \pm 0.03\%$), while the relative abundance of Acaulosporaceae, and Ambisporaceae was significantly lower in the OF than in the YF ($P < 0.05$, Table 1).

Table 1 Proportions of Arbuscular mycorrhizal fungi (AMF) phylogroups (VTs) classified by family in the YF and OF.

Family	YF (%)	OF (%)
<i>Glomeaceae</i>	55.95 ± 5.62	57.0 ± 8.15
<i>Paraglomeraceae</i>	37.14 ± 5.85	41.23 ± 8.35
<i>Gigasporaceae</i>	0.08 ± 0.03	$0.60 \pm 0.25^*$
<i>Acaulosporaceae</i>	$2.49 \pm 1.05^*$	0.48 ± 0.41
<i>Ambisporaceae</i>	$4.29 \pm 1.17^*$	0.48 ± 0.11
<i>Achaesporaceae</i>	0.05 ± 0.01	0.21 ± 0.13
<i>Claroideoglomeraceae</i>	0.003 ± 0.001	0.003 ± 0.001

^a Data are shown as the means $\pm$ SD ($n = 12$). ^b YF, young forest; OF, old forest. ^c * indicates that the family differed significantly ($P < 0.05$) between the YF and OF, based on an independent sample t test.

The Shannon index calculated by VTs showed that AMF α diversity was significantly higher in the OF (2.10 ± 0.10) than in the YF (1.81 ± 0.08 , $P < 0.05$, Fig. 2B). Non-metric multi-dimensional scaling (NMDS) based on the relative abundance of VTs also indicated a significant difference in the AMF community between these two forests (Fig. 4). The difference in the AMF community between the YF and OF was also supported by the results of one-way PERMANOVA ($F = 2.56$, $P < 0.05$).

3.2 Relationships between AMF diversity and plant community traits, soil properties and microbial-related indexes

The environmental factors fitted onto the NMDS ordinations

(Fig. 4) showed the explanatory variables (plant community traits, soil properties, and the microbe-related index) to the response variables (AMF community composition) for both the YF and OF. AMF community composition significantly varied with specific plant community traits (tree biomass and diversity), microbe-related indexes (total PLFAs, APA) and soil properties (available N, soil water content, SOC, the ratio of AP/TP and the pH value) ($P < 0.05$). However, AMF community did not have significant correlations with grass biomass/diversity, shrub biomass/diversity, total N or total P in soil

A structural equation model was employed to assess the extent of the direct or indirect influence of the forest type on AMF diversity (Fig. 5). The fitted models met the significance criteria ($X^2/df = 1.38$, $P = 0.21$). The plant community traits, soil properties and microbial index explained 44.2% of the variation in AMF diversity. The forest type mediated AMF diversity indirectly through plant, soil and microbial factors (Fig. 5B). Plant community traits (diversity and biomass) were the strongest driving factors for AMF diversity, with a total path coefficient of 0.66 (Fig. 5B). AMF were also influenced by soil nutrients and microbes, with total path coefficients of 0.24 and 0.05, respectively, although the influence were not significant ($P > 0.05$, Fig. 5B).

4 Discussion

4.1 AMF community composition differed between the YF and the OF

The significant difference in AMF diversity and community composition between the young forest (YF) and the old-growth forest (OF) ($P < 0.05$, Figs. 2, 4) confirmed our first hypothesis, suggesting that the OF harbors higher AMF diversity than the YF. The higher AMF diversity in the OF can probably be explained by the higher plant diversity (Peng and Wang, 1983) and biomass (Tang et al., 2011), more severe P

limitation (Huang et al., 2013), and a greater amount of photosynthesis carbon allocated belowground in the OF than in the YF (Tang et al., 2011). Other studies found higher AMF diversity helps plants take up more nutrients (Koide and Kabir,

Fig. 4 Non-metric multidimensional scaling (NMDS) of the community composition of arbuscular mycorrhizal fungi in the young forest (red ellipse, YF) and the old forest (dark ellipse, OF) (stress = 0.19). Significant variables ($P < 0.05$) of soil properties (SOC, AP/TP, aN, pH and SWC), plant properties (tree diversity and tree biomass) and microbial properties (TM, AMFb and APA) were fitted onto the NMDS graph according to the results of “envfit” function analysis in R. Tree diversity, AMF tree diversity; tree biomass, biomass of AMF trees; SOC, soil organic carbon; AP/TP, available P/total P; aN, available N; pH, pH value; SWC, soil water content; APA, acid phosphatase activity; TM, total biomass of microbes (total PLFAs); AMFb, AMF biomass (16:1ω5).

