



Erosion-deposition positively reconstruct the bacterial community and negatively weaken the fungal community

Wanglin Hao^{a,b,c}, Bin Xia^{a,b}, Mingxiang Xu^{a,b,d,*}

^a State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, 712100 Yangling, Shaanxi, China

^b University of Chinese Academy of Sciences, 100190 Beijing, China

^c Department of Life Sciences, LyuLiang University, 033000 Lvliang, China

^d Institute of Soil and Water Conservation, Northwest A&F University, 712100 Yangling, Shaanxi, China

ARTICLE INFO

Keywords:

16s rRNA
ITS1
Erosion
Deposition
Diversity
Microbial communities

ABSTRACT

Soil erosion and deposition are general ecological processes that have been widely described in terms of their effects on the physical and chemical properties of soil. However, their effects on soil microbes remain unclear, especially how microbial communities respond to erosion–deposition in soils with different organic carbon levels. A long-term field experiment was conducted to examine the effects of erosion and deposition on soil microbial communities across full slopes with different organic carbon levels on the Loess Plateau of China. The results showed that erosion reduced soil bacterial alpha diversity, weakened bacterial network complexity while deposition increased bacterial alpha diversity, and enhanced the complexity of the bacterial network. However, both erosion and deposition caused a decrease in fungal alpha diversity and network complexity. There was a weak reverse cooperative covariation relationship between bacterial and fungal alpha diversity. There was a higher bacterial and fungal diversity at the eroded and depositional sites with high soil organic carbon (SOC) level than low and medium SOC levels. An increase in the SOC level effectively strengthened the network complexity of bacteria and fungi at the eroded and depositional sites. Erosion-deposition and SOC levels significantly increased variation in bacterial community structure. In contrast, the fungal community structure only differed at the eroded and depositional sites at high SOC levels. The key factors driving variation in bacterial community structure in soil properties were not significantly affected by SOC levels. Conversely, key factors resulting in differences in fungal community structure were regulated by the SOC level. Our results demonstrate that erosion–deposition reconstruct the bacterial community and weakens the fungal community, organic carbon regulate soil microbial communities and functions by controlling earth surface processes induced by erosion–deposition.

1. Introduction

Soil erosion, destruction, stripping, transportation, and displacement of soil from the location of its formation by external agents (e.g., raindrops, runoff, wind, gravity, etc.), and deposition at low-lying areas, is a universal natural geological phenomenon (Lal, 2003; Lal, 2020). Soil erosion depletes soil fertility, changes the particle size distribution, destroys the structure of soil aggregates, reduces the effective rooting depth, and destroys the most basic natural resources (Borrelli et al., 2018; Gu et al., 2018; Ouyang et al., 2018). Conversely, deposition at lying areas increases soil clay particles, accumulation of organic matter, and accumulation of soluble nutrients, which increase the amount of soil

cation substitution and soil water holding capacity (Berhe et al., 2007; Gu et al., 2018; Nadeu et al., 2012; Pacala et al., 2001). In sum, soil erosion–deposition is a selective process that is both directional and non-directional, resulting in a series of soil hydraulic, physical, and chemical properties, which have an important effect on the healthy ecological environment development.

Soil microorganisms, recognized as “Earth’s dark matter” (Jansson, 2013) and as important decomposers, are the most active part of the soil ecosystem. They participate in many key soil processes and terrestrial ecosystem services such as the formation and transformation of organic matter (Cortez and Bouché, 2001), development of soil physical properties (Gu et al., 2018), plant nutrition (Kuz'yakov et al., 2000; Singh

* Corresponding author at: 26 Xinong Road Yangling, Shaanxi 712100, China.
E-mail address: xumx@nwsuaf.edu.cn (M. Xu).

<https://doi.org/10.1016/j.catena.2022.106471>

Received 28 February 2022; Received in revised form 18 May 2022; Accepted 12 June 2022

Available online 20 June 2022

0341-8162/© 2022 Elsevier B.V. All rights reserved.

et al., 1989; Wagg et al., 2014), elemental geochemical cycles (Nielsen et al., 2011; Philippot et al., 2013; Veresoglou et al., 2015), primary production, and greenhouse gas emissions (Griffiths and Philippot, 2013; Smith et al., 2003). Soil microorganisms not only drive the formation and transformation of soil substances, but also link the interaction of pedosphere, atmosphere, lithosphere, hydrosphere, and biosphere, playing an irreplaceable role in the global material cycle and energy flow, and are considered the engine of the biogeochemical cycle of the elements of the earth (Gu et al., 2018; Philippot et al., 2013). Owing to their small individual sizes, strong diffusion ability, and extremely high diversity and individual abundance (Torsvik et al., 1990; Van Der Heijden et al., 2008), soil microorganisms are considered to be randomly distributed globally by the early researchers (Finlay, 2002; O'Malley, 2007). Increasing evidence shows that the composition and diversity of soil microbial communities vary with environmental variables, showing a regular spatial distribution (Fierer and Jackson, 2006; Shen et al., 2015). Therefore, exploring soil microbial diversity and community distribution is of great significance for the evaluation of soil ecosystem functions.

The structure and diversity of soil microbial communities provide insight into the elements circulation, energy flow, soil stability, and health assessment of the soil ecosystem (Jackson et al., 2003; Van Bruggen and Semenov, 2000; Wortman et al., 2013). They are widely affected by soil pH, texture, temperature, moisture, nutrient content, and organic carbon matrix (Brockett et al., 2012; Cookson et al., 2007; Hansel et al., 2008; Kallenbach et al., 2016). Erosion does not only cause a large amount of organic carbon migration and transformation, but also changes the physical and chemical properties of the soil and the hydrothermal environment (Berhe et al., 2007; Nadeu et al., 2012). This inevitably leads to the response of the soil microbial community structure, diversity of keystone taxa, and co-occurrence networks (Lauber et al., 2008; Rasche et al., 2011).

Soil degradation induced by soil erosion is often caused by the depletion of organic matter (Zhao et al., 2020). Organic carbon can improve the stability of soil aggregates (Peixoto et al., 2006), regulate soil chemical processes (Jia et al., 2014), maintain the metabolic activities of various organisms in the soil, and effectively inhibit soil erosion and other forms of soil degradation (Kaschuk et al., 2006; Pastorelli et al., 2013). Except for differences in climate and soil physical–chemical properties between regions, differences in soil are largely due to the background of organic carbon. Soil organic carbon is an important substrate required for soil microbial metabolism and plays a decisive role in the growth of microbial populations (Jiang et al., 2021; Stefanowicz et al., 2020). The decomposition of organic carbon and the efficiency of substrate utilization directly drive the diversity, structure, and co-occurrence network of microbial communities (Bonner et al., 2018; Borken and Matzner, 2009; Colman and Schimel, 2013; Davidson and Janssens, 2006).

Therefore, we hypothesized that erosion–deposition inducing changes of soil properties may significantly affect on the community structure of bacteria and fungi. Community structure will differ between bacteria and fungi owing to various response mechanisms. Furthermore, the backgrounds of soil organic carbon may affect the erosion–deposition process, change soil properties, and regulate the differentiation of microbial community structure. From 2011 to 2019, long-term experiments were established in slopes with different organic carbon levels. We measured a range of soil physical and chemical properties. After long-term erosion, we quantified the diversity, community composition, and co-occurrence network of bacteria and fungi using 16s rRNA and ITS1 amplicon sequencing. This study aimed to (1) explore effects of long-term erosion–deposition on bacterial and fungal community diversity, community composition, and co-occurrence network, (2) analyze the driving mechanism of soil properties changes induced by erosion–deposition on bacterial and fungal community structure, and (3) clear the regulation of organic carbon backgrounds in the differentiation of microbial communities under the influence of

erosion–deposition.

2. Methods

2.1. Experimental site and climatic conditions

Our study was conducted at the Ansai Soil and Water Conservation Test Station of the Chinese Academy of Sciences (108°11'–109°26'N, 36°31'–37°19' E), at the central area of the Loess Hilly Region, in the Shaanxi Province, China. The experimental site was located in the semi-arid monsoon climate zone at approximately 1371.9 m above sea level. The average annual air temperature of this area is 8.8 °C (the maximum temperature is 36.8 °C and the minimum temperature is –23.6 °C) with total annual precipitation of 540 mm, approximately 70% of which occurs from July to September. The regional soil mainly comprises loess soil developed on the loess parent material, and has poor resistance to erosion, thus becomes seriously eroded. The main types of soil erosion are rill and ephemeral gully erosion.

2.2. Plots and sampling

An “S” shaped slope was designed with a water-retaining weir at the foot of the slope in September 2011. The top, middle, and foot of the slope were divided into control, erosion, and deposition sites, and the slopes of them were approximately 5°, 20°, and 5°, respectively (Fig. 1). The erosion and deposition conditions of these three sites were determined according to the erosion needles placed at different parts of the slope. In order to reflect the various characteristics of microbial community on slopes with different soil quality backgrounds after long-term erosion in the actual situation of fertilization on slopes, 3 levels of soil organic carbon (3.03 g kg⁻¹, 6.82 g kg⁻¹, and 10.33 g kg⁻¹) were set by adding well-rotted goat manure, which is a widely used high-quality organic fertilizer on the Loess Plateau, with carbon content of 240–280 g kg⁻¹. There were six plots with a site of 4 m × 17 m (each plot had 3 microplots), including three SOC levels, each of which had two replicates. The plot was bare land with no vegetation cover to eliminate the influence of plant roots.

In October 2019, soil samples were collected from the 0 to 20 cm depth with a 5.0 cm diameter sterilized soil auger at the control site, erosion site, and depositional site of each plot, respectively. 25 samples were combined as 5 composite samples for each plot site. Each sample was divided into three parts after mixing, and a portion of the soil samples was placed in dry ice for amplicon sequencing. Another part was placed in a self-sealed bag in a low-temperature incubator and temporarily stored in a refrigerator at 4 °C for the measurement of soil microbial functional diversity. The remaining samples were air-dried for the measurement of physical and chemical properties.

2.3. Soil analyses

Soil temperature and moisture were measured by monitoring systems (EM50, Decagon Inc., USA) installed at the surface layer (0–20 cm) of different plots. The soil bulk density was measured using the cutting ring method. Soil particle composition was determined using a laser particle size analyzer (Mastersizer APA2000, Malvern Panalytical, UK). The soil particle composition was classified into clay (0.002 mm), silt (0.002–0.05 mm) and, sand (0.05–2.00 mm) based on particle size. The soil aggregates were determined using the improved Yoder wet screen method. Total nitrogen (TN) was measured using the Kjeldahl method. Total phosphorus (TP) was digested by H₂SO₄-HClO₄ and was measured using an ultraviolet–visible spectrophotometer (UV-2600, SHIMADZU Inc., JPN). Soil organic carbon (SOC) was determined using the potassium dichromate volumetric method. Soil pH was measured using a pH meter (PB-10, Sartorius Inc., UK) from a soil–water suspension at a dilution of 1:2.5 (vol/vol).

