Soil & Tillage Research 194 (2019) 104305

Contents lists available at ScienceDirect

Soil & Tillage Research

journal homepage: www.elsevier.com/locate/still

Higher temporal turnover of soil fungi than bacteria during long-term secondary succession in a semiarid abandoned farmland

Jie Wang[a], Guobin Liu[b], Chao Zhang[a,*], Guoliang Wang[a], Linchuan Fang[a], Yongxing Cui[b]

[a] State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Northwest A&F University, Yangling, 712100, PR China

[b] Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling, 712100, PR China

ARTICLE INFO

Keywords:
Soil microbial community
Temporal turnover
Semiarid ecosystem

ABSTRACT

Microorganisms play critical roles in soil biogeochemical processes and the establishment of vegetation communities. However, their long-term successional patterns and associations with environmental factors are not well understood, especially in semiarid areas where plant community composition and species diversity change rapidly. We investigated changes in soil (*Cambisol*) microbial communities across a chronosequence of abandoned farmland comprising six successional stages (0, 11, 35, 60, 100, and 150-years) in the semiarid Loess Plateau of China. We aimed to reveal the long-term patterns and succession rates of microbial communities, and to reveal the driving forces. Bacterial and fungal communities were characterized by sequencing bacterial 16S ribosomal RNA genes and fungal internal transcribed spacers (ITS), respectively. Temporal turnover of microbial succession was investigated using the slope (w value) of linear regression of log-transformed microbial community similarity over time. Succession rate of fungi was approximately three times higher ($w = 0.1477$, $P < 0.0001$) than that of bacteria ($w = 0.0549$, $P < 0.0001$). Bacterial succession was affected by changes in soil NH_4^+-N, total N, organic C, water content, bulk density, and pH, whereas fungi were more susceptible to changes in NO_3^--N, available phosphorus, and C:N ratio. Bacterial communities transitioned from slow-growing oligotrophic groups (*Gemmatimonadetes, Chloroflexi*) to fast-growing copiotrophic groups (*Alpha-* and *Betaproteobacteria*). *Basidiomycota* showed the highest temporal turnover ($w = 0.2000$, $P < 0.0001$), followed by *Armatimonadetes*, *Firmicutes*, *Verrucomicrobia*, *Chloroflexi*, and *Proteobacteria*. These results provide new insights into microbial community dynamics during long-term secondary succession, and enhance our understanding of associations between soil factors and microbes in semiarid ecosystems.

1. Introduction

One of the central themes in ecology is understanding the fundamental ecological patterns and processes of biotic communities during ecosystem succession (Dini-Andreote et al., 2015; Nemergut et al., 2013). Plant community succession has been extensively studied in the past, and changes in plant community composition have been accepted as viable indicators for the evaluation of ecosystem restoration (Odum, 1969; Adler and Lauenroth, 2003). However, the patterns and mechanisms of soil microbial succession after disturbance were less well studied prior to the emergence of next-generation sequencing technologies. Similar to plants, microbial succession is affected by environmental factors (e.g. climate, soils, human activity), nutrient status (e.g. C, N, and P levels), and biological interactions (e.g., competition, amensalism, predation) (Engelhardt et al., 2018; Liang et al., 2015; Zhang and Shangguan, 2016). However, differences in phylogeny, metabolism, and dormancy between plants and microorganisms are likely to result in discrepancies in the successional patterns of microbial communities and their driving mechanisms (Nemergut et al., 2013). In addition, the high sensitivity of microorganisms to environmental changes, and their responses, provide additional information and possibly an early indication of successional progress (Banning et al., 2011).

Bacteria and fungi are important components of the soil microbiota, and are the main drivers of many terrestrial ecosystem processes (Fabian et al., 2017; Wagg et al., 2014). Existing studies have suggested that bacteria and fungi may follow different succession trajectories and be driven by different environmental factors (Brown and Jumpponen, 2014; Poosakkannu et al., 2017). Fernandez-Martinez et al. (2017) found distinct successional trajectories for bacteria and fungi along glacier forefield chronosequences, with bacteria playing an important

* Corresponding author.
E-mail address: zhangchao1985@nwafu.edu.cn (C. Zhang).

https://doi.org/10.1016/j.still.2019.104305
Received 23 June 2018; Received in revised form 18 June 2019; Accepted 20 June 2019

role in the initial stages of succession, whereas fungi could play a predominant role in the later stages. This may be attributed to the differences in phylogeny, phenotype, and life history that exist between fungi and bacteria (Sun et al., 2017). Bacteria are distinguished by metabolic versatility (e.g., heterotrophs, chemoautotrophs, and photoautotrophs) and faster turnover (˜10-fold that of fungi), and are thus, better adapted to life in barren soil (Schmidt et al., 2014). Certain bacteria can fix C and atmospheric N, traits which are not present in fungi (Feng et al., 2018; Salles et al., 2017). Additionally, bacteria are not necessarily as dependent on pre-existing resources as fungi are (Zhang et al., 2018). Previous studies on the effects of succession on bacterial and fungal communities have almost focused on primary succession (Ciccazzo et al., 2016; Dini-Andreote et al., 2015; Tian et al., 2017). Because secondary succession usually occurs on pre-existing soil after disturbance (e.g., wildfire, anthropogenic activities) soils (Zhang et al., 2018; Zhou et al., 2017), changes in microbial communities in the secondary succession may differ from those in the primary succession. However, information concerning microbial secondary succession is lacking, especially in soils from semiarid areas where the plant community composition and species diversity usually change rapidly (Lozano et al., 2014).

Revealing the successional trends and patterns of ecosystems is challenging owing to the requirement for continuous long-term investigation. A chronosequences approach, such as the substitution of space for time, was established to address this challenge, and has been extensively employed to study microbial succession (Dini-Andreote et al., 2015; Walker et al., 2010). However, findings derived from the use of this approach have been inconsistent. For instance, microbial community diversity remained constant in arctic soils (Poosakkannu et al., 2017), whereas the fungi diversity varied on the phylum level along a glacier chronosequence (Tian et al., 2017). These discrepancies have been ascribed to differences in soil conditions, plant communities, and abiotic factors in the process of ecosystem restoration (Urbanova et al., 2015). Soil nutrient levels (e.g. C, N, P) and pH are major drivers of variation in soil microbial community (Harantova et al., 2017; Zhang et al., 2018), because microbes' high dependence on resource availability and acidity for growth in soils (Nemergut et al., 2013; Tripathi et al., 2018). Furthermore, changes in plant communities (e.g. diversity and biomass) could alter the input of C resources into soils through decomposition of litter and release of root exudates, which could indirectly alter microbial diversity and activity (Cline and Zak, 2015).

In the present study, we investigated changes in soil properties, temporal turnover of bacterial and fungal communities, and the association between microbial succession and soil properties along a 150-year successional chronosequence. Our objective was to reveal the patterns and succession rates of bacterial and fungal communities during long-term succession, and to discover their driving forces. We hypothesized that: (1) patterns of bacterial and fungal succession differ, with fungal communities having higher succession rates owing to faster turnover, and (2) that bacterial and fungal community succession is driven by different soil properties during long-term secondary succession in semiarid area. To test our hypothesis, we selected a successional gradient (from abandoned farmland to a climax vegetation community) of six croplands abandoned for 0–150 years in a typical semiarid area, the Chinese Loess Plateau. The bacterial and fungal community compositions were analyzed by sequencing 16S ribosomal RNA (rRNA) and the internal transcribed spacer (ITS), respectively. The microbial successional rate, characterized by temporary turnover, was measured using a time–decay model (Adler and Lauenroth, 2003).

2. Materials and methods

2.1. Study area

Our experiment site was located on the Lianjiabian Forest Farm, Gansu Province (108°10′–109°08′E, 35°03′–36°37′N), part of the Ziwuling Forest, an area of state-owned forest farms with a total area of 23,000 km^2. The region has a mid-temperate continental monsoon climate with a mean annual temperature of 10 °C, and mean annual precipitation of 576.7 mm, 60% of which occurs from July to August (Deng et al., 2014). The soils of this area are *Cambisols*, which developed from secondary loess parent materials according to the FAO classification system (Jian et al., 2017). Throughout this area, the main species of the herbaceous community are *Lespedeza dahurica* and *Bothriochloa ischaemum,* whereas the main species of shrub is *Hippophae rhamnoides*. The dominate communities of pioneer forests are *Populus davidiana* Dode and *Betula platyphylla* Suk (Zou et al., 2002), and the climax vegetation is the *Quercus liaotungensis* Koidz forest (Zhang and Shangguan, 2016).

2.2. Site selection

The present secondary forests of the Ziwuling forest area are the result of natural recovery of abandoned farmland. This followed the emigration of great numbers of local residents as a result of the national conflict of 1842–1866. Some lands were reclaimed for arable cultivation from the 1940s to 1960s, but were subsequently abandoned because of wars and natural disasters. A number of croplands were gradually abandoned because of the "Grain-for-Green Project" of the 2000s (Zhao et al., 2015). Spatially, a complete successional sequence of secondary vegetation characterized by different abandoned ages has formed, which the climax forest (*Q. liaotungensis*) gradually recovering over ˜150 years (Zou et al., 2002). In brief, the secondary succession progressed in the following order: abandoned farmland, pioneer weeds, herbage-shrub mixture, shrub, early forest, and climax forest stages (Wang et al., 2016; Zou et al., 2002). Correspondingly, five successional stages representing 11 years (S11), 35 y (S35), 60 y (S60), 100 y (S100), and 150 y (S150), were chosen to evaluate the effects of long-term secondary succession on the soil microbial community. Meanwhile, an active farmland planted with maize (*Zea mays* L.) was selected as a control (0 years, S0).

