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Characteristics of the soil arbuscular mycorrhizal fungal community along succession stages in tropical forest and its driving factors

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Arbuscular mycorrhizal fungi play an important role in mediating plant-soil interactions across succession stages. However, AMF community dynamics which about the change of community composition and member activity remain unclear. To complete the gap knowledge about microbial community dynamics during restoration succession, soil AMF community composition was studied within a tropical forest ecosystem in the Ganshiling nature reserve using high throughput sequencing methods. The results revealed that soil AMF communities characteristics about speices diversity, species composition and microbial correlation network showed significant differences between shrubland (SC) and secondary forest ecosystems, but the same differences were not found between 40-year recovery secondary forest (SF40) and 60-year recovery secondary forest (SF60). Plant community dynamics were the key factor for regulating soil AMF communities among succession stages. An important biotic factor explaining variance in AMF community composition was root biomass. The correlation network analysis showed that although the nodes were similar among succession stages, the complexity of networks was significant higher in SF40 than in SC and SF60, suggesting that AMF communities were more active in SF40, which verified the hypothesis of intermediate disturbance hypothesis. This study provides new insights into AMF community dynamics and their driving factors across succession stages, as well as expanding knowledge of the ecological value of AMF for tropical forest restoration processes.

KEYWORDS

arbuscular mycorrhizal fungi (AMF), microbial community dynamic, root biomass, secondary succession, tropical forest ecosystems

1 Introduction

Mycorrhizal plant-fungal symbiosis as mediators impact organic matter synthesized by plant photosynthesis to exchange with soil nutrients and increases the root surface 100 or 1,000 times by forming extraradical mycelia, causing water and nutrients to be more efficiently absorbed by roots (Finlay, 2008; Barea et al., 2011). Approximately 80% of plants can be

symbiotically interacted with AMF, which forms mycelia within vegetation root cells and colonizes various ecosystems (de Oliveira Freitas et al., 2014). AMF promote host plant resistance (van der Heijden and Horton, 2009; Achatz and Rillig, 2014; Johnson and Gilbert, 2015) and play key roles in the terrestrial ecosystem.

In recent years, most research has paid attention to AMF community dynamics under restoration secondary succession and its influence factors. The host preference of AMF influences the composition of aboveground vegetation communities with secondary succession. Due to its host preference, AMF drives some host plant to benefit more than others (Janos, 1980). Nutrients and water are transferred between individual plants through an underground mycorrhizal established by AMF community, significantly increasing the competitive ability of specific hosts and altering host growth stability. As a result, the composition of above-ground vegetation changes (Janos, 1980; Kikvidze et al., 2010; Shi et al., 2016). Through mycelia formation in roots, AMF mediates plant-soil feedback across succession stages, altering the traits of host plant and improving the hosts' efficiency for absorbing water and nutrients (Jansa et al., 2011; Jansa et al., 2019). As plant communities progress, AMF colonization is the major factor driving plant community dynamics during secondary succession (Zobel et al., 2014). Mycorrhizal colonization expands and/or complements plant root function: mycorrhizal expands the regional range of resource acquisition by increasing the contact area between roots and soil, and mycelial networks established by AMF enhance the soil nutrition and water acquisition capacity of plants. Host plants' access to soil minerals and nutrients with low mobility is enhanced *via* mycelial networks (e.g., phosphorous, zinc, and copper; Jansa et al., 2011). At the same time, by increasing the input of litter and organic matter, AMF communities are influenced by improving soil properties along succession stages (Casazza et al., 2017; Winagraski et al., 2019).

In addition, the effect of AMF host preferences on plant community structure may induce change in AMF community dynamics. Some studies indicate that the variation of host plants also affects the soil properties, like soil moisture and nutrient availability (Jiao et al., 2011). The variations of soil properties determine the nutrient acquisition patterns of host plants under plant succession. Due to the demand relationship between plants and AMF, AMF community structure was indirectly affected by the availability of soil properties (van der Heijden et al., 2008; Casazza et al., 2017). Moreover, aboveground vegetation communities may direct influence AMF community structure through apoplast chemistry (Li et al., 2020).

AMF communities exhibit significant variation in compositional with plant succession ((Kruger et al., 2017). As succession proceeds, AMF community was composed of some compatible species populations in early succession stages to broad species composition. Meanwhile, several studies have demonstrated the prevalence of stochastic processes in AMF communities in mature ecosystems, favouring builds a broad species composition of AMF communities (Kruger et al., 2017). And with plant succession, increased habitat diversity drives the formation of AMF community patches, also leading to variation in AMF community composition (Walker and del Moral, 2003). In addition, with forest disturbance, AMF communities which are highly resilient and equally resistant had no significant change (Soteras et al., 2015). However, it has also been shown that land degradation affects the AMF community dynamics (Asmelash et al., 2016).

