Impact of Vegetation Restoration on Soil Fungal Community Structure in Karst Rocky Desertification Areas

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Abstract In this paper, managed forest (MF) and natural forest (NF) in the Huajiang Demonstration Zone of Guanling, Guizhou were selected as research objects, and cropland (CL) was taken as control. High-throughput sequencing technology was used to study the characteristics of fungal community composition and species diversity in the surface (0 - 10 cm) soil of each restoration measure, in order to reveal the dominant soil fungal groups and fungal community composition in karst rocky desertification areas, which was conducive to a more comprehensive understanding of the soil conditions of different vegetation restoration measures. Research has shown that vegetation restoration significantly affected the diversity of soil fungal community, with significant increases in Sob index, Ace index, and Chao index. The vegetation restoration has significantly changed the composition of fungal community. The dominant fungi in the CL topsoil are Sordariomycetes (62.28%), Dothideomycetes (12.34%), and Eurotiomycetes (9.12%); the dominant fungi in the MF soil are Sordariomycetes (45.05%), Dothideomycetes (14.74%), and Mortierellomycetes (10.40%); the dominant fungi in the NF soil are unclassified fungal community (26.38%), Sordariomycetes (19.78%), and Agaricomycetes (13.82%). Vegetation restoration has changed the key fungal groups in the soil. Sordariomycetes, *Fusarium*, and Setophoma are the key dominant fungal groups in CL soil; Dioszegia is key dominant fungal group in MF soil; c_unclassified_k_Fungi, p_unclassified_k_Fungi, o_unclassified_k_Fungi, f_unclassified_k_Fungi, g_unclassified_k_Fungi, Teichospora, and *Diaporthe* are key dominant fungal groups in NF soil.

Key words Karst rocky desertification; Vegetation restoration; Soil fungal community; Fungal diversity

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The soil microbial community mainly includes bacteria, fungi, and archaea, which dominate the biogeochemical cycle. It is not only the largest component of global biodiversity, but also provides impetus for cycling of soil organic matter and nutrient elements such as carbon and nitrogen[1-2]. At the same time, soil microorganisms also participate in key processes of forest ecosystems, playing an immeasurable role in the decomposition of soil organic matter and plant litter, maintaining soil structure formation and biodiversity regulation, and ensuring system stability[3]. Soil microorganisms participate in the maintenance and regulation of carbon and nitrogen cycling, organic matter decomposition, energy transfer and transportation, and are the most important component of soil ecosystems. Microbial diversity is closely related to the structure and function of soil ecosystems, and plays an important role in maintaining soil fertility and ecological balance. Its structure and function are particularly sensitive to surrounding environmental conditions and are one of the important indicators of soil changes[4]. In addition, soil microorganisms play a crucial role in soil ecosystem functions and can respond sensitively to changes in the external environment. When carrying out vegetation restoration, there can be significant changes in the quantity, activity, and population structure of soil microorganisms. Due to the influence of different dominant species, the response of microbial community diversity to changes varies. Different species may affect the formation of different microbial communities, and this effect is manifested by affecting the species composition and relative abundance of microorganisms[5].

Different vegetation restoration measures have a significant impact on the composition and structure of soil microbial communities, and affect the stability of soil ecosystems[6]. However, most studies on the impact of vegetation restoration on soil microbial community composition and diversity have used phospholipid fatty acids (PLFA), community level decomposition metabolic profiles (Biolog)™, and polymerase chain reaction - denaturing gradient gel electrophoresis (PCR-DGGE), but these methods still lack the resolution for fine classification of microbial community structure. In recent years, high-throughput sequencing technology has provided an opportunity to gain a deeper understanding of the response of soil microorganisms to vegetation restoration with higher resolution and coverage. For example, Li Qiang[7] found through high-throughput sequencing of 16S rRNA and 18S rRNA that there are significant differences in soil microbial community structure among four vegetation types in karst fault basins; using 16S rRNA high-throughput sequencing technology, Yang Rui *et al.*[8] found that there were significant differences in the composition of rhizosphere microbial communities in *Zanthoxylum bungeanum* planted for different years; Zhu Jianning *et al.*[9] also used high-throughput sequencing technology to find significant differences in soil microbial composition in the cropland of Sanjiang Plain counties. Although there have been many studies on