The ages of different succession stages of vegetation were determined through two methods (Wang et al., 2016). For shrub and herbaceous communities that regenerated for no more than 60 years, we verified the restoration age both by interviewing local elders and by examining land contracts between farmers and the government. For forest communities with more than 60 years of recovery, we investigated the restoration age by counting growth rings and referring to related documents (Zou et al., 2002). A more detailed description of the method used to identify the ages of the communities can be found in previous studies (Deng et al., 2014; Wang et al., 2016). All sites had similar elevations, slope gradients, slope aspects, and land use histories. Site descriptions are presented in Table 1.

2.3. Sampling and physicochemical analysis

Soil samples were collected in April 2017. Six replicate plots were established randomly at each stage of succession, and the distance between adjacent plots was large enough (80–100 m) that there was no spatial dependence (< 13.5 m) for most soil variables (Marriott et al., 1997). The plots were 5 × 5 m in the herbaceous communities, 10 × 10 m in the shrub communities, and 20 × 20 m in the forest community. Surface litter was removed, following which the top 20 cm of soil was collected using a stainless steel corer with a 5 cm of diameter. Ten cores were collected in an S-shape pattern in each plot and mixed to form one sample. After removing the roots, litter, debris, and stone, the collected soil was divided into two subsamples. One subsample (approximately 100 g) was immediately stored at −80 °C for DNA analysis, and the other (approximately 500 g) was air-dried for physicochemical analysis.

Soil organic carbon (OC) was measured using the potassium dichromate oxidation method (Nelson and Sommers, 1982). Soil pH was

Table 1
Geographical and vegetation features at different succession stages in the Ziwuling Mountains of the Loess Plateau.

Sites	Successional Stage	Latitude	Longitude	Elevation(m)	Slope(°)	Vegetaion community	Companion Species
S0	Farmland	36°4'25"	108°28'6"	1435	10~15	–	–
S11	Pioneer Weeds	36°5'2"	108°31'37"	1335	8~12	*B. ischaemun*	*L. dahurica,C. lanceolata*
S35	Herbage-shrub mixture	36°5'15"	108°31'35"	1378	10~15	*B. ischaemun* + *L. bicolor*	*H. rhamnoides*
S60	Shrub	36°5'16"	108°31'34"	1411	8~10	*H. rhamnoides*	*S. schneideriana,B. ischaemun,C.lanceolata*
S100	Early Forest	36°2'56"	108°31'36"	1452	10~15	*P. davidiana* + *Q. liaotungensis*	*C. lanceolata,S. schneideriana*
S150	Climax Community	36°2'55"	108°32'16"	1477	10~15	*Q. liaotungensis*	*C. lanceolata,S.Salicifolia,O. davidiana Decaisne, C. lanceolata*

B. ischaemun: Bothriochloa ischaemun; L. dahurica: Lespedeza dahurica; C. lanceolata : Carex lanceolata; L. bicolor: Lespedeza bicolor; H. rhamnoides: Hippophae rhamnoides; S. schneideriana: Spiraea schneideriana; P. davidiana: Populus davidiana; Q. liaotungensis: Quercus liaotungensis; O. davidiana Decaisne: Ostryopsis davidiana Decaisne.

Table 2
Characteristics of soil properties duringthe secondary succession in Ziwuling Mountains.

Soil variables	Sites							
	S0	S11	S35	S60	S100	S150	$F_{5,36}$	*P*
Organic C (g kg^{-1})	12.36 ± 1.19 d	14.48 ± 0.89 c	15.60 ± 0.11 c	18.80 ± 0.17 b	20.64 ± 0.71 a	22.08 ± 0.78 a	36.85	< 0.001
Total N (g kg^{-1})	1.31 ± 0.12 b	1.26 ± 0.08 b	1.28 ± 0.05 b	1.91 ± 0.08 a	1.95 ± 0.11 a	2.02 ± 0.09 a	16.19	< 0.001
Available P (mg kg^{-1})	4.95 ± 0.43 b	3.65 ± 0.20 c	4.71 ± 0.10 b	5.57 ± 0.80 ab	5.74 ± 0.48 a	7.21 ± 0.41 a	8.26	< 0.001
NO_3^--N (mg kg^{-1})	12.63 ± 0.10 a	2.62 ± 0.56 c	3.98 ± 0.50 b	4.52 ± 0.46 b	5.69 ± 0.58 b	6.05 ± 0.75 b	344.61	< 0.001
NH_4^+-N(mg kg^{-1})	5.83 ± 0.29 c	7.21 ± 0.51 b	7.68 ± 0.38 b	9.25 ± 0.53 a	10.26 ± 0.50 a	11.41 ± 0.98 a	13.77	< 0.001
pH	8.33 ± 0.02 a	8.25 ± 0.03 a	8.21 ± 0.00 b	8.13 ± 0.02 b	8.11 ± 0.03 b	8.08 ± 0.03 c	16.60	< 0.001
Total P (g kg^{-1})	0.66 ± 0.02 a	0.57 ± 0.02 b	0.62 ± 0.01 a	0.64 ± 0.01 a	0.65 ± 0.01 a	0.65 ± 0.01 a	5.22	0.0015
C/N	9.40 ± 0.11 b	11.67 ± 0.73 a	12.29 ± 0.54 a	9.93 ± 0.38 b	10.85 ± 0.60 a	10.94 ± 0.60 a	4.10	0.0059
Water content (%)	2.41 ± 0.13 c	11.88 ± 1.73 b	12.04 ± 0.55 b	12.88 ± 1.50 b	16.55 ± 1.09 a	20.24 ± 1.88 a	38.81	< 0.001
Bulk density(g cm^{-3})	1.29 ± 0.02 a	1.22 ± 0.03 b	1.11 ± 0.04 b	1.11 ± 0.03 b	1.01 ± 0.04 c	0.88 ± 0.05 d	13.49	< 0.001

Values are means ± standard error (n = 6). The last two columns showed the *F* values and the significance of the linear mixed models, respectively. Different letters indicate the significant difference at the level of 0.05 between the successional stages.

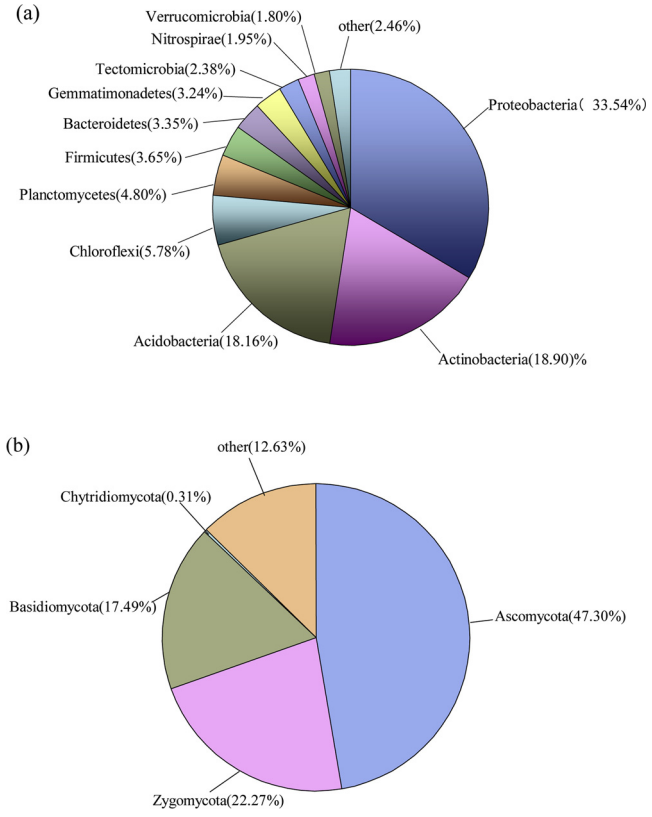

Fig. 1. Major bacterial and fungal taxa at the phylum level.

measured with a combination pH electrode in a soil-to-water ratio of 2.5:1 (v/w). Total nitrogen (TN) was measured using the Kjeldahl method (Bremner and Mulvaney, 1982). Soil NH_4^+-N and NO_3^--N were analyzed using a continuous flow autoanalyzer after extraction with 2 M KCl in a 1:5 ratio. Total phosphorus (TP) was measured using melt-molybdenum, antimony, and scandium colorimetry. Available phosphorus (AP) was measured using the Olsen method (Olsen and Sommers, 1982). Soil water content (WC) was measured gravimetrically by drying the samples at 105 °C overnight, and expressed as a percentage of the dry weight. Soil bulk density was measured according to the method of Deng et al. (2014).