In tropical rainforest ecosystems, AMF symbiosis with aboveground vegetation has revealed their potential importance for biogeochemical cycling (Jansa et al., 2011; Parihar et al., 2020), although it is unclear how environmental factors relate to AMF across succession stages. The tropical forest in Ganshiling, Hainan Province was subjected to large-scale logging in the 1980s, making it an important study area for ecosystem succession (Qi et al., 2014). This study addresses the following two questions: i) to explore the change of AMF community composition and its response mechanism and ii) the most influential environmental factors in AMF community dynamic during restoration succession. Revealing AMF community dynamics in the Ganshiling area during restoration succession is of great significance in vegetation restoration, and it could provide insights in regional ecological protection and the sustainable management of forests. Therefore, the characteristics and influencing factors of soil AMF communities were investigated in different forest succession stages of Ganshiling.

2 Materials and methods

2.1 Study area

Ganshiling Natural Reserve served as the site of the study (109°37'~109°41′E, 18°19'~18°24′N), a typical tropical lowland rainforest from 50 to 681 m, and the slope is <50°. It is a typical lowland hilly landform with a tropical marine monsoon climate on Hainan Island, China. The annual average precipitation and temperature are 1800 mm and 25.4°C, respectively. The soil parent material was granite and the main plant species in this area include *Hopea reticulata, Vatica mangachapoi, Koilodepas hainanense, Rhodomyrtus tomentosa, Melastoma sanguineum, Scleria elata* and *Blechnum orientale* (Qi et al., 2014; Mao et al., 2021).

2.2 Sampling collection and environmental variables

Three succession stages in Ganshiling Natural Reserve were studied: 1) the shrub forest (SC; 109°39'~109°41′E, 18°22'~18°23′N), was subjected to logging and formed by artificial disturbance such as construction of nature reserve, and the main plant species include: *Aporosa dioica* and *Olea hainanensis*; 2) the 40 years recovery secondary forest after logging ceased in 1979 (SF40; 109°39'~109°40′E, 18°21'~18°23′N), and the main plant species include: *Garcinia oblongifolia* and *Vatica mangachapoi*; and 3) the 60 years recovery secondary forest after logging ceased in 1959 (SF60; 109°39'~109°40′E, 18°22'~18°23′N), and the main plant species include: *Vatica mangachapoi* and *Hopea reticulata*. Detailed information of each sample were shown in Supplementary Table S1.

In August 2019, five soil samples of 0–10 cm depth were obtained in each plot from three plots of 900 m^2 (30 m × 30 m) in each succession stage. These samples were then divided into portions intended for AMF community (stored at −80°C) and soil property assessment. The soil moisture was measured by gravimetric method (Blake, 1965). A 2 mm screen sieve was used to sieve air-dried soil samples for analyzing soil pH, soil organic carbon (SOC), total nitrogen (TN), and total phosphorus (TP), as well as soil stoichiometric characteristics (e.g., C/N ratio, C/P ratio, and N/P

TABLE 1 Alpha diversity index of AMF community among three successional stages.

Alpha diversity	SC	SF40	SF60
Shannon-Wiener	2.72 ± 0.15[a]	2.29 ± 0.23[b]	2.84 ± 0.17[a]
Simpson	0.83 ± 0.03[a]	0.69 ± 0.06[b]	0.83 ± 0.04[a]
Richness	133.93 ± 4.41[c]	150.87 ± 8.12[b]	177.53 ± 4.08[a]
Pielou	1.28 ± 0.07[a]	1.04 ± 0.10[a]	1.26 ± 0.07[a]
Chao1	173.55 ± 9.1[b]	202.34 ± 11.04[a]	219.15 ± 5.64[a]
Ace	169.49 ± 5.76[c]	193.24 ± 7.92[b]	221.17 ± 5.29[a]
Sobs	133.93 ± 4.41[c]	150.87 ± 8.12[b]	177.53 ± 4.08[a]
Phylogenetic diversity (PD)	7.78 ± 0.23[b]	9.54 ± 0.52[a]	10.41 ± 0.33[a]

Data are presented as mean ± standard deviation. Statistical significance is indicated by different superscript letters ($p < 0.05$).

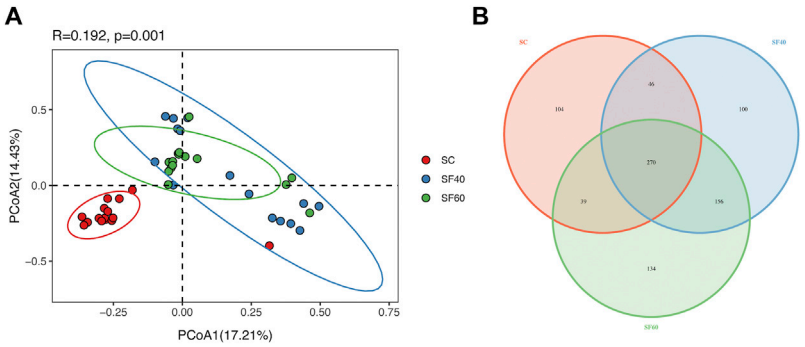

FIGURE 1
Principal coordinate analysis (PCoA) of AMF community **(A)** in succession. Point represent samples with points in the same colour representing samples of the same group. OTUs represent common or unique OTUs to a group in the Venn diagram **(B)**. SC, shrub forest; SF40, the 40a secondary forest; SF60, the 60a secondary forest.

ratio). In order to measure soil pH, soil suspensions were mixed with distilled water. An analysis of the soil TN and TP was conducted using sulfuric acid and potassium sulfate after digestion with sulfuric acid, and then followed with the protocol described by Kjeldahl (Bremner, 1960; Taylor, 2000).

