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Changes in soil microbial communities from exposed rocks to arboreal rhizosphere during vegetation succession in a karst mountainous ecosystem

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ABSTRACT

To provide information that can support natural vegetation restoration in karst areas, we investigated the change rules of soil microbial communities during vegetation succession from bare rock to arboreal forest using high-throughput sequencing. The results showed that vegetation succession did not cause significant changes in alpha diversity of soil microbial communities. The main bacterial phyla were *Proteobacteria*, *Actinobacteria*, and *Acidobacteria* during vegetation succession. There was a shift from *Ascomycota* to *Basidiomycota* during succession, and the relative abundance of *Basidiomycota* in arboreal rhizosphere soil was the highest; this promoted mycorrhizal formation with the trees and mineral nutrient absorption by the host. Most of the symbiotic networks between soil microorganisms showed cooperative relationships. We propose that the dominant microbes contributed to the biological weathering of limestone and soil evolution under vascular plants. Furthermore, the findings of this study can help improve soil properties by providing insight into how to adjust microbial composition.

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Karst mountain ecosystem; vegetation succession; soil microorganism; microbial diversity; ecological functions

1. Introduction

Karst is second only to desert as the most fragile natural ecosystem. Southwest China is one of the three major karst areas in the world (He et al. 2008; Xue et al. 2017). Degeneration of original vegetation types in Southwest China has continued since the 1970s due to anthropogenic reasons (Yao et al. 2001); vegetation coverage has sharply declined (Wang 2003), and the phenomenon of rocky desertification has intensified (Wang et al. 2010). Therefore, Southwest China has been designated as a key ecological restoration area by the Chinese government (Zhu et al. 2012).

Microbial communities and their diversity are important indicators of ecosystem health and sustainability (Lewis et al. 2010). Soil microbial communities play an important role in biodiversity establishment and terrestrial ecosystem function maintenance by driving biogeochemical processes and regulating nutrient turnover (Doran and Zeiss 2000; Bardgett and van der Putten 2014). Previous studies have demonstrated that diverse soil physicochemical properties and potential interactions among taxa during vegetation restoration may jointly affect the bacterial community structure in karst rocky desertification regions (Xue et al. 2017; Pang et al. 2019). Soil microbial diversity is positively correlated with plant species diversity (Zhu et al. 2010). With vegetation succession, soil quality was found to improve (Zhao et al. 2019). These studies have provided important evidence that can help promote natural vegetation restoration in rocky desertification areas.

The natural vegetation restoration steps of rocky desertification in karst areas include mainly rock weathering, lower plant covering, and higher plant succession. In the early stages, microorganisms first settle on exposed rock surfaces and play a pioneering role in the processes of rock weathering and pedogenesis (Borin et al. 2010; Lian et al. 2010; Tang et al. 2012). Biological weathering by microorganisms promotes the release of mineral elements in rocks and provides abundant organic matter for soil formation and evolution (Banfield et al. 1999; Chen et al. 2016). Through functions of their metabolic products, extracellular secretion, and redox exchange, the existence of soil microorganisms enhance and increase the rate of mineral decomposition and rock weathering. Thus, microbes can improve the soil ecological environment and affect surface vegetation coverage and succession, and changes in the soil ecological environment and vegetation coverage correspondingly affect soil microbial communities (Zhang et al. 2018; Liu et al. 2019; Zhao et al. 2019). With vegetation succession, mycorrhizal fungal emergence contributes to arboreal and gramineous plant growth and reproduction (Bever et al. 2010; Peay et al. 2016). In the global forest inventory database, 60% and 80% of trees form host-specific associations with ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) fungi, respectively (Davison et al. 2015; Steidinger et al. 2019). Thus, it is crucial to research the microbial community characteristics of rock and soil in karst environments during vegetation restoration and succession. However, most previous studies focused on the soil microbial community after vascular plant colonization, or only preliminarily

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investigated the microbes on the rock surfaces. Currently, it is still unclear how the microbial community continuously changes during vegetation restoration and succession, which can be divided into three stages: primitive bare rock, low-grade vegetation appearance, and stable top-level vegetation community formation. In particular, response of soil microbial community and ecological function to vegetation succession changes in karst environments has not previously been researched in detail.

We speculated that karst vegetation succession affects changes of soil physical and chemical properties, directly or indirectly affects the distribution and symbiosis patterns of soil microbial communities, and impacts the ecological function of microbial communities. This study was conducted to: (i) demonstrate the effect of vegetation succession on soil microbial community dynamics, structural composition, and the presence of unique taxa; (ii) reveal the connections of soil environmental variables with bacterial and fungal communities; (iii) recognize the function and metabolic characteristics of bacterial and fungal communities; and (iv) determine the effects of vegetation succession on soil microorganism network patterns and topological properties. In this study, we elucidated the relationships among vegetation succession, soil physicochemical properties, and microbial communities using high-throughput sequencing and geochemical technologies.

2. Materials and methods

2.1. Study area and sample collection

The study area is located on Tianlong Mountain (26° 14′ 48″ N, 105° 45′ 51″ E, 1402–1512 m a.s.l.) in Puding County, Anshun City, Guizhou Province, China (Figure 1). Tianlong Mountain is a representative region, with typical characteristics of most karst mountain ecosystems in southwestern China. Yang et al. (2012) and Liu et al. (2016) reported the detailed geological, geographical, and climatological characteristics of Tianlong Mountain, which provided us with basic information on the study area and background. According to those studies, Tianlong Mountain is a solitary mountain in a karst peak cluster landform with an area of approximately 50 hectares, a relative elevation difference of 110 m, and a moderately steep slope with an average grade of 31.0° ± 14.0° (Yang et al. 2012; Liu et al. 2016). The vegetation on Tianlong Mountain is typical karst native vegetation that underwent complete karst vegetation evolutionary processes (Yang et al. 2012; Liu et al. 2016). Limestone outcrops are ubiquitous, with an average coverage of 44.7% ± 25.8% (Liu et al. 2016). The main soil type in the study region is brown limestone soil, known as 'Cambisols' in the World Reference Base (WRB) soil classification system (USS Working Group WRB 2015), with a thickness of 100–800 mm (Liu et al. 2016). The climate in the study area is classified by the intersection of the north subtropical monsoon humid climate and the central subtropical monsoon humid climate (Yang et al. 2012), with an average annual temperature of 15.1°C, annual precipitation of 1397 mm, and sunshine duration of 1202 h (Liu et al. 2016).

After multiple field surveys, we selected the south slope of Tianlong Mountain as the study area because the slope gradients are uniform and the effects of light, rainfall, wind, and other climate factors throughout this area are similar. In addition, the south slope of Tianlong Mountain contains abundant and typical vegetation types, and our research precisely focused on the relationship between vegetation type and microbial community. Sampling points of all vegetation cover types were located in an area of approximately 1000 m^2 on the same slope, with a relative height difference of less than 50 m. The sampling sites contained six typical vegetation succession sites (Figure 1): naked rock, lichen-covered, moss-covered, herbaceous, shrub-covered, and arboreal forest areas. In September 2019, the samples were collected from naked rock debris (0–20 mm) on NR, surface debris of rock covered with lichen (LR), soil on the interface of moss (Hypnaceae) roots and rock (MS), soil in the rhizosphere of gramineous plants (*Imperata cylindrica* (L.) Beauv.) (GS), soil in the rhizosphere of shrub vegetation (*Pyracantha fortuneana* (Maxim.) Li) (SS), and soil in the rhizosphere of arbors (*Lithocarpus confinis* Huang) (AS). A 10 m×10 m experimental quadrat was randomly selected from each type of vegetation for random sampling. Four parallel samples were collected from each stage, and a total of 24 soil samples were obtained. Each sample was homogenized and evenly divided into two parts. One part was stored at −80°C for bacterial and fungal DNA extraction and high-throughput sequencing, and the other was air-dried for physical and chemical analysis.