Soil microbial biomass carbon (SMBC) was analyzed by chloroform

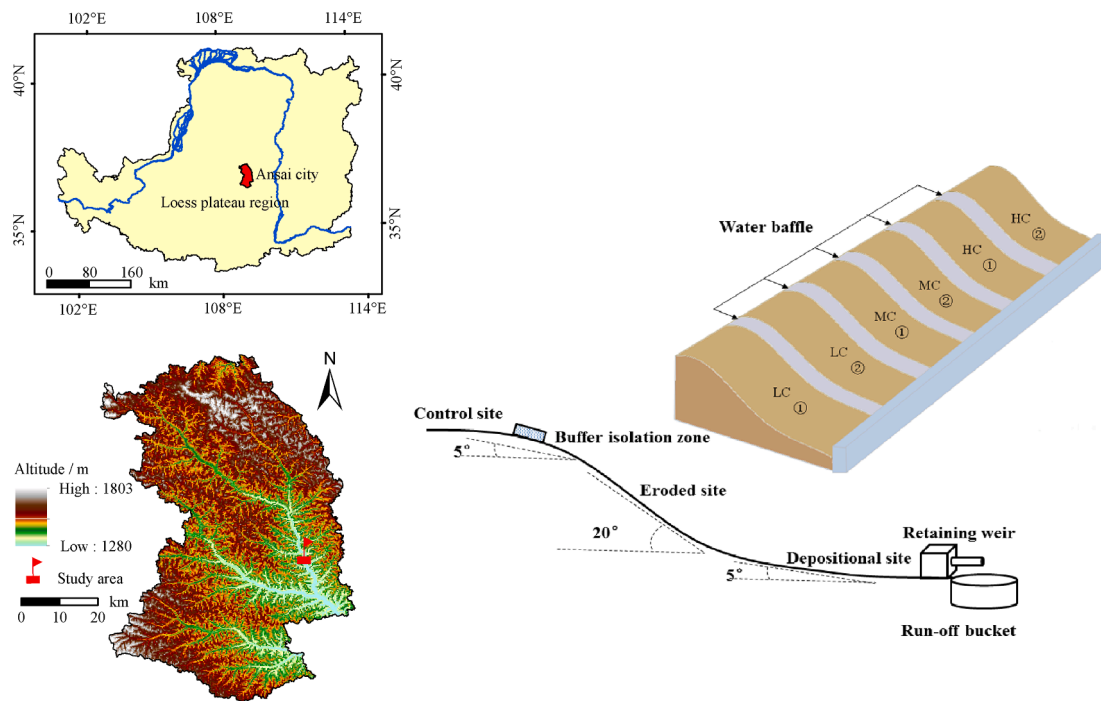


Fig. 1. The map of plot.

fumigation extraction method (Vance et al., 1987). The fresh soil was first placed in plastic jars, the soil water content was adjusted to about 17%, and the bottle mouth was sealed with plastic film containing micropores. Then these samples were cultivated at 25 °C for 7 days to eliminate the influence of water and temperature variations at sampling time on the measurement results of microbial biomass carbon. After the cultivation, 25 g fresh soil was fumigated with chloroform for 24 h, and then extracted with 0.5 M K₂SO₄ for 2 h on a shaker (185 rpm). The extracts were centrifuged and filtered (Whatman 42). Similar sets of non-fumigated sample were extracted the same way. Carbon concentration in the extracted solutions was measured by a TOC analyser (TOC-V wp, SHIMADZU Inc., JPN.). Microbial biomass carbon concentration was calculated following the method of Wu et al. (Wu et al., 1990):

$$SMBC = (F - C)/K_c$$

where *SMBC* is soil microbial biomass carbon, *F* and *C* is the carbon concentrations in the extracts of fumigated and non-fumigated soils respectively, and $K_c = 0.45$, which is the proportionality factor to convert (*F*–*C*) to *SMBC*.

Dissolved organic carbon (DOC) was extracted from 30 g of fresh soil with an addition of 60 ml of distilled water (Xu et al., 2010). The mixture was shaken for 30 min on a shaker (200 rpm) at 20 °C, centrifuged for 20 min at 3500 rpm and the supernatant liquid was filtered through 0.45 μm cellulose nitrate membrane filter. Dissolved organic carbon in extracts was measured by a TOC analyzer (TOC-V wp, SHIMADZU Inc., JPN.).

2.4. Amplicon sequencing

Soil microbial DNA was extracted from fresh soil (0.5 g) using a FastDNA SPIN kit (MP Bio-medicals, USA). The DNA concentration was evaluated using a Nanodrop ND-1000 spectrophotometer (Thermo Scientific, Wilmington, NC, USA). The quality of DNA was determined using 1.2 % agarose gel electrophoresis, and DNA was stored at –20 °C. Primers 338F and 806R (5'-ACTCTACGGGAGGCAGCAG-3' and 5'-GGACTACHVGGGTWTCTAAT-3') were used to amplify the V3–V4 hypervariable region of the 16S rRNA gene in bacteria (Mori et al., 2014).

The ITS rRNA gene in fungi was amplified using PCR primers ITS1F and ITS2R (5'-CTTGGTCATTTAGAGGAAGTAA-3' and 5'-GCTGCGTTCTTCATCGATGC-3') (Bazzicalupo et al., 2013). High-throughput sequencing of 16S rRNA and ITS rRNA genes in the soil samples was performed by Irun Biotechnology Co. Ltd. using the Illumina HiSeq2500 platform. The raw sequences obtained were subjected to quality control using the QIIME software. Operational taxonomic units (OTUs) were clustered at a similarity level of 97% (Edgar et al., 2011). Bacterial sequences and fungal sequences were taxonomically identified based on the Silva database (Quast et al., 2012) and the Unite database (Kõljalg et al., 2013) using the QIIME2. Alpha and beta diversity indices for bacteria and fungi were obtained using the QIIME2.

2.5. Statistical analyses

Correlation analysis and analysis of variance were performed using R version 4.0.2. Graphing analysis was performed using Origin 2021 software (Origin Lab, USA). Two-way analysis of variance was used to analyze the effects of SOC level and erosion on soil properties, considering treatment (SOC level and erosion site) as the fixed effect, replication as the random effect, and time of measurement as the repeated measure variable. Means were separated using the least significant difference test.

Structural equation models (SEMs) were analyzed using AMOS 25 graphics (IBM Corp., Armonk, NY, USA). All of these factors were used to quantify the direct and indirect factors driving microbial diversity. In general, we established a base model based on correlation analyses between the forcing variables, response variables, and empirical knowledge. We then optimized the base model according to the actual model fits, including the chi-square (χ^2) statistic, whole-model *p*-value, goodness of fit index (GFI), and root-mean-square error of approximation (RMSEA). Significant effects were determined at $p < 0.05$, and $p < 0.01$, unless otherwise stated.

The relationships between the relative abundances of major microbial phyla and soil properties were analyzed using Pearson correlations. Based on pairwise Bray-Curtis and Unifrac dissimilarities, nonmetric multidimensional scaling (NMDS) was performed using “metaMDS” in the vegan package (R version 4.0.2) was used to identify variations in

soil microbial communities across different erosion sites and SOC levels. Redundancy analysis (RDA) was conducted using “rda” in the vegan package to analyze the relationships between soil microbial communities and soil properties.

Co-occurrence networks were built for bacterial and fungal communities at different erosion sites and SOC levels. OTUs with relative abundance >0.1% (bacteria) and >0.0% (fungi) in all samples were selected. Spearman correlation coefficients (ρ) > 0.6 and p -values < 0.05, were used to construct co-occurrence networks, and the p -values were adjusted using the Benjamini-Hochberg method. Various indicators (the number of nodes and edges, modularity, clustering coefficient, average path length, network diameter, average degree, and graph density) were calculated to describe the overall network topology characteristics. Statistical analysis and visualization of the networks of different erosion sites and SOC levels were performed using Gephi (Bastian et al., 2009). We also used vulnerability to describe the stability of the network (Yuan et al., 2021). The vulnerability of a network was indicated by the maximum vulnerability of nodes in the network.

3. Results

3.1. Erosion events and soil properties

The average annual rainfall in the study area was approximately 558 mm, and erosion events occurred approximately 18 times at different SOC levels. The average erosion rate ranged from 5670 to 6256 t km⁻² yr⁻¹, and the average deposition rate ranged from -2964 to -3408 t km⁻² yr⁻¹. As the SOC level increases, the erosion rate decreases at eroded sites but increases at depositional sites (Table 1).

Soil moisture, bulk density (BD), sand, TN, TP, SOC, SMBC, and DOC at the eroded sites were significantly lower than those at the non-eroded sites, while they were higher at the depositional sites than at the non-eroded sites ($p < 0.05$, Table 2). The soil clay, silt, mean weight diameter (MWD) of aggregates, and pH value at the eroded sites were higher than those at the non-eroded sites, but were lower at the depositional sites than at the non-eroded sites ($p < 0.05$, Table 2). The effect of erosion deposition on soil temperature was not significant ($p > 0.05$, Table 2). With the increase in SOC level, soil moisture, MWD, BD, and soil nutrients (SOC, TN, TP, SMBC, and DOC) content increased significantly, pH decreased significantly, and soil particle composition improved significantly (Table 2).

Table 1
Erosion and deposition occurrence at different plots under three SOC levels in 2011–2019.

| year | Rainfall (mm) | Erosion event | SOC level | Experiment site | Erosion modulus (t km ⁻² yr ⁻¹) |
|-------------------|-----------------------|--------------------------|-----------|-----------------------|--|
| 2011 ~ 2019 | 391 ~ 959 (558) | 14 ~ 24 (18) | LC | Non-eroded sites (CK) | — |
| | | | | Eroded sites (E) | 3328 ~ 9384 (6256) |
| | | | | Depositional sites(D) | -2074 ~ -4446 (-2964) |
| | | | MC | Non-eroded sites (CK) | — |
| | | | | Eroded sites (E) | 3678 ~ 9208 (6130) |
| | | | | Depositional sites(D) | -2144 ~ -5056 (-3064) |
| HC | Non-eroded sites (CK) | — | | | |
| | Eroded sites (E) | 2182 ~ 8806 (5670) | | | |
| | Depositional sites(D) | -2088 ~ -5548 (-3408) | | | |

Positive values indicate erosion and negative values indicate deposition.

3.2. Soil microbial composition

We obtained high-quality sequences from the 16 rRNA and ITS1 gene sequencing in all soil samples (bacteria: 90.6% of total sequences; fungi: 90.7% of total sequences). An average of 6,628 OTUs were identified in bacterial sequences for each sample (Fig. S1a), and all detected OTUs were classified into 33 bacterial phyla. The most abundant phyla in each sample were Proteobacteria, Actinobacteria, Acidobacteria, and Chloroflexi, accounting for approximately 82.34% of all bacteria, and other phyla were Gemmatimonadetes, Bacteroidetes, Cyanobacteria, Verrucomicrobia, Patascibacteria, and Armatimonadetes (Fig. 2a). An average of 355 OTUs were identified in fungal sequences for each sample (Fig. S1b). All detected OTUs were classified into 12 fungal phyla; the most abundant phyla in each sample were Ascomycota and Basidiomycota, accounting for approximately 86.67% of all fungi (Fig. 2a), and the others were Mortierellomycota, Glomeromycota, and Chytridiomycota (Fig. 2b). In the bacterial phyla, erosion–deposition significantly affected the abundance of Actinobacteria, Acidobacteria, Patascibacteria, and Armatimonadetes. Except for Acidobacteria and Cyanobacteria, SOC levels had a significant effect on the other eight dominant bacterial phyla, but the interaction effect of SOC levels and erosion site was not significant (Table S1). In the fungal phyla, erosion–deposition significantly affected Ascomycota and Basidiomycota, and SOC levels significantly affected Ascomycota and Glomeromycota. The interaction effect of SOC level and erosion site was not significant (Table S2). Differences in bacteria and fungi at various erosion sites and SOC levels are shown in Figs. S2 and S3.