At the same time, vegetation surveys and root samples were conducted on sample plots to obtain aboveground plant community characteristics. Using gravimetric method to measure root biomass. And the vegetation survey data were used to calculate the Shannon-Wiener index, Margalef index and Pielous index.

2.3 DNA extraction and amplicon sequencing

Using the MIO-BIO PowerSoil DNA Isolation Kit (MO BIO Laboratories, Carlsbad, CA, United States), soil DNA was extracted from 250 mg soil samples. The NanoDrop ND-2000 Spectrophotometer (Thermo Fisher Scientific, Waltham, MA, United States) was used to analyze and quantify DNA, which was prepared at a standard concentration for PCR amplification.

For PCR amplification, AMV4.5NF (5′-AAGCTCGTAGTT GAATTTCG-3′) and AMDGR (5′-CCCAACTATCCCTATTAA TCAT-3′) were used as primers (Lumini et al., 2010). An AMF library was constructed using two-step PCR amplification. Target fragments were amplified using specific primers. Later, an Illumina adapter sequence, a primer pad, and a barcode were added into both the forward and reverse target fragments. A 50 ml reaction volume was used for PCR of each sample, comprising 10 ml of 5x buffer, 1 ml of dNTP (10 m/M), 1 U of Phusion DNA High-Fidelity polymerase (New England Biolabs, Ipswich, MA, United States), 1 ml of forward and reverse phasing primers, and 5–50 ng of target sequencing. The reaction volume was supplemented to 50 µl with RNase free ultrapure water. An ABI9700 PCR amplifier (Applied Biosystems, Waltham, MA, United States) was used to amplify AMF. Amplification products were kept warm at 10°C. With the assistance of an AxyPrepDNA Gel Recovery Kit (Axygen Scientific, Corning, NY, United States), electrophoresis was used on an agarose gel to pool and purify PCR products. FTC 3000TM real-time PCR (Fungyln Biotech, Richmond Hill, Ontario, Canada) was used to quantify purified DNA and mixed to an equal molar ratio to perform the second PCR amplification. When the second PCR amplification, the reaction volume change to 40 µl: 5x buffer (8 µl), dNTP (1 µl, 10 m/M), Phusion High-Fidelity polymerase (0.8 U, New England Biolabs, Ipswich, MA, United States), both forward and reverse phasing primer (1 µl), respectively, and DNA template (5 µl) and RNase free ultrapure water (5 µl).

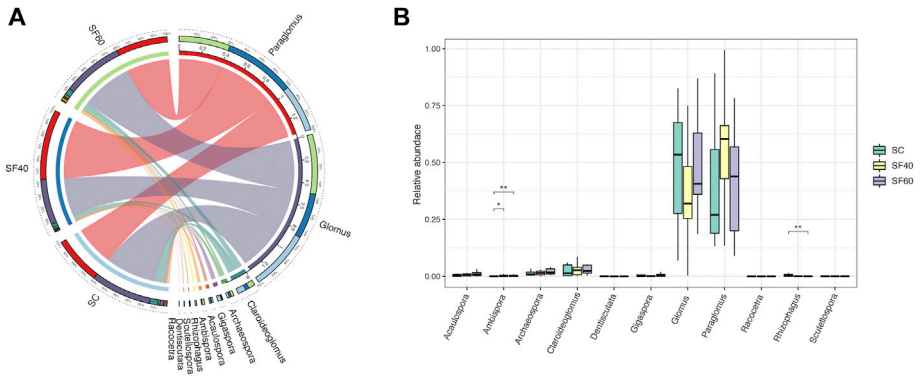

FIGURE 2
The Circos diagram **(A)** represents the AMF community's contribution in succession across groups based on genera. Each colour represented a gene and the columnar size shows the relative abundance. The AMF contribution was combined with different colour columnar. The significant test of genera differences relative to abundance in multi-groups **(B)**, which is analysed using Wilcoxon rank-sum test. * ($p < 0.05$); ** ($p < 0.01$); SC, shrub forest; SF40, the 40a secondary forest; SF60, the 60a secondary forest.