2.2. Soil physicochemical parameter determination

The soil physicochemical parameters of the samples were detected with proven technical approaches used by previous studies. The soil organic carbon (SOC), total carbon (TC), and total nitrogen (TN) contents were determined by an organic element analyzer (vario MACRO cube, Elementar, Germany) (Liu et al. 2014). The soil moisture (SM) content was measured by weighing the soil and calculating the mass loss from drying until a constant weight was reached at 105°C for 24 h (Xue et al. 2017). The pH value of soil was determined with a soil-to-water ratio of 1:2.5 (w/v) using a pH meter (pHS-3C, Xiao-Sheng Instruments, China) (Xue et al. 2017). Soil exchangeability of K^+, Na^+, Ca^{2+}, and Mg^{2+} ions was extracted by EDTA–ammonium acetate solution and measured by inductively coupled plasma emission spectroscopy (Xing et al. 2010). Soil available Cu^{2+}, Zn^{2+}, Fe^{2+}, Mn^{2+}, and Al^{3+} were extracted by ammonium bicarbonate–diethylene triamine penta acetic acid and determined by inductively coupled plasma emission spectroscopy (Soltanpour and Schwab 1977). Total phosphorus (TP) was determined by the NaOH fusion molybdenum–antimony colorimetric method (NY/T 88–1988). Available phosphorus (AP) was identified by $NaHCO_3$ extraction (NY/T 1121.7–2014).

2.3. DNA extraction and Illumina MiSeq sequencing

Total microbial DNA in each soil sample was extracted via the PowerSoil® DNA isolation kit (MOBIO Laboratories, QIAGEN Inc., USA) according to the manufacturer's protocol (Che et al. 2019). The DNA extract was checked on a 1% agarose gel, and DNA concentration and purity were determined with a NanoDrop 2000 UV-vis spectrophotometer (Thermo Scientific, USA). The hypervariable V3–V4 region of the bacterial 16S rRNA gene was amplified with the primer pair 338F (5′-ATC CCT ACG GGA GGC AGC AG-3′) and

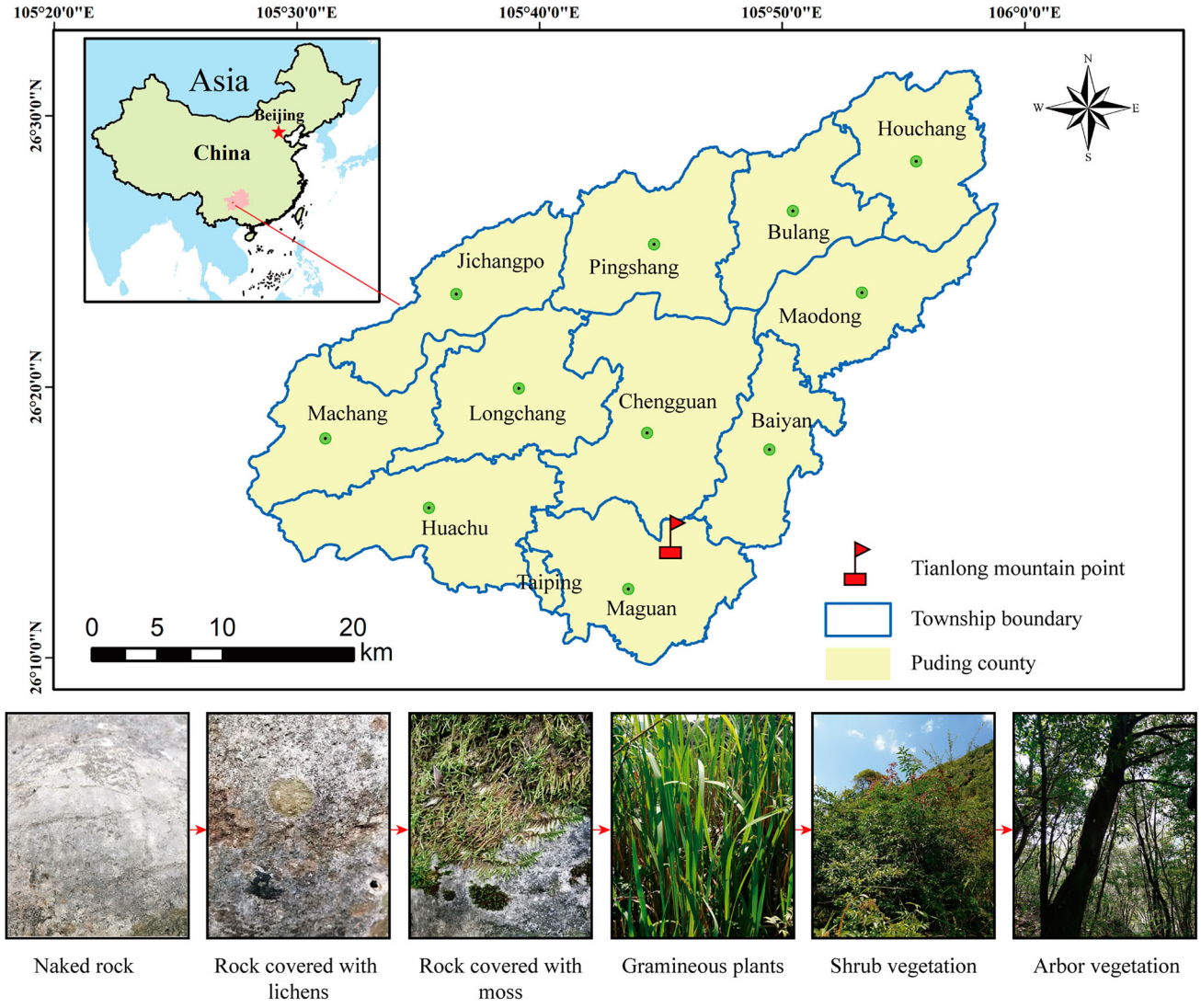

Figure 1. The study site and representative vegetation at each successional stage.

806R (5′-GGA CTA CHV GGG TWT CTA AT-3′) (Mori et al. 2014; Xu et al. 2016). The fungal ITS1 region was amplified by ITS1F (5′-CTT GGT CAT TTA GAG GAA GTA A-3′) and ITS2R (5′-GCT GCG TTC TTC ATC GAT GC-3′) (Adams et al. 2013). Specific amplification procedures are described in **Supplementary S2.3**. NEXTFLEX® Rapid DNA-Seq Kit was used to build the database (Campana et al. 2014). Illumina's MiSeq PE300 platform was used for sequencing (Shanghai Majorbio Bio-pharm Technology Co., Ltd., China). The Illumina library kit used for sequencing was the TruSeq™ DNA Sample Prep Kit. The high-throughput sequencing datasets used in this study can be found in the NCBI SRA database (https://www.ncbi.nlm.nih.gov/) (SRP279039 for 16S rRNA gene sequences and SRP279046 for ITS gene sequences).

2.4. Data processing

We obtained the unprocessed FASTQ files for analysis, and Trimmomatic (version 0.33, http://www.usadellab.org/cms/?page=trimmomatic) was used for double-ended data filtering (Bolger et al. 2014). FLASH (version 1.2.11, https://ccb.jhu.edu/software/FLASH/) was applied for sequence merging (Magoc and Salzberg 2011). Mothur (version 1.35.1, http://www.mothur.org) was used for sequence quality control (Schloss et al. 2009). Operational taxonomic units (OTUs) of both prokaryotes and fungi were clustered using UPARSE (version 7.1, http://drive5.com/uparse/) (Edgar 2013; Che et al. 2018) with 97% similarity (Che et al. 2019), and chimeric sequences were identified and removed. Taxonomic classification was determined by RDP Classifier (http://rdp.cme.msu.edu/) according to the 16S rRNA database (*i.e.* Silva 132) and the fungal ITS database (*i.e.* Unite 8.0) with a confidence threshold of 0.7 (Kóljalg et al. 2005; Quast et al. 2013).

2.5. Statistical analyses

Mean and standard deviation of values and significance of difference analysis were analyzed using SPSS Statistics (version 20.0, IBM, Armonk, NY, USA). The difference between mean values was determined by LSD post-hoc testing ($P < 0.05$). All statistical analyses and figures were developed using R statistical software (version 3.6.1; R Core 2021). Soil bacterial and fungal community alpha diversity was determined via Sobs, Chao index, Shannon index, PD index, Good's coverage, and Pielou's evenness index which were calculated using the vegan package.

