Differences in soil microbial communities with successional stage depend on vegetation coverage and soil substrates in alpine desert shrublands

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Abstract

Background and aims In semiarid ecosystems, changes in plant communities are promoted under shrub canopies during restoration, but the link between shrub community restoration dynamics and changes in soil microbe communities is still unclear.

Methods We characterized the community structure and plant interactions of soil microbes by combining different methodological approaches (including high-throughput sequencing of the 16S rRNA gene and ITS gene, analysis of phospholipid fatty acids (PLFAs) and chloroform fumigation) and the key driving factors along a successional gradient of Sophora moorcroftiana shrub community in the middle reaches of the Yarlung Zangbo River.

Results Soil microbial biomass carbon (MBC) and nitrogen (MBN), total PLFAs, and alpha diversity increased significantly as the successional stage advanced, and MBC and MBN were positively correlated with the carbon and nitrogen contents in the soil. Mantel test showed that successional stage-induced changes in soil microbial beta diversity were mainly associated with shrub coverage and soil physicochemical properties. The relative abundances of bacterial PLFAs, particularly those of gram-negative bacteria, such as Bacteroidetes, Alphaproteobacteria and Betaproteobacteria, significantly decreased with succession; the opposite was true for Acidobacteria, Planctomycetes, Gemmatimonadetes Deltaproteobacteria and Gammaproteobacteria. However, the proportion of fungi did not significantly differ among the four successional stages; the dominant phyla were Ascomycota and Basidiomycota.

Conclusion We suggest that shrubs directly shape soil microbial communities or indirectly affect such communities by altering soil substrates. Our findings advance the current understanding of sand-stabilizing plant–soil interactions during natural restoration and the reversal of desertification in stressful desert ecosystems.

Introduction

Desertification is defined as one of the most serious eco-environmental land degradation problems associated with wind erosion on the Tibetan Plateau (Shen et al. 2012; Zhan et al. 2021) and is mainly characterized by the loss of natural vegetation and wildlife; degradation of physical, chemical and biological soil characteristics; and surface sand drift (UNCCD 1994; Feng et al. 2021). Desertification severely degrades soil quality, reduces land resources and creates sandstorms, leading to further restrictions in local economic development (Liu et al. 2020). Ecological restoration is seen as a global priority for restoring degraded ecosystems (Aronson and Alexander 2013; Liu et al. 2018). Vegetation is the most important biological component in sand dune habitats and directly affects the stability and resilience of sand dune structures (Liu et al. 2014; Wang et al. 2019). In particular, native shrub species have been proposed as one of the most effective ways to achieve ecological restoration due to their ability to mitigate desertification and prevent soil erosion (Xiao et al. 2019). Vegetation restoration in degraded ecosystems has been proposed as the dominant measure for protecting soil surfaces from wind erosion (Zhang et al. 2022). Previous studies indicated that the successional gradient of vegetation community restoration in desert ecosystems is actually one type of disturbance gradient, with the disturbance to the surface layer decreasing with increasing vegetation cover (e.g. Bai et al. 2018; Bai et al. 2020). In such arid environments, soil nutrient content, water use efficiency, and microbial community structure vary simultaneously with community succession (Lozano et al. 2014; Liu et al. 2018; Bai et al. 2020). However, how soil microbes affect plant–soil interactions along community successional gradients in alpine desert ecosystems remains unclear.

It is well known that microbes are regarded as ideal indicators for soil quality and health and play key roles in the transformation of soil nutrients, mineralization of natural compounds, regulation of soil ecosystem functions and ecological processes (Schloter et al. 2003; Biswas and Kole 2017; Schloter et al. 2018). They also influence plant growth and community evolution by regulating soil nutrient availability (Zhang et al. 2019), and plants in turn affect the soil microbial community structure and drive changes in physicochemical soil properties (van der Putten et al. 2013).

Previous studies have demonstrated that vegetation restoration in arid and semiarid environments significantly alters soil microbial community structure and diversity (e.g. Zhang et al. 2013; An et al. 2022). For instance, the abundances of total phospholipid fatty acids (PLFAs) and the PLFAs of microbial functional groups significantly increased following vegetation restoration (Hu et al. 2020). Bacterial diversity and richness increased with the establishment of *Haloxylon ammodendron* on shifting sand dunes, and the structure of bacterial communities was significantly altered (An et al. 2022). Studies have showed that changes in microbial community composition are influenced by factors such as carbon inputs (Lozano et al. 2014); plant-microbial interactions (Bai et al. 2020); soil pH and carbon, nitrogen and phosphorus contents (Banning et al. 2011; Song et al. 2019). Poosakkannu et al. (2017) found that succession strongly affects the distribution of microbial species, but fungi and bacteria may not follow the same successional trajectories, in sand dune ecosystems. These studies indicated that the expansion of native shrubs can increase soil bacterial and fungal community diversity and microbial biomass and select for different fungal community compositions and fungal: bacterial (F:B) ratios (Hollister et al. 2010; Yannarell et al. 2014; Collins et al. 2016). Such published reports on soil microbial changes with plant community succession, however, lacked sufficient information (e.g. microbial biomass, community composition and activity) to help explain such variations in dry or semiarid environments.

Some new and young endemic vegetation was found in sandy environments on the Tibetan Plateau (Shen 1996). These species are exposed to harsh environmental conditions (e.g. low oxygen, extremely low temperatures, drought and salinity) and have evolved unique physiological and biochemical adaptation strategies to cope with these multiple stresses (Li et al. 2017). *Sophora moorcroftiana* (Benth.) Baker, a perennial leguminous shrub, is an endemic species to Tibet and is limited to hillsides, sandy gravel floodplains, sandy areas and alluvial fans of the wide valley in the middle reaches of the Yarlung Zangbo River (Cheng et al. 2017). Ecologically, it is one of the most important sand-fixing plant species; it exhibits strong tolerances to drought, cold, barren land and sand burial, and acts as a pioneer species for vegetation restoration and reconstruction in this region (Zhao et al. 2007; Guo et al. 2014; Liao et al. 2021). It plays an irreplaceable role in water and soil conservation, the fixation of sand dunes and the prevention of shifting sands in the middle reaches of the Yarlung Zangbo River (Guo et al. 2009). To our knowledge, desert shrubs can have specific and obvious “morphological, physiological or behaviour” effects in these extreme and harsh environmental conditions; these adaptations strongly affect the basal soil organic matter (SOM), nutrient contents, salinity and other conditions and affect the activity, quantity and diversity of soil microorganisms (Yu and Steinberger 2012). However, the impact of *S. moorcroftiana* shrub community succession on soil microbial communities has not yet been studied, and the ecological role of soil microbes in mediating plant–soil interactions along successional gradients in alpine desert ecosystems has not been determined. Thus, *S. moorcroftiana* shrub community succession in alpine desert ecosystems provides a very interesting scenario to study the impact of vegetation restoration processes on soil microbial communities under climate change. To the best of our knowledge, due to fluctuations in environmental conditions and extreme spatial heterogeneity, alpine soil microbial communities can be highly specialized and can vary widely across vegetation types, soil properties, and microclimates (Donhauser and Frey 2018; Fierer 2017). Therefore, understanding the effects of vegetation succession on soil microbial communities and the underlying key drivers of community assembly of alpine desert ecosystems will greatly advance existing knowledge about the underlying mechanisms that drive plant community succession in desertified alpine areas.

In this study, we hypothesized that the soil microbial community structure under *S. moorcroftiana* shrubs would differ by successional stage and would change in biomass, diversity, and composition. We also hypothesized that shrub coverage and soil physicochemical properties would be the key drivers structuring soil microbial communities. Our objective was to obtain an in-depth understanding of the potential links between soil microbial and plant–soil interactions during vegetation-soil system restoration. To do this, we used fumigation-extraction and PLFA and Illumina sequencing to evaluate the alterations in soil microbial biomass, diversity and community composition and the key

driving factors of these changes along a successional gradient of *S. moorcroftiana* shrub community restoration in the middle reaches of the Yarlung Zangbo River, southern Tibetan Plateau.

Materials And Methods

Study area

This study was conducted in the middle reaches of the Yarlung Zangbo River (28°59'–29°26' N, 88°04'–93°18' E) (Fig. 1, Table S1). The middle reaches of the Yarlung Zangbo River basin from Lizi to Pai town in Mainling county, are approximately 1293 km in length, with an area of 60,000 km^2, which is 5% of the Tibet Autonomous Region (Zhong et al. 2014; Zeng et al. 2018). The region is mainly characterized by a monsoon and semiarid plateau climate. The average annual temperature is approximately 6–8 °C, with summer temperatures of ≥15 °C and winter temperatures below -2 °C, and the average annual precipitation is 300–600 mm, which falls mainly from July to August (Sun et al. 2019; Ling et al. 2020). In winter and spring, there are strong winds in the basin. The wind velocity is extremely high at 32.5 m/s, the monthly maximum wind velocity is 4.7 m/s, and the number of windy days is as high as 172 days per year (Shen et al. 2012). The altitude ranges from 3032 to 4019 m. The soil type is mainly mountainous shrub steppe soil and alpine steppe soil. The natural vegetation mainly consists of mountain shrub grassland, with *S. moorcroftiana*, *Ceratostigma minus*, *Aristida triseta*, *Orinus thoroldii*, and *Pennisetum flaccidum* as the dominant species. In alpine grasslands, *Stipa purpurea*, *Artemisia* and *O. thoroldii* are constructive species.