Correlations between soil properties and relative abundances of dominant bacterial and fungal phyla are shown in Figs. S4 and S5. In terms of erosion sites, the relative abundance of Proteobacteria had a significant positive correlation with MWD, SOC, and TN at the three different erosion sites ($p < 0.05$). The relative abundance of Actinobacteria was significantly negatively correlated with BD, MWD, SOC, TN, SMBC, and DOC at three different erosion sites ($p < 0.05$), while the relative abundance of Actinobacteria and Chloroflexi at the depositional site, and Acidobacteria at the erosion site were significantly positively correlated with soil moisture, while the relative abundance of Proteobacteria at the eroded and depositional sites was significantly negatively correlated with soil moisture ($p < 0.05$, Fig. S4). There was a significant positive correlation between the relative abundance of Ascomycota and soil moisture at the erosion sites ($p < 0.05$, Fig. S5). In terms of SOC levels, the relative abundance of Proteobacteria at the middle SOC level was significantly positively correlated with BD, and significantly negatively correlated with MWD ($p < 0.05$), while the relative abundance of Actinobacteria at low SOC levels was significantly negatively correlated with moisture, BD, SOC, and TN, and the relative abundance of Acidobacteria at high SOC levels were significantly negatively correlated with soil moisture ($p < 0.05$, Fig. S4). The relative abundance of Basidiomycota at the middle SOC level was significantly positively correlated with soil temperature ($p < 0.05$, Fig. S5).

3.3. Soil microbial diversity

The Shannon index was used to evaluate the alpha diversity of the microbial communities (Fig. 3, Table S3). Bacterial alpha diversity was not significantly different between the erosion sites, but there were significant differences between the different SOC levels ($p < 0.05$, Table S3). At each SOC level, the Shannon index of bacteria was higher at the depositional site than at the non-eroded site, while it was lower at the eroded site than at the non-eroded site. At the same erosion site, an increase in SOC level increased the Shannon index of bacteria (Fig. 3a). Fungal alpha diversity was not only significantly affected by the erosion sites, but was also significantly regulated by SOC levels ($p < 0.05$, Table S3). At each SOC level, the fungal Shannon index was higher at the non-eroded site than at the eroded and depositional sites. At the same erosion site, the fungal Shannon index was higher at high SOC levels, but

Table 2
Soil properties on various of experiment sites with different SOC levels.

| SOC level | Experiment site | T °C | M % (V/V) | BD g cm ⁻³ | Clay % | Silt % | Sand % | MWD mm | SOC g kg ⁻¹ | TN g kg ⁻¹ | TP g kg ⁻¹ | SMBC mg kg ⁻¹ | DOC mg kg ⁻¹ | pH |
|-----------|-----------------|-----------------|----------------|-----------------------|-----------------|----------------|-----------------|----------------|------------------------|-----------------------|-----------------------|--------------------------|-------------------------|---------------|
| LC | CK | 21.42 ± 1.39Aab | 6.64 ± 0.40Bb | 1.16 ± 0.03Bc | 11.68 ± 0.57ABa | 57.51 ± 0.72Aa | 30.81 ± 1.28Ba | 1.04 ± 0.22ABb | 2.94 ± 0.21Bc | 0.33 ± 0.02Bc | 0.54 ± 0.01Ba | 81.17 ± 14.26Bc | 162.43 ± 16.53Bc | 8.69 ± 0.03Aa |
| | | 22.07 ± 0.88Aab | 6.23 ± 0.24Bb | 1.05 ± 0.09Cc | 12.62 ± 0.47Aa | 60.78 ± 1.28Ab | 26.59 ± 1.75Bb | 1.20 ± 0.11Ac | 2.70 ± 0.34Cc | 0.32 ± 0.02Cc | 0.55 ± 0.04Aa | 78.86 ± 10.40Bc | 157.75 ± 13.60Bc | 8.63 ± 0.02Bb |
| | D | 20.81 ± 0.93Aa | 7.32 ± 0.31Aa | 1.28 ± 0.05Aa | 11.33 ± 0.34Bb | 58.14 ± 1.48Ab | 30.53 ± 1.82Cc | 0.77 ± 0.08Bc | 3.59 ± 0.32Ac | 0.35 ± 0.01Ac | 0.55 ± 0.01Aa | 94.27 ± 4.97Ac | 188.51 ± 14.72Ac | 8.59 ± 0.02Cb |
| MC | CK | 23.28 ± 1.30Aa | 6.82 ± 0.37Bab | 1.23 ± 0.01Bb | 11.47 ± 0.89Bab | 58.29 ± 0.90Aa | 30.24 ± 1.78Ba | 1.21 ± 0.08Aa | 4.68 ± 0.10Bb | 0.45 ± 0.07Ab | 0.55 ± 0.00Ba | 85.54 ± 3.54Bb | 171.08 ± 7.09Bb | 8.60 ± 0.06Bc |
| | | 23.05 ± 0.82Aa | 6.69 ± 0.25Ba | 1.16 ± 0.04Cb | 11.41 ± 0.43Ba | 60.92 ± 0.43Aa | 27.67 ± 0.86Bab | 1.27 ± 0.28Ab | 4.29 ± 0.59Cb | 0.42 ± 0.10Bb | 0.54 ± 0.01Ca | 84.38 ± 5.60Bb | 168.79 ± 6.40Bb | 8.64 ± 0.04Aa |
| | D | 21.58 ± 1.02Aa | 7.69 ± 0.32Aa | 1.27 ± 0.04Aa | 9.99 ± 0.55Bb | 57.33 ± 1.18Ab | 32.68 ± 1.72Cb | 0.93 ± 0.02Bb | 5.49 ± 0.49Ab | 0.47 ± 0.01Ab | 0.57 ± 0.00Aa | 98.30 ± 11.19Ab | 196.61 ± 19.99Ab | 8.61 ± 0.05Ba |
| HC | CK | 17.57 ± 1.51Ab | 6.83 ± 0.40Ba | 1.28 ± 0.02Aa | 10.08 ± 0.21Ab | 56.82 ± 0.14Bb | 33.10 ± 0.11Ab | 1.25 ± 0.14Ba | 6.51 ± 0.62Ba | 0.50 ± 0.01Ba | 0.54 ± 0.01Ba | 116.19 ± 6.19Ba | 249.03 ± 18.78Ba | 8.63 ± 0.02Bb |
| | | 19.81 ± 1.01Ab | 6.80 ± 0.27Ba | 1.19 ± 0.03Ba | 11.17 ± 0.09Bb | 59.25 ± 0.39Cb | 29.58 ± 0.30Ab | 1.33 ± 0.16Aa | 5.45 ± 0.21Ca | 0.47 ± 0.02Ca | 0.59 ± 0.02Aa | 104.52 ± 9.39Ca | 232.38 ± 12.39Ca | 8.64 ± 0.01Aa |
| | D | 16.80 ± 1.05Ab | 8.20 ± 0.39Aa | 1.28 ± 0.03Aa | 8.80 ± 0.02Ba | 55.84 ± 0.18Ca | 35.36 ± 0.21Aa | 1.13 ± 0.19Ca | 7.81 ± 0.42Aa | 0.55 ± 0.01Aa | 0.59 ± 0.00Aa | 140.52 ± 19.69Aa | 281.16 ± 19.76Aa | 8.52 ± 0.04Cc |
| F | Cl | 18.09 | 3.35 | 414.20 | 1561.58 | 729.60 | 398.11 | 210.36 | 9768.07 | 1676.73 | 310.47 | 5364.62 | 1533.74 | 113.77 |
| | ES | 2.95 | 23.00 | 1204.65 | 1321.06 | 1516.41 | 1575.85 | 420.07 | 1767.87 | 146.58 | 260.16 | 879.96 | 530.72 | 459.61 |
| P | Cl × ES | 0.51 | 0.67 | 103.22 | 111.09 | 51.10 | 37.27 | 20.67 | 159.19 | 11.83 | 107.93 | 27.91 | 52.04 | 160.34 |
| | ES | <0.001 | 0.0354 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |
| R2 | Cl × ES | 0.0529 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |
| | ES | 0.7305 | 0.6115 | 0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |
| RMSE | | 0.13 | 0.14 | 0.74 | 0.83 | 0.78 | 0.76 | 0.52 | 0.95 | 0.74 | 0.55 | 0.91 | 0.77 | 0.58 |
| | | 10.59 | 3.52 | 0.04 | 0.49 | 1.34 | 0.91 | 0.17 | 0.37 | 0.04 | 0.02 | 13.17 | 10.29 | 0.04 |

CK non-erosion, E erosion, D deposition, T temperature, M moisture, BD bulk density, MWD mean weight diameter of soil aggregates, SOC soil organic carbon, TN total nitrogen, TP total phosphorous, SMBC soil microbial biomass carbon, DOC dissolved organic carbon, Cl organic carbon levels, ES experiment site. Capital letters are significant between different sites of slopes with the same SOC level ($P < 0.05$), and lowercase letters are significant between the same site of slopes with different SOC level ($P < 0.05$).

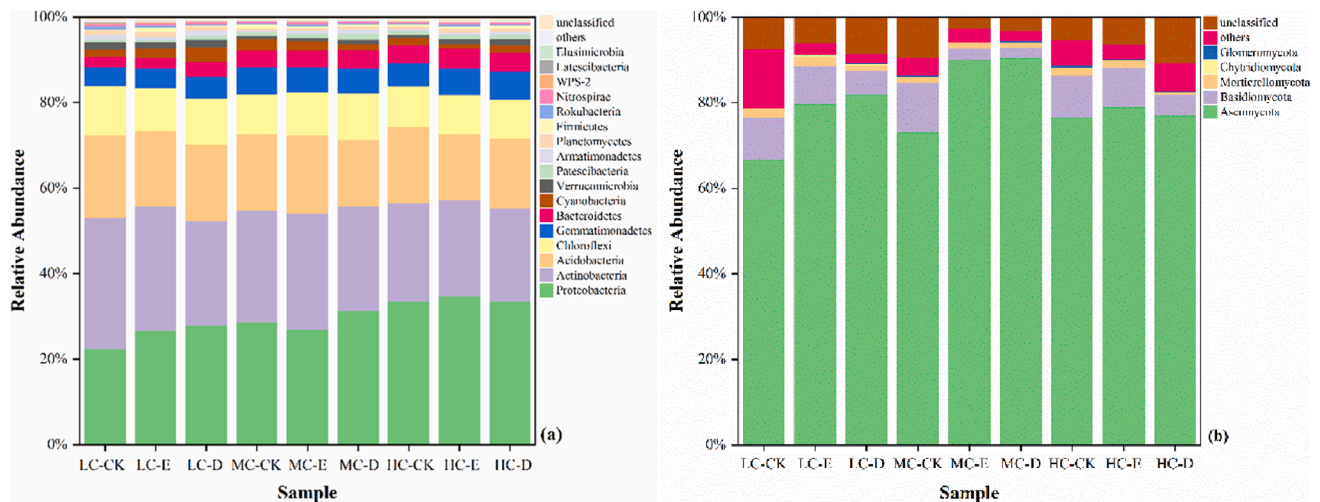


Fig. 2. The relative abundance of bacteria (a) and fungi (b) at phylum level in soils on various sites of slopes with different SOC levels. LC: low SOC level; MC: middle SOC level; HC: high SOC level; CK: non-eroded sites (control sites); E: eroded sites; D: depositional sites.