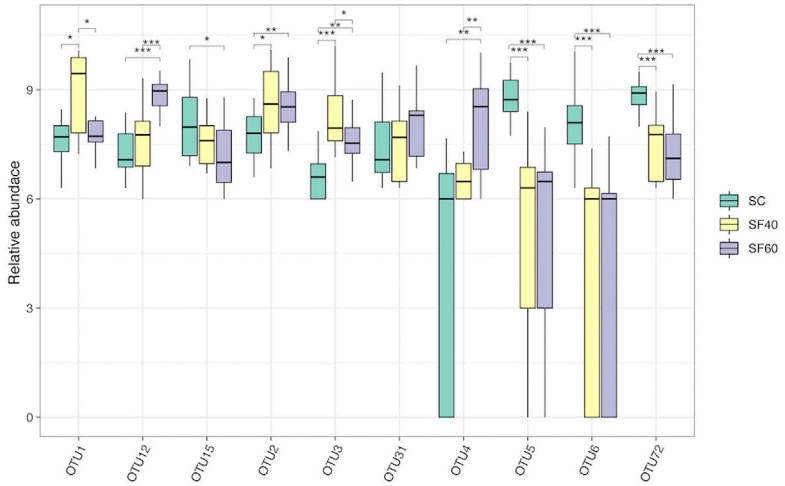

FIGURE 3
The significant test of difference of the top10 OTUs relative abundance in multi-group. The significant difference is analysed using analyzed by Wilcoxon rank-sum test. * ($p < 0.05$); ** ($p < 0.01$); *** ($p < 0.001$); SC, shrub forest; SF40, the 40a secondary forest; SF60, the 60a secondary forest.

Using different barcodes to identity sequences of different samples in the parallel sequencing test, the sequence with a complete barcode was regarded as a valid sequence and extracted to a dataset stored in the FASTQ format. Quality assurance and splicing was performed on the valid sequences, the specific process for which follows: 1) using the Trimmomatic program, poorly overlapped and low-quality sequences (quality score <20, window size <5) were removed (Bolger et al., 2014); 2) a merged pair of reads as a sequence was used to refer to the overlap relationship of PEreads (>10 bp) by the FLASH program (Magoc and Salzberg, 2011); and 3) merge sequences were screened according to error ratio (<0.2). By using mothur V.1.39.5, quality control of merge reads was performed by removing sequences that were ambiguous, homologous, or chimeras generated during PCR amplification (Schloss et al., 2009). Analysis of species information and operational taxonomic units (OTUs) clustering was based on the clean tags. OTUs were selected using UPARSE with a cutoff of 97% similarity (Edgar, 2013). The dataset was screened for chimeric reads using UCHIME in reference database mode (Edgar et al., 2011). Through USEARCH_global, all sequences were compared to OTU representative sequences to obtain the OTU table. The identity of OTU taxonomy was determined by using Blast to compared representative sequences with the Maarjam database (Zhang et al., 2000; Opik et al., 2010). The taxonomy of OTU was obtained for species which had the highest similar identity with OTU representative sequences in the Maarjam database, except for uncultivated environmental information. Some OTUs without species information were marked 'Unidentified'. The library preparation and sequencing were performed by TinyGene Bio-Tech (Shanghai, China). Raw sequence data has been submitted to NCBI's Sequence Read Archives (accession no. PRJNA884298).

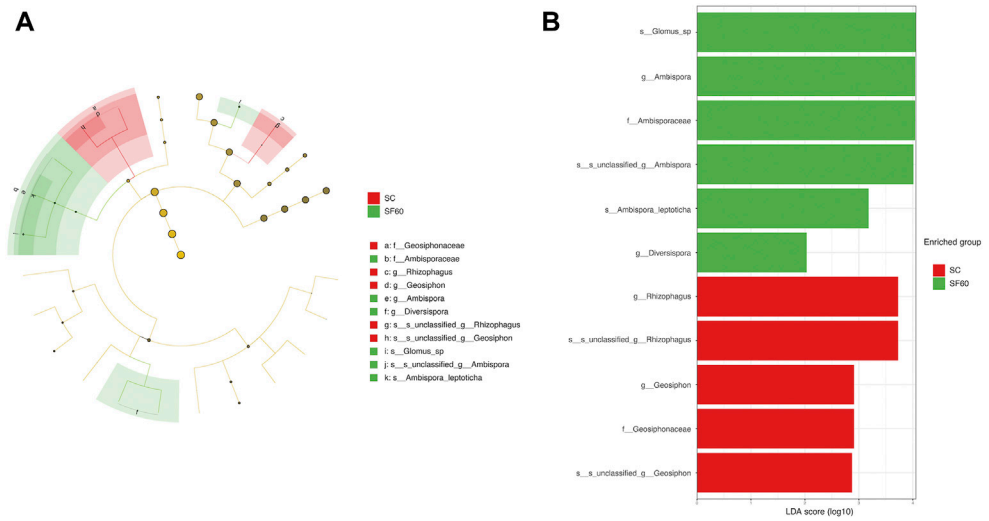

FIGURE 4
Linear discriminant analysis effect size (LEfSe) analysis in AMF composition across succession. Phylum to species is represented by the cladogram circle **(A)**. Points at different taxonomy levels represent microbial groups within that level, and their diameters represent relative abundances. Similarly colored enriched points are represented in a group. The yellow point represents microbes with no significant differences. The microbial groups with LDA score >2 are in the histogram **(B)**. SC, shrub forest; SF40, the 40a secondary forest; SF60, the 60a secondary forest.