Clustering analysis of bacterial and fungal communities under the six vegetation types was conducted based on

OTU abundance-based Bray–Curtis similarity coefficients and using the ggplot2 package for drawing. The 50 most abundant OTUs among the six vegetation types were analyzed using the hierarchical clustering software Cluster and visualized as a heatmap using the RColorBrewer and gplots packages. Non-metric multidimensional scaling (NMDS) analysis was performed to calculate the gradient in compositional changes of bacterial and fungal microbial communities (based on Bray–Curtis) using the ggplot2 package, and differences in bacterial and fungal communities between different samples were analyzed by Adonis test. Canonical variance inflation factor (VIF) analysis was used to screen environmental factors to remove factors with strong multicollinearity relationships (filter out environmental factors with VIF > 10). Detrended correspondence analysis (DCA) was used to determine whether redundancy analysis (RDA) or canonical correspondence analysis (CCA) analysis should be used for association analysis of environmental factors. According to the DCA results (axis lengths of DCA1 were 3.3587 for bacteria and 4.3032 for fungi), the RDA was performed to analyze the correlations between selected environmental factors and bacterial communities, and the CCA was conducted to analyze the correlations between selected environmental factors and fungal communities. The VIF analysis, CCA, RDA, and Mantel tests were performed using the vegan and permute packages. Additionally, the ecological functions of soil bacteria and fungi were separately analyzed using FAPROTAX (Louca et al. 2016) and FUNGuild (Nguyen et al. 2016). The co-occurrence networks were calculated using the WGCNA package and visualized using the interactive platform Gephi (version 0.9.2, https://gephi.org/) (Bastian et al. 2009). We removed OTUs with a relative abundance less than 0.01% for bacterial and fungal communities (Ma et al. 2016). We considered a valid co-occurrence event to have a Spearman's correlation coefficient ($r > 0.6$, $P < 0.05$) (Steinhauser et al. 2008). P-values were adjusted by Benjamini and Hochberg false discovery rate test (Benjamini et al. 2006).

3. Results

3.1. Microbial community diversity and composition in different vegetation succession stages

The alpha diversity analysis results revealed that the bacterial community richness, diversity, community evenness, and phylogenetic diversity index in the LR stage were significantly lower than those in the other stages ($P < 0.05$) (Table 1). As shown in Table 1, the fungal community richness in the MS stages was the largest among all vegetation succession stages, and the fungal community diversity and evenness of in the LR stage were the lowest. Furthermore, the alpha diversity of soil bacterial and fungal communities in different vegetation types did not show an obvious trend among different stages.

Taxonomic analysis of the rock and soil samples collected in the areas with different vegetation types revealed that the dominant bacterial phyla across all samples were *Proteobacteria* (26.58%–38.09%), *Actinobacteria* (12.18%–34.43%), *Acidobacteria* (6.87%–22.63%), *Chloroflexi* (2.66%–15.38%), and *Bacteroidetes* (6.84%–2.54%) (Figure 2(A)). In addition, there were characteristic dominant bacterial phyla in different succession stages. The *Cyanobacteria* abundances in the NR (5.61%) and LR (43.23%) stages were higher than those in the other stages. In the MS stages, the relative abundance of *Actinobacteria* (34.43%) was higher than those in the other stages. With the emergence of vascular plants (in the GS, SS, and AS stages), the relative abundances of *Acidobacteria*, *Proteobacteria*, and *Candidatus Rokubacteria* displayed an increasing trend. As shown in the heatmap (Supplementary Figure S1), the abundance of these 50 dominant OTUs differed among the different vegetation succession stages, and the dominant OTUs in each stage also differed.

The taxonomic analysis of fungal communities revealed that *Ascomycota* and *Basidiomycota* were the dominant phyla from bare rock surface to shrub rhizosphere soil (Figure 2(B)). In the NR stage, the relative abundance of *Ascomycota* was 82.29%, which rapidly increased to 94.19% during lichen coverage (the LR stage). In the MS stage, the abundance of *Ascomycota* decreased (62.23%), whereas the abundances of *Mortierellomycota* (17.64%) and *Basidiomycota* (15.04%) increased. The rhizosphere fungi of Gramineae and shrubs were similar, and *Ascomycota* and *Basidiomycota* were the dominant phyla. At the AS stage, *Basidiomycota* (60.03%) became the dominant species and was significantly higher in abundance than in the other vegetation stages (Figure 2(B)). As shown in the heatmap (Supplementary Figure S2), the abundance of these 50 dominant fungal OTUs differed among the different vegetation succession stages, and the dominant fungal OTUs in each stage also differed. The dominant OTUs in the NR and LR stages were mostly *Ascomycota*, and in the MS stage were mostly *Mortierellomycota*. OTUs with high relative abundance in the AS stage mostly belonged to *Inocybe*, *Geminibasidium*, *Tomentella*, *Sebacina*, and *Russula*, which belong to *Basidiomycota*, and a few belonged to *Mortierellomycota* (Supplementary Figure S2).

The NMDS analysis results showed that the bacterial species compositions of the NR, LR, and MS stages were similar, and those of the GS, SS, and AS stages were similar (Figure 3(A)). The distribution of fungal communities was similar to that of bacteria (Figure 3(B)). Clustering analysis revealed that the 24 bacterial community samples clustered into six stages that corresponded very well to the six vegetation types (Supplementary Figure S3A). Clustering analysis of fungal samples showed that the NR, LR, and MS stages had good similarity in community composition within each stage; however, the GS, SS, and AS stages overlapped, which indicated that these stages had little difference in fungal community composition (Supplementary Figure S3B).

3.2. Physicochemical properties of rock surface debris and soil at different vegetation succession stages and their effects on microbial community composition

As shown in Table 2, with vegetation succession, the soil pH value of samples gradually decreased and tended to be neutral. The contents of TOC, TC, TN, TP, AP, AK, and exchangeable Ca, Mg, Cu, Zn, and Al in the MS stage were significantly higher than those in other stages. In general, the contents of TOC, TN, C/N ratio, TP, AP, Mg, Cu, Fe, and Mn increased with vegetation succession from NR to AS, except in the MS stage.

According to VIF analysis, the combination of the environmental variables 'pH + TC + Ca + K + Na + Mg +

Table 1. Soil microbial richness and diversity indices under different types of vegetations.

Samples		Sobs	Chao 1	Shannon	Pielou's evenness index	PD index	Good's Coverage
Bacteria	NR	1899 ± 210.61a	2445 ± 254.97a	6.40 ± 0.26a	0.84 ± 0.02a	182.33 ± 18.49a	0.97 ± 0.00b
	LR	952 ± 367.65b	1420 ± 551.44b	4.69 ± 0.30b	0.69 ± 0.03b	102.47 ± 28.24c	0.98 ± 0.01a
	MS	1936 ± 105.92a	2522 ± 121.08a	6.35 ± 0.20a	0.84 ± 0.02a	172.77 ± 3.87ab	0.97 ± 0.00b
	GS	1744 ± 86.83a	2401 ± 146.77a	6.19 ± 0.04a	0.83 ± 0.01a	160.22 ± 8.66ab	0.97 ± 0.00b
	SS	1667 ± 112.94a	2249 ± 180.69a	6.19 ± 0.14a	0.83 ± 0.01a	152.22 ± 9.78b	0.97 ± 0.00b
	AS	1711 ± 199.71a	2276 ± 167.52a	6.22 ± 0.32a	0.84 ± 0.03a	150.54 ± 10.77b	0.97 ± 0.00b
Fungi	NR	484 ± 164.18b	561 ± 191.94bc	3.37 ± 0.91b	0.55 ± 0.13a	135.67 ± 43.71b	1.00 ± 0.00a
	LR	297 ± 66.96c	440 ± 150.87c	2.05 ± 0.83c	0.36 ± 0.13b	69.60 ± 15.12c	1.00 ± 0.00a
	MS	934 ± 74.53a	1117 ± 68.36a	4.45 ± 0.12a	0.65 ± 0.02a	200.09 ± 16.55ab	0.99 ± 0.00b
	GS	581 ± 125.94a	648 ± 156.90bc	3.76 ± 0.144ab	0.59 ± 0.03a	165.16 ± 32.16ab	1.00 ± 0.00a
	SS	538 ± 98.08bb	631 ± 103.09bc	3.92 ± 0.21ab	0.62 ± 0.02a	135.77 ± 17.86b	1.00 ± 0.00a
	AS	646 ± 182.11b	732 ± 226.42bc	3.94 ± 0.43ab	0.61 ± 0.06a	183.02 ± 50.63ab	1.00 ± 0.00a

Note: Statistical significance was assessed by one-way ANOVA followed by LSD, $P < 0.05$. In the same column, different lowercase letters show statistically significant differences. NR: naked rock; LR: rock covered with lichen; MS: soil in the moss roots; GS: soils in the rhizosphere of gramineous plants; SS: soil in the rhizosphere of shrub vegetation; AS: soil in the rhizosphere of arboreal vegetation. (both here and below)

Cu + Fe + Mn + Al + TP' had the strongest correlation with bacterial community composition (Mantel test, $r = 0.779$, $P = 0.001$), and 'pH + TC + Ca + K + Al + TP + TN + Mg + Fe + Mn' had the strongest correlation with fungal community composition (Mantel test, $r = 0.609$, $P = 0.001$). The RDA results indicated that available K ($r^2 = 0.75$, $p = 0.001$) and Al ($r^2 = 0.64$, $p = 0.001$) were the main environmental factors that affected bacterial communities (Figure 4(A)). Moreover, the CCA results indicated that pH ($r^2 = 0.77$, $p = 0.001$) and available Mn ($r^2 = 0.67$, $p = 0.001$) were the main environmental factors that affected fungal communities (Figure 4(B)). Spearman analysis showed that available K and Al had significant positive correlations with the alpha diversity index of bacteria. The pH and exchangeable Na were significantly negatively correlated with the fungal α diversity index, whereas TOC, TN, C/N ratio, TP, available P, K, Mg, Cu, Zn, Mn, and Al were significantly positively correlated with the fungal α diversity index (Supplementary Table S1).