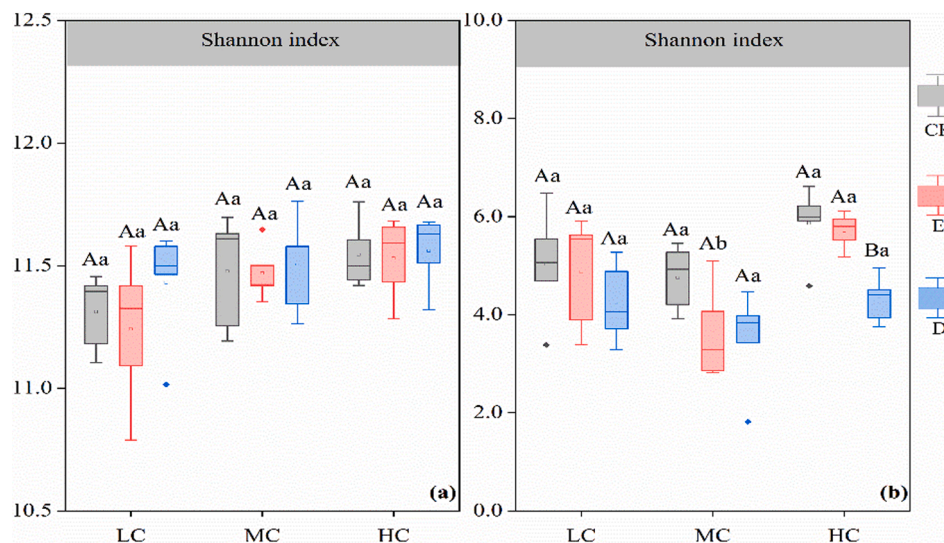


Fig. 3. Alpha diversity of soil bacteria (a) and fungi (b) as affected by soil erosion on various sites of slopes with different SOC levels. Box lines are the maximum and minimum values, respectively. The hollow square represents mean of alpha diversity index. Capital letters are significant between different sites of slopes with the same SOC level ($P < 0.05$), and lowercase letters are significant between the same site of slopes with different SOC level ($P < 0.05$).

lower at low SOC levels than at the middle SOC level. The rate of change (ROC) was used to measure the change in bacterial and fungal Shannon indices with SOC levels (Fig. S6). With the increase in SOC level, the ROC of bacteria at the eroded site presented a decreasing trend, and the rate became increasingly slower. The ROC of bacteria at the depositional site showed an increasing trend, and the rate of increase gradually slowed down. However, regardless of the eroded and depositional sites, the ROC of fungi showed a decreasing trend with an increase in SOC level.

We used a structural equation model (SEM) to analyze the direct and indirect effects of soil properties on soil bacterial and fungal diversity caused by erosion–deposition and SOC levels (Fig. 4). We incorporated the most relevant soil property variables into the structural equation model and obtained the optimal model (Chi-square:2.962, $p = 0.479$, GFI = 0.998, RMSEA = 0.000) by constructing the initial model, checking model, and correction model. Erosion-deposition and SOC levels had direct or indirect effects on bacterial alpha diversity through moisture, MWD, TN, pH, and TP, while erosion–deposition and SOC levels directly or indirectly affected fungal alpha diversity through

moisture, MWD, TN, and pH. The diversity of bacteria and fungi presented a reverse cooperative covariation relationship, which together caused changes in soil microbial biomass carbon.

3.4. Soil bacterial community structure

NMDS was used to evaluate the differences in bacterial and fungal community structures, and the results were reliable (Stress < 0.2, Fig. 5). At the three SOC levels, the bacterial community structure at the control check site, eroded site, and depositional site were diverse, while the fungal community structure of the erosion sites was different at high SOC levels compared with low and medium SOC levels (Fig. 5). ANOSIM showed that there were distinct differences in bacterial communities at different SOC levels and erosion sites ($p < 0.05$, Table S4). There was no obvious difference in the fungal community structure at each part of the erosion sites at low SOC levels. At high SOC levels, the fungal community structure at the control site was similar to that at the eroded site, but all of them significantly differed from that at the eroded site ($p < 0.05$, Table S4).

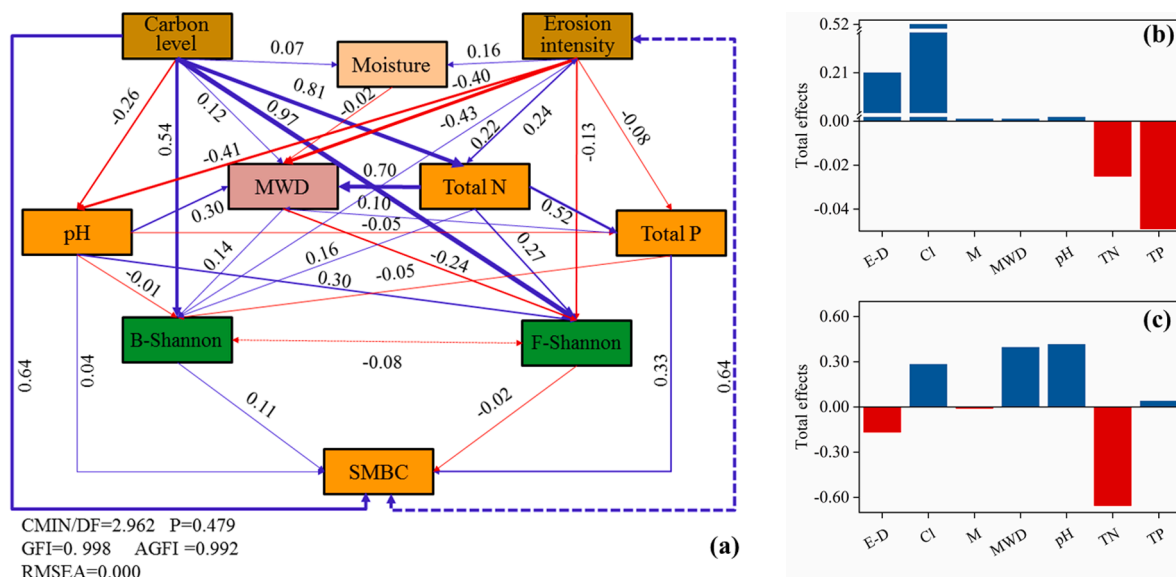


Fig. 4. Effects of soil properties on soil bacterial and fungal diversity in different site under three carbon levels. SEM analyzes effects of moisture, MWD, soil pH value, total nitrogen, total phosphorous, soil microbial biomass carbon on bacterial and fungal diversity (a). Blue and red lines indicate significant positive and negative effects, respectively. The numbers adjacent to the arrows are path directions and coefficients, while the width of the arrows is proportional to the strength of the path coefficients. The dotted line represents the covariant relationship between variables. The bar chart (b), (c) present the total effect of soil properties on soil bacteria and fungi diversity, respectively.

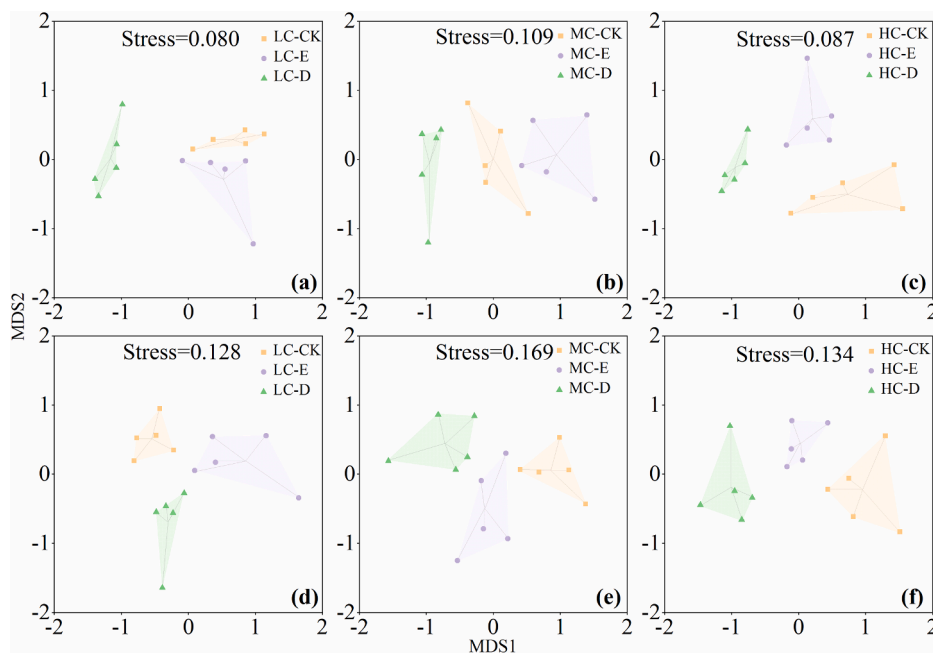


Fig. 5. NMDS of soil bacterial (a, b, c) and fungal (d, e, f) communities across three different sites at three SOC levels based on Bray-Curtis distances.

RDA revealed that MSTR, MWD, Cy, and SOC were the main environmental predictors affecting bacterial community structure (Fig. 6a, b, and c), explaining 32.25%, 32.43%, and 34.94% of the community variation at the low, middle, and high SOC levels, respectively. TEMP, MSTR, MWD, BD, Caly, SOC, TN, TP, and pH were considered as the main environmental predictors controlling fungal community structure (Fig. 6d, e, and f). The process of soil properties affecting fungal communities at different erosion sites was restricted by SOC levels, and crucial controlling factors were converted at low, middle, and high SOC levels.

3.5. Soil microbial co-occurrence network complexity

Bacterial and fungal co-occurrence networks were constructed for different erosion sites and SOC levels (Figs. 7, 8, and 9). The nodes and edges of the bacterial networks for different erosion sites and SOC levels are shown in Table S5. Network analysis identified Actinobacteria, Proteobacteria, Acidobacteria, and Chloroflexi as keystone OTUs at different erosion sites and SOC levels (Fig. 7). Actinobacteria and Acidobacteria were more connected at the eroded site, and Proteobacteria and Chloroflexi had many connections at the depositional site (Fig. 9a). Actinobacteria, Acidobacteria, and Chloroflexi were more connected at low and middle SOC levels, and Proteobacteria were more