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the impact of vegetation restoration measures on soil microbial community structure, the results obtained are controversial and even contradictory. Some studies have found that vegetation restoration can alter the diversity and composition of soil microbial communities[10-11]. And some studies have shown that the impact on α diversity of soil microorganisms is not significant[12]. The main reason may be that the composition and diversity of soil microbial communities are influenced by many biological and abiotic factors[13]. Fungi are one of the main groups of soil microorganisms, which can not only decompose substances difficult to be degraded such as lignin and cellulose in plant residues, but also form pathogens or symbiotes that closely interact with plants, promoting plant metabolism and nutrient absorption. They play an important role in soil nutrient accumulation, transformation, and material cycling, and have made significant contributions to maintaining the stability of soil ecosystems[14]. Domestic and foreign studies have shown that changes in vegetation types have a significant impact on the structure of soil fungal communities[5,15-18]. Different community structures are closely related to changes in soil physicochemical properties, especially effective phosphorus, which is one of the main driving factors for changes in soil fungal community structure and composition[19]. Vegetation restoration plays an important role in soil fungal communities, especially after 30 years of vegetation restoration, the number of soil fungal communities significantly increases. There are also significant differences in soil biological activity formed by different types of plants. Compared to soil bacteria, soil fungi are more adaptable to harsh environments. There are significant differences in fungal species, diversity, and relative abundance among different types of soil. The changes in soil fungal community are closely related to the changes in SOC content and fraction, and may be driven by them[20]. The composition of microbial PLFA varies with different restoration strategies, and the abundance of phospholipid fatty acids of arbuscular mycorrhizal in natural soil restoration is significantly higher than that in managed vegetation restoration[21]. There are significant differences in the rich and rare groups of soil microbial communities under different vegetation conditions[22]. The composition of fungal communities is most closely related to changes in soil nutrient conditions. Extractable soil phosphorus may be an important regulatory factor for soil fungal communities. The changes in dominant fungal groups may be related to changes in specific soil characteristics[23]. Previous studies have shown that soil moisture content, total nitrogen, organic carbon, and alkaline nitrogen have significant effects on fungal communities. Different plants have different nutrient absorption abilities in the soil, so there is a certain relationship between plant root distribution and soil organic matter content, and soil moisture content is one of the important factors determining soil biological activity. When improving soil moisture content, it will provide a favorable environment for the formation of microbial communities, and the diversity of microbial communities is also showing a significant upward trend[24]. The increase in soil organic carbon creates favorable conditions for the accumulation of soil nutrients and the growth of soil fungi. These studies have shown that vegetation restoration has a significant impact on soil fungal communities, but the important regulatory factors affecting soil fungal communities vary in different regions. Perhaps the dominant fungal groups in different regions have different requirements for soil properties. Vegetation restoration affects the structure and diversity of soil fungal communities by altering soil properties.

Based on this, Huajiang Karst Canyon Rocky Desertification Control Demonstration Zone in Zhenfeng County, Guizhou Province was taken as the research area. Using 16S rRNA high-throughput sequencing technology, the changes in physicochemical properties and fungal community structure of the surface soil (0 – 10 cm) in CL, NF, and MF were contrasted. The purposes of this paper were to ① analyze the impact of afforestation on soil fungal communities, ② elucidate the response of soil fungal communities to afforestation, and ③ determine the dominant fungal groups under different vegetation restoration measures. It aimed to provide theoretical basis for the response of soil microbial communities to ecological restoration in karst rocky desertification areas.