3.3. Prediction of soil microbial ecological function at different vegetation succession stages

The FAPROTAX analysis showed that these functional groups were mainly correlated with the geochemical cycles of C, N, O, S, H, Fe, Cl, and other elements (Figure 5). In the NR stage, the relative abundances of functional stages related to C, H-cycles (*e.g.* knallgas bacteria, dark hydrogen oxidation, methylotrophy, and methanol oxidation) and N-cycles (*e.g.* nitrate ammonification, nitrate reduction, nitrite denitrification, and nitrate denitrification), which were related to chemoautotrophic and chemoheterotrophic bacteria, were higher than those for the other stages (Figure 5). In the LR stage, functional stages were mainly related to photosynthesis (*e.g.* chloroplasts, photoheterotrophy, aerobic anoxygenic phototrophy, photoautotrophy, cyanobacteria, and oxygenic photoautotrophy) and hydrocarbon degradation (*e.g.* hydrocarbon degradation, aromatic hydrocarbon degradation, and aliphatic non-methane hydrocarbon degradation). In the MS stage, functional stages were mostly associated with chemoheterotrophy (*e.g.* aerobic chemoheterotrophy and chemoheterotrophy), N cycle (*e.g.* nitrate respiration, nitrogen respiration, and ureolysis), fermentation, and degradation of aromatic compounds. In the GS stage, the functional stages were mainly related to human diseases and chitin dissolution, which are related to chemoheterotrophic bacteria. In the SS stage, functional stages were mainly associated with human diseases (*e.g.* human pathogens that cause pneumonia), carbohydrate degradation (*e.g.* xylanolysis and chitinolysis), parasitic relationships (*e.g.* intracellular parasites, animal parasites, or symbionts, and predatory or exoparasitic agents), the S cycle (*e.g.* respiration of sulfur compounds and sulfate respiration), and the Mn cycle (manganese oxidation). In the AS stage, functional stages were mainly related to the N cycle (*e.g.* aerobic nitrite oxidation and nitrification), the Cl cycle (*e.g.* chlorate reducers), the Fe cycle (*e.g.* iron respiration), anaerobic respiration (*e.g.* fumarate respiration), and plant pathogens.

As showed in FUNGuild analysis results, a total of nine nutrient types were detected in all samples (Figure 6(A)), and symbiotrophy, saprotrophy–symbiotrophy, and saprotrophy were the main methods of nutrient acquisition. After removing unallocated OTUs, the distribution of fungal nutrient types in different vegetation succession stages showed significantly different trends ($p < 0.05$, one-way ANOVA). The fungal guilds varied with vegetation succession (Supplementary Figure S4). In the NR and LR stages, the relative abundance of lichenized species was higher, especially in the LR stage. In the MS stage, the relative abundance of saprotrophs and plant pathogens rapidly increased. The abundances of undefined saprotrophs and soil saprotrophs were higher in the GS and SS stages. In the AS stage, the relative abundance of ectomycorrhizal fungi rapidly increased, and the relative abundance of saprotrophs was relatively high. As important plant symbiotic mycorrhizal fungi, AM fungi and ECM fungi were significantly different in all vegetation succession stages ($F = 4.436$, $P = 0.008$ and $F = 45.769$, $P < 0.001$, respectively) (Figure 6(B, C)). The AM fungi were mostly not distributed in the LR and MS stages, but existed in the NR, GS, SS, and AS stages. The relative abundance of AM fungi decreased from the GS to AS stage (0.80 ± 0.41%, 0.77 ± 0.21%, and 0.34 ± 0.37%, respectively) (Figure 6(B)). The relative abundance of ECM fungi was highest in the AS stage, where it reached 49.95 ± 14.41% (Figure 6(C)).

3.4. Symbiotic network relationship of soil microorganisms in different vegetation cover stages

Based on the non-random co-occurrence network analysis results, we found that the symbiotic networks of soil bacteria and fungi were quite different in different vegetation succession stages. As shown in Figure 7 and Table 3, the number of positively correlated edges in each stage was much larger

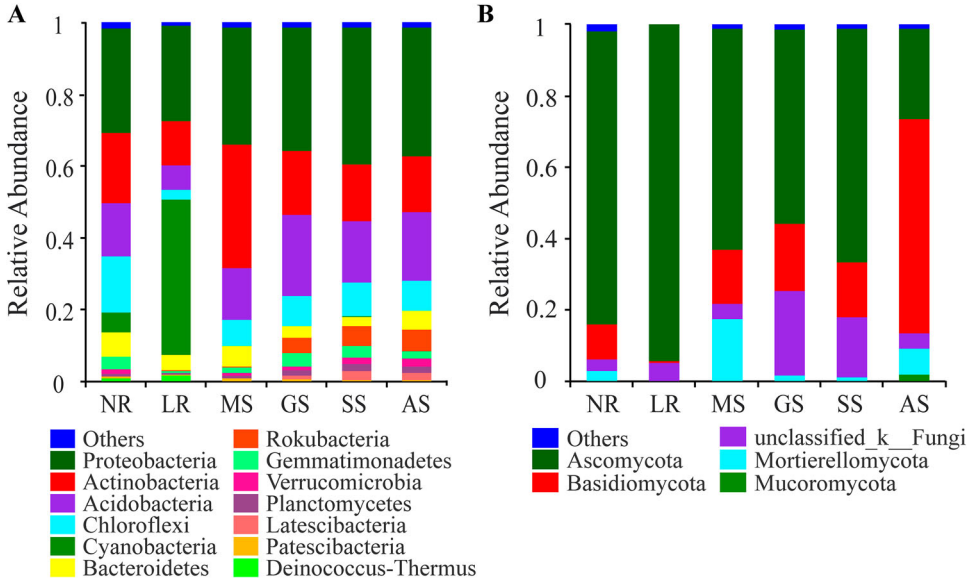

Figure 2. Relative abundance of the bacterial (A) and fungal (B) communities at the phylum level. 'Others' include phyla with less than 1% average relative abundance. Data represent the mean of four replicate samples.

than the number of negatively correlated edges, which indicated that most soil microbial communities were cooperative rather than competitive relationships. The average degrees of nodes in the NR, AS, and SS stages were higher, which demonstrated that the soil microbial coupling relationships were stronger between the bare rock surface, arboreal forest, and shrubbery.

The modularity index of each stage was greater than 0.4, which revealed that each stage network was a co-occurrence network with modular structure; however, the MS stage was significantly more modular than the other stages. The modules of each network were divided based on the modularity index (Supplementary Figure S5). From the total of the first four modules in each stage, NR > AS > SS > GS > MS > LR.

4. Discussion

4.1. Microbial community formation in rock surface and soil with vegetation succession

In this study, the bacterial alpha diversity of the LR stage was lowest, but there was no significant difference among the other stages. Fungal alpha diversity was the lowest in the LR stage and highest in the MS stage, but there was no significant difference among the other stages (Table 1). In the initial stage of karst vegetation succession, the bacterial communities that first colonized the surface of the bare rock played a key role in rock weathering. The bacterial and fungal diversity in the NR stage was not significantly different from that in soil (Table 1), which contradicts the results of some previous studies. We speculate that, because bare rock surface is nutritionally poor, different microbial species simultaneously compete for limited nutrients and there is no dominant community to monopolize nutrient resources; therefore, more species have a chance to survive. Consequently, the diversity and richness of microbial species on bare rock surface were not significantly different from those in relatively nutritionally rich soil.