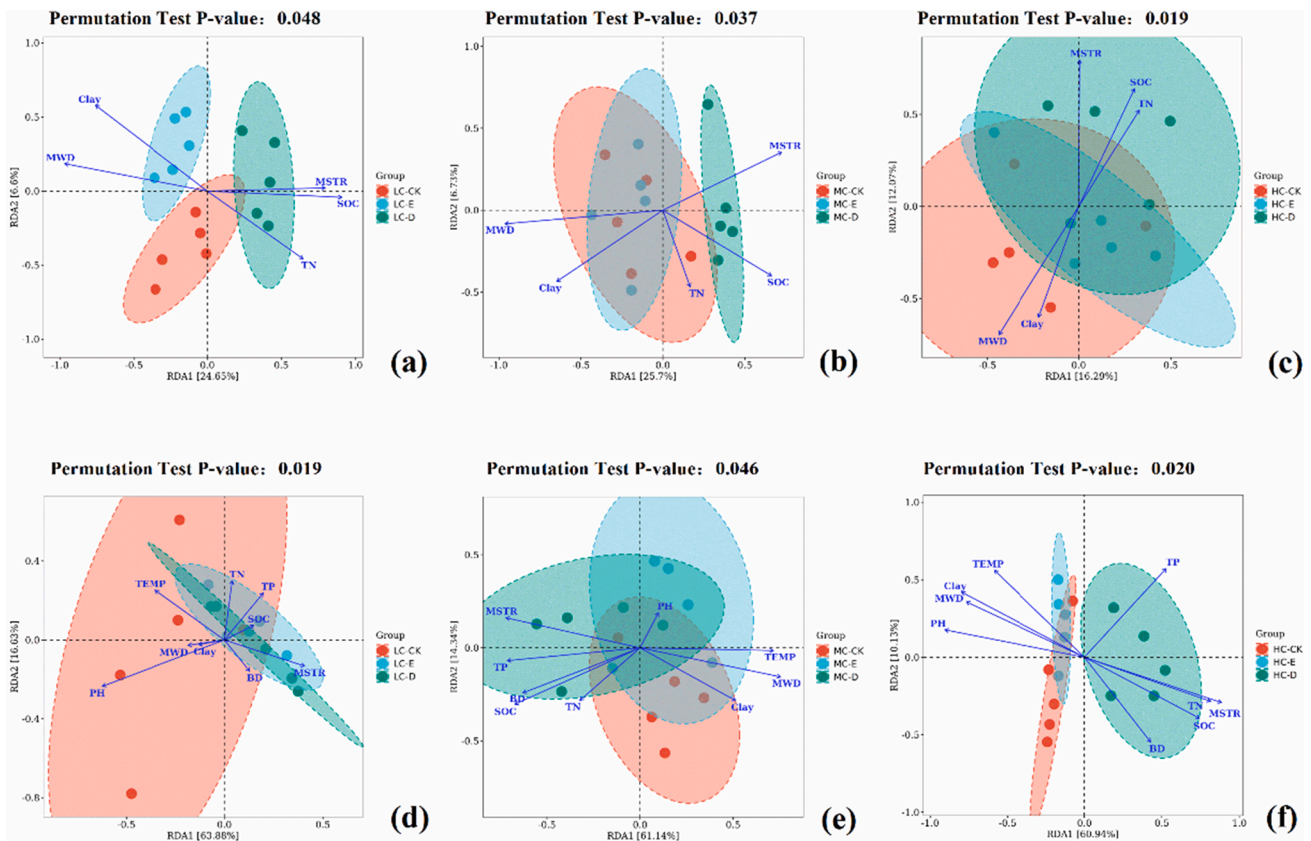


Fig. 6. The redundancy analysis (RDA) of soil bacterial (a, b, c) and fungal (d, e, f) communities across three sites at three SOC levels. RDA identify relationships of the relative abundance of dominant bacteria and fungal phylum to soil properties. MSTR: soil moisture; TEMP: temperature; pH: soil pH value; SOC: soil organic carbon; TN: total nitrogen; TP: total phosphorous; SMBC: soil microbial biomass carbon; BD: soil bulk density; MWD: mean weight diameter of soil aggregates; Clay: Soil clay content.

connected at high SOC levels (Fig. 9b). The nodes and edges of the fungal networks for different erosion sites and SOC levels are shown in Table S6. Ascomycota and Basidiomycota were considered keystone OTUs at different erosion sites and SOC levels (Fig. 8). Ascomycota and Basidiomycota were more connected at the eroded site and high SOC levels (Fig. 9c, d).

The network topological characteristics of bacteria and fungi are shown in Tables S5 and S6. The modularity of the bacterial network at the control check, eroded, and depositional sites were 0.271, 0.371, and 0.240, respectively; the modularity bacterial networks at low, middle, and high SOC levels were 0.313, 0.222, and 0.139, respectively (Table S5). This indicates that more functional communities were present at the depositional site than at the eroded and control check sites. We also found that as SOC levels increased, more communities that are functional increased in the bacterial networks. The bacterial network vulnerability was also on average lower in depositional sites (0.135) and higher in eroded sites (0.162) than in control sites (0.143) and decreased with increase of SOC level (Table S5). The modularity of the fungal network at the control, eroded, and depositional sites were 0.444, 0.663, and 0.661, respectively, and they were 0.830, 0.740, and 0.504, at low, middle, and high SOC levels, respectively. Erosion-deposition reduced the functional communities of the fungal network, and an increase in SOC level promoted functional communities in the fungal network (Table S6). The fungal network vulnerability was on average higher in depositional sites (0.201) and eroded sites (0.195) than in control sites (0.181) and decreased with increase of SOC level (Table S6).

4. Discussion

4.1. Changes in soil properties induced by erosion–deposition and SOC levels

In this study, erosion caused an uneven distribution of soil moisture, but it did not have a significant effect on soil temperature. This was because that erosion caused an uneven distribution of soil aggregate structure, capillary number, and porosity, resulting in significant differences in soil moisture at each erosion site (Soinnie et al., 2016; Wang et al., 2014). Although changes in soil structure caused by erosion led to changes in thermal conductivity, resulting in changes of temperature, changes of temperature at soil-air interface may be further weakened with the increase of soil layer. Therefore, temperature in our test layer did not have a significant response to erosion. However, soil organic carbon did not only significantly affect soil moisture at the eroded and depositional sites, but also affected the variation characteristics of soil temperature. This was because that, with the increase of soil organic carbon content, soil aggregate structure increased, distribution of soil porosity evened out, number of capillaries increased, capacity of water absorption and holding improved, and soil moisture also increased (Adhikari and Bhattacharyya, 2015; Carrizo et al., 2015; Zinn et al., 2011). The change in moisture may affect the soil thermal conductivity, which indirectly leads to local differences in soil temperature.

Erosion stripped off the topsoil, and the spatial distribution pattern of soil porosity and aggregate structure was reset, resulting in a decrease in the bulk density at the eroded site. (Jankauskas et al., 2008). The bulk density at the sedimentary site increased due to the accumulation of fine soil and reconstruction of the soil texture (Morvan et al., 2018). The aggregates were destroyed during the entire erosion process, and the

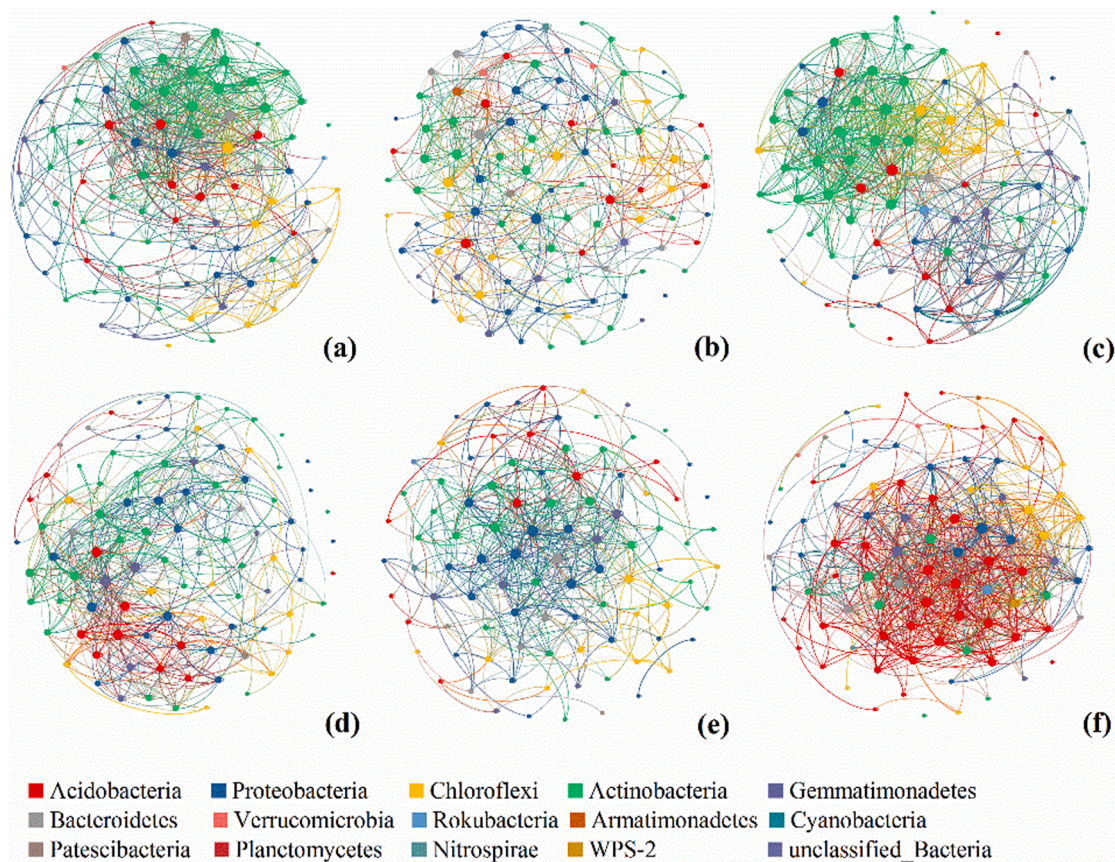


Fig. 7. Bacterial co-occurrence networks of non-eroded sites (a), eroded sites (b), depositional sites (c), low SOC level (d), middle SOC level (e), high SOC level (f). A connection denotes a significant correlation (Spearman's $\rho > 0.6$, $P < 0.05$), and a node represents an operational taxonomic unit (97% sequence identify threshold, ASV/OTU) in the sample. The size of each node is directly proportional to the degree of connectivity, and the thickness of connection between two nodes is directly proportional to the values of Spearman's correlation coefficient.

stability of the aggregates accumulated at the depositional site was weakened (Xu et al., 2016). Therefore, the average weight diameter of aggregates at the eroded site was higher than that at the control site, whereas it was lower at the depositional site ($p < 0.05$). The soil particle composition at the eroded site was significantly different from that at the depositional site. This is due to the classification of soil particles during the erosion–deposition process. (Xu et al., 2016). To a large degree, the level of SOC directly determines the pattern of soil bulk density and stability of soil aggregates (Zinn et al., 2011). When eroded soil particles are destroyed and transported by erosion, soil nutrients are lost along with the migration of soil particles, and are buried along with silt deposition (Borrelli et al., 2018; Gu et al., 2018; Pacala et al., 2001). As a result, TN, TP, SOC, SMBC, and DOC at the eroded site were significantly lower than those at the control site were, while they were higher at the depositional site ($p < 0.05$). The process of migration, deposition, and the increase in organic carbon levels may cause a decrease in soil pH. This is because the loss of soil mineral nutrients caused by erosion will increase the relative concentration of soil acid-causing ions, which in turn promotes a decrease in soil pH (Bezdicke et al., 2003; Jarasiunas and Kinderiene, 2016).

Therefore, damage, transportation, migration, and redistribution of the topsoil caused by erosion will directly lead to topsoil decay (Zhang et al., 2004), drastic changes in the hydrothermal environment (Starr et al., 2000), topsoil nutrient loss (Borrelli et al., 2018), and directional and nondirectional changes in soil properties (Lal, 1998), which in turn causes soil quality degradation. In the deposition process, the transported and migrated soil fine particles were accumulated, the topsoil structure was rebuilt, and the nutrients lost due to erosion were intercepted and buried, which would make more available nutrients stored at

the depositional site. This series of processes promoted the formation of two environments where the soil texture was “reconstructed” and the nutrient “rich and poor” differed at the eroded and depositional sites. Moreover, the SOC background regulated the formation of these two environments.