1 Materials and methods

1.1 Research area and experimental design The research area is located at the border of Guanling County, Anshun City, Guizhou Province and Zhenfeng County, Qianxinan Autonomous Prefecture, in the Huajiang karst rocky desertification control demonstration area (25°39′13″ – 25°41′00″ N, 105°00′36″ – 105°46′30″ E, Fig. 1). The altitude is 500 – 1 200 m, with a total area of 51.6 km^2, of which the karst area is about 87.92%. The research area has a typical subtropical dry hot valley climate, with an average annual temperature of 18.4 ℃ and an annual precipitation of about 1 100 mm. 80% of the total precipitation is mainly concentrated from May to October. The soil in this area is mainly limestone soil. Long-term unreasonable human activities and land use have resulted in low surface vegetation coverage, high rock exposure rate, and developed intensity of rocky desertification in the area. Three sampling areas were set up within the research area, with a distance of 500 – 1 500 m between each sampling area. Control cropland (CL), managed forest (MF), and natural forest (NF) were selected in each sampling area. MF and NF in each sampling area are adjacent to CL, ensuring that the terrain and soil types of each land use type are basically the same. NF is natural fallow for 15 – 20 years, and the main vegetation species are *Toona sinensis*, *Koelreuteria paniculata*, *Mallotus barbatus*, *Viburnum dilatatum*, *Mallotus philippensis*, *Vernicia fordii*, *Alangium chinense*, *etc.* MF is the main ecological restoration economic forest in the local area, planted for about 15 – 20 years. Local residents pick *Z. bungeanum* and trim their branches from July to September every year. The main cultivation of CL is maize (*Zea mays* L.), which has been planted for more than 50 years. Corn is harvested in September every year, and the corn straw is removed.

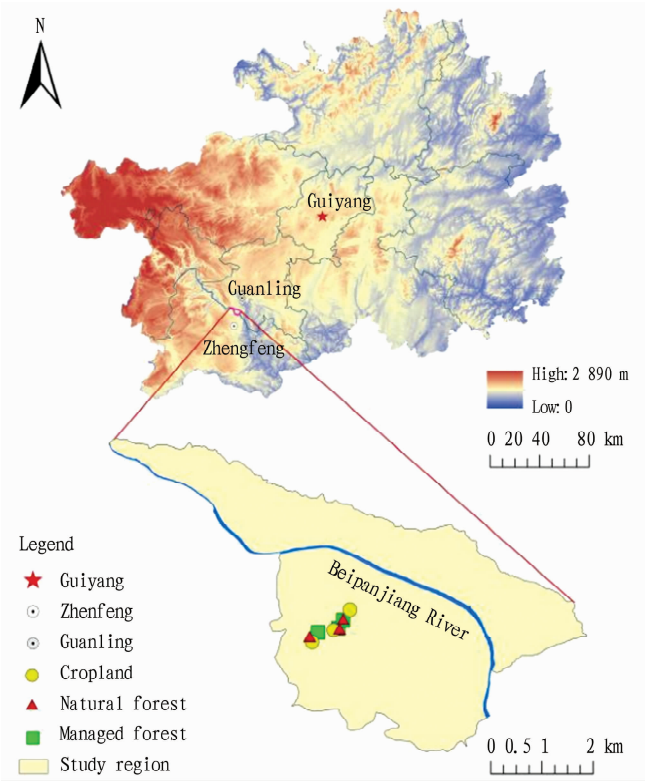

Fig. 1 Research location

1.2 Site setting and sample collection Three different vegetation restoration measures (CL, NF, and MF) were selected as the research objects in the study area. Three sample plots (10 m × 10 m) were set up for each land type, and 0 – 10 cm of undisturbed soil was collected using sterile bags for each plot. Three points were mixed into one point. Using a shovel, 2 kg of soil samples from a 0 – 10 cm of soil layer was taken. After sieving out stones and plants, the soil was mixed evenly, and the samples were sealed in plastic bags for the determination of soil physical and chemical properties. Approximately 25 g of soil was collected using sterilized gloves, and was placed in a sterilized centrifuge tube. It was transported back to the laboratory on the same day using a portable outdoor refrigerator, and was immediately frozen in a −80 ℃ of freezer for the determination of soil fungal community structure.