Plant investigation and soil sampling

In August 2020, a sampling site was established in an *S. moorcroftiana* dominated shrub grassland, on gentle terrain; the area had not been subjected to anthropogenic disturbances and included an aeolian sandy surface located along the middle reaches of the Yarlung Zangbo River basin. The transect contains different types of aeolian sand (moving dune, semi-fixed dune, fixed dune, etc.) In the initial stage of community succession, on moving sand dunes, the vegetation community consisted of the shrub *S. moorcroftiana* with sparse sand-stabilizing herbaceous plants. With succession, the dominance of *S. moorcroftiana* increased, ultimately resulting in a fixed sandy area. The climax of sand-stabilizing vegetation succession in the middle reaches of the Yarlung Zangbo River is the shrub community, with *S. moorcroftiana* being the dominant species (Zhao et al. 2007). Thus, we classified the entire successional gradient of the community restoration process into four stages based on vegetation cover and surface features (Shen et al. 2012). The first stage was dominated by *S. moorcroftiana*, with sparse sand-stabilizing herbaceous species on moving dunes and vegetation cover < 10%. In the second stage, the importance value of *S. moorcroftiana* gradually increased, and herbaceous species gradually recovered in the presence of nurse shrubs, transitioning into the semifixed dune stage with vegetation cover of 10%-30%. In the third stage (sandy gravel stage), the coverage of *S. moorcroftiana* shrubs further increased, with vegetation cover of 30%-60%; this marked a transitional stage from semi-fixed sandy land to fixed sandy land, and the sandy land type is in a fixed state at this stage. In the last stage, the community entered the fixed dune stage, and the vegetation coverage of the climax shrub community with *S. moorcroftiana* as the dominant species reached 70%. Fig. 1, Table 1 and Table S1 outline these stages.

In this study, 24 sample sites were selected in the four successional stages of the *S. moorcroftiana* shrub community, all of which had a similar topographic position (flat sandy land). Three 100 m^2 (10 m × 10 m) plots were randomly selected in each identified site, giving a total of 72 plots. The distance between any two plots was greater than 10 m. We measured the shrub coverage (SBC) of each plot along three parallel lines, each with a length of 10 m (Bai et al. 2020). In each plot, we established five diagonal 1 m × 1 m subplots in which to determine the grass biomass (GB) and grass coverage (GC). For the plant investigation, we chose 8–10 vigorous *S. moorcroftiana* shrubs in each plot and measured their diameter at breast height (DBH), shrub height (SH), and shrub crown size (SCS) (its shape approximated an ellipse)

by taking the east–west and north–south diameters through the centre of the fullest part of the canopy (MartinezMeza and Whitford 1996). Plant samples were dried at 105 °C for approximately 15 min to minimize respiration and decomposition. Subsequently, the plant samples were oven-dried to a constant mass at 65 °C.

For soil sampling, nine soil cores were taken in an S shape at a depth of 0 to 20 cm using a 5 cm inner diameter soil auger under the canopy of each *S. moorcroftiana* shrub and then thoroughly mixed and pooled into a composite soil sample after removing visible gravel and plant litter. Soil samples were first passed through a 2 mm mesh sieve and then subdivided into three parts: a portion of the fresh soil from the field was stored at -80 ℃ for molecular and PLFA analysis, and the second portion was refrigerated at 4 °C for microbial biomass (carbon, nitrogen, and phosphorus), inorganic N (nitrate and ammonium) and available phosphorus analyses. The third portion was air-dried and stored at room temperature for soil physicochemical property analysis.

Analysis of plant and soil properties

Soil bulk density (BD) (0–20 cm) was measured by collecting soil in a steel ring (volume 100 cm^3), drying it in an oven at 105 °C (± 2 °C) for 24 h, and then weighing the dry mass. Soil pH was measured in a 1:5 soil:water suspension after 30 min of shaking at room temperature. Soil moisture (SM) was measured after oven drying at 105 °C to a constant mass. Soil and plant organic carbon concentrations were assayed by $K_2Cr_2O_7$ oxidation and the $FeSO_4$ titration method (Huang et al. 2014). Total nitrogen (TN) was determined by a Cleverchem 200+ instrument (Chilehaus A, Fischertw iete2-20095 Hamburg, Germany) after digestion with H_2SO_4-H_2O_2. Total phosphorus (TP) was determined with the molybdenum antimony colorimetric method following digestion with H_2SO_4-$HClO_4$. Soil dissolved organic carbon (DOC) was extracted with 0.5 M K_2SO_4 and analysed with a vario TOC instrument (Elementar-Straβe1·63505, Langenselbold, Germany). Soil inorganic nitrogen was extracted with 1 M KCl for 30 min on a shaker at room temperature, and the filtrates were analysed by a Cleverchem 200+ instrument (Chilehaus A, Fischertw iete2-20095 Hamburg, Germany). Soil available phosphorus was measured using the molybdenum blue method (Yang and Liu, 2019). Soil microbial biomass C (MBC), N (MBN) and P (MBP) were all determined by the chloroform fumigation extraction method (Brookes et al. 1985; Vance et al. 1987; Wu et al. 2000). Soil MBC, MBN and MBP were estimated as the difference between fumigated and unfumigated soil measurements and based on extraction measurement efficiency (conversion coefficient *k*) (k_C = 0.45 for MBC, k_{EN} = 0.45 for MBN, k_P = 0.40 for MBP) (Brookes et al. 1985; Vance et al. 1987; Joergensen and Mueller 1996).

Phospholipid fatty acids (PLFAs)

PLFA extraction process was based on the method described by Bossio and Scow (1998). Eight grams of each freeze-dried soil sample was accurately weighed; chloroform, methanol, and phosphate extract were added at a volume ratio of 1:2:0.8; and the extracts were analysed with a gas chromatograph (Hewlett Packard 6890 series GC, FID) using the MIDI software system (MIDI, Inc., Newark, DE). The concentration of each PLFA component was calculated based on 19:0 methyl internal standard concentrations. The 14:0, i14:0, 15:0, i15:0, a15:0, 15:0 DMA, 16:0, i16:0, i16:0, a16:0, 17:0, 18:0, 20:0, 16:1ω7c, 16:1ω9c, i17:0, a17:0, cyl7:0ω7c, 17:1ω8c, i17:1ω9c, 18:1ω5c, 18:1ω7c, cy19:0ω7c and cy19:0ω9c values were used as total bacterial biomarkers (Frostegård and Bååth 1996; Bach et al. 2010; Huang et al. 2014). The values of 18:1ω9c, 18:2ω6c and 18:3ω6c were used as fungal PLFA biomarkers (Sun et al., 2021). The i14:0, a15:0, i15:0, a16:0, i16:0, a17:0 and i17:0 values were used as a gram-positive bacterial PLFA biomarkers (Frostegård and Bååth 1996; Sampedro et al. 2006; Zheng et al. 2021). The 16:1ω7c, 16:1ω9c, cy17:0ω7c, 17:1ω8c, i17:1ω9c, 18:1ω5c, 18:1ω7c, cy19:0ω7c and cy19:0ω9c values were used as gram-negative bacterial PLFA biomarkers (Frostegård and Bååth 1996; Bach et al. 2010; Guan et al. 2018). In addition, the PLFA 16:1ω5c value was used as a biomarker for AMF, and the values of 10Me16:0, 10Me17:0 and 10Me18:0 were treated as biomarkers for actinomycete PLFAs (Frostegård and Bååth 1996; Bossio and Scow 1998). Additionally, the F:B ratio (the ratio of all the fungal PLFA biomarkers to all the

bacterial PLFA biomarker biomass ratios) and the G^+:G^- ratio (the ratio of gram-positive bacterial PLFA biomass to gram-negative bacterial PLFA biomass) were also calculated. The bacterial stress indicators were also calculated as follows: the cy:pre ratio was represented by the ratio of (cy17:0 + cy19:0) to (16:1 ω7c + 18:1ω7c), and the sat:mono ratio was represented by the ratio of total saturated PLFAs (14:0 + 15:0 + 16:0 + 17:0 + 18:0 + 20:0) to total monounsaturated PLFAs (16:1ω7c + 16:1ω5c + 17:1ω8c + 18:1ω5c + 18:1ω7c + 18:1ω9c + 18:2ω6c) (Bossio and Scow 1998; Moore-Kucera and Dick 2008).

DNA extraction, amplification and Illumina sequencing

Total genomic DNA was extracted using the FastDNA® SPIN Kit for Soil (MP Biomedicals, Santa Ana, CA) according to the manufacturer's instructions. The integrity of genomic DNA was detected through agarose gel electrophoresis, and the concentration and purity of genomic DNA were detected through the NanoDrop 2000 and Qubit@3.0 Spectrophotometer (Thermo Scientific, Wilmington, USA). The V4-V5 hypervariable regions of the 16S rRNA gene were amplified with the primers 515F (5'-GTGCCAGCMGCCGCGG-3') and 907R (5'-CCGTCAATTCMTTTRAGTTT-3') (Biddle et al. 2008). The fungal ITS and ITS1 hypervariable regions of the ITS1 gene were amplified with the primers ITS1 (5'-CTTGGTCATTTAGAGGAAGTAA-3') and ITS2 (5'-GCTGCGTTCTTCATCGATGC-3') (Wang et al. 2022). PCR was performed in triplicate in 10 μL mixtures containing 1 μL of 10 × Toptaq buffer, 0.8 μL of 2.5 mM dNTPs, 0.2 μL of F/R primer (10 μM), 0.2 μL of Toptaq DNA polymerase, 1~3 μL template DNA, and up to 10 μL ddH_2O. The thermal cycling parameters for PCR amplification were as follows: initial denaturation at 94 °C for 2 min; 94 °C for 30 s, 55 °C for 30 s, 72 °C for 1 min; 25~27 cycles of denaturing at 72 °C for 10 min, and hold at 4 °C. Each sample was independently amplified three times. The PCR products were checked by agarose gel electrophoresis, and the PCR products from the same sample were pooled. The pooled PCR product was used as a template, and index PCR was performed by using index primers to add the Illumina index to the library. The amplification products were checked using gel electrophoresis and purified using the Agencourt AMPure XP Kit (Beckman Coulter, CA, USA). The purified products were the indexed in the 16S V4–V5 library. The library quality was assessed on the Qubit@3.0 Fluorometer (Thermo Scientific, Wilmington, USA) and Agilent Bioanalyzer 2100 (Agilent Technologies, USA) systems. Finally, the purified amplicons from all the samples were pooled in equimolar concentrations, and then the pooled library was sequenced on a NovaSeq 6000 platform (Illumina, San Diego, USA), SP-Xp (PE250) using a 2 × 250-paired-end sequencing kit in Genesky Biotechnologies Inc., Shanghai, 201315 (China).