4.2. Responses of soil microbial community characteristics to erosion–deposition and SOC levels

The sensitivity of soil microbes to disturbances is different, and may exhibit resistance, resilience, and “functional redundancy” effects to disturbances (García-Palacios et al., 2018). In this study, erosion caused a decrease in bacterial and fungal alpha diversity. This was because of the continuous stripping of the topsoil layer, destruction of soil aggregate structure, reduction in soil moisture, and entrainment of nutrients by the sediment during the erosion processes (Table 2). The reduced substrate that is required for microbial life activities and the habitat of bacteria and fungi was severely affected and became barren. Changes in habitats and loss of niches have been shown to reduce the diversity of fungi and bacteria (Bahram et al., 2018; Zhang et al., 2018). Although bacteria and fungi respond differently to the environment, long-term erosion has produced a negative response to the diversity of bacteria and fungi. The fine particles of topsoil transported and stripped by erosion were intercepted and buried in low-lying areas, and soil moisture increased at the depositional sites (Table 2). Under the influence of the water-activated aggregate structure (Wang et al., 2018), the availability of enriched nutrients increased, bacteria proliferated rapidly, both types and numbers improved, and the bacterial diversity increased (Tiemann and Billings, 2011). The composition of the fungal community

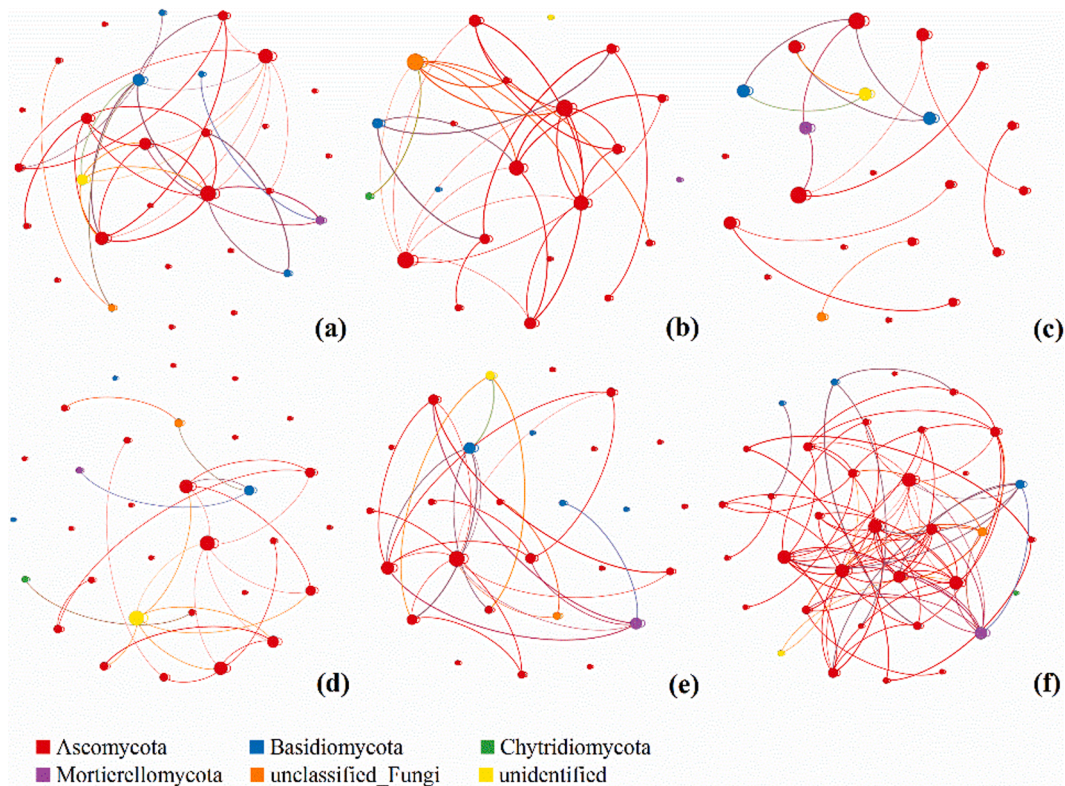


Fig. 8. Fungal co-occurrence networks of non-eroded sites (a), eroded sites (b), depositional sites (c), low SOC level (d), middle SOC level (e), high SOC level (f). A connection denotes a significant correlation (Spearman’s $\rho > 0.6$, $P < 0.05$), and a node represents an operational taxonomic unit (97% sequence identify threshold, ASV/OTU) in the sample. The size of each node is directly proportional to the degree of connectivity, and the thickness of connection between two nodes is directly proportional to the values of Spearman’s correlation coefficient.

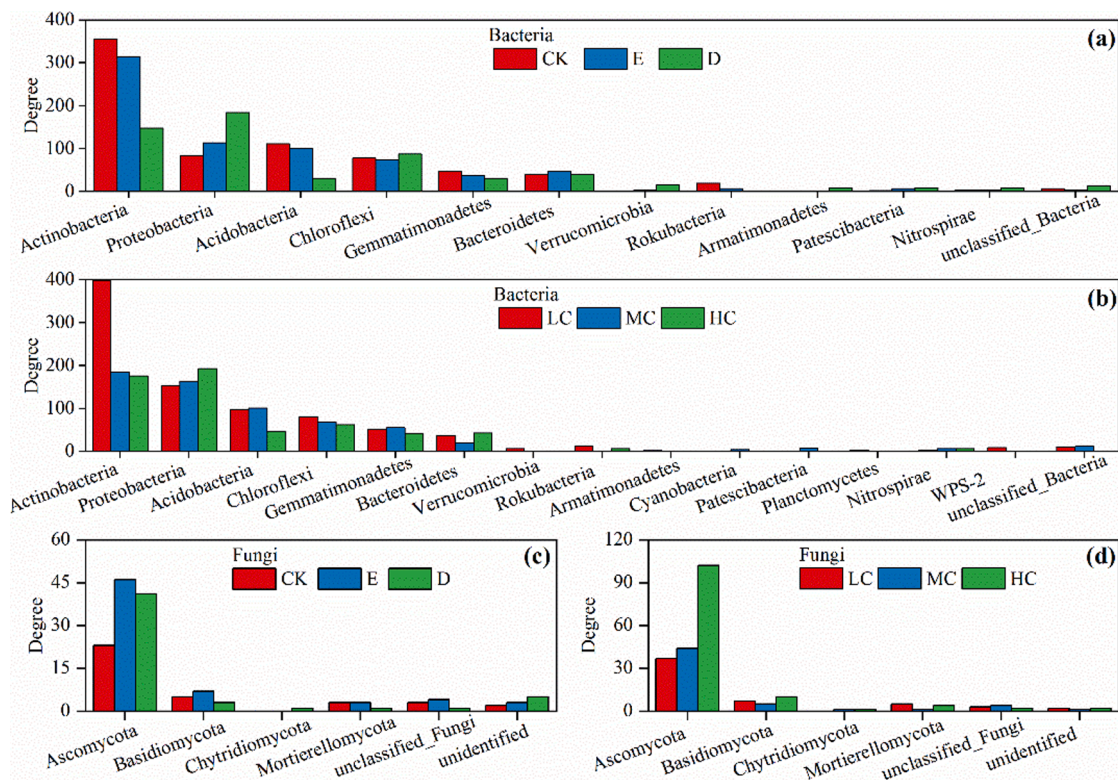


Fig. 9. The effects of experiment sites and SOC levels on the distribution of degree of connectivity at the taxonomic level of bacterial (a, b) and fungal (c, d) phylum.

was more dependent on habitat availability, and continuous deposition may result in the attenuation of habitat effectiveness, which is not conducive to the colonization of scattered spores and propagules (Kasel et al., 2008). In addition, fungi have strong water tolerance and high evolutionary levels (De Vries et al., 2018; De Vries et al., 2012), which means that, in the process of long-term habitat destruction, the recovery ability and mechanism of fungi were far behind bacteria, and fungal communities did not return to their original state or even flourish after the environmental reconstruction. This also confirmed the “retention effect” of the soil environment on the fungal community. Once destroyed, it is difficult to recover completely, which affects the function of the soil ecosystem (Meisner et al., 2018; Preece et al., 2019).

Many studies have shown that the available water content and pH in soil are considered to be the most important factors affecting soil microbial abundance (Delgado-Baquerizo et al., 2019; Fierer and Lennon, 2011; Shen et al., 2014; Tedersoo, 2017; Treseder, 2008). Notably, in this study, although soil moisture did not have a direct effect on bacterial and fungal diversity, it had an indirect effect on bacterial and fungal diversity by driving soil aggregates. These results suggest that soil moisture affects microbial diversity mainly through aggregates, which are considered as the basic places of microbial metabolism. Previous studies have suggested that pH can actively drive bacterial diversity, but has little or weak negative effects on fungal diversity (Peay et al., 2016; Zhou et al., 2016). In our study, with decreases in pH, bacterial diversity increased, and pH close to neutral may be more conducive to bacterial diversity. However, a decrease in pH drives the loss of fungal diversity. Therefore, when soil is stripped and transported from eroded sites to depositional sites, the pH decreases, which increases bacterial diversity and reduces fungal diversity. There was a weak antagonistic effect on the bacterial and fungal diversity. TN and SOC, as the nutrients supplied for soil microbial metabolism activities, directly affect microbial diversity (Shen et al., 2015; Singh et al., 2013). SMBC is a part of soil active components, which are regarded as indicators of variation in bacterial and fungal diversity. The effect of TP on fungal diversity was not obvious, but it had an adverse effect on bacterial diversity.

Compared with the control sites, bacterial and fungal communities differed at the eroded and depositional sites (stress < 0.2, Fig. 5). At the phylum level, erosion-sedimentation significantly affected the relative abundance of Actinobacteria and Acidobacteria (Table S1). This may be caused by changes in the structure of soil aggregates, soil aeration, and pH during the processes of erosion and deposition (Fierer and Jackson, 2006). At the phylum level, erosion-deposition significantly affected Ascomycota and Basidiomycota (Table S1). This should result from the resetting of soil moisture, nutrients, texture, and other resources caused by erosion-deposition (Bennett et al., 2009). RDA analysis showed that the regulators of bacterial community structure were MSTR, MWD, clay, and SOC, while factors, such as TEMP, MSTR, MWD, BD, Caly, SOC, TN, TP, and pH regulated various fungal communities. Thus, these factors (e.g., TEMP, pH, TN, and TP) significantly regulated the fungal community compared to the bacterial community, and the regulatory mechanism of fungi is relatively complex. A combination of these factors affects the availability of soil fungal community habitats, which in turn affects the colonization of fungal scattered spores and propagules after soil changes (Kasel et al., 2008). In summary, destruction and reconstruction of the habitat may cause the recovery of the fungal community structure to be delayed or even irreversible, but the response of the bacteria was relatively weak.

Organic carbon is the core of eroded soil quality (Bonner et al., 2018; Van Oost et al., 2007), and it is also a substrate for maintaining microbial metabolism. Its quality has a significant effect on the growth of microbes (Takriti et al., 2018). Although erosion and deposition had different effects on bacteria and fungi, both bacterial and fungal diversity increased with an increase in the SOC level. In contrast, various bacterial and fungal communities became more obvious as the SOC level increased. This indicates that an increase in SOC levels can regulate the metabolic process of microorganisms by changing the availability and

composition of nutrients and soil structure at the erosional and depositional environments (Hobbie and Hobbie, 2012), which does not only increase microbial diversity, but also contribute to the growth and differentiation of functional microorganisms.