1.3 Soil DNA extraction and quantification Soil DNA was stored in an environment of −20 ℃, and sample DNA was extracted from 0.15 – 0.35 g of fresh soil using a DNA kit. The quality and concentration of DNA were measured using a Nanodrop 2000 spectrometer (Thermo Fisher Scientific, Wilmington, DE, United States). The quality of DNA extraction was detected by 1% agarose gel electrophoresis. Through polymerase chain reaction (PCR), amplification of the V3 – V4 variable region was performed using primers 338F (5'-ACTCCTACGGAGGGCAGAG-3') and 806R (5'- GGACTACHVGGGTWTCTAAT-3'). The reaction conditions were: initial denaturation at 95 ℃ for 5 min, followed by denaturation at 95 ℃ for 30 s, primer annealing at 58 ℃ for 30 s, and extension at 72 ℃ for 1 min, with 3 replicates per sample. After mixing the PCR products of the same sample, they were eluted with Tris HCl buffer, and PCR amplification was detected with 2% agarose gel electrophoresis. The AxyPrepDNA gel recovery kit (AXYGEN Company) was used to cut and recover the PCR products, and QuantiFluor™-ST blue fluorescence quantitative system was used for detection and quantification of the recycled products. The amplified products were sequenced using the Illuminian HiSeq2500 PE250 platform at Shanghai Meiji Biopharmaceutical Technology Co., Ltd.

1.4 OTU classification According to different vegetation restoration measures, 9 sampling points were divided into 3 groups. Annotation on species taxonomy of OTU was performed, and the corresponding abundance information of each OTU annotation result in each sample was calculated. Based on the taxonomic annotation results, sequence information was extracted from two levels: phylum and class, and the relative abundance of each species was calculated. Those with abundance <0.01 were merged into one category and recorded as others.

1.5 Data analysis One-way ANOVA was used to compare whether there was a significant difference ($P<0.05$ and $P<0.01$) between α diversity of soil fungi under different vegetation restoration measures. One-way ANOVA and LSD test were conducted using SPSS 22.0 statistical software. α diversity index involving community diversity (Shannon and Simpson), community richness (Chao1, Sobs and Ace), and community coverage (Coverage) was calculated by Mothur (v. 1.30.2 version, https://mothur.org/wiki/calculators/). The R language package (version 2.4.3) was used for non-metric multidimensional scaling (NMDS) and ANOSIM analysis of Bray-Curtis dissimilarity to compare and visualize the similarity of soil bacterial communities among different land use types. Linear discriminant analysis (LDA) effect size (LefSe, http://huttenhower.sph.harvard.edu/galaxy/root?tool_id=lefse_upload) was used to identify species with differences between communities, and further determine specific fungal groups under different vegetation restoration measures. Inter group microbial differences can be obtained, and microbial species with differences between groups can be identified, which is of great significance for microbial diversity protection and predicting soil quality change patterns.

2 Results and analysis

2.1 Optimization of high-throughput sequencing data The dilution curve is a method of randomly selecting a certain number of sequences from a sample, calculating the Alpha diversity index of the corresponding samples, and determining whether the sequencing data is sufficient based on whether the curve has reached a plateau. The Core species curve is used to describe the changes in total and core species as the sample size increases. Based on whether the Pan/Core species curve has reached a plateau, it can be evaluated whether the sample size for this sequencing is sufficient. As shown in Fig. 2, the dilution curve and Core species analysis curve tended to flatten with the increase of sample size, indicating that the sample size for this test was sufficient, and the data was reliable.