The raw read sequences were processed in QIIME2 (Bolyen et al. 2019). The adaptor and primer sequences were trimmed using the cutadapt plugin. Raw reads at any site with an average quality score < 20 were truncated, reads contaminated by the adapter were removed and reads having fewer than 100 bp were eliminated by TrimGalore. The DADA2 plugin was used for quality control and to identify amplicon sequence variants (ASVs) (Callahan et al. 2016). The remaining unique reads were checked for chimaeras by compaison with the gold.fa database (http://drive5.com/uchime/gold.fa) and clustered into operational taxonomic units (OTUs) by UPARSE with a 97% similarity cut-off (http://drive5.com/uparse/) (Edgar 2013). Taxonomic assignments of 16S rRNA and ITS ASV representative sequences were performed with confidence thresholds of 0.8 and 0.6 by a pretrained naive Bayes classifier trained on RDP (version 11.5) and UNITE (version 8.2), respectively.

Statistical analysis

OTU abundance information was normalized and homogenized using a standard sequence number corresponding to the sample with the lowest number of sequences. Alpha diversity indices including the Chao1, ACE, Shannon, Simpson and Good's coverage indices, were analysed by Mothur. Nonmetric multidimensional scaling (NMDS) was used to test differences in microbial communities among successional stages. Additionally, the similarity of community composition in the above abovementioned communities was evaluated sequentially using the ‘Adonis’ and ‘ANOSIM’ functions (999

permutations) of the ‘vegan’ R package (Luo et al. 2022). One-way analysis of variance (ANOVA) and least significant difference (LSD) tests were used to examine differences in plant and soil properties, soil microbial biomass, PLFAs and dominant microbial phyla among the different successional stages. Pearson's correlation was used to investigate correlations between microbial community composition and plant and soil characteristics. All the statistical analyses were performed using SPSS 20.0 (SPSS Inc., Chicago, IL, USA) and Origin 2021 software (Origin Lab Inc., Northampton, USA). The Mantel test was used to analyse the relationships between the beta diversity of microbial (bacterial or fungal) communities and plant and soil properties. Redundancy analysis (RDA) was used to evaluate the associations between soil microbial community compositions and plant and soil properties. Forward selection of environmental variables was applied to identify environmental factors that contributed significantly to the variation in the soil microbial community compositions. Monte Carlo permutation tests were conducted with 999 permutations to test the significance of the constrained ranking model. Structural equation modelling (SEM) was used to determine the effects of plant and soil characteristics on soil microbial community compositions. Data reduction was necessary due to the number of plant and soil factors (17 environmental factors). The final variables used in SEM were comprehensively determined based on Pearson's correlation analysis and PCA ordinations. Finally, SBC, GC, SH, DBH, SCS and GB were selected as measured variables contributing to the latent variable “vegetation”. We tested the fit of the models using the χ^2 goodness of fit test and the RMSEA test. The SEM analyses were performed using AMOS version 24.0 software (IBM SPSS Inc.) and RDA was carried out using CANOCO 4.5. $P < 0.05$ was considered statistically significant.

Results

Changes in soil microbial biomass at different successional stages

There was an overall increase in soil MBC, MBN and all PLFA groups with increasing community succession, but MBP did not significantly change among successional stages (Figs. 2 and 3). In detail, soil total PLFAs and the major functional groups of microbial PLFAs (bacteria, funga, AMF and actinomycetes) in the fixed dune and sandy gravel land stages were significantly higher than those in the semifixed dune and moving dune stages (Fig. 3). The soil microbial biomass C:P and N:P ratios also increased, however, community succession showed no significant effects on the soil microbial biomass C:N ratio, but the microbial biomass C:N ratio of the stabilized (fixed) sand dunes was higher than that of the semi-fixed sand dunes and mobile sand dunes (Fig. 2d-f). Soil MBC was positively correlated with soil MBN ($r = 0.86$, $P < 0.01$). Soil MBC, the biomass of total PLFAs and the PLFAs of the major groups were significantly correlated with SBC, GC, SH, SCS, DBH, SM, BD, SOC, DOC, STN, the soil C:N ratio, available N and available P ($P < 0.05$) (Table S2, Table S3). In addition, the mean r F:B and G^+:G^- atios were 0.22 ± 0.01 and 0.77 ± 0.01 respectively. The F:B ratio increased significantly in the sandy gravel land stage, while the G^+:G^- ratio decreased significantly in the sandy gravel land stage; the cy:pre ratio and sat:mono ratio, i.e. stress indicators, did not differ significantly among the successional stages (Fig. 4).

Responses of microbial diversity to successional stages

A total of 4,702,900 and 4,624,877 read pairs were obtained from bacterial and fungal sequences across the 72 soil samples after quality trimming and filtering and removal of the chimeric sequences, with an average number of retained sequences per sample of 65,318 and 64,234, ranging from 51,523 to 69,767 and from 45,571 to 70,715, respectively. These sequences were classified into 2324 bacterial OTUs and 567 fungal OTUs at the 97% similarity threshold. All the alpha diversity (bacterial and fungal) indices indicated that there were significant differences ($P < 0.05$) among the different successional stages (Table 2). The bacterial and fungal Chao1, ACE and Shannon indices tended to increase with successional stage, while the bacterial Simpson index tended to decrease with successional stage. However, the Simpson index of the fungal community decreased from the moving dune stage to the semi-fixed dune stage and then significantly increased from the semi-fixed dune stage to the sandy gravel land stage after which it tended to decrease.

The bacterial and fungal alpha diversities increased or decreased significantly from the semi-fixed dune stage to the sandy gravel land (or fixed dune) stage. The Good's coverage values for all the samples were > 97%, indicating that the number of sequences obtained represented the microbial communities well. Correlation analysis of the plant and soil properties and bacterial and fungal alpha diversity indices showed that the bacterial Simpson index and coverage were negatively correlated with the SBC and STN contents, and the Shannon, Chao1 and Ace indices were positively correlated with the SBC and STN contents, but negatively correlated with the soil C:N ratio (Fig. 5). Similar results have been found previously in fungal communities.

According to the NMDS results, the soil microbial community compositions significantly differed between successional stages (Fig. 6). For the bacterial community, the sampling sites in the fixed dune and sandy gravel land stages were well separated from those in the semi-fixed dune and moving dune stages (Adonis: R^2 = 0.23, P < 0.001; ANOSIM: R = 0.53, P < 0.001; Fig. 6a). For the fungal community, the aggregation degrees of the sample points from the fixed dunes were distant from those of the sample points from sandy gravel land, and both successional stages were very distant from the sample points in the semi-fixed dune and moving dune stages (Adonis: R^2 = 0.19, P < 0.001; ANOSIM: R = 0.50, P < 0.001; Fig. 6b). The Mantel test showed that microbial (bacterial and fungal) beta diversity was positively related to the changes in SBC, SH, SM, SOC, DOC, STN, and NH_4^+-N (Table 3).

Responses of microbial compositions to successional stages

The order of the microbial PLFA composition of the *S. moorcroftiana* shrub community was as follows: bacteria (64.03% ± 0.39%) > fungi (11.73% ± 0.18%) > actinomycetes (9.50% ± 0.40%) > AMF (2.97% ± 0.08%) (Table 4). In detail, the relative abundance of bacterial PLFAs significantly decreased with succession, mainly for the G^- bacterial PLFAs. However, no significant differences in the proportion of fungal PLFAs were found among the different successional stages. Taxonomic assignments of ASV representative sequences using the RDP classifier identified the dominant bacterial phyla (relative abundance >1%), i.e. Actinobacteria, Proteobacteria, Acidobacteria, Bacteroidetes, Chloroflexi, Planctomycetes, Gemmatimonadetes, Firmicutes, Verrucomicrobia, and Armatimonadetes, from all the samples (Fig. 7a, Table S4). Notably, except for the phylum Armatimonadetes, the relative abundances of all the dominant bacterial phyla varied significantly among the successional stages (P < 0.05). The relative abundances of Actinobacteria, Proteobacteria and Bacteroidetes significantly decreased from the moving dune stage to the fixed dune stage; those of both Acidobacteria and Planctomycetes significantly increased with community succession; those of Gemmatimonadetes and Verrucomicrobia were higher in the sandy gravel land stage, while that of Chloroflexi was lower in the moving dune stage; and that of Firmicutes first increased and then decreased with advancing successional stage, and was lowest in sandy gravel land. At the class level (Table S4), Alphaproteobacteria and Betaproteobacteria were the most dominant Proteobacteria, and their relative abundances significantly decreased with succession (P < 0.001); the relative abundances of two other Proteobacteria classes, Deltaproteobacteria and Gammaproteobacteria, increased with community succession (P < 0.001). We compared the bacterial community at the order level (Table S4), and Rhizobiales, Sphingomonadales, Rhodospirillales, Rhodobacterales and Caulobacterales, branches of Alphaproteobacteria, showed different trends among the successional stages. In detail, the relative abundance of Rhodospirillales significantly increased with succession, while those of the other branches significantly declined (P < 0.05); Rhizobiales was the most abundant Alphaproteobacteria. Within Actinobacteria, the relative abundance of the order Actinomycetales decreased significantly from the moving dune stage to the fixed dune stage.