4.3. Erosion-deposition and SOC levels affect microbial co-occurrence network and keystone taxa

Microbial network studies have mainly analyzed the interactions among different microbial species in complex soil ecosystems. The interactions among microbial species are critical to ecosystem stability, especially in the soil microbial community (Bascompte, 2007; Qi et al., 2019; Zhou et al., 2011). Our results show that erosion reduces the network complexity of bacteria and fungi, while deposition increases the complexity of bacterial networks, but reduces the network complexity of fungi. An increase in the SOC level can further strengthen the network complexity of bacteria and fungi at various sites. This is because microbial co-occurrence networks in erosion and deposition sites are largely driven by resources rather than phylogeny (Banerjee et al., 2016b), and the complexity of microbial networks differed due to changes in land management and disturbance (Li et al., 2017; Sul et al., 2013). Erosion leads to a decrease in the availability of soil water, organic carbon, and other nutrients, and resource limitations inevitably damage the complexity of bacterial and fungal networks (Banerjee et al., 2019; Barberán et al., 2012; De Vries et al., 2018). Deposition trapped and buried soil nutrients, increased soil moisture, and created a relatively resource-rich environment. This environment is more conducive to the repair of the bacterial network. In contrast, fungal mycelia crossed soil porosity and promoted the movement of the community to new resource patches (Kohlmeier et al., 2005), but the cycle of niche re-differentiation and re-recovery lasted longer, and it was difficult to recover to the original state under “retention effect” (Meisner et al., 2018; Preece et al., 2019). As a substrate of microbial metabolism, an increase in organic carbon content has a positive effect on the complexity of bacterial and fungal community networks (Xue et al., 2020).

Keystone taxa play a pivotal role in driving the microbial community structure and function (Banerjee et al., 2016a). In this study, Actinobacteria, Proteobacteria, Acidobacteria, and Chloroflexi were identified as bacterial keystone taxa (Fig. 7), Ascomycota and Basidiomycota were identified as fungal keystone taxa (Fig. 8), which is consistent with previous studies (Banerjee et al., 2018; Deng et al., 2012; Ling et al., 2016). Actinobacteria and Acidobacteria are highly connected generalists at the eroded sites. This was because Actinobacteria had good adaptability to low-water environments, and Acidobacteria is an oligotrophic bacterial phylum, which had good adaptability to relatively poor soil at the eroded sites. Proteobacteria and Chloroflexi are highly connected generalists at the depositional sites (Fig. 9a). Proteobacteria is a eutrophic bacterial phylum, and the trapped and enriched nutrients at the depositional sites provide a rich substrate for their proliferation. Chloroflexi, involved in the CO₂ fixation reaction, rapidly proliferated in environments with compact and reconstructed soil structures. There were more connections of Actinobacteria, Acidobacteria, and Chloroflexi in low and middle SOC levels, while Proteobacteria had more connections at high SOC levels (Fig. 9b), which indicates that Proteobacteria was more suitable to grow in a high-humidity and organic carbon enriched environment, whereas Actinobacteria, Acidobacteria, and Chloroflexi were more adapted to proliferate in low and medium SOC environments. Ascomycota and Basidiomycota are highly connected generalists at the eroded sites and high SOC levels (Fig. 9c and d). This suggests that Ascomycota and Basidiomycota had high adaptability in an environment of structural destruction and nutrient loss, as well as an environment with abundant substrates. In summary, various keystone taxa should be attributed to changes in soil properties and differences in organic carbon substrates caused by erosion and deposition.

Modularity indicates how well a network can be subdivided into modules or compartments, which may originate from specific interactions, habitat heterogeneity, resource partitioning, or niche overlap. Less modularity is interpreted as a more functional community (Deng et al., 2012; Olesen et al., 2007). In this study, there was less modularity of the bacterial network at the depositional sites than at the eroded sites (Table S5), suggesting that more bacterial functional communities were present at the depositional sites than at the eroded sites. There was higher modularity of the fungal network at the eroded and depositional sites than at the control sites (Table S6), which suggests that both erosion and deposition caused a reduction in fungal functional communities. As the SOC level increased, the bacterial and fungal modules decreased (Tables S5, 6), suggesting that an increase in SOC levels effectively increased bacterial and fungal functional communities. Similarly, the clustering coefficient of the bacterial and fungal co-occurrence networks also confirmed our results. Lower clustering coefficient in bacterial erosion network, higher clustering coefficient in the bacterial depositional network, and increases in clustering coefficient with SOC levels indicate that deposition enhanced the functional communities compared with erosion, and an increase in SOC levels further enhanced the functional communities in each network. Interestingly, clustering coefficients in the erosion and depositional networks reduced, and increased SOC levels also effectively strengthened the clustering coefficients, indicating that both erosion and deposition reduced functional communities, but an increase in SOC levels effectively improved the functional communities. In general, the bacterial deposition network is larger and more complex than the erosion network. This is because the more efficient resources at the depositional sites supported an increase in network complexity, improving bacterial community stability and nutrient transfer efficiency (Wang et al., 2018). Environments at the eroded sites were more susceptible to disturbance, which had a negative effect on the ecological functions of the bacteria in the habitat. This was confirmed by the vulnerability of bacterial communities as well. The bacterial network vulnerability was lower in depositional sites and higher in eroded sites than in control sites. Moreover, erosion and deposition networks were disturbed to varying degrees and became fragmented, and the niches were further differentiated, which was not conducive to the stable proliferation of fungal communities. Furthermore, an increase in SOC level undoubtedly had a positive effect on bacterial and fungal co-occurrence networks, which promoted the building of bacterial and fungal communities with more organization and were more functional (Ling et al., 2016).

5. Conclusion

In this study, long-term erosion and deposition continuously created two environments, where soil texture was “reconstructed” and nutrients differed between “rich and poor”. In such an environment, bacterial communities were constantly being destroyed and remodeled, and staying in a process of continuous improvement of their functions. However, due to its slow recovery cycle, weak repair ability, and lack of available external forces (no vegetation, root system and soil intrusion in this study), fungal community destroyed by erosion cannot be quickly reconstructed and recovered in the deposition site, which greatly increased the risk of decline or even loss of functional diversity. The internal mechanisms of bacterial and fungal community structure construction and maintenance were different, and the response to environmental factors and soil properties were also different. The bacterial community structure was mainly affected by SOC, MSTR, TN, MWD, Clay, while change in fungal community structure was driven by MSTR, TEMP, pH, SOC, TN, TP, BD, MWD, and Clay. Remarkably, Increase in organic carbon level was beneficial to inhibit erosion, reduce the polarization of soil properties in erosion and deposition areas, and effectively improved the reconstruction of bacterial and fungal community structure, but it did not mean that the decline of the fungal community caused by long-term erosion–deposition can be completely eliminated.

The decline of fungal community function may be more conducive to the retention of inert organic matter and slow down the mineralization of soil organic matter. Our results bring a new insight into understanding changes in microbial life processes and survival strategies induced by erosion–deposition. These findings also give a new revelation that organic carbon can be used to control earth surface processes induced by erosion–deposition, regulating and stabilizing soil microbial communities and functions, and promoting the normal functioning of soil ecosystems.

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.

Acknowledgements

This study was funded by National Natural Science Foundation of China (No. 42177345, 41771318), Scientific and Technological Innovation Programs of Higher Education Institutions in Shanxi (No. 2020L0680), and Key research and development program in Lvliang City (No. 2020SHFZ45). We thank the Ansaï Farmland Ecosystem National Observation and Research Station for providing experimental site and research support.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.catena.2022.106471>.

References

- Adhikari, G., Bhattacharyya, K.G., 2015. Correlation of soil organic carbon and nutrients (NPK) to soil mineralogy, texture, aggregation, and land use pattern. *Environ. Monit. Assess.* 187 (11), 735.
- Bahram, M., Hildebrand, F., Forslund, S.K., Anderson, J.L., Soudzilovskaia, N.A., Bodegom, P.M., Bengtsson-Palme, J., Anslan, S., Coelho, L.P., Harend, H., Huerta-Cepas, J., Medema, M.H., Maltz, M.R., Mundry, S., Olsson, P.A., Pent, M., Pölme, S., Sunagawa, S., Ryberg, M., Tedersoo, L., Bork, P., 2018. Structure and function of the global topsoil microbiome. *Nature* 560 (7717), 233–237.
- Banerjee, S., Baah-Acheamfour, M., Carlyle, C.N., Bissett, A., Richardson, A.E., Siddique, T., Bork, E.W., Chang, S.X., 2016a. Determinants of bacterial communities in Canadian agroforestry systems. *Environ. Microbiol.* 18 (6), 1805–1816.
- Banerjee, S., Kirkby, C.A., Schmutter, D., Bissett, A., Kirkegaard, J.A., Richardson, A.E., 2016b. Network analysis reveals functional redundancy and keystone taxa amongst bacterial and fungal communities during organic matter decomposition in an arable soil. *Soil Biol. Biochem.* 97, 188–198.
- Banerjee, S., Schlaeppi, K., van der Heijden, M.G.A., 2018. Keystone taxa as drivers of microbiome structure and functioning. *Nat. Rev. Microbiol.* 16 (9), 567–576.
- Banerjee, S., Walder, F., Büchi, L., Meyer, M., Held, A.Y., Gättinger, A., Keller, T., Charles, R., van der Heijden, M.G.A., 2019. Agricultural intensification reduces microbial network complexity and the abundance of keystone taxa in roots. *ISME J.* 13 (7), 1722–1736.
- Barberán, A., Bates, S.T., Casamayor, E.O., Fierer, N., 2012. Using network analysis to explore co-occurrence patterns in soil microbial communities. *ISME J.* 6 (2), 343–351.
- Bascompte, J., 2007. Networks in ecology. *Basic Appl. Ecol.* 8 (6), 485–490.
- Bastian, M., Heymann, S., Jacomy, M., 2009. Gephi: An Open Source Software for Exploring and Manipulating Networks. In: *Proceedings of the Third International Conference on Weblogs and Social Media, ICWSM 2009*, San Jose, California, USA, May 17–20, 2009.
- Bazzicalupo, A.L., Bálint, M., Schmitt, I., 2013. Comparison of ITS1 and ITS2 rDNA in 454 sequencing of hyperdiverse fungal communities. *Fungal Ecol.* 6 (1), 102–109.
- Bennett, L.T., Kasel, S., Tibbitts, J., 2009. Woodland trees modulate soil resources and conserve fungal diversity in fragmented landscapes. *Soil Biol. Biochem.* 41 (10), 2162–2169.
- Berhe, A.A., Hartel, J., Harden, J.W., Torn, M.S., 2007. The significance of the erosion-induced terrestrial carbon sink. *Bioscience* 57, 337–346.
- Bezdicsek, D.F., Beaver, T., Granatstein, D., 2003. Subsoil ridge tillage and lime effects on soil microbial activity, soil pH, erosion, and wheat and pea yield in the Pacific Northwest, USA. *Soil Tillage Res.* 74, 55–63.
- Bonner, M.T.L., Shoo, L.P., Brackin, R., Schmidt, S., 2018. Relationship between microbial composition and substrate use efficiency in tropical soil. *Geoderma* 315, 96–103.