Previous studies have shown that low-temperature, nutrient-poor, drought-prone regions had high microbial diversity (Neufeld and Mohn 2005; Niederberger et al. 2008). Therefore, we believe that it is reasonable to have high microbial diversity on nutrient-poor rock surfaces. Consequently, the bacterial community diversity in the NR stage

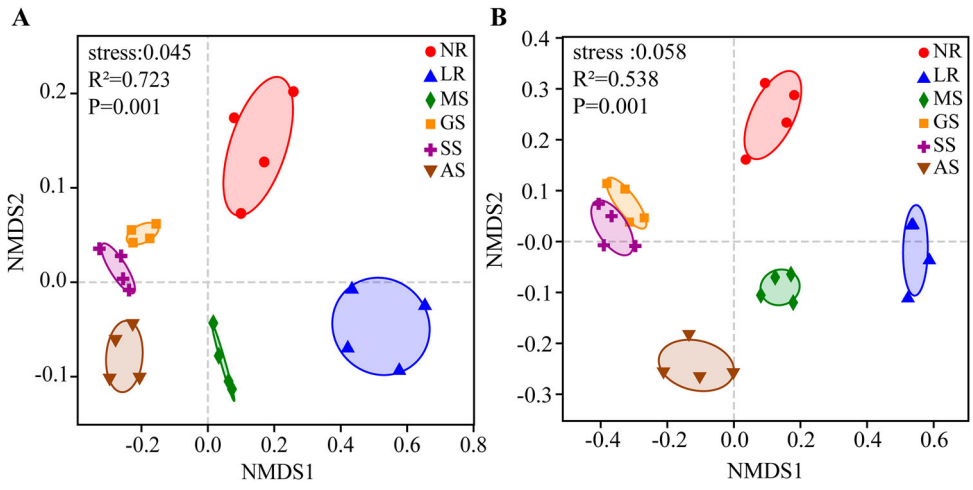

Figure 3. Non-metric multi-dimensional scaling analysis of bacteria (A) and fungal (B) communities. The distance between the points indicates differentiation in the community.

Table 2. Soil physico-chemical properties of the experimental samples.

Physicochemical factor	Sample ID					
	NR	LR	MS	GS	SS	AS
pH	8.50 ± 0.21a	8.57 ± 0.27a	7.32 ± 0.10c	7.81 ± 0.07b	7.66 ± 0.10b	7.03 ± 0.11d
SM	––	––	––	35.71 ± 6.99b	40.25 ± 5.18ab	48.67 ± 9.81a
TOC	0.05 ± 0.02d	0.05 ± 0.00d	22.97 ± 4.13a	3.27 ± 0.11c	3.35 ± 0.46c	6.77 ± 1.15b
TN	0.03 ± 0.01c	0.03 ± 0.00c	2.11 ± 0.48a	0.32 ± 0.01bc	0.33 ± 0.02bc	0.46 ± 0.13b
C/N ratio	1.56 ± 0.38c	1.53 ± 0.12c	11.05 ± 0.86b	10.28 ± 0.38b	10.13 ± 0.77b	15.69 ± 5.62a
TC	10.72 ± 1.84b	12.45 ± 0.06b	27.37 ± 6.49a	4.69 ± 0.79c	4.19 ± 0.51c	6.25 ± 2.13c
TP	0.20 ± 0.05bc	0.01 ± 0.00c	1.25 ± 0.35a	0.36 ± 0.01b	0.35 ± 0.03b	0.31 ± 0.03b
Available elements						
AP	2.6 ± 0.44c	2.90 ± 0.24bc	34.95 ± 1.66a	4.68 ± 1.25b	4.19 ± 1.24bc	4.65 ± 1.63b
AK	336.78 ± 127.79b	19.00 ± 5.19d	492.03 ± 31.57a	234.94 ± 30.22c	268.50 ± 66.66bc	207.78 ± 52.25c
Ca	16.30 ± 3.31b	17.24 ± 0.51b	21.30 ± 3.91a	14.88 ± 1.13b	14.52 ± 1.57b	7.34 ± 1.37c
Na	30.42 ± 9.38a	30.67 ± 5.80a	20.28 ± 2.91b	22.64 ± 0.85b	23.35 ± 1.52b	24.56 ± 0.62ab
Mg	195.20 ± 26.10c	116.43 ± 12.39c	1057.82 ± 249.08a	508.29 ± 109.67b	322.68 ± 133.45bc	960.55 ± 301.71a
Cu	0.95 ± 0.09d	0.72 ± 0.03d	4.49 ± 0.57a	3.94 ± 0.54b	3.78 ± 0.13b	2.84 ± 0.27c
Zn	0.61 ± 0.06b	0.61 ± 0.11b	64.91 ± 10.70a	2.98 ± 0.63b	3.03 ± 1.62b	4.51 ± 1.25b
Fe	47.71 ± 15.02b	10.69 ± 3.13c	43.57 ± 4.33bc	61.09 ± 17.23b	62.38 ± 8.88b	150.69 ± 48.37a
Mn	5.68 ± 1.26b	3.51 ± 1.17b	56.26 ± 11.79a	47.27 ± 12.20a	61.66 ± 20.96a	55.28 ± 10.74a
Al	1.85 ± 0.23b	0.19 ± 0.08d	3.80 ± 0.58a	1.19 ± 0.14c	1.29 ± 0.06c	2.27 ± 0.51b

Note: Statistical significance was assessed by one-way ANOVA followed by LSD, $P < 0.05$. In the same row, different lowercase letters represent statistically significant differences. pH, potential of hydrogen; SM, soil moisture, %; TOC, total organic carbon, %; TN, total nitrogen, %; C/N ratio, soil carbon-to-nitrogen ratio; TC, total carbon, %; TP, total phosphorus, g kg^{-1}; Ca, exchangeable calcium, g kg^{-1}; AP, available phosphorus, mg kg^{-1}; AK, available potassium, mg kg^{-1}; Na, exchangeable sodium, mg kg^{-1}; Mg, exchangeable magnesium, mg kg^{-1}; Cu, available copper, mg kg^{-1}; Zn, available zinc, mg kg^{-1}; Fe, available iron, mg kg^{-1}; Mn, available manganese, mg kg^{-1}; Al, available aluminum, mg kg^{-1}.

was higher than that in the LR stage, but that in the NR stage was not significantly different from those in the MS, GS, SS, and AS stages (Table 1). With further rock weathering, lichenized fungi became the dominant microbial community on the rock surface. Therefore, the bacterial and fungal diversity decreased in the LR stage. These results are consistent with the results of Liu et al. (2019), who studied microbial community changes under different vegetation covers in sandstone areas. When moss appears, it coexists with algae, bacteria, and fungi on exposed limestone, which forms a moss shell that plays an important role in degraded karst ecosystem restoration (Cao et al. 2020).

In this study, the diversity of bacterial and fungal communities in the MS stage was the highest, which was due to litter and leaf accumulation on the moss-covered rock surface for years forming a thin layer of humus, which is extremely nutrient-rich. This laid the foundation for mass reproduction of microorganisms and further accelerated the process of rock weathering and soil formation. Bryophytes and their symbiotic microorganisms are considered pioneers of vegetation restoration in karst areas (Cao et al. 2020). After vascular plant emergence, the role of microorganisms gradually changed from pioneers of rock weathering to decomposers and maintainers of the soil environment (Liu et al. 2019). In this study, there was no significant difference in bacterial and fungal diversity in the GS, SS, and AS stages after vascular plants appeared. The result of this study was similar to those of previous studies (Liu et al. 2019; Liu et al. 2020).

During karst vegetation succession, the composition of dominant bacteria and fungi only changed quantitatively, but there was no significant difference at the phylum level. For example, *Proteobacteria*, *Actinobacteria*, and *Acidobacteria* were the dominant bacterial phyla in all samples (Figure 2(A)). Previous studies also showed that the bacterial community was mainly composed of *Proteobacteria*, *Actinobacteria*, and *Acidobacteria*, regardless of succession length (Kim et al. 2014; Li et al. 2014; Lin et al. 2014; Liu et al. 2020). In addition, the relative abundances of *Cyanobacteria* in the NR and LR stages were higher than in the other stages (Figure 2A). *Cyanobacteria* can survive in extremely barren environments and drive the biogeochemical cycle of multiple elements by fixing C and N, thereby improving soil fertility (Lett and Michelsen 2014; Rodriguez-Caballero et al. 2018; Sepehr et al. 2019), and *Cyanobacteria* can coexist with fungi (such as *Ascomycota*) to form lichens on rock surfaces or weathered crusts and secrete acid to accelerate rock erosion (Chen et al. 2000).