Fig. 5 Structural equation model (panel A, theoretical model; panel B, practical model) showing the hypothesized causal relationships among soil properties, the microbial index, plant-related parameters and AMF diversity (Shannon index). The width of the arrow represents the strength of the standardized path coefficient (*, $P < 0.05$; **, $P < 0.01$). The e value indicates residuals.

2000; Chagnon et al., 2014), therefore, the greater AMF diversity in the OF likely promotes higher plant nutrient uptake and lower interspecific competition, allowing more tree species to coexist. A comparative study revealed higher AMF diversity in macrocosms with a diverse plant composition, alleviating P deficiency to a greater extent than in macrocosms with lower AMF diversity, implying more efficient P uptake by a more diverse AMF community (van der Heijden et al., 1998). Therefore, plants and AMF may facilitate mutual promotion. Alternatively, the diversity of both partners could be indirectly mediated by environmental factors.

VT348 (classified as Paraglomeraceae) was the richest phylogroup (Fig. 3), and Paraglomeraceae was one of the most dominant AMF families in our study sites (Table 1). Paraglomeraceae could not be identified by traditional spore-based techniques (Morton and Redecker, 2001), and identification was possible only when molecular-based phylogenetic techniques became available because the spores of Paraglomeraceae are very similar to Glomeraceae (Oehl et al., 2003). Paraglomeraceae is a significant component in tilled agricultural soil under organic management, and this family was not related to soil physiochemical characteristics (Gosling et al., 2014). Glomeraceae was the secondary dominant family in our study sites (Table 1), which is consistent with studies conducted in several ecosystems, such as a moso bamboo forest (Qin et al., 2017), grassland (Li et al., 2015), and farmland (Hijiri et al., 2006). The high abundance of Glomeraceae occurred because this family protects host roots from pathogen infections (Powell et al., 2009) and/or because of the high tolerance of these species to low pH levels (Qin et al., 2017). Unlike Glomeraceae, the percentages of both Gigasporaceae and Acaulosporaceae differed significantly between the OF and the YF (Table 1). The higher proportion of Gigasporaceae found in the OF and the negative correlations with the available P/total P ratio suggest that Gigasporaceae is beneficial for P uptake in tropical forests, especially in the OF (Appendix B and C). Other studies have found that the well-developed hyphae (Powell et al., 2009) and the P transporter operon (Treseder, 2005) of Gigasporaceae enable these fungi to acquire nutrients and alleviate plant P deficiency. Acaulosporaceae was more abundant in the YF than in the OF but showed no significant correlation with any of the examined environmental factors (Appendixes B and C). The high extracellular phosphatase activity observed in Acaulosporaceae (Vosatka and Dodd, 1998) suggests a strong competitive advantage in low-P soils; in this respect, it was unexpected that this family was more common in the YF than in the OF. This might be due to different AMF infection strategies in different forests since P is also deficient in YF. Differences in morphological, physiology or phenological traits among plant taxa that affect the demand or supply of P lead to variation in plant responses to mycorrhizal infection (Johnson, 2010). Considering the distinct difference in plant composition in these two forests at our study sites (Appendix A), the balance between costs and

benefits of mycotrophy may also insert influence on the composition of AMF community. The underlying mechanism by which AMF regulate plant P acquisition deserves intensive study in the future.