2.4 Bioinformatic and environmental correlation analyses

In order to explore the AMF community dynamics, the change in distribution and composition of AMF were analyzed. Furthermore, the impact of environmental factor on AMF community dynamics were explored.

For bioinformation analysis, some OTUs that the classification results could not identify specific genus, and <5 sequences were not used. The species diversity was calculated in R package "vegan". The non-metric multidimensional (NMDS) and principal coordinate analysis (PCoA) were analyzed using Bray-Crutis dissimilarity with R. The Venn diagram was used to demonstrate the distribution of OTUs during succession stages by R version 4.1.2.

Based on this dataset, the genus level was used to explore AMF composition differences which had the clearest taxonomy annotations. To explored the AMF community difference across groups, the OTU level was used for analysis. The top 10 relative abundances under genera and OTUs were selected for multi-group differential analysis.

Using R package 'microbiomeMarker', the linear discriminant analysis effect size (LEfSe) and linear discriminant analysis (LDA) were performed (Segata et al., 2011). Screening the OTUs which it frequency of occurrence >70% in samples for the following calculation. According to Spearman's correlation coefficient (p-value ≤0.05), the dominant OTUs was selected to construct microbial network. The microbial network was using selected dominant OTUs as nodes and its strong correlations as edges. The screened of dominant OTUs and visualize data preparation were completed by R, and the microbial network visualized with Gephi (Sirova et al., 2018; Nauta et al., 2020).

By using R version 4.1.2, the mantel test, two-factor correlation heatmap and distance-based redundancy analysis (db-RDA) was analyzed. The significances of environmental factors with AMF were tested using Monte Carlo permutation ANOVA (Tamminen et al., 2018).

3 Result

3.1 The distribution of soil AMF community across succession stages

Among alpha diversity indices, the Chao1, ACE, and phylogenetic diversity (PD) of the soil AMF community showed significant differences between shrubland and secondary forest ($p < 0.05$). These indices showed an increasing trend with succession. Compared with other succession stages, SF60 group had the highest Chao1, ACE, and PD (Table 1). Conversely, Simpson and Shannon-Wiener indices showed no significant differences across succession stages (Table 1).

NMDS, PCoA, Venn, differential, and beta diversity analyses revealed significant differences in soil AMF communities between shrubland and secondary forest, but not between SF40 and SF60 (Figure 1A; Supplementary Figures S2, S3).

The Venn diagram showed that there were 270 shared OTUs in different groups, and the number of shared OTUs between SC and SF40 and between SC and SF60 were 46 and 39, respectively. However, the number of shared OTUs between SF40 and SF60 was 156 (Figure 1B). Kuklospora and Redeckera were just present in SC, and Diversispora were only present in secondary forests, respectively. In summary, AMF community distribution was influenced by succession, and the differences between shrubland and secondary forest were especially obvious.

3.2 The composition of soil AMF community

As succession stages progressed, the composition of soil AMF community changed. As a result, Paraglomus and Glomus emerged as dominant genera, with Paraglomus exhibiting higher relative abundances in SF40. In contrast, the higher relative abundance of Glomus and Claroideoglomus was present in SC and SF60 (Figure 2A).