Ascomycota and *Basidiomycota* were the dominant fungal phyla throughout succession, and *Ascomycota* had absolute dominance in the NR and LR stages (Figure 2(B)). Tang and Lian (2012) reported that *Ascomycota* have an absolute advantage in fungal communities on the surfaces of dolomite and limestone outcrops. Our results revealed a shift from *Ascomycota* to *Basidiomycota* during succession (Figure 2B), which is consistent with the findings of previous studies and indicates soil nutrient accumulation and ecosystem maturation (Nara 2008; Chai et al. 2019). *Basidiomycota* can form mycorrhizas in symbiosis with plants and participate in nutrient absorption and transportation in plant roots, which is beneficial to tree cultivation and afforestation (Garbaye 1994).

As saprophytes, *Mortierellomycota* survive in organic matter such as soil humus or rotted leaves, and a few can form mycorrhizal fungi with arboreal plants (Zhang et al. 2011; Wagner et al. 2013). *Mortierella* can dissolve phosphorus, which can increase crop yield and establish a symbiotic relationship with plants (Fröhlich-Nowoisky et al. 2015; Grzadziel and Galazka 2019). In this study, *Mortierellomycota* and *Mortierella* significantly accumulated in both the MS and AS stages, which indicated that good soil quality is related to the high relative abundance of *Mortierellomycota* (Figure 2(B) and Figure S2). Consequently, the dominant microbial community in different vegetation succession stages played substantial roles in rock and soil evolution.

4.2. Correlation between environmental factors and microbial communities in karst vegetation succession

The contents of TOC and other elements in the soil of the MS stage were significantly higher than those in the other

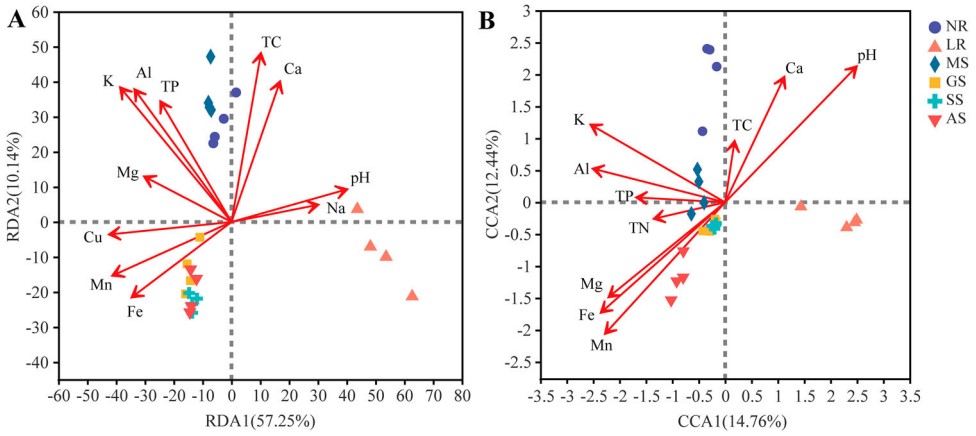

Figure 4. Redundancy analysis (RDA) plots of Bacteria (A) and canonical correspondence analysis (CCA) plots of Fungi (B).

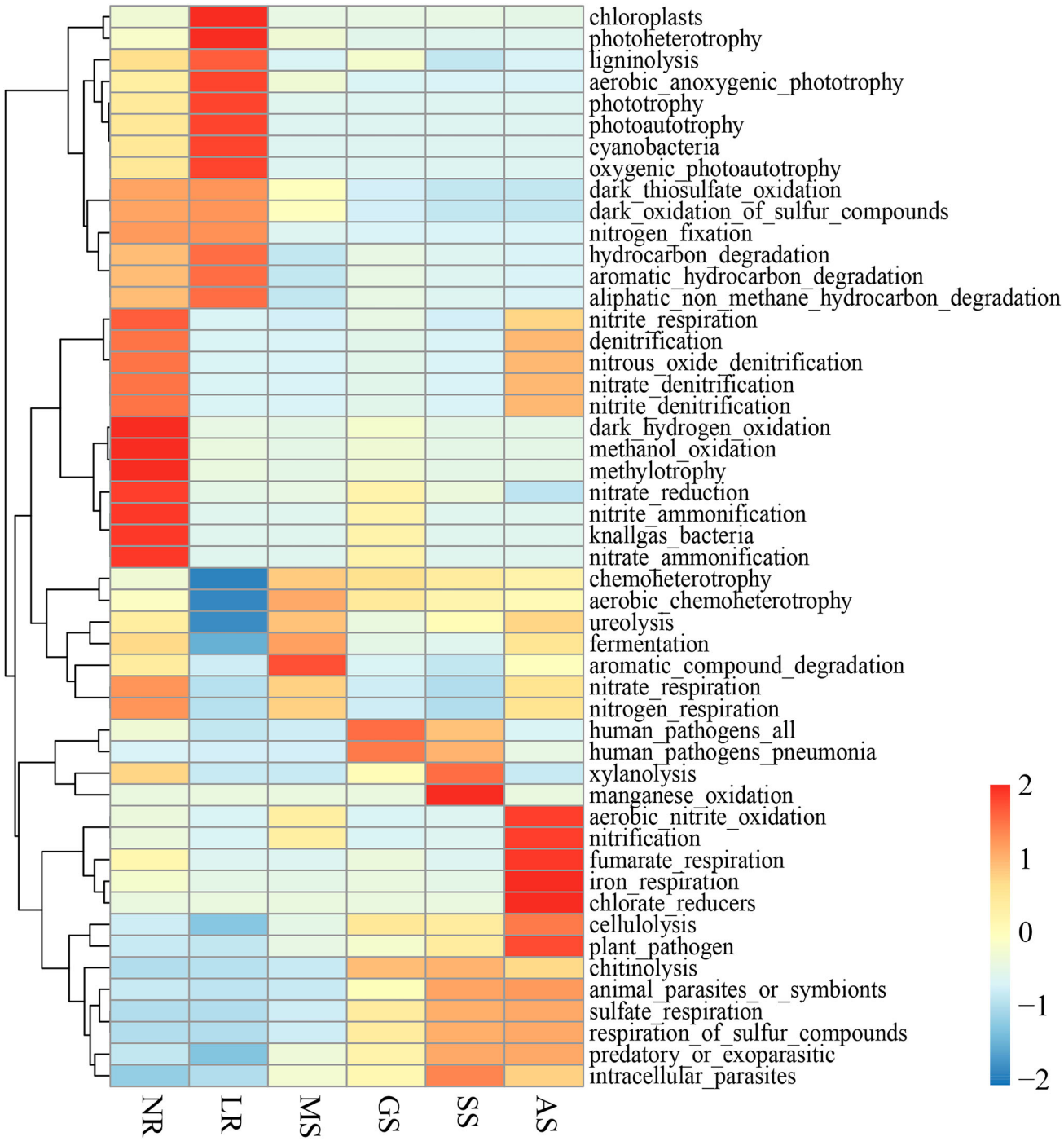

Figure 5. Distribution of bacterial function in the FAPROTAX database within different stages of vegetation succession.