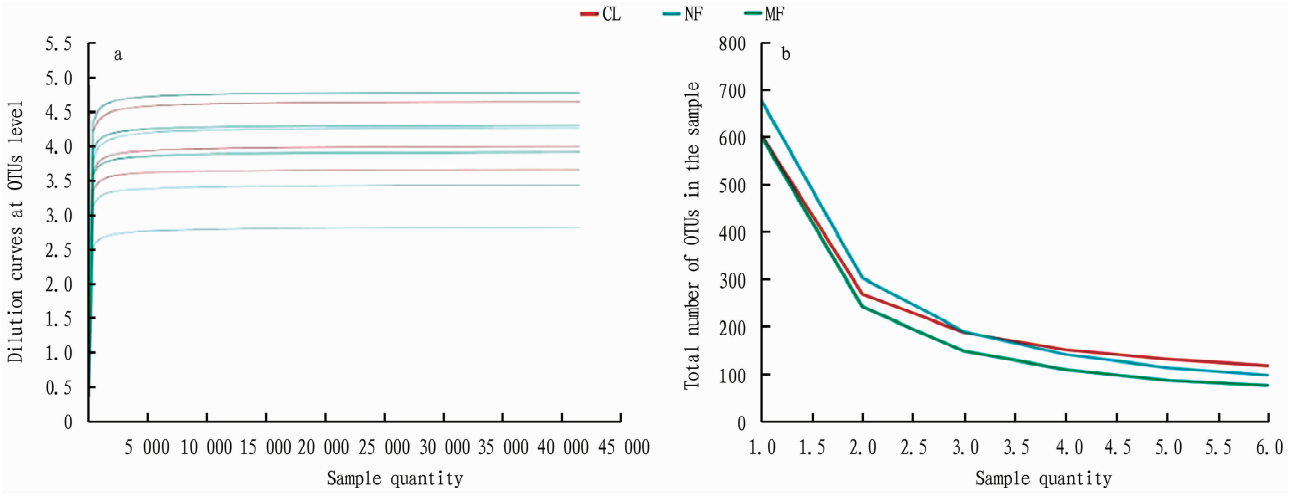

Fig. 2 Dilution curves (a) and Core species analysis curves (b) for different samples

A total of 524 949 valid sequences were obtained from 9 soil samples through high-throughput sequencing and analysis (Table 1), with 41 563 valid sequences obtained from each sample. The number of OTUs was 2 703, belonging to 12 phyla, 44 classes, 113 orders, 259 families, and 561 genera.

Table 1 Sequencing results

Land type	Real sequence	Effective sequence	Number of OTUs	Range
CL	177 562	124 689	1 297	0.994
MF	150 739	124 689	1 422	0.995
NF	196 648	124 689	1 393	0.993

2.2 Diversity of soil fungal communities Common α diversity index of soil fungi includes Shannon index, Sobs index, Simpson index, Ace index, Chao index, and Coverage index. The Sobs index represents the actual number of observed species, and the higher the value, the more microorganisms in the sample. The Shannon index is used to estimate the diversity of microorganisms in a sample, and the higher the value, the higher the diversity of microbial communities in the sample. The Simpson index refers to the probability that the number of individuals obtained from two consecutive sampling of a community belongs to the same species. The higher the value, the lower the diversity of the microbial community in the sample. The Ace index is used to evaluate the richness and evenness of species composition in a sample. The larger the value, the richer the microbial species in the sample, and the more uniform the distribution of each species. The Chao index is used to estimate the number of species, and the higher its value, the more species there are; the Coverage index represents the coverage of sequencing results, and the higher its value, the closer the sequencing results are to the actual situation. According to Table 2, there was no significant difference in the Sob and Shannon indexes among the three land types. The Ace and Chao indexes in NF were significantly higher than those in CL ($P<0.05$). Similarly, the Simpson diversity index of NF was significantly higher than that of MF ($P<0.05$), and there was no significant difference in the Simpson diversity index between MF and CL. The coverage index of CL was different from that of NF, but there was no significant difference compared to MF.

Table 2 Alpha diversity index of soil fungi under different vegetation restoration measures

Land type	Sobs	Shannon	Simpson	Ace	Chao	Coverage
CL	660 ± 55.34 a	4.10 ± 0.29 a	0.05 ± 0.02 ab	742.27 ± 68.39 b	741.80 ± 68.47 b	1.00 ± 0.000 4 a
NF	778 ± 88.70 a	3.52 ± 0.42 a	0.12 ± 0.03 a	981.03 ± 60.50 a	957.43 ± 61.36 a	1.00 ± 0.000 1 b
MF	684 ± 22.01 a	4.34 ± 0.25 a	0.04 ± 0.10 b	773.75 ± 23.19 b	774.97 ± 20.38 ab	1.00 ± 0.000 2 a

Note: Different lowercase letters in the same column indicate significant differences ($P<0.05$).

Non-metric multidimensional scaling, also known as NDMS, was used to explore the similarity and differences of microbial communities in different soil ecological environment samples, and analyze their inter group differences. As shown in Fig. 3, stress = 0.019 < 0.05 indicated that this analysis had good representativeness. There were differences in the composition of soil fungal communities under three different vegetation restoration measures. The concentration of CL and MF points indicated that the community structure of CL was similar to that of MF. The dispersion of NF was relatively open and far away from CL and MF, indicating significant differences in the soil fungal community structure between NF and CL, MF, and the soil fungal community structure of each NF sample point was not similar.