2.4. DNA extraction and Illumina MiSeq high-throughput sequencing

Microbial DNA was extracted from 0.25 g of soil using a FastDNA spin kit (MP Biomedicals, Cleveland, USA). The final DNA concentration and purity were measured using a NanoDrop 2000 UV–vis spectrophotometer (Thermo Scientific, Wilmington, USA), and DNA quality was checked by 1% agarose gel electrophoresis. The V4-V5 hypervariable regions of the bacterial 16S rRNA gene were amplified by PCR (GeneAmp 9700, ABI, USA) using primers 515 F (5′-GTGCCAGCMGCCGCGGTAA-3′) and 907R (5′−CCGTCAATTCCTTTGAGTTT-3′). The ITS 1 region of the fungal 18S rRNA gene was amplified using primers ITS5-1737 F (5′ -GGAAGTAAAAGTCGTAACAAGG-3′) and ITS2-2043R (5′-GCTGCGTTCTTCATCGATGC-3′). PCR reactions were performed in a volume of 30 μL containing 2 μL of sterile ultrapure water, 15 μL of Phusion Master Mix (2×), 3 μL of primer 6 μM and 10 μL of template DNA (5~10 ng). The PCR procedure was initial denaturation at 98 °C for 60 s; followed by 30 cycles of 98 °C for 10 s, 50 °C for 30 s, and 72 °C for 30 s; final elongation at 72 °C for 5 min; and hold at 4 °C. Successful PCR amplification was verified by 2% agarose gel electrophoresis. PCR products were mixed in equal proportions. Then, PCR product mixtures were purified with a Qiagen Gel Extraction Kit (Qiagen, Germany). Sequencing libraries were generated using a TruSeq® DNA PCR-Free Sample Preparation Kit (Illumina, USA), and index codes were added. Library quality was assessed on a Qubit 2.0 Fluorometer (Thermo Scientific) and Agilent Bioanalyzer 2100 system. Finally, the library

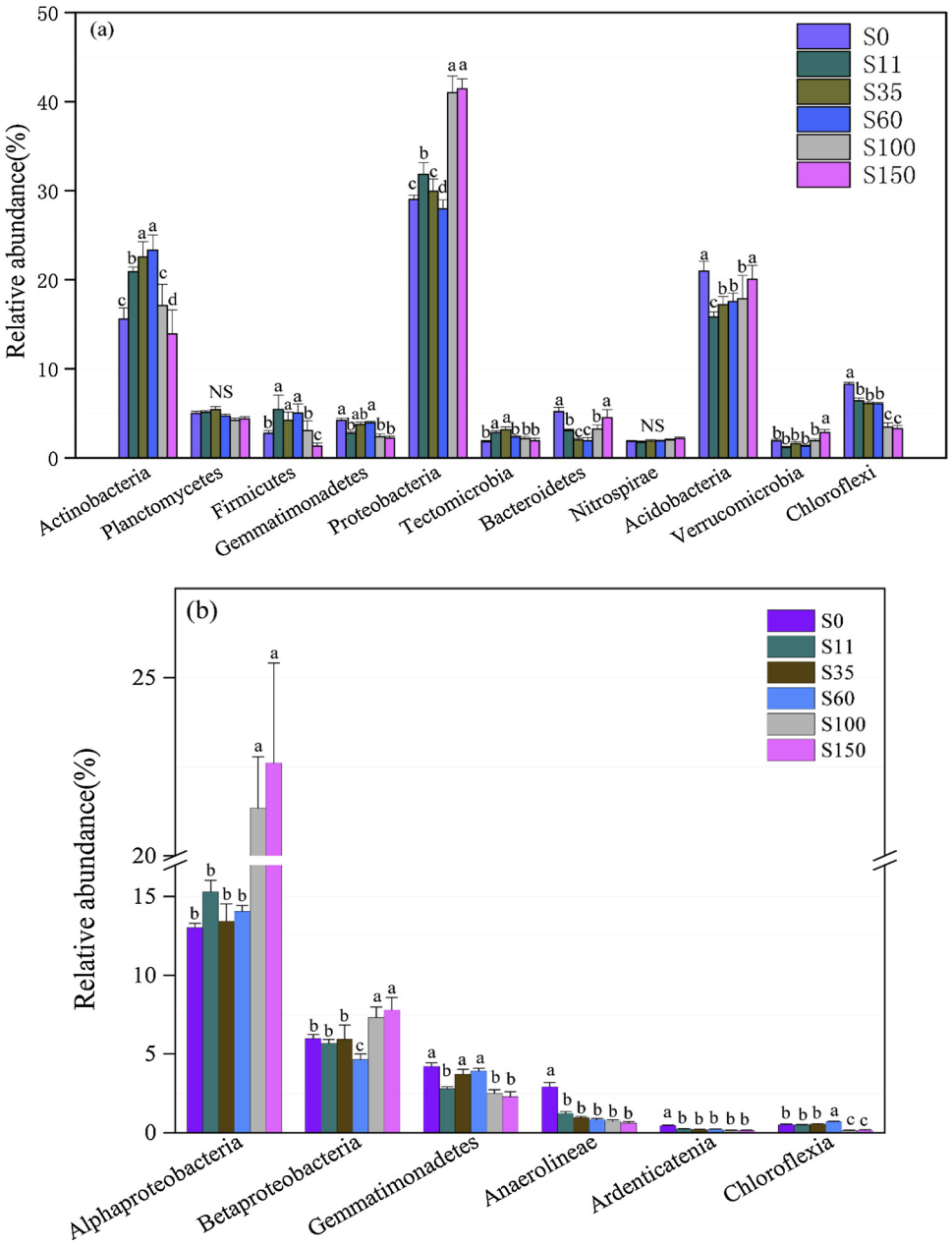

Fig. 2. Mean relative abundance of bacterial communities at the (a) phylum or (b) class level. Values are the mean ± standard error (n = 6). Different letters indicate the significant difference at the level of 0.05 between the successional stages.

was sequenced on an Illumina HiSeq 2500 platform, and 250 bp paired-end reads were generated. The raw reads were deposited into the NCBI Sequence Read Archive (SRA) database (accession number: SRP149331).

2.5. Processing of sequencing data

Raw fastq files were demultiplexed, and the sequences were quality-filtered and chimera checked using the Quantitative Insights into Microbial Ecology (QIIME) workflow (Caporaso et al., 2010). In brief, quality filtering of the raw tags was performed under specific filtering conditions to obtain the high-quality clean tags according to the QIIME quality control process (Bokulich et al., 2013). Sequences with the same barcode were sorted into the same sample (Edgar, 2013). Bacterial and fungal tags were compared with reference databases (Gold database, http://drive5.com/uchime/uchime_download.html; Unite database, https://unite.ut.ee/, respectively) using the UCHIME algorithm to detect chimera sequences, and then the chimera sequences were removed (Caporaso et al., 2010). Then, the effective tags were finally obtained. The remaining sequences were clustered by UPARSE software (Edgar, 2013) and assigned to OTUs at similarities of 97%. Bacterial taxonomic identity was determined using the Silva reference database (http://www.arb-silva.de) via the RDP classifier, and fungi were identified using the Unite database (https://unite.ut.ee/) with the BLAST tool and QIIME software (http://qiime.org/index.html). Finally, a total of 2391714 bacteria sequences (on average, 66437 per sample) and 2915831 fungal sequences (on average, 80995 per sample) were obtained. Relatively high Good's coverage values ranging from 0.973 to 0.999 were obtained. The average lengths of sequences for bacteria and fungi were 374 bp and 234 bp, respectively.

2.6. Statistical analyses

A linear regression method was used to detect the relationship

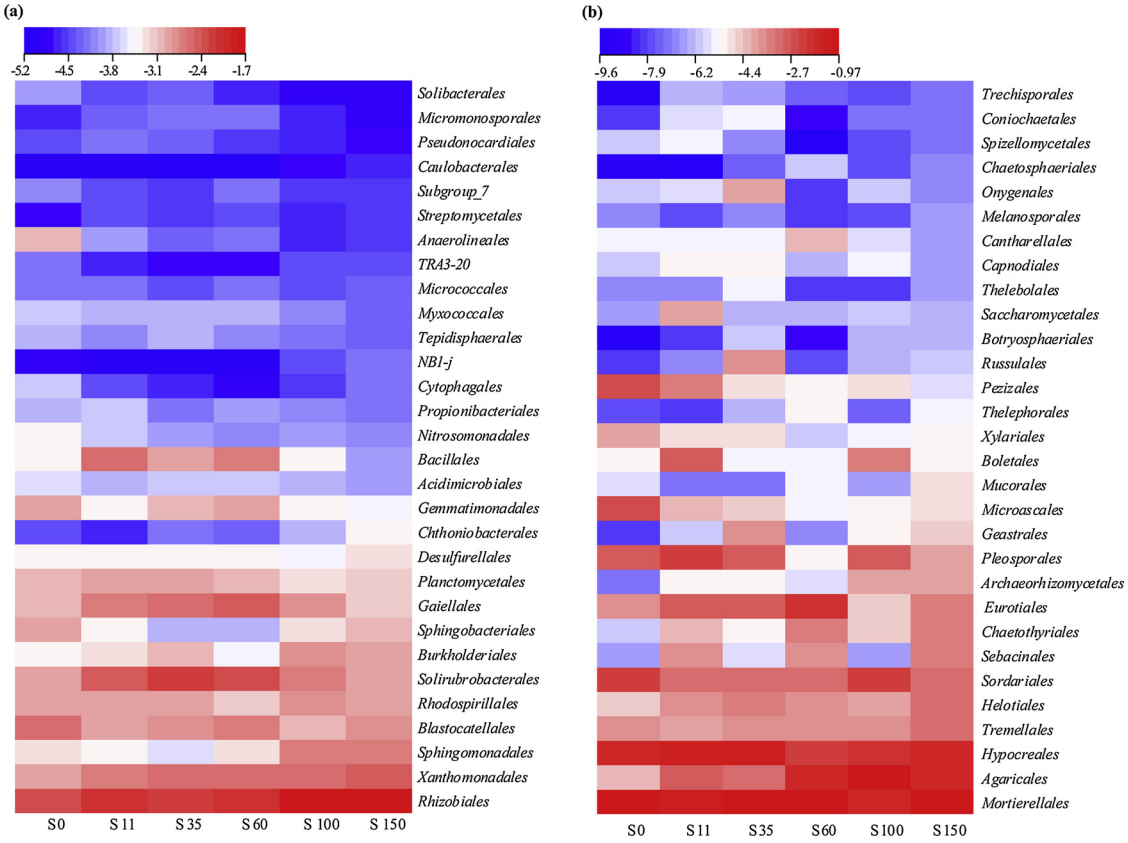

Fig. 3. Heatmap of the top 30 abundant microbial families during the succession. The color intensity in each cell indicates the transformed relative abundance [Ln (x)] of a family, referring to the color key at the left top of the figure. The relative abundance is expressed as the average percentage of the targeted sequences to the total high-quality (a) bacterial and (b) fungal sequences of samples.

between the temporal distance between samples and their similarity in terms of microbial community composition (Horner-Devine et al., 2004). The Bray–Curtis distance was used as a taxon-based metric of differences in community composition. An Arrhenius (log–log) plot was used to model the species–time relationship in the form ln(*Ss*) = constant – *w*ln(*T*), where *Ss* is the pairwise similarity in community composition, *T* (year) is the time interval of sampling the two compared samples, *w* is the regression coefficient of ln(*Ss*) with ln(*T*) and constant as intercepts, and *w* is a metric of the rate of species turnover across time. The significance of *w* values among different estimations was also determined by bootstrapping (999 times), followed by a pairwise *t*-test (Horner-Devine et al., 2004). The significance comparison of *w* values between different microbial communities was performed using the function diffslope of the software package "samba" (Jurasinski, 2012).