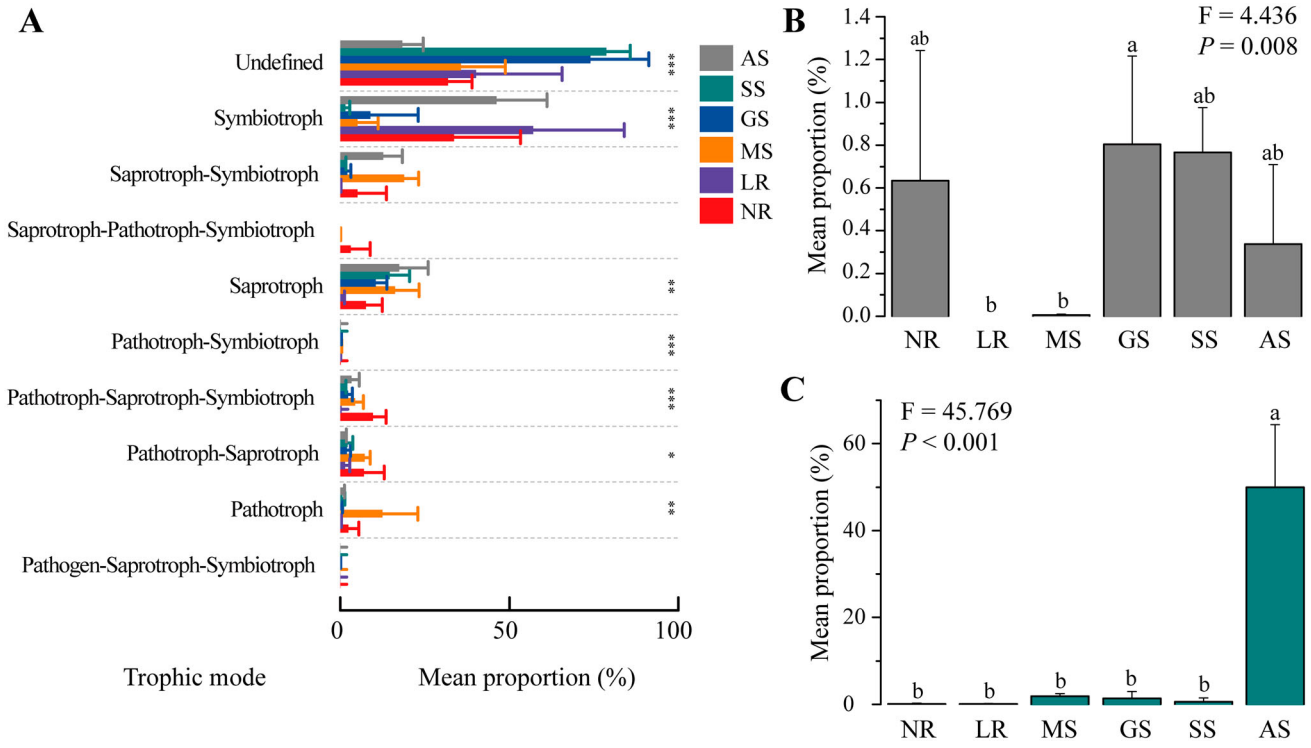

Figure 6. Function predictions of fungal communities using FUNGuild against UNITE database. (A) FUNGuild. (B) Arbuscular mycorrhizal fungi. (C) Ectomycorrhizal fungi.

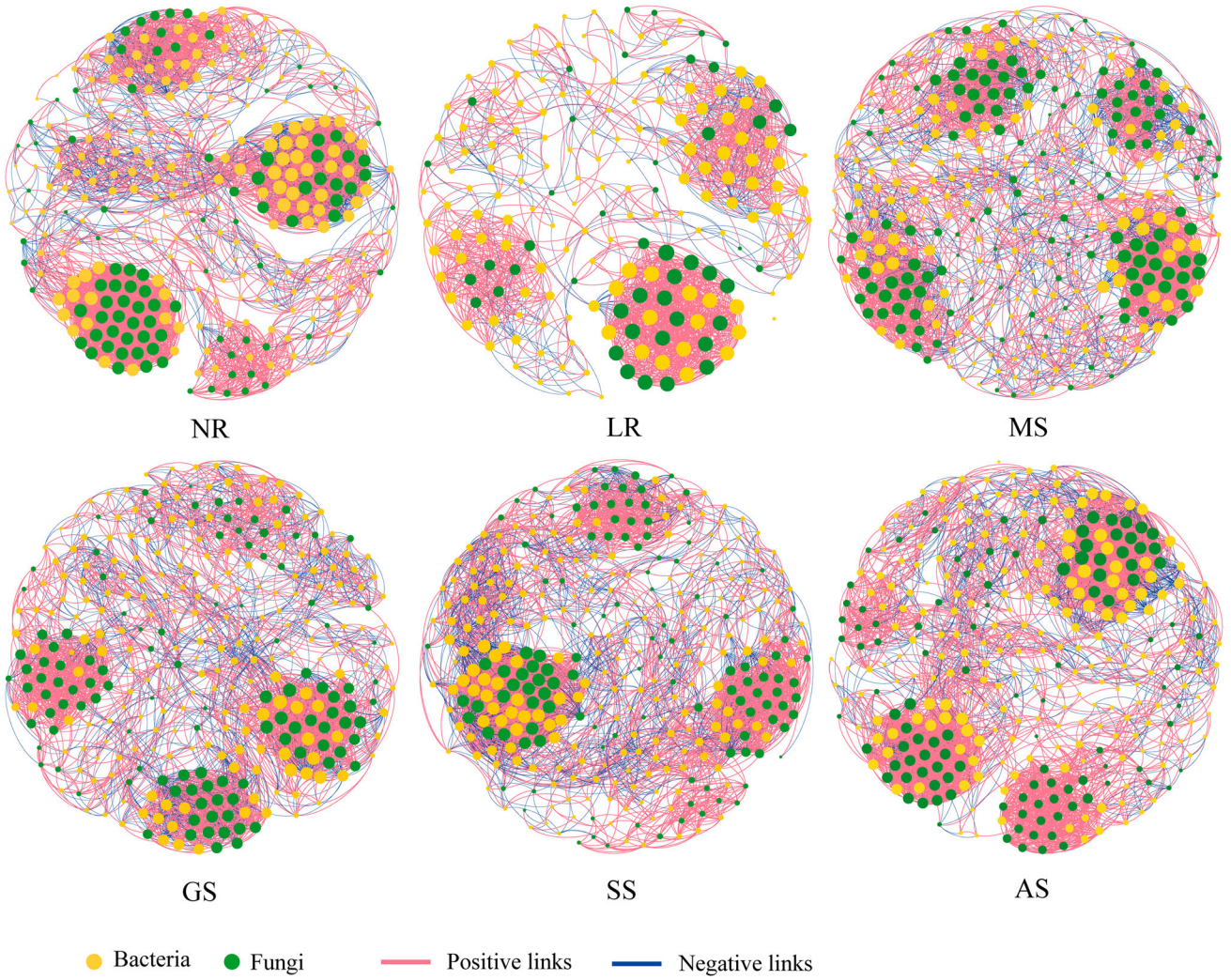

Figure 7. Network co-occurrence analysis of microbial communities (OTUs with relative abundance greater than 1%) within each groups of different vegetation succession stages. A connection denotes a strong (Spearman's $r > 0.6$) and significant (P-value < 0.05) correlation. Each point represents unique OTUs in the datasets. The size of each node is proportional to the relative abundance.

Table 3. Topological properties for the networks obtained within different stages of vegetation succession.

	Groups of different vegetation succession stage					
Network metrics	NR	LR	MS	GS	SS	AS
Number of nodes[a]	314	189	342	329	342	331
Bacterial nodes[b]	218 (69.43%)	142 (75.13%)	199 (58.19%)	215 (65.35%)	220 (64.33%)	219 (66.16%)
Fungal nodes[c]	96 (30.57%)	47 (24.87%)	143 (41.81%)	114 (34.65%)	122 (35.67%)	112 (33.84%)
Total number of edges[d]	4012	1561	3703	3404	4162	4087
Number of positive correlations[e]	3160 (78.76%)	1264 (80.97%)	2448 (66.11%)	2322 (68.21%)	2876 (69.1%)	3184 (77.91%)
Number of negative correlations[f]	852 (21.24%)	297 (19.03%)	1225 (33.89%)	1082 (31.79%)	1286 (30.9%)	903 (22.09%)
Average degree[g]	25.554	16.519	21.655	20.693	24.339	24.695
Modularity[h]	1.059	0.879	1.729	1.522	1.464	1.078
Number of communities[i]	9	16	7	7	7	13
Average clustering coefficient[j]	0.724	0.735	0.644	0.650	0.654	0.695
Eigenvector centrality[k]	0.042	0.037	0.094	0.073	0.053	0.061
Average path length[l]	4.443	5.091	4.258	4.341	4.196	4.320

Note: [a] Microbial taxon at OTU level (relative abundance > 0.1%). [b] Bacterial taxon at OTU level. [c] Fungal taxon at OTU level. [d] Number of connections/correlations obtained by Gephi software. [e] Number of positive correlation ($r > 0.6$ with $p < 0.05$). [f] Number of negative correlation ($r > 0.6$ with $p < 0.05$). [g] Average number of connections per node in the network, that is, the node connectivity. [h] Capability of the nodes to form highly connected communities, that is, a structure with high density of between nodes connections. [i] A community is defined as a group of nodes densely connected internally. [j] How nodes are embedded in their neighborhood and the degree to which they tend to cluster together. [k] A measure of node importance based on node connections. [l] Average network distance between all pair of nodes or the average length off all edges in the network.