The fungal communities varied less among the successional stages than the bacterial communities (Fig. 7b, Table S5). The dominant fungal phyla in all the samples were Ascomycota (66.01%), Basidiomycota (15.93%), Chytridiomycota (1.84%), and Mortierellomycota (1.83%). The relative abundance of each fungal taxon across taxonomic levels (phyla, class, and order) varied inconsistently between the successional stages. The sandy gravel land stage had the lowest relative abundance of Ascomycota, whereas the relative abundance of Basidiomycota was highest in this stage.

Sordariomycetes, Dothideomycetes and Agaricomycetes were the dominant fungal classes in all four successional stages, accounting for more than 60% in the variation of the fungal classes (Table S5). In addition, at the order level (Table S5), Hypocreales, Pleosporales and Agaricales accounted for 57.00% of the variation, and the sandy gravel land stage had the lowest relative abundance of Hypocreales and the highest relative abundance of Agaricales ($P <$ 0.001). The mean relative abundances of unassigned fungi and unidentified Ascomycota were 10.08% and 9.31%, respectively.

Responses of plant and soil properties to successional stages

The plant and soil properties were significantly affected by successional stage, but showed differential responses (Table 5, Table S6). In general, among the plant characteristics, GC, SH and GB were high in the fixed dune stage, while DBH and SCS were higher in the moving dune stage than in the other stages ($P < 0.05$); SBC significantly increased with successional stage (F = 50.24, $P < 0.001$). In terms of soil characteristics, the content of SM, SOC, DOC, STN, STP, NH_4^+-N and available P increased with succession, although no significant changes among sites were found in several cases from the mobile dune stage to semi-fixed to fixed dune (including sandy gravel land) stages. In contrast, the soil C:N ratio significantly decreased with succession. These findings indicated that sand dune stabilization and revegetation improved the soil fertility level. Soil pH, BD and NO_3^--N did not differ among the different successional stages, but NO_3^--N was higher in the stabilized (or basically stable) sand dune sites than in the active sand dune sites.

Relationships between the microbial community compositions and environmental variables

The RDA showed that microbial (bacterial and fungal) taxa responded differently to variations in the plant and soil environmental factors at different taxonomic levels (phylum, class, and order) (Fig. 8, Fig. S1, Table S7, S8). These results indicated that plant environmental factors, especially SBC, greatly impacted the soil bacterial community composition, but, had little effect on the fungal community composition. Soil substrates, particularly soil total nitrogen (STN), were responsible for many of the changes in bacterial community compositions, while the soil C:N ratio affected the fungal community compositions (Table S7, Table S9). The ordination diagram (Fig. 8a) between the relative abundances of the dominant bacterial phyla and plant and soil factors showed that the abundances of Acidobacteriota, Actinobacteria, Planctomycetota, Proteobacteria, Bacteroidetes and Chloroflexi were significantly correlated with SBC, SCS, STN and the soil C:N ratio. For Proteobacteria, SBC, SCS, STN and the soil C:N ratio were related to the abundances of Rhodospirillales, Rhodobacterales, Rhizobiales, Sphingomonadales, Caulobacterales, Burkholderiales and Xanthomonadales (Fig. S1b), which belong to the Alphaproteobacteria, Betaproteobacteria and Gammaproteobacteria branches (Table S4). However, in contrast, among the plant and soil environmental factors, only the abundance of Mortierellomycota was significantly positively correlated with SBC, but negatively correlated with the soil C:N ratio (Fig. 8b). The Basidiomycota, Agaricomycetes and Tremellomycetes classes and their respective orders were correlated with SCS, STN and the soil C:N ratio. Among Ascomycota, the abundance of the Sordariomycetes class and Hypocreales and Sordariales orders were positively correlated with the soil C:N ratio (Fig. S1c, d).

The final structural equation model adequately fit the data, illustrating the interactions among the plant and soil characteristics and microbial community compositions (Fig. 9). The model indicated that vegetation characteristics and SOC had a direct positive effect on soil bacterial community composition, whereas the soil C:N ratio had a direct negative effect on bacterial community composition. The fungal community composition increased as the soil C:N ratio decreased. Vegetation may have indirectly affected microbial community compositions by affecting DOC and NO_3^--N contents. SEM also showed that soil pH and SM had both indirect positive and negative effects on microbial community compositions.

Discussion

Effects of successional stages on soil microbial biomass

The results of this study showed that the soil microbial communities had higher biomass in the stabilized sand dune stage than in the other stages, corresponding to similar trends with higher shrub coverage along the successional gradients of *S. moorcroftiana* shrub community restoration (Figs. 1 and 2, Table S2 , Table S3). These results were consistent with previous reports that plant and microbial communities displayed a similar pattern characterized by an increase in soil microbial biomass and activity and linked to an increase in plant cover and diversity along successional stages in dry ecosystems (Lozano et al. 2014). This may be because greater plant cover may improve soil microenvironments and microbial communities and thereby stimulate SOM decomposition (Li et al. 2018). Previous studies have also indicated that SOM provides substrates for soil microbial growth (Moscatelli et al. 2007), thereby contributing to the accumulation of microbial biomass in the soil. In addition, the increase in plant cover enhances the input of organic material such as litter and roots in soils, which is beneficial to the accumulation of soil organic carbon (Yang et al. 2009; Pugnaire et al. 2011). Thus, it was not surprising that a significant relationship between soil microbial biomass (MBC, MBN, the total amount of PLFAs and the major functional groups of microbial PLFAs) and SOC, DOC and STN was observed along the successional stages (Table S2, Table S3). However, there were no significant differences in the soil MBP concentrations among the different successional stages (Fig. 2c). These differences were due to P-limitation promoting homeostasis in P-poor sites, while organic P was mineralized outside the cells by extracellular enzymes and P was taken up more slowly than C by the microorganisms (Heuck et al. 2015). We suggest that vegetation restoration enriches the accumulation of microbial biomass and improves soil quality.

Effects of successional stages on microbial diversity as well as community composition

Our results showed that succession alters the composition and diversity of soil microbial communities (Figs. 4, 6 and 7, Tables 3 and 5, Table S4, Table S5). The soil bacterial communities were dominated by the phyla Actinobacteriota, Proteobacteria, and Bacteroidetes, which play a crucial role in soil C, N, P, and S cycling (Kersters et al. 2006; Guo et al. 2019) and contain copiotrophic taxa (Hortal et al., 2013), and the relative abundance of these bacterial taxonomic groups decreased as the successional stage advanced (Fig. 7, Table S4). For instance, Actinobacteria was the most abundant phylum across successional stages, and the abundance of Actinobacteria decreased with community succession and was negatively related to SBC, STN and STP (Fig. 7, Table S4, Table S9), possibly because this phylum was adapted to resource-limited conditions (Siles and Margesin 2016). Similar results were found in other studies in a dry environment (Lozano et al. 2014). Notably, although Proteobacteria and Bacteroidetes were found in soils with high carbon availability (Fierer et al. 2017; Eilers et al. 2010) we did not find any positive association with SOC; however, we did find a positive association of these phyla with SCS (Fig. 8), further supporting the hypotheses that their abundances increase with community maturity (Fierer et al. 2017; Hortal et al. 2013). Alphaproteobacteria were the most abundant Proteobacteria. In particular, Rhizobiales, a branch of the class Alphaproteobacteria, establish a symbiotic relationship with legumes to fix N (Hodkinson and Lutzoni 2010) and should be more active beneath shrub canopies than in other environments (Bai et al. 2020; Table S4). Bacteroidetes are good at rapidly decomposing organic matter, whereas Proteobacteria dissolve phosphorus by releasing enzymes and organic acids into the soil (Bai et al. 2020; An et al. 2022). Burkholderiales, a key taxon in Betaproteobacteria that increases in abundance with shrub growth, are considered potential plant growth-promoting organisms (Hortal et al. 2013) and are highly efficient mineral weathering bacteria (Uroz et al. 2011). Studies have shown that Burkholderiales can also play a role in N_2 fixation and confer resistance to water stress (Hortal et al. 2013). In addition, the relative abundances of Chloroflexi, Planctomycetes, Gemmatimonadetes increased with the successional stage (Fig. 7, Table S4), which may be related to increased soil nutrient availability, potentially benefiting the recruitment and growth of soil microbes (Bai et al. 2020). Therefore, we suggest that these bacteria play a particularly important role in severe environments, such as nutrient-limited arid or semiarid ecosystems.

Gram-negative bacteria are typically considered fast-growing microbes due to their tendency to decompose more labile organic materials (i.e. act as copiotrophs), while gram-positive bacteria mainly decompose low-quality or recalcitrant organic matter (i.e. act as oligotrophs) (Chen et al. 2019). It has been shown recently that the changes in the abundances of copiotrophic and oligotrophic flora during vegetation restoration are consistent with their physiological abilities to decompose the biochemical structures of plant litter (An et al. 2022). Our results showed that with the decrease in the coverage of *S. moorcroftiana* shrubs and the intensification of wind-sand (sand burial) disturbance, the proportion of gram-positive bacteria increased more than that of gram-negative bacteria, and the G^+:G^- ratio increased (Table 3, Fig. 4). This may be because gram-positive bacteria have much thicker and stronger cell walls than gram-negative bacteria, making them more resistant to environmental stress than gram-negative bacteria (Wang et al. 2018). This result was consistent with a previous report by Djukic et al. (2010), which found that gram-positive bacteria may be more successful in resource-limited areas.