Linear mixed models (LMMs) were used to assess the effects of successional stages on soil properties and microbial community. The models included the "successional year" as a fixed effect (i.e. 'S0', 'S11', 'S35', 'S60', 'S100', and 'S150') and the "sampling site" as a random effect. All residuals were checked for normality and homogeneity of variance. Response variables (e.g. soil physicochemical properties and microbial taxon) that did not meet the assumptions of normality and homoscedasticity were log-transformed. If there was a significant effect, a comparison among means was conducted using Tukey's honest significant difference (HSD) test at the level of 0.05. Nonmetric multidimensional scaling analysis (NMDS) was employed to assess differences in microbial community structure based on Bray-Curtis distance among the different successional stages, with significance testing performed using analysis of similarities (ANOSIM). Redundancy analysis (RDA) and Pearson correlation analysis were performed to ascertain the effects of environmental variables on microbial community structure. LMMs were conducted using the *lme* function of the "nlme" package (Gałecki and Burzykowski, 2013), and the HSD test was conducted using the *glht* function in the "multcomp" package (Hothorn et al., 2008).

3. Results

3.1. Soil physicochemical properties

Succession caused differing variation ($P < 0.05$) in soil physicochemical properties (Table 2). The organic C, NH_4^+-N, and water content of soil increased significantly over time. No significant differences were found in the TN and AP concentrations in the previous 35 years; thereafter, they increased significantly and peaked at the 150-year site. Soil pH and TP concentrations were restricted to narrow ranges (8.08–8.33 and 0.57–0.66 g/kg, respectively). A sharp decrease in NO_3^--N concentration was found in soils in the pioneer weeds stage (S11) compared with original farmland, which was followed by a subsequent gentle increase with successional time. The ratio of C:N increased from 9.40 in farmland to 12.29 in the herbage-shrub mixture stage (S35), and then remained stable over the next 60 years. Bulk soil density decreased significantly with successional time.

3.2. Changes in microbial community composition during succession

Soil communities were assigned to a total of 41 bacterial and 8 fungal phyla. *Proteobacteria* was the most abundant bacterial phylum across all succession stages, accounting for 33.54% of all sequences, followed by *Actinobacteria* (18.90%), *Acidobacteria* (18.16%), *Chloroflexi* (5.78%), *Planctomycetes* (4.80%), *Firmicutes* (3.65%), *Bacteroidetes* (3.35%), and *Gemmatimonadetes* (3.24%) (Fig. 1a). The relative abundances of *Proteobacteria* and *Acidobacteria* in the early

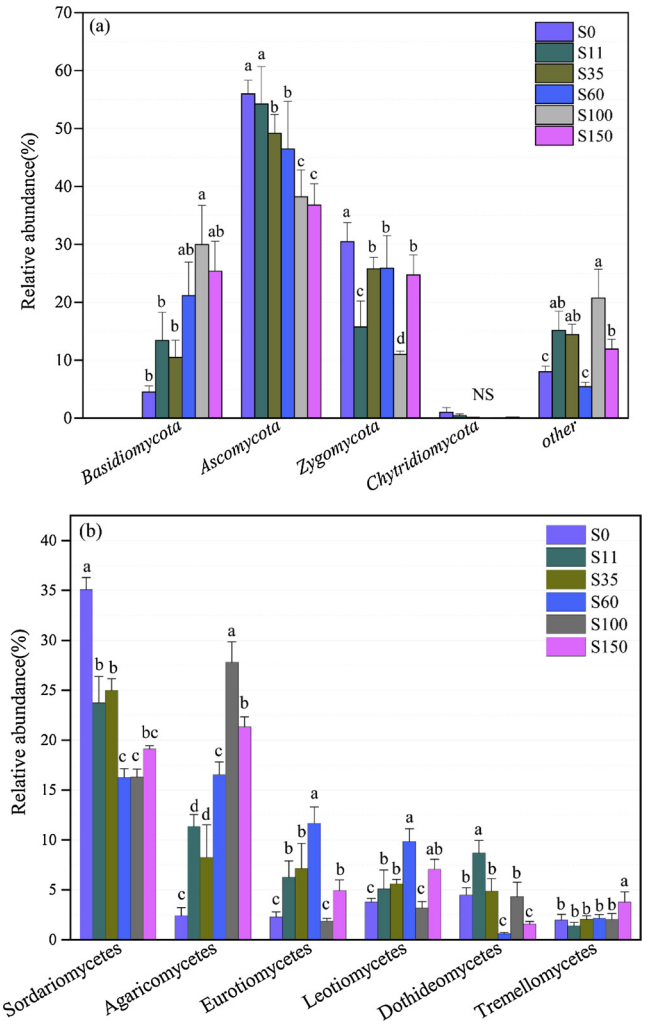

Fig. 4. Mean relative abundance of fungi communities at the (a) phylum or (b) class level. Different letters indicate the significant difference at the level of 0.05 between the successional stages.

forest community and climax community stages were significantly higher than in the other stages, whereas the abundances of *Gemmatimonadetes* and *Chloroflexi* showed the opposite trend (Fig. 2a). At the class level, *Alpha-* and *Betaproteobacteria* were more abundant during later stages (S100 and S150) of succession than in the former stages (Fig. 2b), which was obvious in the order of *Rhizobiales, Sphingomonadales*, and *Caulobacterales* (Fig. 3a). In contrast, the relative abundances of class *Anaerolineales*, *Micrococcales*, and *Gemmatimonadales* decreased markedly as succession time increased.

The fungal community was dominated by the phylum *Ascomycota* (47.30%), followed by *Zygomycota* (22.27%), *Basidiomycota* (17.49%), and *Chytridiomycota* (0.31%) (Fig. 1b). The relative abundance of *Ascomycota* decreased with succession time (Fig. 4a), and was obvious in order *Microascales* belonging to the class *Sordarimoycetes* (Fig. 4b). The relative abundance of *Basidiomycota* increased with time, and was characterized by a higher abundance of class *Agaricomycetes* and order *Tremellales* (Figs. 4b and 3 b).

The ordination of NMDS (Fig. 5a and b) and ANOSIM analysis (Table 3) uncovered clear variations in bacterial and fungal community composition. Bacterial communities could be classified into four groups: farmland and 11-year sites were clearly separated from each other, 35- and 60-year sites tended to group together, and 100- and 150-year sites tended to group together and were clearly separated from other sites (Fig. 5a). The profiles of the fungal communities at the six successional stages were clearly separated from each other (Fig. 5b).

3.3. Changes in microbial temporal turnover during succession

There was a significant difference in temporary turnover between bacterial and fungal communities with succession (Fig. 6). The slope in the fungal communities ($w = 0.1477$, $P < 0.0001$) was significantly steeper ($P = 0.001$) than that in the bacterial communities ($w = 0.0549$, $P < 0.0001$), indicating an almost three times faster rate of succession for fungi than for bacteria. At the phylum/class level (Table 4), the highest temporary bacterial community turnover was found in *Armatimonadetes* ($w = 0.1089$, $P < 0.0001$), followed by *Firmicutes* ($w = 0.1086$, $P < 0.0001$), *Verrucomicrobia*, *Chloroflexi*, *Proteobacteria*, and *Bacteroidetes*. *Proteobacteria* showed a significant variation in turnover ($w = 0.0903$, $P < 0.0001$), characterized by the class *Alpha-* and *Betaproteobacteria*. In the fungal community, *Basidiomycota* ($w = 0.2000$) and *Ascomycota* (0.0331), showed significant ($P < 0.0001$) temporal turnover during succession.

3.4. Linkage between microbial succession and soil properties

The first two axes of RDA explained the 67.9% and 61.4% of the variation in the bacterial and fungal communities, respectively (Fig. 7a and b). Soil NH_4^+-N, TN, OC, AP, pH, water content, and bulk density were significantly correlated with the first two axes of soil bacterial community composition ordination plot, whereas NO_3^--N, AP, and the C:N ratio were significantly correlated with the first two axes of soil fungal community composition plot. Pearson correlation analysis (Table 5) showed that of NH_4^+-N, TN, OC, and AP concentrations, as well as water content, were positively correlated with the abundance of *Proteobacteria*, and negatively correlated with the abundance of *Chloroflexi* and *Gemmatimonadetes*. Bulk density and pH were negatively correlated with *Proteobacteria* and positively correlated with *Chloroflexi* and *Gemmatimonadetes*. In addition, water content, organic C, AP, NO_3^--N, and the C:N ratio were positively correlated with *Basidiomycota* and negatively correlated with *Ascomycota*.