4.2 Relationships among AMF diversity and plant community traits, soil properties and microbial-related indexes

The positive correlation between AMF community composition and plant-related indexes (Fig. 4) is explained by the different nutrient demands of different plants (Smith and Read, 2008). van der Heijden et al. (1998) suggested that AMF represent a major factor contributing to plant biomass and diversity because a diverse AMF community increases plant P use efficiency. The significant positive relationship between tree diversity and AMF community composition (Fig. 4) suggests that the higher diversity of one symbiotic partner promotes higher diversity of the other. AMF diversity was significantly correlated with plant biomass in DBR forests (Fig. 4), which is consistent with studies conducted in old-field ecosystems in North America and a tropical low-flooding forest in Mexico, but inconsistent with the results of grass pot culture experiments (van der Heijden et al., 1998; Koch et al., 2012; Solis-Rodriguez et al., 2020). In addition, the OF was proven as N-rich (Lu et al., 2014) and P-limited (Huang et al., 2013; Hou et al., 2015) forest, plants and AMF may form strong mutualism according to Johnson's trade balance model (Johnson, 2010). Previous study on carbon allocation found greater portion of NPP allocated to belowground in the OF than in the YF (Tang et al., 2011), higher plant C supply in the OF also suggested higher AMF demand (Johnson 2010), which may result in higher AMF diversity in the OF compared with the YF.

Soil-related factors (such as soil organic carbon, and available N) significantly affected AMF community composition (Fig. 4). The synthetical index of all the above factors was observed to be one of the most important factors influencing AMF diversity, with a total path coefficient of 0.24 (Fig. 5B). However, this path coefficient was offset by the negative effect of the AP/TP ratio on AMF diversity and the positive effect of pH on AMF diversity. The positive correlation between the AMF community and soil available N probably resulted from greater plant investment in N-rich extracellular phosphatase (approximately 15% N) (Treseder and Vitousek, 2001) although N is rich at our study sites, phosphatase decomposes organic P to enhance available P for uptake by plants (Houlton et al., 2008). Therefore, AMF probably contributes to plant N uptake due to the large N requirement associated with this P strategy. AMF can provide a considerable amount of P to plants especially at the growth stage when plants have a higher nutrient requirements in wetlands (Bao et al., 2019). The positive correlation between the AMF community and APA and the availability of P (AP/TP, Fig. 4) at our study sites suggests that AMF contributes to P supply in DBR forests, especially in OF, because AMF hyphae can expand the

surface area to absorb P, while AMF extraradical hyphae exhibit high extracellular phosphatase activity, to break down organic P (Vosatka and Dodd, 1998; Khade et al., 2010).

The AMF community composition was also influenced by microbial biomass (Fig. 4, Appendix B). Studies suggest that the microbial community can influence the AMF community. For example, Comamonadaceae species act as mycorrhizal helper bacteria and promote infection by *Glomus mosseae* (Pivato et al., 2009). The significant correlation between AMF diversity and microbial biomass found in our study suggests that AMF interact with the microbial community, although the specific functions of such interactions are unknown (Scheublin et al., 2010). Our results suggested that other microbes probably play a significant role in AMF community assembly, although which specific microbe contributes to AMF diversity was unclear in our study.

5 Conclusions

In conclusion, our results showed that different forests exhibited a significantly different AMF community composition. AMF diversity is influenced by plant community traits, soil physicochemical properties and microbe-related factors, which partly explained the observed variance of the AMF community composition. Among all of the evaluated factors, plant community traits (diversity and biomass) were the dominant factors that influenced the AMF community assembly. This study also revealed a possible connection between the different colonization strategies of various AMF families in different forests. For example, Gigasporaceae, a family showing different strategies for alleviating P deficiency, was richer in the OF than in the YF, due to P deficiency being more severe in the OF than in the YF. This study provides deeper insight into the factors influencing AMF assembly in two natural forests with a rich plant species composition, although a large-scale study is needed in natural tropical forests rich in plant species.

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Conflict of interest

The authors declare that they have no conflict of interest.

Author contributions

J.Z. and X.T. designed the research, J.Z., C.Q. and G.C. collected the samples, J.Z. and Z.L. performed the experiments and analyzed the data and J.Z., C.Q., L.M. and X.T. wrote the manuscript.

Electronic supplementary material

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