Previous studies have demonstrated that fungal communities are relatively stable (Pan et al., 2021). Similar results were found in this study, in which the relative abundances of fungal taxa differed nonsignificantly among the different successional stages (Table 3). The fungal community along the succession gradient was dominated by the phyla Ascomycota, Basidiomycota, Chytridiomycota and Mortierellomycota, consistent with descriptions of desert-grassland ecosystems (Pan et al. 2021; Wang et al. 2021) (Fig. 7). Ascomycota and Basidiomycota metabolize organic substrates deposited in the rhizosphere, and their abundances are influenced by SOM dynamics due to the decomposition of plant residues (Ren et al. 2018). Our study confirmed that these dominant phyla were mainly affected by the soil C:N ratio (Fig. 9, Table S9). Additionally, the classes Agaricomycetes and Tremellomycetes and their respective orders were correlated with SCS, STN and the soil C:N ratio (Fig. S1c and d). This was because the growth of shrubs improved the microclimate conditions under the canopy, and root exudates were available for use as growth substrates (Hortal et al. 2013). The comprehensive bacterial community composition response supported the second hypothesis that microbial community compositions were primarily affected by SBC, SCO, STN and the soil C:N ratio as the successional advanced. These results are consistent with the results of Waldrop et al. (2017) and Wang et al. (2021), which indicated that plant productivity and SOM ultimately determine microbial community compositions at a continental scale. This differs from many studies that identified soil pH as the most important factor regulating microbial community composition in the Namib Desert (Scola et al. 2018) and global dryland soils (Maestre et al. 2015).

Microbial alpha diversity has been widely used to explore the structure of microbial communities (Lozupone and Knight 2008; Wang et al. 2021). Our results showed that the bacterial and fungal alpha diversities (Chao1 and Shannon indices) increased along the successional gradient, moving dune stage to the fixed dune stage (Table 4). The observed increase in microbial diversity may be associated with greater plant biomass and the increasing presence of herbaceous plant species (mainly organic substrates), which provide soil microbes with more diverse resources and niches (An et al. 2022). In this study, there were linear relationships between SBC, STN and the soil C:N ratio and the Shannon, Chao1, and ACE indices of bacteria and fungi (Fig. 5). However, Hortal et al. (2013) did not observe an increase in bacterial diversity with vegetation cover or plant species richness. In fact, this knowledge gap largely limits our understanding of the interdependency of microbial diversity with plant diversity (Hortal et al. 2013). The effect of soil microbial diversity on aboveground properties appears to vary from positive to negative, depending on the context (Wardle et al. 2004). In general, beta diversity is used to describe the assembly of microbial communities along environmental gradients (Scola et al. 2018; Wang et al. 2021). In our research, NMDS analysis showed that soil microbial beta diversity was similar between the fixed dune and sandy gravel land and between the semi-fixed dune and moving dune along the successional stage, except for clearly separated between the fixed dune and sandy gravel land in the fungal community (Fig. 6). A possible explanation for this finding is that the responses of soil bacteria and fungi differ according to their morphological characteristics, utilization strategies and sensitivity to the environment (Chen et al. 2019; Wang et al. 2021). Moreover, numerous studies of many ecosystems have noted that bacterial communities are more diverse than

fungal communities (Wallenstein et al. 2007; Prewitt et al. 2014; Chen et al. 2019; Wang et al. 2021); this finding was confirmed by our results in a desert ecosystem (Table 4). The results of the Mantel test indicated that microbial beta diversity was highly related to SBC, SOC, DOC, STN and NH4+-N (Table 4). This strong relationship was because greater vegetation cover and denser vegetation increased litter input and root exudation, resulting in increased soil organic carbon and thus altered microbial community composition (Ding and Eldridge 2021; Kuzyakov and Blagodatskaya 2015; Ochoa-Hueso et al. 2018; Yu et al. 2022). Moreover, the accumulation of carbon sources was accompanied by the presence of shrubs in each of the successional stages in the desert ecosystem (Zhou et al. 2017; Zhao et al. 2019; Yu et al. 2022). Similar results suggested that differences in vegetation coverage might contribute to the high heterogeneity of soil microbial communities (Waymouth et al. 2020). We also observed that SM was responsible for differences in soil microbial beta diversity (Table 4), consistent with the results of Pugnaire et al. (2011), indicating that nurse shrubs also cause changes in the factors affecting the abiotic environments beneath their canopy (such as soil water content), thus influencing the composition of the soil microbial community. Overall, we suggest that shifts in microbial activity are affected not only by plant coverage, but also by the soil environment.

Conclusion

Changes in soil microbial community composition as well as increases in microbial biomass and activity, but not MBP, do occur along successional gradients of created by *S. moorcroftiana* shrub community restoration. We suggest that plant biomass and species richness under shrub canopies increase with community restoration, favouring species with easily decomposable litter that would also stimulate microbial biomass and activity. The results from our study also showed that bacterial and fungal communities responded differently to environmental change, especially bacterial community structure, and that SBC, SOC, STN and the soil C:N ratio were vital environmental factors. Our results provide insights into the complex interactions between microbial communities and plant–soil interactions through changes in microbial community structure, biomass and activity during plant–soil system restoration in desertified alpine areas.

Declarations

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Tables

Table 1

Types and indicators of aeolian sandy land in the middle reaches of the Yarlung Zangbo River basin.

Indicators	Wind-eroded sand land	Wind-deposited sand land		
	Sandy gravel land	Fixed dunes	Semi-fixed dunes	Moving dunes
Surface feature	Flat sandy gravel land, soil surface environment is basically stable	Flat sand land, no obvious wind erosion, surface environment is stable or basically stable	Flat sand land, the distribution is relatively uniform, but there is still a more obvious sand movement.	Sand movement, mountain slope sand land, barchan dune and dune chain, complex dune
Vegetation cover	30–60%	≥30%	10–30%	< 10%
Main species	*Artemisia wellbyi, Oxytropis serioopetala, Trikeraia hookeri, S. moorcroftiana*	*S. moorcroftiana,* *Artemisia wellbyi,* *Artemisia younghusbandii*	*S. moorcroftiana,* *Artemisia wellbyi,* *Orinus thoroldii, Artemisia younghusbandii*	*Orinus thoroldii, S. moorcroftiana.*

Table 2

The richness and diversity of soil microbial community along the stages of succession.

	Stages	Alpha-diversity of microbial community				
		Chao1	ACE	Shannon	Simpson	Coverage
Bacterial	FD	2563.61±28.78a	2545.23±28.44a	7.21±0.02a	0.002±0.000b	0.9977±0.0006b
	SGL	2653.95±101.94a	2636.19±99.95a	7.24±0.05a	0.002±0.000b	0.9975±0.0019b
	SFD	2122.70±97.03b	2110.86±96.01b	6.78±0.10b	0.006±0.001a	0.9983±0.0014a
	MD	1938.44±59.33b	1927.30±42.29b	6.64±0.05b	0.007±0.003a	0.9986±0.0010a
Fungal	FD	641.28±18.28a	642.13±18.31a	4.86±0.06a	0.024±0.002ab	0.9996±0.0004b
	SGL	679.06±71.19a	680.51±71.40a	4.61±0.31ab	0.077±0.033a	0.9996±0.0010b
	SFD	469.30±32.30b	469.90±32.17b	4.28±0.17b	0.041±0.009ab	0.9997±0.0004ab
	MD	421.03±24.87b	421.19±24.92b	4.14±0.12b	0.050±0.007b	0.9988±0.0003a

FD: fixed dunes; SGL: sandy gravel land; SFD: semi-fixed dunes; MD: moving dunes. Values were presented as mean with SE. Different lower-case letters indicate significant difference among the different successional stages at $p < 0.05$. Chao1: richness estimator; ACE: abundan

Table 3

Mantel test for the relationships between beta diversity and plant and soil properties.

plant and soil properties	Bacterial beta diversity		Fungal beta diversity	
	Mantel r	*P* value	Mantel r	*P* value
Shrub coverage (SBC)	**0.413**	**0.001**	**0.412**	**0.001**
Grass coverage (GC)	0.042	0.212	0.036	0.229
Shrub height (SH)	**0.207**	**0.001**	**0.209**	**0.001**
Shrub crown size (SCS)	-0.009	0.480	-0.009	0.492
Diameter at breast height (DBH)	-0.029	0.617	-0.029	0.620
Grass biomass (GB)	-0.076	0.831	-0.082	0.853
pH	-0.049	0.834	-0.050	0.836
Soil moisture (SM)	**0.351**	**0.002**	**0.353**	**0.001**
BD	-0.020	0.512	-0.022	0.507
SOC	**0.182**	**0.010**	**0.182**	**0.015**
DOC	**0.247**	**0.008**	**0.244**	**0.013**
STN	**0.303**	**0.001**	**0.300**	**0.003**
STP	0.002	0.429	-0.002	0.417
C:N	0.047	0.207	0.046	0.229
NH_4^+-N	**0.247**	**0.006**	**0.244**	**0.010**
NO_3^--N	0.044	0.202	0.042	0.194
Available P	0.117	0.090	0.116	0.071

Table 4

The proportion of individual PLFAs (mol %) among different successional stages.

type	Relative abundance PLFAs (mol %)						
	Bacteria	G^+	G^-	Other B	Fungi	Act	AMF
FD	62.57±0.40b	19.80±0.30b	27.32±0.26b	15.44±0.24a	11.65±0.28a	11.08±0.46a	3.05±0.11a
SGL	60.77±0.72b	18.24±0.41b	27.24±0.58b	15.30±0.25a	11.27±0.35a	11.13±0.76a	3.92±0.20a
SFD	66.94±0.73a	23.12±0.59a	29.62±0.56a	14.19±0.42b	11.59±0.28a	7.68±0.85b	2.57±0.12ab
MD	67.17±0.50a	23.26±0.41a	30.02±0.69a	13.89±0.45b	12.33±0.41a	6.15±0.69c	2.51±0.10b
F	20.623	27.356	9.854	5.153	1.145	14.289	13.920
P	**< 0.001**	**< 0.001**	**< 0.001**	**0.003**	0.337	**< 0.001**	**< 0.001**

FD: fixed dunes; SGL: sandy gravel land; SFD: semi-fixed dunes; MD: moving dunes**.** Values were presented as mean with SE. Different lower-case letters indicate significant difference among the different successional stages at $p < 0.05$.