4. Discussion

4.1. Changes in composition of microbial community during secondary succession

During the succession, soil bacterial community development could be classified into four phrases: pioneer stage (farmland), initial stage (11 years), intermediate stage (35–60 years), and late stage (100–150 years) (Fig. 5a). During each phase, the bacterial community seemed to harbor increasingly similar bacterial assemblages. In contrast, the fungal community could be classified into six different phrases (Fig. 5b). These results supported our hypothesis that bacterial and fungal communities display different successional patterns. Consistent with previous studies (Lozano et al., 2014; Zeng et al., 2017), the bacterial community in soils was mainly composed of *Proteobacteria*, *Actinobacteria*, *Acidobacteria*, *Bacteroidetes*, *Chloroflexi*, *Gemmatimonadetes*, and *Planctomycetes* (Figs. 1a and 2 a). *Proteobacteria* were significantly more abundant in later stages (Fig. 2a) than in the initial stages, suggesting that the forest ecosystem favors *Proteobacteria* populations. This result was in line with the findings of Zhang et al. (2016), who found that the relative abundance of *Proteobacteria* increased with increasing restoration age during secondary succession on a grassland of the Loess Plateau.

Proteobacteria are known to be copiotrophic, and their presence correlates positively with C and N pools (Goldfarb et al., 2011; Zhang et al., 2016). Soil in forest ecosystems was assumed to be a C-rich environment because of abundant nutrient input from litter decomposition, and *Proteobacteria* could therefore be expected to be more abundant in this ecosystem (Li et al., 2014). Improved soil nutrient status

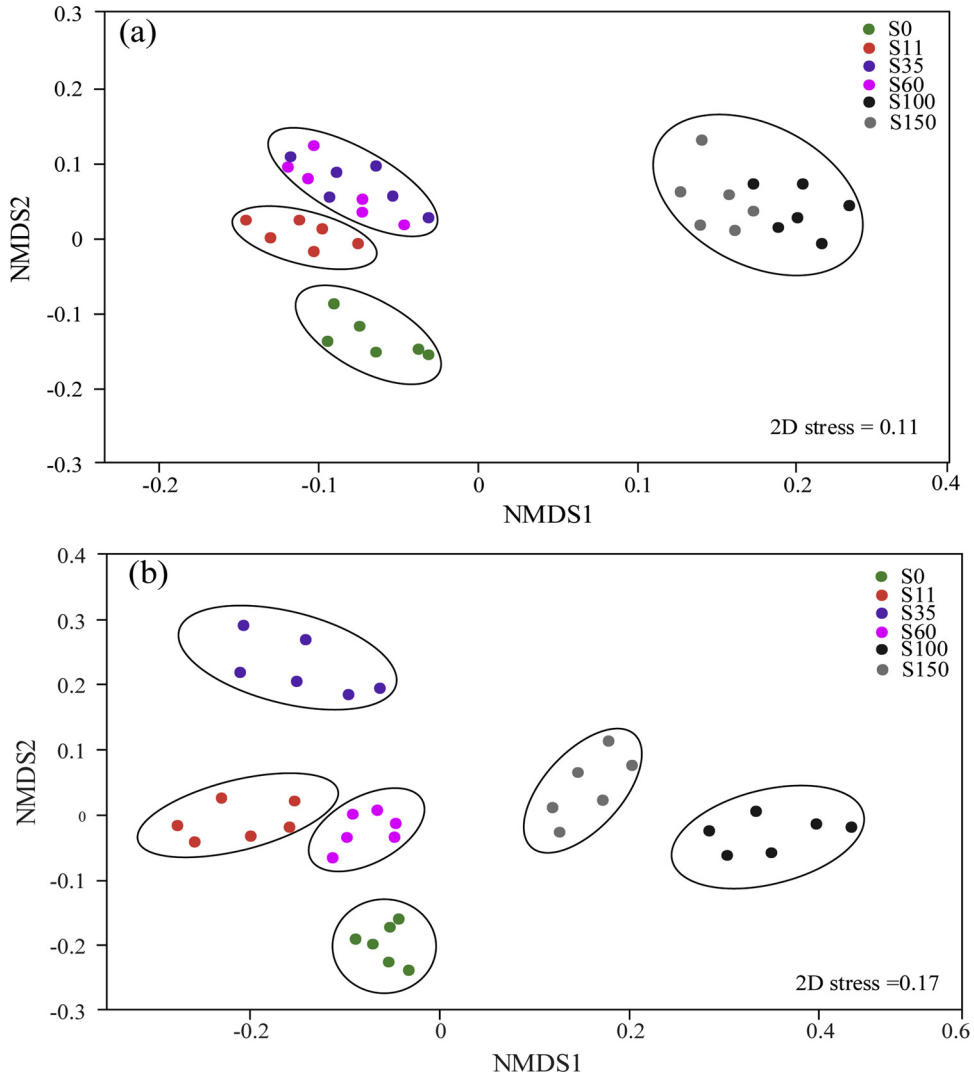

Fig. 5. Nonmetric multidimensional scaling (NMDS) ordinations of (a) bacterial and (b) fungal communities composition at different successional stages.

Table 3
Dissimilarity test of the microbial community composition based on the Bray-Curtis distance on the OUT level by ANOSIM analysis.

Microbial Community	Sites	S0	S11	S35	S60	S100	S150
bacteria	S0		(0.870,0.005)	(0.850,0.003)	(0.980,0.003)	(0.876,0.003)	(0.991,0.003)
	S11			(0.444,0.003)	(0.461,0.002)	(0.854,0.004)	(0.894,0.001)
	S35				(0.191,0.068)	(0.813,0.002)	(0.848,0.005)
	S60					(0.841,0.006)	(0.930,0.002)
	S100						(0.028,0.367)
fungi	S0		(0.620,0.002)	(0.974,0.004)	(0.967,0.001)	(0.978,0.001)	(0.961,0.004)
	S11			(0.574,0.002)	(0.337,0.005)	(0.943,0.005)	(0.806,0.001)
	S35				(0.663,0.005)	(0.998,0.003)	(0.883,0.002)
	S60					(0.954,0.001)	(0.815,0.002)
	S100						(0.456,0.005)

Data in each cell above is *R*-statistic/*P*-value of ANOSIM analysis by paired test respectively.

was also responsible for the decreasing abundance of *Gemmatimonadetes* and *Chloroflexi*, which belong to oligotrophic groups and prefer nutrient-poor soil (Davis et al., 2011; Koyama et al., 2014). These results suggested that belowground communities transitioned from slow-growing oligotrophic groups to fast-growing copiotrophic groups which use labile organic substrates at later successional stages. Among the *Proteobacteria*, *Alphaproteobacteria* was the largest subgroup at different successional sites (Fig. 2b), with samples from those sites containing significant populations of *Rhizobiales*, an N-fixing bacterium (Fig. 3a). Given the importance of *Rhizobiales*-related phylotypes in the N cycling of soils, their presence in this degraded area may be ecologically significant. Additionally, given that most members of the *Anaerolineae* and *Ardenticatenia* classes are anaerobic populations (Davis et al., 2011); their decreasing abundance is possible evidence of an improvement in soil aeration. This assumption was confirmed by the decreased soil bulk density along succession (Table 2).

In contrast to the bacterial communities, whose compositions tended to overlap (Fig. 5a), the distinct differences in fungal community

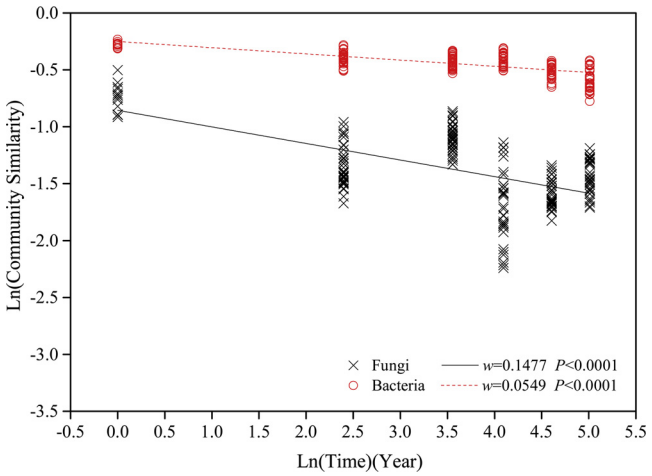

Fig. 6. The time-decay curves for fungal and bacterial communities. The slopes of all lines was significantly less than zero and significantly different for pairwise comparison.

Table 4
Temporal turnover of bacterial and fungal groups.

Groups	Turnover		Permutation test	
	w	*P*-value	*t*	*P*-value
Bacterial				
All OTUs	0.0549	< 0.0001	−497.2	< 0.0001
Acidobacteria	0.0450	< 0.0001	−334.5	< 0.0001
Actinobacteria	0.0390	< 0.0001	−260.7	< 0.0001
Bacteroidetes	0.0880	< 0.0001	−391.7	< 0.0001
Armatimonadetes	0.1089	< 0.0001	−327.3	< 0.0001
Verrucomicrobia	0.0997	< 0.0001	−393.2	< 0.0001
Nitrospirae	0.0675	< 0.0001	−324.0	< 0.0001
Tectomicrobia	0.0163	0.0012	−97.7	< 0.0001
Gemmatimonadetes	0.0659	< 0.0001	−371.5	< 0.0001
Firmicutes	0.1086	< 0.0001	−207.5	< 0.0001
Planctomycetes	0.0386	< 0.0001	−478.5	< 0.0001
Proteobacteria	0.0903	< 0.0001	−505.6	< 0.0001
Alphaproteobacteria	0.0695	< 0.0001	−397.2	< 0.0001
Betaproteobacteria	0.0636	< 0.0001	−514.2	< 0.0001
Deltaproteobacteria	0.0541	< 0.0001	−338.6	< 0.0001
Gammaproteobacteria	0.0323	< 0.0001	−171.1	< 0.0001
Chloroflexi	0.0970	< 0.0001	−444.1	< 0.0001
Fungi				
All OTUs	0.1477	< 0.0001	−472.4	< 0.0001
Ascomycota	0.0331	< 0.0001	−221.3	< 0.0001
Chytridiomycota	0.0621	0.3370	32.6	< 0.0001
Basidiomycota	0.2000	< 0.0001	−224.7	< 0.0001
Zygomycota	0.0226	0.1220	50.2	< 0.0001

[t] and *P*-values are from t-tests on bootstrapping (999 times) for testing significance of *w* values.

composition between successional stages suggested that fungi were more sensitive to environmental changes than the bacteria (Fig. 5b). This result agreed with the study by Sun et al. (2017), who found large changes in fungal communities during forest ecosystem restoration. A possible reason could be the faster succession rate of fungi compared to bacteria, as outlined in the section discussing microbial temporal turnover (Fig. 6). As expected, the fungal communities displayed clear succession along the chronosequence. *Agaricomycetes*, the largest class of *Basidiomycota*, increased in abundance with succession time and dominated at the late stages, replacing the class *Sordariomycetes* (from the phylum *Ascomycota*), which dominated the early-stage community (Fig. 4b). This finding was in line with that of Banning et al. (2011), who reported a distinct pattern of change in fungal communities during progression from grassland to forest. The results of the investigation into bacterial and fungal community compositions confirmed our hypothesis that there is a distinction between the patterns of succession of bacterial and fungal communities.