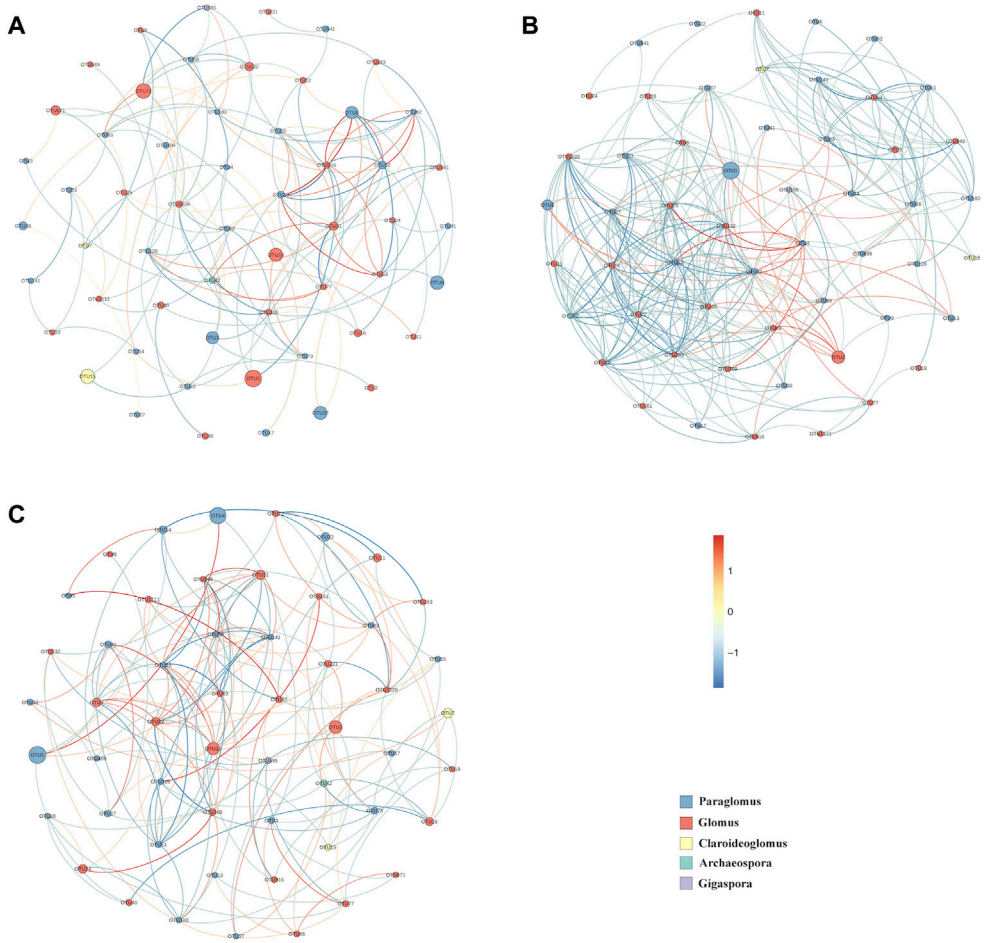

FIGURE 5
The correlation network of AMF community in SC **(A)**, SF40 **(B)** and SF60 **(C)**. Strong and significant correlations (Spearman's r > 0.5) indicate a connection. Positive correlations are represented by red edges, while blue edges represent negative correlations. The size of the nodes represents OTUs abundance. Nodes represented by the same colour belong to the same genera.

TABLE 2 Mantel test on the correlations between the relative abundance of OTUs and biotic or abiotic variables.

Variables	*r*	*p*-Value
Margalef + Shannon + Pielou + RB	0.608	0.004
SOC + TN + TP + Margalef + Shannon + Pielou + RB	0.564	0.005
SOC + TN + TP + SBK + moisture + pH + RB	0.539	0.004
SOC + TN + TP + SBK + moisture + pH	0.339	0.04
SOC + TN + TP	0.343	0.036

Variables combine of environmental factors, and *r* is the correlation coefficient. $p < 0.05$ indicates statistical significance. SOC, soil organic carbon; TN, total nitrogen; TP, total phosphate; SBK, soil bulk; RB, root biomass; Margalef, the richness index of aboveground vegetation; Shannon; Shannon-Wiener diversity index of aboveground vegetation; Pielou, the pielou index of aboveground vegetation.

At the genera level, the multi-group differential analysis showed the variation of Paraglomus and Glomus were non-significant during succession. In addition, Ambispora and Rhizophagus were differential genera in succession, and Ambispora was significantly less abundant in shrubland than in secondary forest. In addition, Rhizophagus had the highest relative abundance in shrubland, and showed a decreasing trend with succession (Figure 2B).

At the OTUs level, the multi-group differential analysis showed that most of the Top 10 OTUs belonged to Paraglomus and Glomus, and only OTU15 belonged to Claroideoglomus. Multi-group differential analysis showed that the relative abundance of OTU1 and OTU4 increased along succession stages. The relative abundances of OTU5, OTU6, and OTU72 were greater in SC than in SF40 and SF60. OTU1, OTU2 and OTU3 were higher in SF40 than in SC and SF60 (Figure 3).

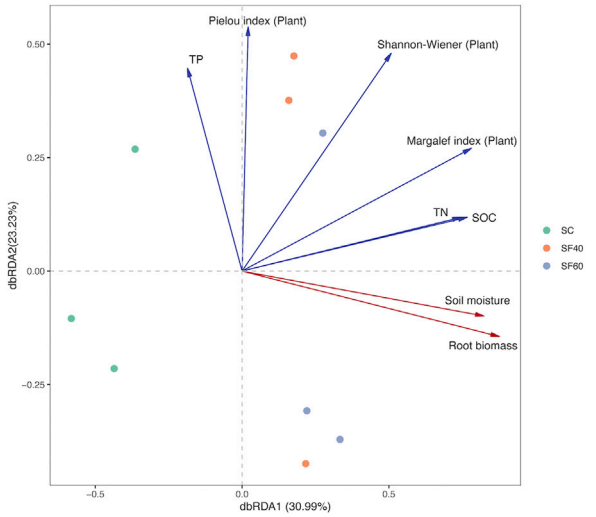

FIGURE 6
The db-RDA analysis based on Bray-Crutis distance in OTU levels. Relationships between AMF community and environment plotted. Each point represents a plot with the same colour in each group. SOC, soil organic carbon; TN, total nitrogen; TP, total phosphate; RB, root biomass.