Table 5

Plant and soil characteristics among different successional stages.

Plant properties	F	*P*	Soil properties	F	*P*
Shrub coverage (%)	50.243	**<0.001**	pH	2.516	0.066
Grass coverage (%)	21.951	**<0.001**	Soil moisture (%)	3.974	0.011
Shrub height (cm)	2.776	0.048	BD (g cm^{-3})	1.122	0.346
Shrub crown size (m^2)	3.778	0.014	SOC (g kg^{-1})	6.177	0.001
Diameter at breast height (cm)	4.884	0.004	DOC(mg kg^{-1})	12.357	**<0.001**
Grass biomass (g m^{-2})	7.658	**<0.001**	STN (g kg^{-1})	16.537	**<0.001**
			STP (g kg^{-1})	2.890	0.042
			C:N	11.711	**<0.001**
			NH_4^+-N (mg kg^{-1})	3.694	0.016
			NO_3^--N (mg kg^{-1})	1.176	0.325
			Available P (mg kg^{-1})	2.135	0.104

BD: soil bulk density; SOC: soil organic carbon; DOC: dissolved organic carbon; STN: soil total nitrogen; STP: soil total phosphorus; C:N ratio: ratio of soil organic carbon to soil total nitrogen.

Figures

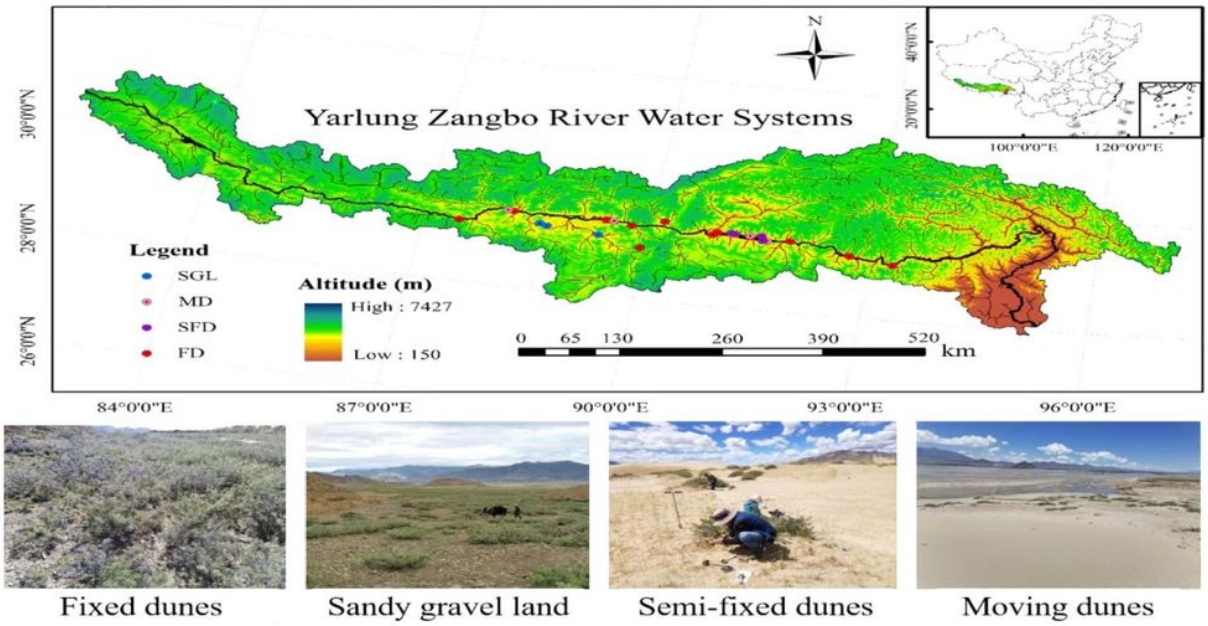

Figure 1

Location of the Yarlung Zangbo River basin on the southern Tibetan Plateau of China, the sampling sites and landscape main aeolian sandy land types of *S. moorcroftiana* (plotted by Arcgis9.3).

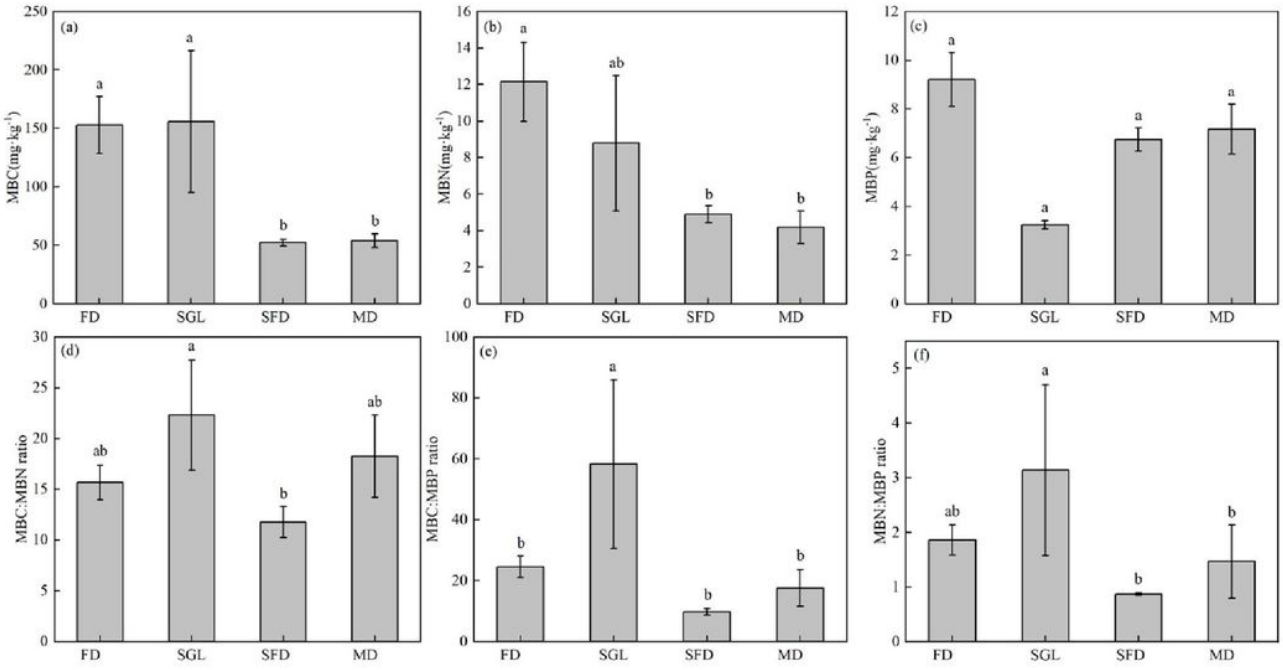

Figure 2

Soil microbial biomass C (MBC), N (MBN) and P (MBP) and their ratios along the different successional stages. Bars indicate mean ± SE. Different uppercase letters denote significant difference ($P < 0.05$) among the four succession stages. FD: fixed dunes; SGL: sandy gravel land; SFD: semi-fixed dunes; MD: moving dunes.

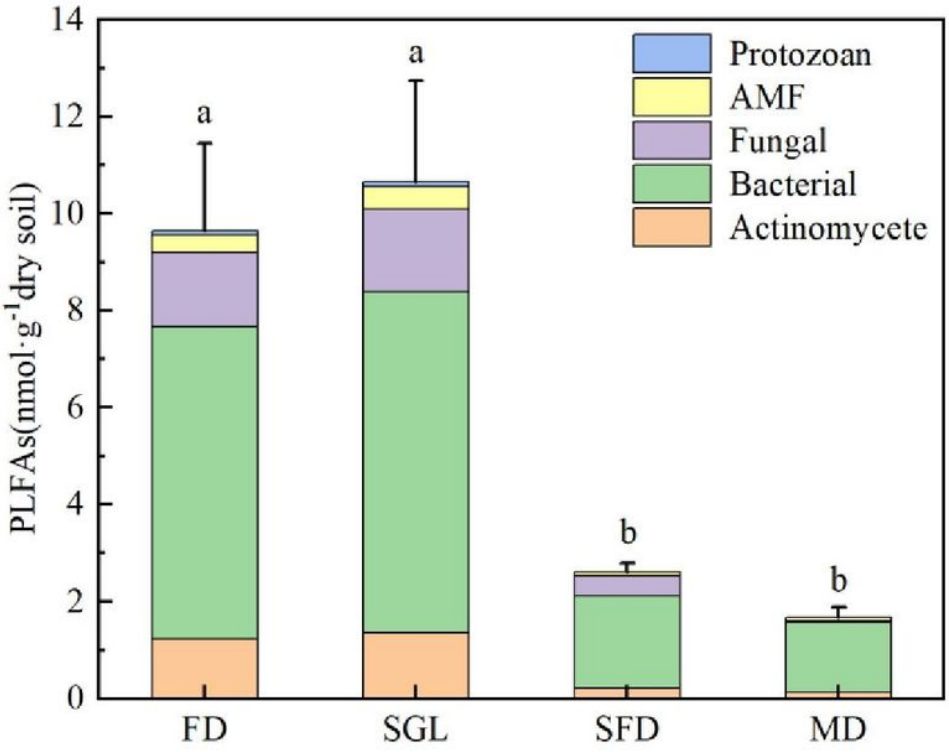

Figure 3

Comparison of the biomass of functional groups PLFAs at different successional stages. Different uppercase letters indicate significant difference ($P < 0.05$). AMF: arbuscular mycorrhizal fungi. FD: fixed dunes; SGL: sandy gravel land; SFD: semi-fixed dunes; MD: moving dunes.