4.2. Distinct temporal turnover of bacteria and fungi during secondary succession

In the case of the 150-year succession, we found a significantly linear decrease in bacterial and fungal similarity over time (log transformed) (Fig. 6; Table 4). Generally, the turnover values of the bacterial and fungal communities (0.016–0.200) displayed the same magnitudes as those described in other studies, ranging from 0 to 0.3 (Liang et al., 2015; Shade et al., 2013). As we hypothesized, the fungal community showed a higher succession rate than did the bacterial community, characterized by an almost three-times-higher temporary turnover. A possible explanation could be the unique biological attributes of microbes, which include massive population sizes, rapid dispersal rates, high asexual reproduction, and resistance to extinction. Furthermore, the temporal turnover of small soil microbes is usually lower than that of larger microbes (Shade et al., 2013). Fungi tend to be much larger than bacteria, and their communities are less diverse owing to their lower cell count (Rousk and Baath, 2007). Thus, the succession rate of the fungal community was higher, possibly owing to colonization by new species or an increased extinction rate of extant species. Our result was in line with that of (Zhang et al., 2017), who reported that the succession rate of eukaryotes ($w = 0.3251$, $P < 0.0001$) was higher than that of bacteria ($w = 0.2450$, $P < 0.0001$) during dredging disturbance. The temporary turnover of the bacterial and fungal communities might suggest the decreased stability and reassembly of microbial populations during succession.

Different microbial populations showed diverse slopes of the time–decay relationships during succession, which reflected the differences in sensitivity of the diverse microbial phylogenetic groups to environmental change. Some populations, such as the phyla *Basidiomycota*, *Firmicutes*, *Proteobacteria*, and *Chloroflexi*, showed higher turnover than other microbes (Table 4). These results were in partial agreement with the study by Liang et al. (2015), who found a high turnover of *Proteobacteria* and *Firmicutes* in a long-term experiment which transplanted soil from a warm temperate zone to a cold zone, but were in contrast to the finding that *Actinobacteria* showed a higher temporary turnover and higher sensitivity than other microbes to environmental change. This discrepancy could be related to the living habits of the *Actinobacteria* community. In general, populations of *Actinobacteria* tend to be highly susceptible to temperature compared with other microbes (Mohammadipanah and Wink, 2016), whereas this did not occur in our study because of a stable temperature (data not shown).

4.3. Soil nutrients and properties as drivers of microbial community changes

In our study, 67.9% and 61.4% of the variation in soil bacterial and fungal communities was explained by the selected soil properties (Fig. 7a, b), respectively, indicating that the shift in microbial community composition was largely correlated with soil properties during succession. Because of the different responses of microbial populations to elevated soil nutrients, such as the preference of copiotrophic *Proteobacteria* for enriched nutrient soil, and preference of oligotrophic *Gemmatimonadetes* for nutrient-poor soil, different associations between microbial communities and soil properties were found. The investigation of Zhang et al. (2013) showed that increased N concentration was the major factor influencing bacterial and fungal communities in permafrost soils supporting different vegetation types on the Tibetan Plateau. However, bacteria and fungi differed in their responses to N forms. In our study, bacteria were sensitive to NH_4^+-N concentration, whereas fungi tended to sensitive to NO_3^--N concentration (Fig. 7a, b) in soils on the Loess Plateau. These results showed a selective response of the microbes to the N form.

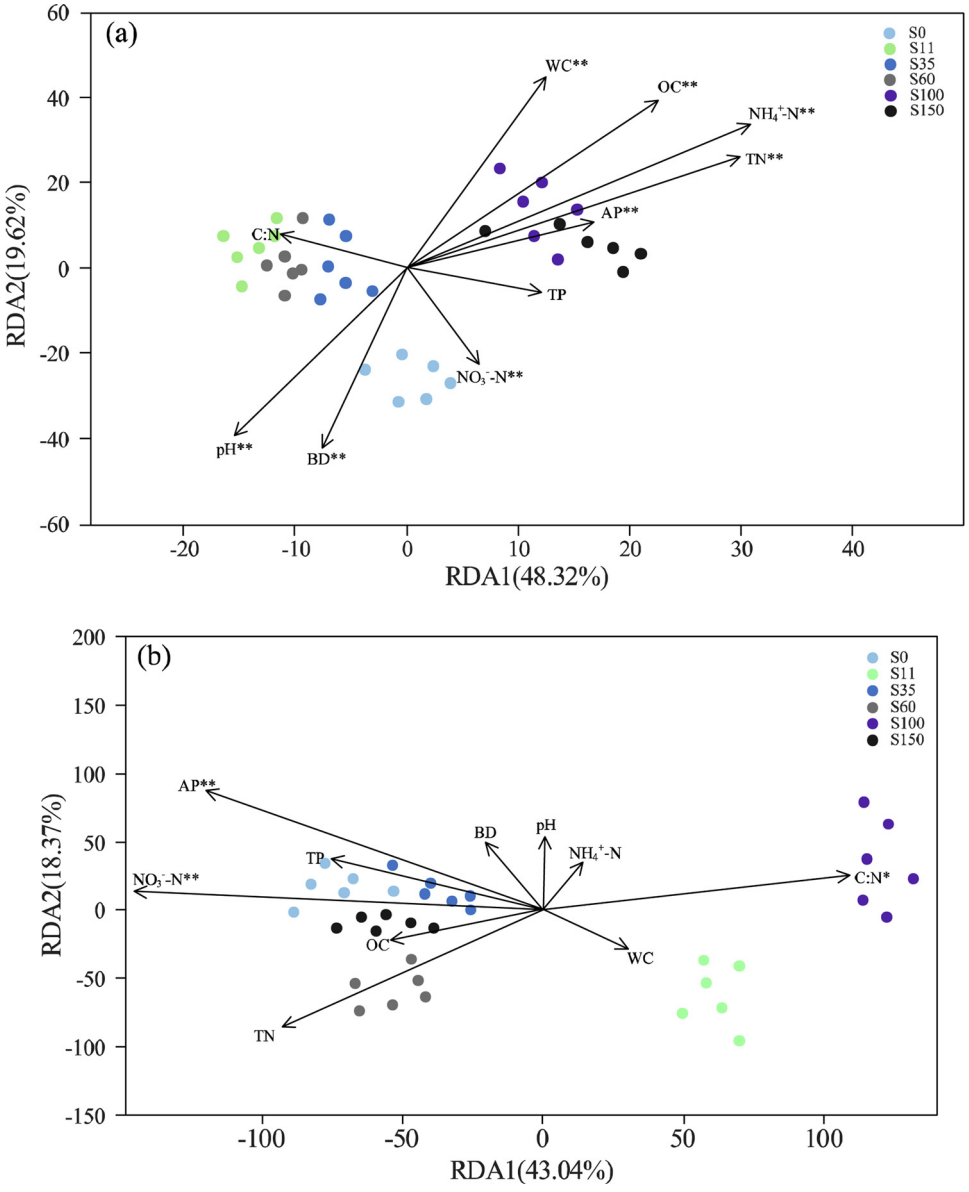

Fig. 7. Ordination plots of the results from the redundancy analysis to identify the relationships among the dominant (a) bacterial population and (b) fungal population based on genus level. OC: organic C, TN: total N, TP: total P, AP: available P, BD: bulk density, WC: water content. The asterisk in ordination plot indicates that the soil variables were significantly correlated with the first two axes of RDA ordination biplot. *: $P < 0.05$; **: $P < 0.01$.

Table 5
Pearson coefficient between soil properties and the abundance of the dominant microbial groups.