LEfSe analysis showed that Rhizophagus and Geosiphon were specific genus in SC, but Ambispora and Diversispora were specific genus in SF60 (Figure 4).

3.3 Correlation network construction of AMF community

The correlation network analysis showed AMF community co-occurrence patterns were significantly different between succession stages. Although the nodes were similar among the three groups, the edges were significantly higher in SF40 (nodes = 54, edges = 272) than in SC (nodes = 56, edges = 145) and SF60 (nodes = 53, edges = 170). Furthermore, the SF40 network had higher network topological properties (average degree, network diameter, and clustering coefficient) than SC and SF60. Although most of modes in these networks were similar, the interaction between nodes were significantly different among groups (Figure 5).

3.4 Relationship between environmental factors and AMF community

In the Mantel test, aboveground plants community characteristics were the major factor in varieties of soil AMF community composition (r^2 = 0.608, p = 0.004; Table 2). Likewise, the db-RDA analyses also showed that the Margalef index, Shannon-Wiener index, Pielou index, and root biomass of aboveground vegetation were drivers in changes of AMF community composition (Figure 6). In addition, the soil moisture, SOC, and total N—which belong to abiotic factors—also affect AMF community composition significantly (Supplementary Table S2). The composition of AMF communities could be explained by 54.2% of these factors. Among them, root biomass was the key factors which influenced AMF community composition (r^2 = 0.789, p = 0.012; Figure 6; Supplementary Table S4).

The two-factor correlation heatmap of network attributes and environmental factors showed that C/N ratio significantly correlated to Harmonic geodesic distance (HD), network transitivity (Trans), and average clustering coefficient (avgCC), while root biomass (RB) and Margalef significantly correlated with total nodes (Figure 7).

4 Discussions

4.1 Characteristics of AMF community among the forest succession

With succession, the dominant vegetation gradually evolves from shrubs to trees, and it showed an increase trend in vegetation community complexity. Consistent with the variation of aboveground vegetation communities, AMF species richness and spectral diversity were increased during succession stages in this study (Table 1), and it could be confirmed that the AMF is closely related to host plants, which have host preferences (Janos, 1980; Xu T. et al., 2016; Li et al., 2020). It could be further found that the composition of AMF communities is highly similar in higher taxonomy levels during restoration succession, and it contrasted to vegetation communities composition had significant differences with succession (Leal et al., 2013; Reyes et al., 2019). For example, AMF community composition was similar at the genera level during succession in this study (Figure 2B), and the differences in AMF community composition were significant at the OTU level (Figure 3). In this study, Paraglomus and Glomus dominated in AMF community during succession, which benefits from its biological characteristics that have wide biogeographic distributions and vegetation cover (Figure 2A) (Lovelock et al., 2003). This study demonstrates that the importance of OTUs varied significantly between groups. This dynamic is associated with changes in the AMF niche and functionality at the OTUs level and it confirms that the host preference of AMF community was reflected in changes to the species importance and many coexisting microorganisms have functional redundancy at the OTU level (Louca et al., 2018). The niche analysis of keystone microbial taxa at different successional stages proof that the niche of these keystone taxa at each stage was clearly differentiated (Supplementary Figure S5). In generally, AMF functional redundancy and niche changes are likely response mechanisms to help AMF adapt the habitat changes during succession which consistent with previous studies (Varela-Cervero et al., 2015; Alguacil et al., 2016).

4.2 Influencing factors of AMF community

This study showed solid correlation between plant communities and soil AMF communities (r^2 = 0.608, p = 0.001; Table 2). As an important factor, the host plants could affect the AMF community dynamic by altering the microhabitat (McGuire et al., 2012; Chai et al., 2019). With the change in vegetation community, the host plant reshapes the AMF community composition by secreting apoplast chemistry and root exudates (Goldmann et al., 2015; Hanif et al., 2019; Li et al., 2020). This effect further impacts the uptake of nutrients and water by vegetation (McGuire et al., 2012; Nakayama et al., 2019). In this study, the root biomass also has the strongest correlation with soil AMF community (r^2 =