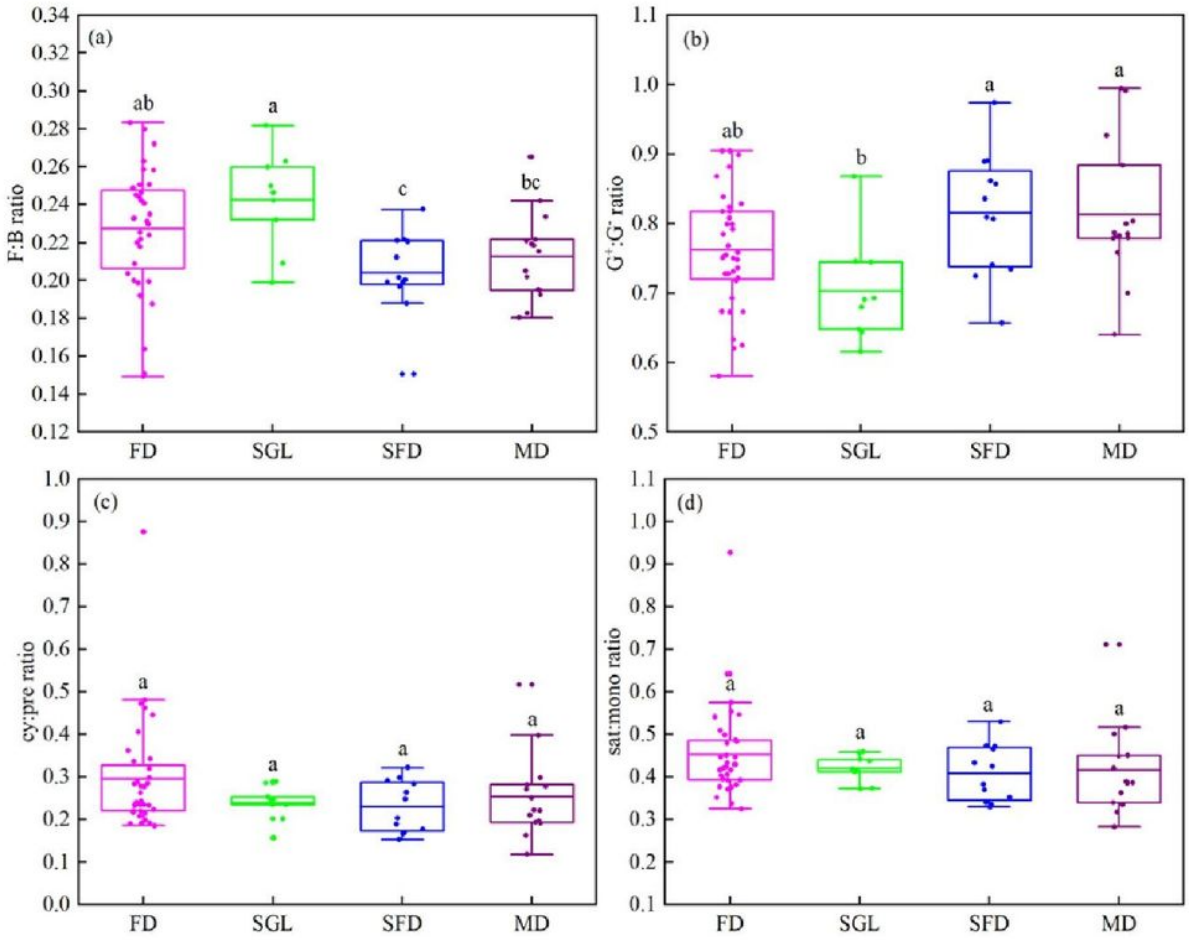

Figure 4

Stress indicators at different successional stages. The boxes show the median surrounded by the 25th and 75th percentiles; F:B ratio: ratio of fungal to bacterial PLFAs; G^+:G^- ratio: ratio of gram-positive to gram-negative bacterial PLFAs cy:pre ratio: ratio of cy17:0 + cy19:0 to 16:1ω7c + 18:1ω7c, sat:mono ratio: ratio of total saturated to total monounsaturated PLFAs.

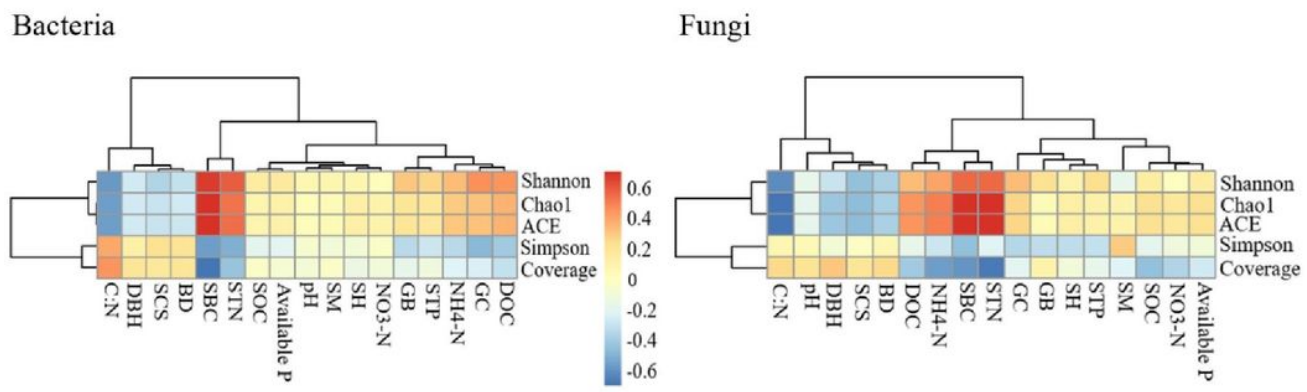

Figure 5

Heat maps showing significant correlations between alpha diversity indices and plant and soil physicochemical properties.

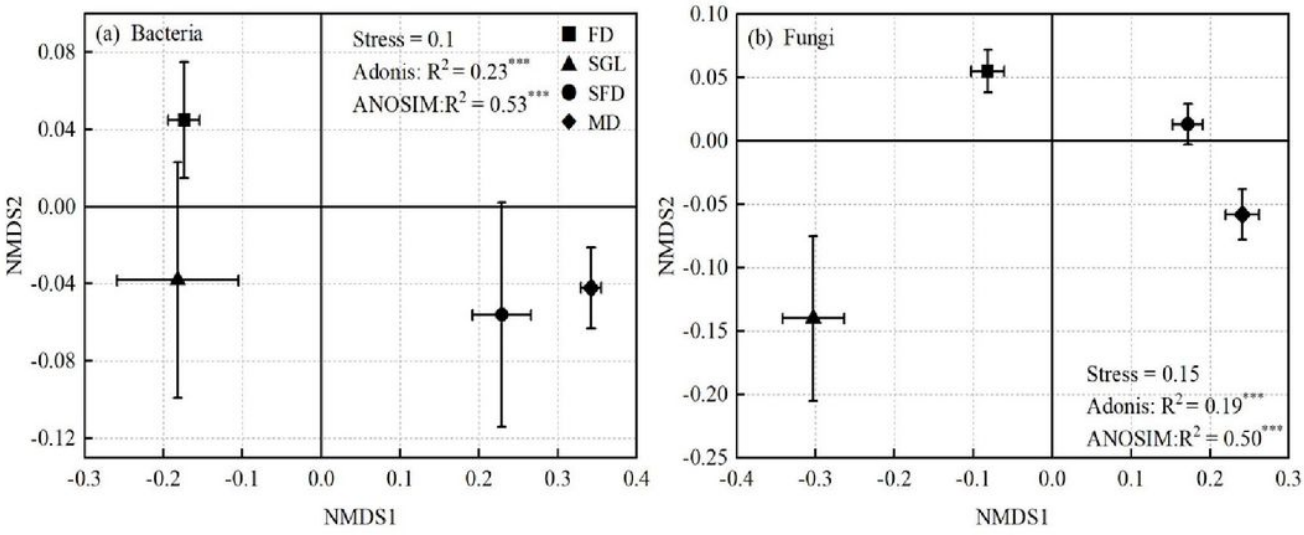

Figure 6

Changes of soil bacterial (a) and fungal (b) beta diversity along the different successional stages. FD: fixed dunes; SGL: sandy gravel land; SFD: semi-fixed dunes; MD: moving dunes.