Parameter	WC	BD	OC	TN	NO_3^--N	NH_4^+-N	TP	AP	C:N	pH
Proteobacteria	0.610**	−0.599**	0.617**	0.534**	−0.120	0.716**	−0.124	0.497**	−0.012	−0.510**
Actinobacteria	−0.092	0.118	−0.167	−0.303	−0.402	−0.092	−0.329	−0.249	0.333*	0.043
Acidobacteria	−0.102	0.040	0.068	0.256	0.436**	−0.142	0.308	0.083	−0.361*	0.064
Chloroflexi	−.763**	0.762**	−0.740**	−0.584**	0.327	−0.748**	0.102	−0.473	−0.138	0.609**
Planctomycetes	−0.302	0.360*	−0.435**	−0.534**	0.016	−0.460**	−0.165	−0.418*	0.305	0.360*
Firmicutes	−0.174	0.179	−0.276	−0.277	−0.278	−0.187	−0.076	−0.214	0.125	0.152
Gemmatimonadetes	−0.553**	0.590**	−0.434**	−0.338*	0.334*	−0.607**	−0.012	−0.351*	−0.089	0.390*
Bacteroidetes	−0.142	0.038	−0.102	0.047	0.563**	−0.130	0.304	0.129	−0.334*	0.161
Tectomicrobia	0.032	−0.014	−0.143	−0.317	−0.451**	−0.302	−0.522**	−0.392*	0.387*	0.152
Nitrospirae	0.416*	−0.338*	0.476**	0.432**	0.034	0.192	0.030	0.167	−0.094	−0.292
Verrucomicrobia	0.373*	−0.275	0.404*	0.336	0.256	0.286	0.330*	0.454**	−0.054	−0.256
Basidiomycota	0.597**	−0.412*	0.523**	0.326	0.487**	−0.215	0.122	0.523**	0.412*	−0.421*
Ascomycota	−0.471**	0.284	−0.540**	−0.294	−0.425**	0.119	−0.207	−0.412*	−0.394*	0.259
Zygomycota	−0.313	0.375*	−0.129	−0.050	0.310	−0.216	0.237	0.167	−0.175	0.242
Chytridiomycota	−0.291	0.212	−0.126	−0.038	0.305	−0.205	0.304	−0.106	−0.133	0.382*

**Correlation is significant at $P < 0.01$ (two-tailed);*Correlation is significant at $P < 0.05$(two-tailed); OC: organic C, TN: total N, TP: total P, AP: available P, BD: bulk density, WC: water content.

Soil pH and bacterial community changes have been shown to be strongly correlated in different soil ecosystems (Shen et al., 2013; Tripathi et al., 2018). Whereas pH correlates well with bacterial community change in semiarid soils and in our investigation, it does not correlate well with fungal community changes. A possible reason could be adaption of fungal species to broad variations in soil pH (Rousk et al., 2010). Additionally, our results showed that the bacterial community's composition was closely correlated with water content of soil, but not with fungal community composition, a result agreeing with the generally greater resistance of fungi to dry conditions (de Vries and Shade, 2013), as well as the more stable properties of fungal-based food webs (de Vries et al., 2012; Engelhardt et al., 2018). We also showed a close correlation between AP and fungal community, suggesting the importance of AP in the establishment of fungal communities in soil. However, other studies found no evidence of a close association between P and bacterial community (Zeng et al., 2017; Zhang et al., 2016). It is thus not clear which processes account for the patterns of change between these two communities. One possible factor is pedogenesis because of predictable chemical and physical changes that correlate with these numerous dynamics during ecosystem development (Zhang et al., 2014). However, this speculation needs to be further investigated.

Soil bulk density was an important factor affecting the microbial community. Decreased bulk density along succession correlated with increased soil porosity and improved aeration; this could be favorable for the survival and growth of many aerophile bacteria (most species in soils are aerophilic). Moreover, the C:N ratio greatly affected fungal communities, in line with previous studies (Yang et al., 2013; Zhang et al., 2014). Given the contribution of aboveground litter and belowground roots to soil nutrient status, it can be assumed that the variation in the C:N ratio along the chronosequence could be driven by the C:N ratio in litter and roots, which was ultimately determined by the aboveground community structure (Zhang et al., 2016).

It is worth mentioning that the results obtained in our study were based on a space for time substitution. When carried out at large scales, this type of approach can suffer from pseudo-replication as each part of the chronosequence is not replicated. When replicate samples are taken from a single experimental unit differences between experimental units are confounded with the differences induced by the treatment. In large scale studies such as the one presented here, it is difficult to avoid due to the high cost of establishing replicated experimental units at the field scale. We therefore determined whether the relative spatial proximity of the samples taken from within a single experimental unit might have affected the soil and microbial properties measured (Ramette and Tiedje, 2007) using linear mixed models and this was not the case. This reinforces the idea that changes in bacterial community properties were due to changes in soil properties caused by succession.

5. Conclusions

Changes to soil microbial communities during 150-year succession supported our hypothesis that bacterial and fungal succession patterns in soils differ. The fungal community showed a higher succession rate than did the bacterial community, characterized by an almost three-times-higher temporary turnover. Bacterial succession was affected by changes in soil NH_4^+-N, total P, organic C, water content, bulk density, and pH, whereas fungal succession was affected to a greater extent by NO_3^--N, available P, and C:N ratio. *Basidiomycota* had the highest temporal turnover; followed by *Armatimonadetes*, *Firmicutes*, *Verrucomicrobia*, *Chloroflexi*, and *Proteobacteria.* These results enhance our understanding of the association between soil properties and microbial community structure and succession during long-term restoration in semiarid ecosystems.

Acknowledgements

This work was financially supported by the National Natural Sciences Foundation of China (41771554), and the National Key Research and Development Program of China (2016YFC0501707). The authors thank Professor Zhao Xu in the statistical analysis of data, and also thank the two anonymous reviewers and editors of the journal for their valuable comments, suggestions, and revisions of this manuscript.

References

Adler, P.B., Lauenroth, W.K., 2003. The power of time: spatiotemporal scaling of species diversity. Ecol. Lett. 6, 749–756.
Banning, N.C., Phillips, I.R., Jones, D.L., Murphy, D.V., 2011. Development of microbial diversity and functional potential in bauxite residue sand under rehabilitation. Restor. Ecol. 19, 78–87.
Bokulich, N.A., Subramanian, S., Faith, J.J., Gevers, D., Gordon, J.I., Knight, R., Mills, D.A., Caporaso, J.G., 2013. Quality-filtering vastly improves diversity estimates from Illumina amplicon sequencing. Nat. Methods 10, 57–U11.
Bremner, J.M., Mulvaney, C.S., 1982. Nitrogen-total. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Eds.), Methods of Soil Analysis, Part 2, Chemical and Microbial Properties. Agronomy Society of America, Agronomy Monograph 9, Madison, Wisconsin pp. 595e624.
Brown, S.P., Jumpponen, A., 2014. Contrasting primary successional trajectories of fungi and bacteria in retreating glacier soils. Mol. Ecol. 23, 481–497.
Caporaso, J.G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F.D., Costello, E.K., Fierer, N., Pena, A.G., Goodrich, J.K., Gordon, J.I., Huttley, G.A., Kelley, S.T., Knights, D., Koenig, J.E., Ley, R.E., Lozupone, C.A., McDonald, D., Muegge, B.D., Pirrung, M., Reeder, J., Sevinsky, J.R., Tumbaugh, P.J., Walters, W.A., Widmann, J., Yatsunenko, T., Zaneveld, J., Knight, R., 2010. QIIME allows analysis of high-throughput community sequencing data. Nat. Methods 7, 335–336.
Ciccazzo, S., Esposito, A., Borruso, L., Brusetti, L., 2016. Microbial communities and primary succession in high altitude mountain environments. Ann. Microbiol. 66, 43–60.
Cline, L.C., Zak, D.R., 2015. Soil microbial communities are shaped by plant-driven changes in resource availability during secondary succession. Ecology 96, 3374–3385.
Davis, K.E.R., Sangwan, P., Janssen, P.H., 2011. Acidobacteria, Rubrobacteridae and Chloroflexi are abundant among very slow-growing and mini-colony-forming soil bacteria. Environ. Microbiol. 13, 798–805.
de Vries, F.T., Liiri, M.E., Bjornlund, L., Bowker, M.A., Christensen, S., Setala, H.M., Bardgett, R.D., 2012. Land use alters the resistance and resilience of soil food webs to drought. Nat. Clim. Change 2, 276–280.
de Vries, F.T., Shade, A., 2013. Controls on soil microbial community stability under climate change. Front. Microbiol. 4.
Deng, L., Wang, K.B., Shangguan, Z.P., 2014. Long-term natural succession improves nitrogen storage capacity of soil on the Loess Plateau, China. Soil Res. 52, 262–270.
Dini-Andreote, F., Stegen, J.C., van Elsas, J.D., Salles, J.F., 2015. Disentangling mechanisms that mediate the balance between stochastic and deterministic processes in microbial succession. Proc. Natl. Acad. Sci. U. S. A. 112, E1326–E1332.
Edgar, R.C., 2013. UPARSE: highly accurate OTU sequences from microbial amplicon reads. Nat. Methods 10, 996.
Engelhardt, I.C., Welty, A., Blazewicz, S.J., Bru, D., Rouard, N., Breuil, M.-C., Gessler, A., Galiano, L., Carlos Miranda, J., Spor, A., Barnard, R.L., 2018. Depth matters: effects of precipitation regime on soil microbial activity upon rewetting of a plant-soil system. ISME J. 12, 1061–1071.
Fabian, J., Zlatanovic, S., Mutz, M., Premke, K., 2017. Fungal-bacterial dynamics and their contribution to terrigenous carbon turnover in relation to organic matter quality. ISME J. 11, 415–425.
Feng, M., Adams, J.M., Fan, K., Shi, Y., Sun, R., Wang, D., Guo, X., Chu, H., 2018. Long-term fertilization influences community assembly processes of soil diazotrophs. Soil Biol. Biochem. 126, 151–158.
Fernandez-Martinez, M.A., Perez-Ortega, S., Pointing, S.B., Green, T.G.A., Pintado, A., Rozzi, R., Sancho, L.G., de los Rios, A., 2017. Microbial succession dynamics along glacier forefield chronosequences in Tierra del Fuego (Chile). Polar Biol. 40, 1939–1957.
Gałecki, A., Burzykowski, T., 2013. Linear Mixed-Effects Models Using R. Springer.
Goldfarb, K.C., Karaoz, U., Hanson, C.A., Santee, C.A., Bradford, M.A., Treseder, K.K., Wallenstein, M.D., Brodie, E.L., 2011. Differential growth responses of soil bacterial taxa to carbon substrates of varying chemical recalcitrance. Front. Microbiol. 2.
Harantova, L., Mudrak, O., Kohout, P., Elhottova, D., Frouz, J., Baldrian, P., 2017. Development of microbial community during primary succession in areas degraded by mining activities. Land Degrad. Dev. 28, 2574–2584.
Horner-Devine, M.C., Lage, M., Hughes, J.B., Bohannan, B.J.M., 2004. A taxa-area relationship for bacteria. Nature 432, 750–753.
Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biomet. J. 50, 346–363.
Jian, H., Wang, H., Li, Z., 2017. Relationship between plants and soil resource patterns on forest land at different scales using a new theoretical model. Ecol. Model. 349, 33–40.
Jurasinski, G., 2012. Simba: a Collection of Functions for Similarity Analysis of Vegetation Data.
Koyama, A., Wallenstein, M.D., Simpson, R.T., Moore, J.C., 2014. Soil bacterial