2.3 Composition of soil fungal community

2.3.1 Composition of soil fungal communities at the class taxonomic level. The composition of soil fungi under different vegetation restoration measures was shown in Fig. 4. In CL soil sample, Sordariomycetes was dominant taxa, and its relative abundance was 62.28%, followed by Dothideomycetes (12.34%), Eurotiomycetes (9.12%), Mortierellomycetes (6.08%), unassorted Ascomycota (2.93%). The relative abundance of undetermined fungal groups in NF soil samples was relatively high at 26.38%,

followed by Sordariomycetes (19.78%), Agaricomycetes (13.82%), Leotiomycetes (12.51%), unassorted Ascomycota (10.41%). In MF soil sample, Sordariomycetes was dominant taxa, and its relative abundance was 45.05%, followed by Dothideomycetes (14.74%), Mortierellomycetes (10.40%), Eurotiomycetes (9.26%), and unclassified fungal communities (7.23%). In CL species, Sordariomycetes was significantly more than other plots, and unclassified fungal communities, Agaricomycetes and Leotiomycetes in NF were significantly more than other plots, and Mortierellomycetes in MF was significantly more than other plots. This indicated that the composition of soil fungal communities varied under different vegetation restoration measures, and there were significant differences in NF, CL, and MF.

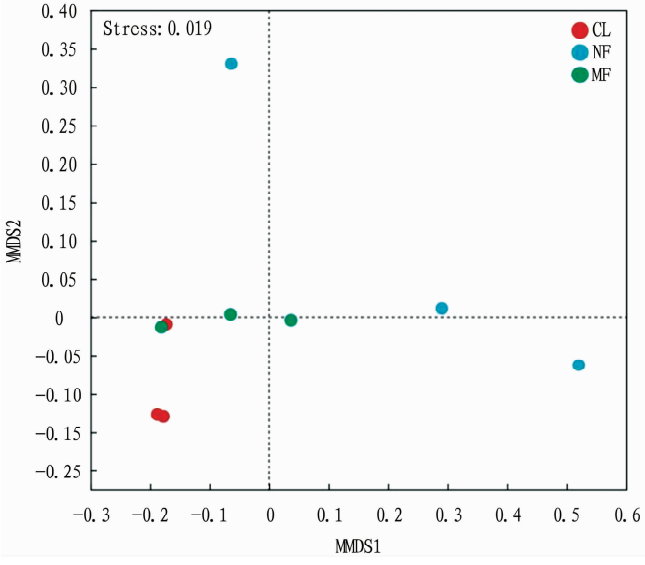

Fig. 3 NMDS analysis of soil fungi under different vegetation restoration measures

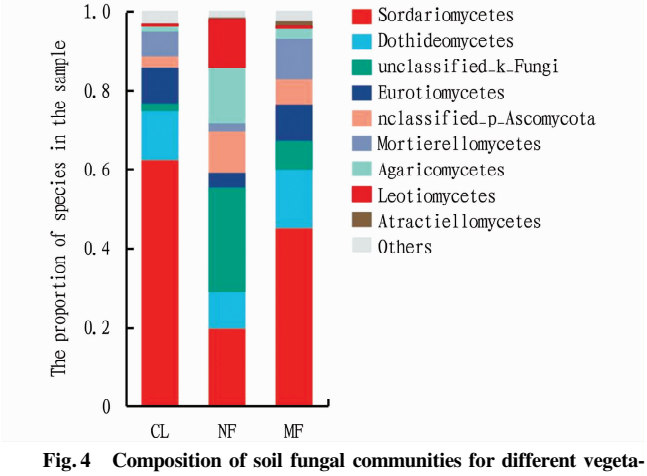

Fig. 4 Composition of soil fungal communities for different vegetation restoration

2.3.2 Venn analysis at the OTU level. Seen from Fig. 5, CL unique species were concentrated in Olpidiomycetes, and NF unique species were concentrated in Dacrymycetes and Arthoniomycetes, and MF unique species were concentrated in Tritirachiomycetes and GS19. There were 452 unique species of CL (at OTU level), 699 unique species of NF, 444 unique species of MF, and a total of 423 core species in the three plots. The restoration measures for vegetation had a significant impact on the composition of fungal communities, especially in NF.