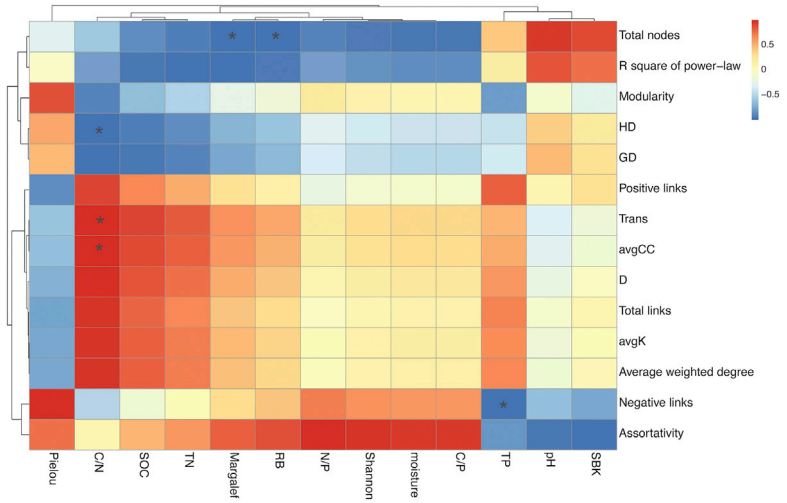

FIGURE 7
The two-factors correlation heatmap. The plot illustrates the relationship between AMF microbial network attributes and environmental factors. * (p < 0.05); HD, Harmonic geodesic distance; GD, Average path distance; Trans, Transitivity; avgCC, Average clustering coefficient; D, Density; avgK, Average degree; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphate; RB, root biomass.

0.789, p = 0.012; Figure 6; Supplementary Table S4) because microbial activity and growth could be stimulated by roots (Wang et al., 2017). By altering root turnover and/or root exudation, the change in root biomass may affect resource availability for the soil AMF community (Philippot et al., 2013). As well as influencing soil microbial community nutrient uptake, root exudates act as signaling molecules and attractants, as well as inhibitors or repellents (Baetz and Martinoia, 2014). Therefore, the soil AMF community might be regulated by changes in root biomass during succession (Eisenhauer et al., 2017).

In addition, soil properties and AMF community composition correlated strongly (Figure 6). Decomposition rates of organic matter and nutrient cycling were directly influenced by soil properties, which contributed to a diverse community of soil AMF (Xu X. et al., 2016). The alternations in AMF community also react upon nutrient cycling (Phillips et al., 2013). As an important environmental factor, the soil moisture drive for soil AMF community characteristics (r^2 = 0.689, p = 0.036; Figure 6; Supplementary Table S4). There is a direct relationship between soil moisture and nutrient effectiveness, which could impact on the soil microbial diversity and abundance through affect microbial nutrient uptake, and it could further affect in soil AMF community composition (Deepika and Kothamasi, 2015; Peng et al., 2021). In addition, soil moisture had clear legacy effects on soil properties, the nutrient uptake of plants, the formation of AMF, and mycorrhizal responsiveness, which would alter the synergistic relationship between AMF and host plants (Cavagnaro, 2016).

4.3 Influence factors of AMF correlation network

This study's results showed that the most complex network occurs in SF40 (Figure 5). In the Ganshiling Nature Reserve, the aboveground vegetation suffered extensive deforestation in the 1980s and gradually recovered to become a tropical lowland rainforest after successive anthropogenic disturbances. With increasing restoration years, the intensity of disturbance to the successional stages which were selected for this study varied. With further explored, it could be found that SF40 suffer intermediate disturbance frequency compared with other. According to intermediate-disturbance hypothesis (IDH), the SF40 with intermediate disturbance frequency could keep the most active AMF community. Moderate ecological scale disturbances keep off interspecific competition and provide supportive environment for microbial species which about both early and late succession to survival (Grime, 1973; George et al., 2019).

Moreover, consistent with existing research, the two-factor correlation heatmap showed that changes in AMF community structure were closely related to soil C/N ratios (Figure 7; Wan et al., 2014). It is well established that the Trans and avgCC positively correlated with AMF community activity and HD showed negative correlation with it. In general, a significant positive correlation between change in soil C/N ratio and AMF community activity as succession progressed. Soil C/N ratio responds to soil nutrient status by influencing nutrient mineralization and organic matter decomposition. It has been shown that the soil C/N ratio affects microbial biomass and activity by altering the nutrient effectiveness and quality of the soil substrate in which microorganisms survive (Demoling et al., 2007).

5 Conclusion

Across the succession stages of restoration, significant differences were observed in soil AMF community structure in this study. Moreover, the results not only support that the variation of soil AMF community structure was much higher at the OTU than at the genera, but also confirmed that plant community characteristics are more closely related to the soil AMF community than soil properties.

Root biomass mostly explained the variation in AMF communities during succession stages. Moreover, soil C/N ratio was positively correlated with AMF microbial network complexity significantly.

Overall, this study provided theoretical data relevant to ecological restoration and the sustainable development of tropical forests. The study contributed to the development of knowledge about AMF communities in the tropical forest ecosystem of Hainan.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://www.ncbi.nlm.nih.gov/sra/, PRJNA884298.

Author contributions

The study was conceived and designed by SM and HM. The lab work and the laboratory analysis of YJ, GX, and XW were assisted by these individuals. SM wrote the main manuscript text. Insightful discussions were contributed by QY, HY, TH, and WL. All authors reviewed the manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2022.1110655/full#supplementary-material

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