community composition altered by increased nutrient availability in Arctic tundra soils. Front. Microbiol. 5.
Li, C., Yan, K., Tang, L., Jia, Z., Li, Y., 2014. Change in deep soil microbial communities due to long-term fertilization. Soil Biol. Biochem. 75, 264–272.
Liang, Y., Jiang, Y., Wang, F., Wen, C., Deng, Y., Xue, K., Qin, Y., Yang, Y., Wu, L., Zhou, J., Sun, B., 2015. Long-term soil transplant simulating climate change with latitude significantly alters microbial temporal turnover. ISME J. 9, 2561–2572.
Lozano, Y.M., Hortal, S., Armas, C., Pugnaire, F.I., 2014. Interactions among soil, plants, and microorganisms drive secondary succession in a dry environment. Soil Biol. Biochem. 78, 298–306.
Marriott, C.A., Hudson, G., Hamilton, D., Neilson, R., Boag, B., Handley, L.L., Wishart, J., Scrimgeour, C.M., Robinson, D., 1997. Spatial variability of soil total C and N and their stable isotopes in an upland Scottish grassland. Plant Soil 196, 151–162.
Mohammadipanah, F., Wink, J., 2016. Actinobacteria from arid and desert habitats: diversity and biological activity. Front. Microbiol. 6.
Nelson, D.W., Sommers, L.E., 1982. Total carbon, organic carbon, and organic matter. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis, Part 2. Chemical and Microbial Properties. Agronomy Society of America, Agronomy Monograph 9, Madison, Wisconsin, pp. 539–552.
Nemergut, D.R., Schmidt, S.K., Fukami, T., O'Neill, S.P., Bilinski, T.M., Stanish, L.F., Knelman, J.E., Darcy, J.L., Lynch, R.C., Wickey, P., Ferrenberg, S., 2013. Patterns and processes of microbial community assembly. Microbiol. Mol. Biol. Rev. 77, 342–356.
Odum, E.P., 1969. The strategy of ecosystem development. Science (New York, N.Y.) 164, 262–270.
Olsen, S.R., Sommers, L.E., 1982. Phosphorous. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis, Part 2, Chemical and Microbial Properties. Agronomy Society of America, Agronomy Monograph 9, Madison, Wisconsin, pp. 403–430.
Poosakkannu, A., Nissinen, R., Männistö, M., Kytöviita, M.M.J.E.M., 2017. Microbial community composition but not diversity changes along succession in arctic sand dunes. Environ. Microbiol. 19, 698.
Ramette, A., Tiedje, J.M., 2007. Multiscale responses of microbial life to spatial distance and environmental heterogeneity in a patchy ecosystem. Proc. Natl. Acad. Sci. U. S. A. 104, 2761–2766.
Rousk, J., Baath, E., 2007. Fungal biomass production and turnover in soil estimated using the acetate-in-ergosterol technique. Soil Biol. Biochem. 39, 2173–2177.
Rousk, J., Baath, E., Brookes, P.C., Lauber, C.L., Lozupone, C., Caporaso, J.G., Knight, R., Fierer, N., 2010. Soil bacterial and fungal communities across a pH gradient in an arable soil. ISME J. 4, 1340–1351.
Salles, J.F., Pereira e Silva, M.C., Dini-Andreote, F., Dias, A.C.F., Guillaumaud, N., Poly, F., van Elsas, J.D., 2017. Successional patterns of key genes and processes involved in the microbial nitrogen cycle in a salt marsh chronosequence. Biogeochemistry 132, 185–201.
Schmidt, S.K., Nemergut, D.R., Darcy, J.L., Lynch, R., 2014. Do bacterial and fungal communities assemble differently during primary succession? Mol. Ecol. 23, 254–258.
Shade, A., Caporaso, J.G., Handelsman, J., Knight, R., Fierer, N., 2013. A meta-analysis of changes in bacterial and archaeal communities with time. ISME J. 7, 1493–1506.
Shen, C., Xiong, J., Zhang, H., Feng, Y., Lin, X., Li, X., Liang, W., Chu, H., 2013. Soil pH drives the spatial distribution of bacterial communities along elevation on Changbai Mountain. Soil Biol. Biochem. 57, 204–211.
Sun, S., Li, S., Avera, B.N., Strahm, B.D., Badgley, B.D., 2017. Soil bacterial and fungal communities show distinct recovery patterns during forest ecosystem restoration. Appl. Soil Ecol. 83.
Tian, J.Q., Qiao, Y.C., Wu, B., Chen, H., Li, W., Jiang, N., Zhang, X.L., Liu, X.Z., 2017. Ecological succession pattern of fungal community in soil along a Retreating Glacier. Front. Microbiol. 8, 13.
Tripathi, B.M., Stegen, J.C., Kim, M., Dong, K., Adams, J.M., Lee, Y.K., 2018. Soil pH mediates the balance between stochastic and deterministic assembly of bacteria. ISME J. 12, 1072–1083.
Urbanova, M., Snajdr, J., Baldrian, P., 2015. Composition of fungal and bacterial communities in forest litter and soil is largely determined by dominant trees. Soil Biol. Biochem. 84, 53–64.
Wagg, C., Bender, S.F., Widmer, F., van der Heijden, M.G.A., 2014. Soil biodiversity and soil community composition determine ecosystem multifunctionality. P. Natl. Acad. Sci. U. S. A. 111, 5266–5270.
Walker, L.R., Wardle, D.A., Bardgett, R.D., Clarkson, B.D., 2010. The use of chronosequences in studies of ecological succession and soil development. J. Ecol. 98, 725–736.
Wang, K.B., Ren, Z.P., Deng, L., Zhou, Z.C., Shangguan, Z.P., Shi, W.Y., Chen, Y.P., 2016. Profile distributions and controls of soil inorganic carbon along a 150-year natural vegetation restoration chronosequence. Soil Sci. Soc. Am. J. 80, 193–202.
Yang, Y., Wu, L., Lin, Q., Yuan, M., Xu, D., Yu, H., Hu, Y., Duan, J., Li, X., He, Z., Xue, K., van Nostrand, J., Wang, S., Zhou, J., 2013. Responses of the functional structure of soil microbial community to livestock grazing in the Tibetan alpine grassland. Glob. Change Biol. Bioenergy 19, 637–648.
Zeng, Q., An, S., Liu, Y., 2017. Soil bacterial community response to vegetation succession after fencing in the grassland of China. Sci. Total Environ. 609, 2–10.
Zhang, C., Liu, G., Xue, S., Wang, G., 2016. Soil bacterial community dynamics reflect changes in plant community and soil properties during the secondary succession of abandoned farmland in the Loess Plateau. Soil Biol. Biochem. 97, 40–49.
Zhang, K., Cheng, X., Shu, X., Liu, Y., Zhang, Q., 2018. Linking soil bacterial and fungal communities to vegetation succession following agricultural abandonment. Plant Soil 431, 19–36.
Zhang, N., Xiao, X., Pei, M., Liu, X., Liang, Y., 2017. Discordant temporal turnovers of sediment bacterial and eukaryotic communities in response to dredging: non-resilience and functional changes. Appl. Environ. Microb. 83.
Zhang, X., Xu, S., Li, C., Zhao, L., Feng, H., Yue, G., Ren, Z., Cheng, G., 2014. The soil carbon/nitrogen ratio and moisture affect microbial community structures in alkaline permafrost-affected soils with different vegetation types on the Tibetan plateau. Res. Microbiol. 165, 128–139.
Zhang, X.F., Zhao, L., Xu Jr., S.J., Liu, Y.Z., Liu, H.Y., Cheng, G.D., 2013. Soil moisture effect on bacterial and fungal community in Beilu River (Tibetan Plateau) permafrost soils with different vegetation types. J. Appl. Microbiol. 114, 1054–1065.
Zhang, Y.W., Shangguan, Z.P., 2016. The coupling interaction of soil water and organic carbon storage in the long vegetation restoration on the Loess Plateau. Ecol. Eng. 91, 574–581.
Zhao, Y.G., Liu, X.F., Wang, Z.L., Zhao, S.W., 2015. Soil organic carbon fractions and sequestration across a 150-yr secondary forest chronosequence on the Loess Plateau, China. Catena 133, 303–308.
Zhou, Z., Wang, C., Jiang, L., Luo, Y., 2017. Trends in soil microbial communities during secondary succession. Soil Biol. Biochem. 115, 92–99.
Zou, H.B., Liu, G.B., Wang, H.S., 2002. The vegetation development in North Ziwulin forest region in last fifty years. Xibei Zhiwu Xuebao 22, 1–8 (in Chinese with English abstract).