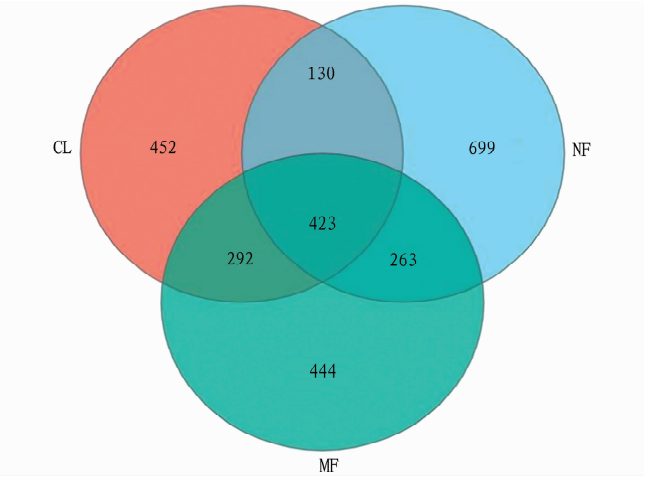

Fig. 5 Venn plot of soil fungi under different vegetation restoration measures

2.3.3 Analysis of key fungal taxa. LEfSe analysis (Fig. 6) revealed significant differences in species among the three types of land use. The LDA score obtained through LDA analysis (linear regression analysis) indicated that the larger the LDA score, the greater the impact of species abundance on differential effects. 7 fungal taxa were enriched in CL soil, namely Sordariomycetes (LDA = 5.33), *Fusarium* (LDA = 4.79), Gymnascella (LDA = 4.29), Setophoma (LDA = 4.15), Hypocreaceae (LDA = 3.78), Pleosporaceae (LDA = 3.60), and Schizothecium (LDA = 3.51). 8 significantly different fungal taxa were detected in NF soil, namely c_unclassified_k_Fungi (LDA = 5.12), p_unclassified_k_Fungi (LDA = 5.10), o_unclassified_k_Fungi (LDA = 5.07), f_unclassified_k_Fungi (LDA = 5.07), g_unclassified_k_Fungi (LDA = 5.06), Immersidiscosia (LDA = 4.17), Teichospora (LDA = 3.97), Bulleribasidium (LDA = 3.73). Fungal taxa enriched in MF was Dioszegia (LDA = 3.68). The results showed that there were significant changes in the relative abundance of soil fungal communities under three different vegetation restoration measures.

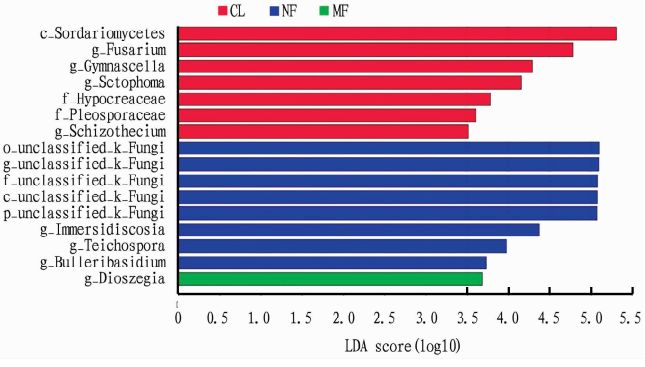

Fig. 6 Columnar distribution of LDA values of soil fungal species under different vegetation restoration measures