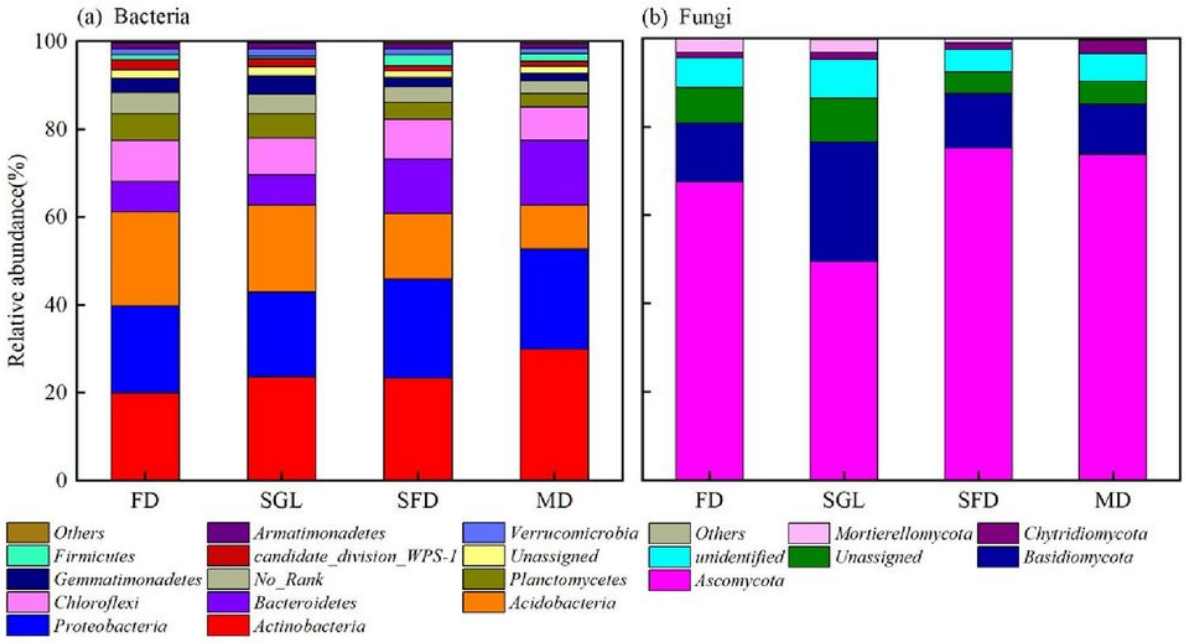

Figure 7

Microbial (bacterial and fungal) community composition (relative abundance > 1%) at the phylum level along the successional stage.

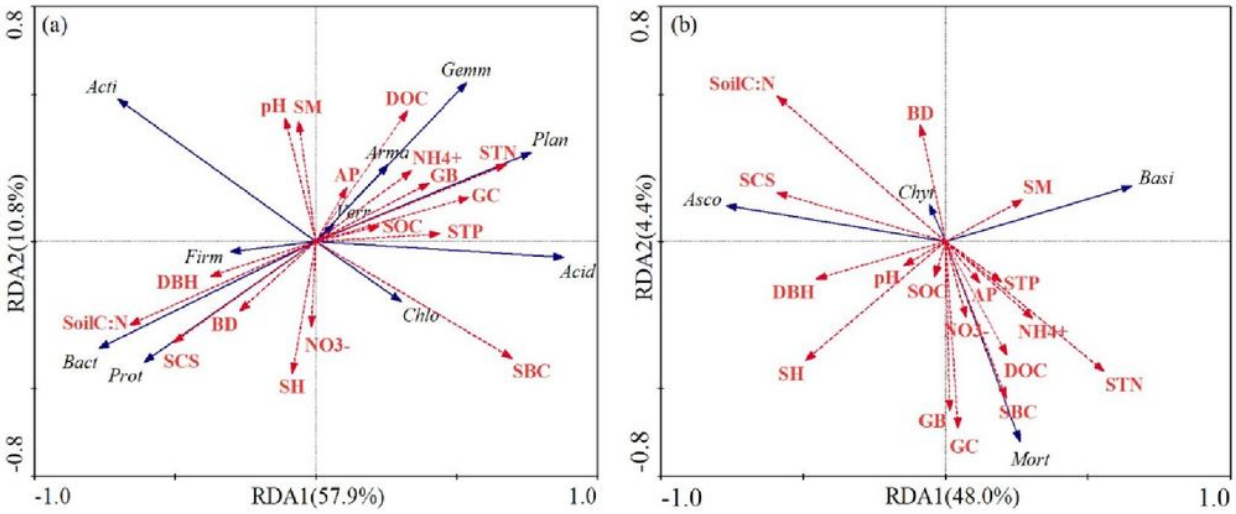

Figure 8

Redundancy analysis (RDA) of the relationships between dominant bacterial (a) and fungal (b) phyla and plant and soil characteristics. Abbreviations: SBC: shrub coverage; GC: grass coverage; SH: shrub height; SCS: shrub crown size; DBH: diameter at breast height; GB: grass biomass; SOC: soil organic carbon; DOC: dissolved organic carbon; STN: soil total nitrogen; STP: soil total phosphorus; BD: soil bulk density; SM: soil moisture; AP: available P; *Prot: Proteobacteria; Acid: Acidobacteria; Acti: Actinobacteria; Bact: Bacteroidetes; Chlo: Chloroflexi; Plan: Planctomycetes; Gemm: Gemmatimonadetes; Firm: Firmicutes; Verr: Verrucomicrobia; Arma: Armatimonadetes; Asco: Ascomycota; Basi: Basidiomycota; Chyt: Chytridiomycota; Mort: Mortierellomycota.*

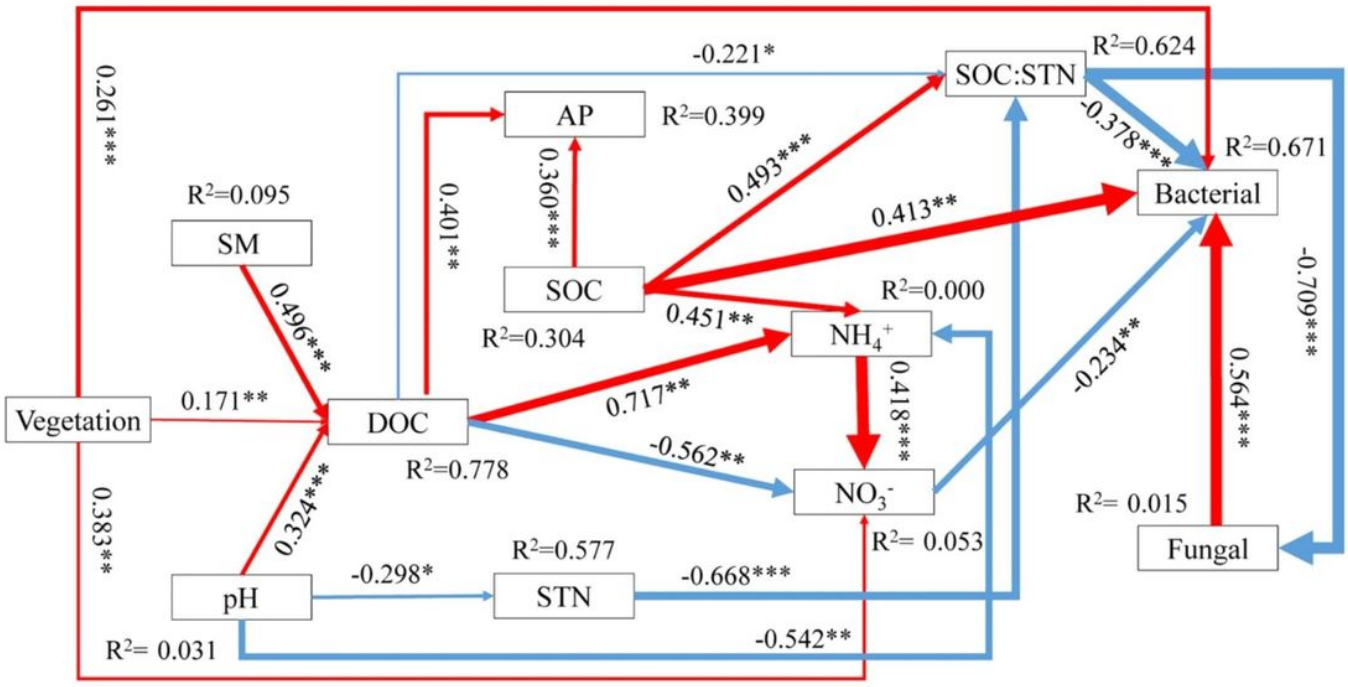

Figure 9

Structural equation modelling (SEM) analysis of the effects of vegetation and soil characteristics on the community compositions of microbial (bacterial and fungal). Vegetation characteristics include shrub coverage (SBC), grass coverage (GC), shrub height (SH), shrub crown size (SCS), diameter at breast height (DBH), grass biomass (GB). Soil variables include soil pH, soil moisture (SM), soil organic carbon (SOC), dissolved organic carbon (DOC), soil total nitrogen (STN), available P (AP), $NH4^+$-N ($NH4^+$), $NO3^-$-N ($NO3^-$) and SOC:STN. Results of model fitting: χ^2 = 38.079, df = 34, P = 0.289, GFI = 0.935, CFI = 0.991, RMSEA = 0.041. Numbers on arrows are standardized path coefficients. Red and blue arrows indicate positive and negative effects, respectively, with the thickness representing the extent of influence. R^2 values represent the proportion of the variance explained for each endogenous variable. ignificance levels are as follows: *P < 0.05, **P < 0.01, and ***P < 0.001.

Supplementary Files

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- Supplementarydata.docx