stages (Table 2); this may be attributed to the fact that the soil of the MS stage mainly comprised organic matter and humus formed by the leaves of moss and other plants. With vegetation succession, the soil pH values showed a downward trend at various stages (Table 2), which was consistent with the findings of previous studies (Holtkamp et al. 2008; Zhao et al. 2014; Xue et al. 2017). The SM values increased from the GS to AS stage (from 35.71% to 48.67%) because the vegetation restoration improved the water-holding capacity of the soil (Korkanc 2014; Zhang et al. 2016). Some soil nutrient contents increased with vegetation succession (Table 2), which confirmed that vegetation succession can improve the physical and chemical properties of soil (Ayoubi et al. 2011; Peng et al. 2013; Deng et al. 2018). Many studies have also shown that soil nutrient concentration increased following vegetation succession (Peng et al. 2013; Deng et al. 2017; Jia et al. 2017), which could be mainly due to the increased biomass above and below the soil (Wang et al. 2018). Moreover, vegetation litter can improve soil properties (Zhao et al. 2017), such as organic matter and soil structure, and reduce nutrient loss due to soil erosion (Saviozzi et al. 2001).

The RDA results revealed that available K and Al were the main environmental factors that affected the bacterial communities, and the CCA results indicated that pH and available Mn were the main environmental factors that affected the fungal communities. This study showed that fungal communities in karst areas were more sensitive to environmental variables than bacterial communities (Table S1). The influences of microhabitats and vegetation communities on soil characteristics during succession can further mediate soil microbial community diversity and composition (Benesperi et al. 2012). Soil pH may indirectly influence microbial communities by regulating soil nutrient availability and ion toxicity (Zhalnina et al. 2015; Hesse et al. 2019). The mineral element K is an essential nutrient for microorganism growth and reproduction. The higher K concentration contributed to the stronger metabolic activity and faster reproduction of microorganisms (Polyakova and Billor 2008). The elemental ratios may affect the microbial community composition because of differences in life strategies (Kaiser et al. 2014). There was a significant positive correlation between available Al and soil microbial community diversity (Figure 4 and Table S1), which supported the idea that low Al content could stimulate soil microbial community to some extent (Liu and Xu 2004).

In karst areas, the rate of karstification and carbonate rock substrate change with topography, resulting in high heterogeneity of soil nutrients and water (Geekiyanage et al. 2019). Topography and slope directly control the migration of soil nutrients and water (Fu et al. 2016; Geekiyanage et al. 2018), and thus affect the growth of karst vegetation (Zhang et al. 2013), which may determine the succession process of karst vegetation and the distribution of soil microbial community. In this study, due to the small changes of topography and slope in the sampling area, their effects on vegetation succession and soil microbial distribution can be ignored. We only focused on the relationship between soil physicochemical properties, soil microbial community composition and vegetation succession in karst areas. In order to better understand the distribution rule and influencing factors of soil microorganisms in the natural vegetation succession in karst areas, it is of great significance to carry out large-scale research with different topographies and slopes in the future.

4.3. Response of soil microbial community ecological function and symbiotic network relationship to vegetation succession processes

Chemoheterotrophic and aerobic chemoheterotrophic bacteria dominated karst vegetation succession (Figure 5). In all ecosystems, chemoheterotrophic bacteria usually act as decomposers that are responsible for *in situ* repair and organic matter recycling (Kämpfer et al. 1993). The ecological functions of bacteria were significantly different in different stages of vegetation succession because of the difference of functional microbiota under different vegetation cover types (Figure 5). In the succession from bare rock to moss cover, the microbial community mainly played a pioneering role in the processes of rock weathering and soil formation, and the ecological functions of bacterial communities in rock

debris were mainly related to nitrate metabolism, carbon inorganic compound metabolism, and photosynthesis (Figure 5). With the forward vegetation succession, vascular plants appeared, soil maturity gradually improved, and soil nutrients improved, which provided more C, N, and other nutrient sources for the soil bacterial communities; additionally, the ecological functional diversity of the bacterial communities also increased.

The main nutritional modes of fungi were shown to be symbiotic, saprophytic, and saprophytic–symbiotic (Figure 6(A)). The relative abundance of symbiotic fungi in karst area vegetation succession was relatively high, especially in the NR, LR, GS, and AS stages. Symbiotic fungi form mutually beneficial cooperative relationships with other organisms, such as with algae to form lichens and with vascular plants to form mycorrhizas. Symbiotic fungi of lichens (such as *Bagliettoa* and *Chaetothyriales*) mainly appeared in the LR stage (Figure S2). Compared with the other stages, a higher abundance of AM fungi was found in the GS stage (Figure 6(B)), which is consistent with previous results (Zhao et al. 2019). The synergistic effect of Gramineae on soil fungal communities was demonstrated through plant tissue structure (Wardle and Nicholson 1996), which was mainly influenced by AM activity related to plant roots or the rhizosphere (Johnson et al. 1992).

When vegetation succession reaches the top-level communities, some dominant forest species (*e.g.* all species in Pinaceae, Fagales, Salicaceae, and Dipterocarpaceae, and some Myrtaceae and Caesalpinioideae species) form ectomycorrhizas with *Basidiomycota* (Koele et al. 2014); therefore, the abundance of ECM in the AS stage was significantly higher than that in the other stages (Figure 6(C and Figure S4)). Under natural conditions, some ECM fungi with low weathering potential can enrich some bacteria with high weathering potential and facilitate the absorption and use of insoluble mineral nutrients through their own high-affinity ion transport system (Sun et al. 2019b). This provides the mineral elements necessary for host plants and their own growth. Moreover, the presence of mycorrhizal fungi also formed a relatively stable rhizosphere microbial community through regulation (Garbaye 1994; Sun et al. 2019a). Previous studies showed that saprophytic fungi are the main decomposers of dead plants and litter in soil and play an important role in organic decomposition and nutrient cycling (Phillips et al. 2014; Chen et al. 2020). Therefore, saprophytic fungi, such as *Fusarium*, *Cladosporium*, *Discosia*, *Knufia*, and *Mortierella*, were relatively abundant in plant rhizosphere soils (Figure 6(A), Figure S2, and Figure S4).

Microbial communities in different vegetation succession stages had non-random co-occurrence patterns, and the microorganism co-occurrence patterns were significantly affected by vegetation succession (Figure 7). The number of positive and negative links approximately reflects the intensity of cooperation and competition among microbial communities, respectively (Deng et al. 2012). According to the number of positive and negative links shown in Table 3, the microbiome mainly had cooperative relationships at each succession stage. In the NR and LR stages, when nutrient levels and availability were poor, microorganisms could obtain the nutrients needed for survival through more collaboration and cooperation. In the final stage of vegetation succession (AS), the soil microecological environment reached a stable state, and the soil microbial communities also evolved into a more stable cooperative symbiotic survival mode. In the co-occurrence network, the existence and distribution of modules in the network can be used to study niche division and synergic relationships (Barberán et al. 2012). With the emergence and development of higher vegetation, the scale of modules increased and the connectivity between species gradually increased (Figure S5), which indicated that the network became more stable.

5. Conclusion

With karst vegetation succession, soil quality gradually improved; however, the soil microbial diversity did not significantly change. The dominant microbial communities in different vegetation succession stages played an important role in the rock and soil evolution. The available K and Al were the main environmental factors that affected the bacterial communities, whereas soil pH and available Mn were the main environmental factors that affected the fungal communities. With vegetation succession, the ecological functions and metabolic patterns of bacterial communities were gradually transformed from those related to chemical autotrophy and photoautotrophy to more complex chemoheterotrophy. The main nutritional types of fungi were symbiotic, saprophytic, and saprophytic–symbiotic. Most of the symbiotic networks between soil bacteria and fungi showed cooperative relationships. Consequently, the change rules of soil microorganisms at all karst vegetation succession stages in this study can provide an important theoretical basis for restoring the ecological environments of karst areas. For example, rock weathering and soil development may be effectively improved by artificially increasing the contents of symbiotic microorganisms, especially the dominant bacteria and fungi on the surface of limestone rocks and in infertile soils.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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