3 Discussion

3.1 Different vegetation restoration measures altering the composition of soil fungal communities The dominant fungi in CL were Sordariomycetes, with a significantly higher relative abundance than NF and MF. The reason may be due to the interference of more human factors on CL, which was consistent with the research results of Gottshall *et al.* Less soil disturbance is conducive to the establishment of fungal hyphal networks, thereby promoting the increase of fungal communities. Moreover, Sordariomycetes belongs to Ascomycota, which is more suitable for survival in agricultural soil. There were significantly more unclassified fungal communities, Agaricomycetes, and Leotiomycetes in NF than in other plots. This may be due to the fact that most of the fungi in Agaricomycetes require higher environmental requirements for survival and are more suitable for survival in natural forests. Many fungal species of Leotiomycetes are plant pathogens, and they need to survive in environments with diverse and large-scale plant species. Mortierellomycetes in MF was significantly more than that in other plots. The possible reason is that the abundance of Mortierellomycetes in soil rich in organic matter is high, playing a crucial role in the transformation of soil carbon and nutrients. The difference in dominant fungi among the three plots may be due to differences in vegetation or soil characteristics within the study area. Vegetation has a significant impact on fungal communities. On the one hand, different plants produce different secretions that affect the composition of soil biological communities. On the other hand, vegetation can coexist with some soil fungi or form mycorrhizal fungi to enhance soil ecosystem stability. The relative abundance of dominant microbial communities and functional genes in soil microbial communities varies under different land use methods, mainly influenced by changes in soil characteristics caused by different land use methods. Soil bulk density, TN, SOC, soil C : N, and mineral nitrogen all affect the changes in fungal communities, while land use has a relatively small impact on fungal nutrient types.

3.2 Impact of different vegetation restoration measures on soil fungal community diversity Soil characteristics are important factors affecting soil fungal diversity. Vegetation restoration significantly affects the diversity of soil fungal communities. Soil bulk density, TN, SOC, soil C : N, and mineral nitrogen all affect changes in fungal communities. Soil bulk density and SOC significantly affect parasitic plant and animal pathogens, endophytic pathogens, and wood saprophytic fungi; soil mineral nitrogen content significantly affects animal pathogens and soil saprophytic bacteria; soil C : N and mineral nitrogen significantly affect orchid mycorrhizal fungi. In this paper, the Shannon index of MF was higher than that of CL. The possible reason was that MF had a rich understory vegetation community and well-developed roots when compared with CL, resulting in better soil bulk density and moisture content than CL and NF. The vegetation population of MF was more abundant and was subject to a small amount of human interference, and the litter covering the surface can be quickly decomposed. CL is prone to soil erosion in rocky desertification areas, resulting in a significant loss of SOC. The Shannon of NF was lower than that of CL, possibly due to the dry season in the study area during sample collection, where many fungi in NF were inactivated, while CL and MF were not significantly affected by human factors.

4 Conclusions

(1) Vegetation restoration significantly affected the diversity of soil fungal communities.

(2) The vegetation restoration has significantly changed the composition of fungal communities. In the CL topsoil, dominant fungi were Sordariomycetes (62.28%), Dothideomycetes (12.34%), Eurotiomycetes (9.12%), Mortierellomycetes (6.08%), unclassified Ascomycota (2.93%); the dominant fungi in the MF soil were Sordariomycetes (45.05%), Dothideomycetes (14.74%), Mortierellomycetes (10.40%), Eurotiomycetes (9.26%), unclassified fungal communities (7.23%); dominant fungi in the NF soil were unclassified fungal communities (26.38%), Sordariomycetes (19.78%), Agaricomycetes (13.82%), Leotiomycetes (12.51%), unclassified Ascomycota (10.41%).

(3) Vegetation restoration has changed key fungal groups in soil, showing as Sordariomycetes, *Fusarium*, and Setophoma were the key dominant fungal groups in the CL soil; Dioszegia was key dominant fungal group in the MF soil; c_unclassified_k_Fungi, p_unclassified_k_Fungi, o_unclassified_k_Fungi, f_unclassified_k_Fungi, g_unclassified_k_Fungi, Teichospora, and *Diaporthe* were key dominant fungal groups in the NF soil.

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(From page 54)

Affected by terrain convergence and enhanced dynamic uplift, it was conducive to the continuity and increase of precipitation.

(5) In this process, the forecast of prefecture- and county-level meteorological departments was more accurately, and their services were fine and timely. The warnings had a good time advance. When issuing high-level warnings, the municipal meteorological bureau decisively called relevant departments 6 h and 14 min before the disaster occurred.

(6) Dehong Prefecture has complex terrain, and there were certain uncertainties in the consideration of topography by model products. Forecasters themselves had insufficient understanding of the triggering effect of complex terrain, and subjective correction was difficult, which was also an important reason for the deviation of heavy precipitation forecast. In the future, business personnel should strengthen the research on the influence mechanism of complex terrain on precipitation and the inspection and application of various model products.

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