- Borken, W., Matzner, E., 2009. Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. *Glob. Change Biol.* 15, 808–824.
- Borrelli, P., Van Oost, K., Meusburger, K., Alewell, C., Lugato, E., Panagos, P., 2018. A step towards a holistic assessment of soil degradation in Europe: Coupling on-site erosion with sediment transfer and carbon fluxes. *Environ. Res.* 161, 291–298.
- Brockett, B.F.T., Prescott, C.E., Grayston, S.J., 2012. Soil moisture is the major factor influencing microbial community structure and enzyme activities across seven biogeoclimatic zones in western Canada. *Soil Biol. Biochem.* 44 (1), 9–20.
- Carrizo, M.E., Alessio, C.A., Cosentino, D., Imhoff, S., 2015. Aggregation agents and structural stability in soils with different texture and organic carbon contents. *Sci Agr* 72 (1), 75–82.
- Colman, B.P., Schimel, J.P., 2013. Drivers of microbial respiration and net N mineralization at the continental scale. *Soil Biol. Biochem.* 60, 65–76.
- Cookson, W.R., Osman, M., Marschner, P., Abaye, D.A., Clark, I., Murphy, D.V., Stockdale, E.A., Watson, C.A., 2007. Controls on soil nitrogen cycling and microbial community composition across land use and incubation temperature. *Soil Biol. Biochem.* 39 (3), 744–756.
- Cortez, J., Bouché, M., 2001. Decomposition of mediterranean leaf litters by *Nicotrilus meridionalis* (Lumbricidae) in laboratory and field experiments. *Soil Biol. Biochem.* 33 (15), 2023–2035.
- Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440 (7081), 165–173.
- De Vries, F.T., et al., 2018. Soil bacterial networks are less stable under drought than fungal networks. *Nat. Commun.* 9, 3033.
- De Vries, F.T., et al., 2012. Land use alters the resistance and resilience of soil food webs to drought. *Nat. Clim. Change* 2, 276–280.
- Delgado-Baquerizo, M., et al., 2019. Changes in belowground biodiversity during ecosystem development. *PNAS* 116, 6891–6896.
- Deng, Y., et al., 2012. Molecular ecological network analyses. *Bmc. Bioinformatics* 13, 113.
- Edgar, R.C., Haas, B.J., Clemente, J.C., Quince, C., Knight, R., 2011. UCHIME improves sensitivity and speed of chimera detection. *Bioinformatics* 27, 2194–2200.
- Fierer, N., Jackson, R.B., 2006. The diversity and biogeography of soil bacterial communities. *PNAS* 103, 626–631.
- Fierer, N., Lennon, J.T., 2011. The Generation and Maintenance of Diversity in Microbial Communities. *Am. J. Bot.* 98, 439–448.
- Finlay, B.J., 2002. Global dispersal of free-living microbial eukaryote species. *Science* 296, 1061–1063.
- García-Palacios, P., Gross, N., Gaitan, J., Maestre, F.T., 2018. Climate mediates the biodiversity-ecosystem stability relationship globally. *PNAS* 115, 8400–8405.
- Griffiths, B.S., Philippot, L., 2013. Insights into the resistance and resilience of the soil microbial community. *FEMS Microbiol. Rev.* 37, 112–129.
- Gu, Z.J., et al., 2018. Quantitative assessment of soil productivity and predicted impacts of water erosion in the black soil region of northeastern China. *Sci. Total Environ.* 637, 706–716.
- Hansel, C.M., Fendorf, S., Jardine, P.M., Francis, C.A., 2008. Changes in bacterial and archaeal community structure and functional diversity along a geochemically variable soil profile. *Appl. Environ. Microbiol.* 74, 1620–1633.
- Hobbie, J.E., Hobbie, E.A., 2012. Amino acid cycling in plankton and soil microbes studied with radioisotopes: measured amino acids in soil do not reflect bioavailability. *Biogeochemistry* 107, 339–360.
- Jackson, L.E., Calderon, F.J., Steenwerth, K.L., Scow, K.M., Rolston, D.E., 2003. Responses of soil microbial processes and community structure to tillage events and implications for soil quality. *Geoderma* 114, 305–317.
- Jankauskas, B., Jankauskiene, G., Fullen, M.A., 2008. Soil erosion and changes in the physical properties of Lithuanian Entic Albeluvisols under different land use systems. *Acta Agriculturae Scandinavica Section B-Soil Plant Sci.* 58, 66–76.
- Jansson, J.K., 2013. FORUM: Microbiology The life beneath our feet. *Nature* 494 (7435), 40–41.
- Jarasunas, G., Kinderiene, I., 2016. Impact of agro-environmental systems on soil erosion processes and soil properties on hilly landscape in Western Lithuania. *J. Environ. Eng. Landscape Manage.* 24, 60–69.
- Jia, Y., Huang, H., Chen, Z., Zhu, Y.G., 2014. Arsenic Uptake by Rice Is Influenced by Microbe-Mediated Arsenic Redox Changes in the Rhizosphere. *Environ. Sci. Technol.* 48, 1001–1007.
- Jiang, B.H., et al., 2021. Analysis of microbial community structure and diversity in surrounding rock soil of different waste dump sites in fushun western opencast mine. *Chemosphere* 269, 128777.
- Kallenbach, C.M., Frey, S.D., Grandy, A.S., 2016. Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls. *Nat. Commun.* 7, 13630.
- Kaschuk, G., Hungria, M., Santos, J.C.P., Berton, J.F., 2006. Differences in common bean rhizobial populations associated with soil tillage management in southern Brazil. *Soil Tillage Res.* 87, 205–217.
- Kasel, S., Bennett, L.T., Tibbitts, J., 2008. Land use influences soil fungal community composition across central Victoria, south-eastern Australia. *Soil Biol. Biochem.* 40, 1724–1732.
- Kohlmeier, S., et al., 2005. Taking the fungal highway: Mobilization of pollutant-degrading bacteria by fungi. *Environ. Sci. Technol.* 39, 4640–4646.
- Köljal, U., et al., 2013. Towards a unified paradigm for sequence-based identification of fungi. *Mol. Ecol.* 22, 5271–5277.
- Kuzyakov, Y., Friedel, J.K., Stahr, K., 2000. Review of mechanisms and quantification of priming effects. *Soil Biol. Biochem.* 32, 1485–1498.
- Lal, R., 1998. Soil erosion impact on agronomic productivity and environment quality. *Crit. Rev. Plant Sci.* 17, 319–464.
- Lal, R., 2003. Soil erosion and the global carbon budget. *Environ. Int.* 29, 437–450.
- Lal, R., 2020. Soil Erosion and Gaseous Emissions. *Appl. Sci.-Basel* 10, 2784.
- Lauber, C.L., Strickland, M.S., Bradford, M.A., Fierer, N., 2008. The influence of soil properties on the structure of bacterial and fungal communities across land-use types. *Soil Biol. Biochem.* 40, 2407–2415.
- Li, X.Q., et al., 2017. Response of soil microbial communities and microbial interactions to long-term heavy metal contamination. *Environ. Pollut.* 231, 908–917.
- Ling, N., et al., 2016. Insight into how organic amendments can shape the soil microbiome in long-term field experiments as revealed by network analysis. *Soil Biol. Biochem.* 99, 137–149.
- Meisner, A., Jacquiod, S., Snoek, B.L., ten Hooven, F.C., van der Putten, W.H., 2018. Drought legacy effects on the composition of soil fungal and prokaryote communities. *Front. Microbiol.* 9, 294.
- Mori, H., et al., 2014. Design and Experimental Application of a Novel Non-Degenerate Universal Primer Set that Amplifies Prokaryotic 16S rRNA Genes with a Low Possibility to Amplify Eukaryotic rRNA Genes. *DNA Res.* 21, 217–227.
- Morvan, X., Verbeke, L., Laratte, S., Schneider, A.R., 2018. Impact of recent conversion to organic farming on physical properties and their consequences on runoff, erosion and crusting in a silty soil. *Catena* 165, 398–407.
- Nadeu, E., Berhe, A.A., de Vente, J., Boix-Fayos, C., 2012. Erosion, deposition and replacement of soil organic carbon in Mediterranean catchments: a geomorphological, isotopic and land use change approach. *Biogeosciences* 9, 1099–1111.
- Nielsen, U.N., Ayres, E., Wall, D.H., Bardgett, R.D., 2011. Soil biodiversity and carbon cycling: a review and synthesis of studies examining diversity-function relationships. *Eur. J. Soil Sci.* 62, 105–116.
- O'Malley, M.A., 2007. The nineteenth century roots of 'everything is everywhere'. *Nat. Rev. Microbiol.* 5, 647–651.
- Olesen, J.M., Bascompte, J., Dupont, Y.L., Jordano, P., 2007. The modularity of pollination networks. *PNAS* 104, 19891–19896.
- Ouyang, W., et al., 2018. Combined impacts of land use and soil property changes on soil erosion in a mollisol area under long-term agricultural development. *Sci. Total Environ.* 613, 798–809.
- Pacala, S.W., et al., 2001. Consistent land and atmosphere-based US carbon sink estimates. *Science* 292, 2316–2320.
- Pastorelli, R., et al., 2013. Consequences on macroporosity and bacterial diversity of adopting a no-tillage farming system in a clayish soil of Central Italy. *Soil Biol. Biochem.* 66, 78–93.
- Peay, K.G., Kennedy, P.G., Talbot, J.M., 2016. Dimensions of biodiversity in the earth mycobiome. *Nat. Rev. Microbiol.* 14, 434–447.
- Peixoto, R.S., et al., 2006. Soil aggregation and bacterial community structure as affected by tillage and cover cropping in the Brazilian Cerrados. *Soil Tillage Res.* 90, 16–28.
- Philippot, L., et al., 2013. Loss in microbial diversity affects nitrogen cycling in soil. *ISME J.* 7, 1609–1619.
- Preece, C., Verbruggen, E., Liu, L., Weedon, J.T., Penuelas, J., 2019. Effects of past and current drought on the composition and diversity of soil microbial communities. *Soil Biol. Biochem.* 131, 28–39.
- Qi, G.F., Ma, G.Q., Chen, S., Lin, C.C., Zhao, X.Y., 2019. Microbial network and soil properties are changed in bacterial wilt-susceptible Soil. *Appl. Environ. Microbiol.* 85, e00162.
- Quast, C., et al., 2012. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucleic Acids Res.* 41, D590–D596.
- Rasche, F., et al., 2011. Seasonality and resource availability control bacterial and archaeal communities in soils of a temperate beech forest. *ISME J.* 5, 389–402.
- Shen, C.C., et al., 2014. Contrasting elevational diversity patterns between eukaryotic soil microbes and plants. *Ecology* 95, 3190–3202.
- Shen, C.C., Ni, Y.Y., Liang, W.J., Wang, J.J., Chu, H.Y., 2015. Distinct soil bacterial communities along a small-scale elevational gradient in alpine tundra. *Front. Microbiol.* 6, 582.
- Singh, D., Shi, L.L., Adams, J.M., 2013. Bacterial Diversity in the Mountains of South-West China: Climate Dominates Over Soil Parameters. *Journal of Microbiology* 51, 439–447.
- Singh, J.S., Raghubanshi, A.S., Singh, R.S., Srivastava, S.C.J.N., 1989. Microbial biomass acts as a source of plant nutrients in dry tropical forest and savanna. *Nature* 338, 499–500.
- Smith, K.A., et al., 2003. Exchange of greenhouse gases between soil and atmosphere: interactions of soil physical factors and biological processes. *Eur. J. Soil Sci.* 54, 779–791.
- Soinne, H., Hyvaluoma, J., Ketoja, E., Turtola, E., 2016. Relative importance of organic carbon, land use and moisture conditions for the aggregate stability of post-glacial clay soils. *Soil Till Res.* 158, 1–9.
- Starr, G.C., Lal, R., Malone, R., Hothem, D., Kimble, J., 2000. Modeling soil carbon transported by water erosion processes. *Land Degrad. Dev.* 11, 83–91.
- Stefanowicz, A.M., Kapusta, P., Zubek, S., Stanek, M., Woch, M.W., 2020. Soil organic matter prevails over heavy metal pollution and vegetation as a factor shaping soil microbial communities at historical Zn-Pb mining sites. *Chemosphere* 240, 124922.
- Sul, W.J., et al., 2013. Tropical agricultural land management influences on soil microbial communities through its effect on soil organic carbon. *Soil Biol. Biochem.* 65, 33–38.
- Takriti, M., et al., 2018. Soil organic matter quality exerts a stronger control than stoichiometry on microbial substrate use efficiency along a latitudinal transect. *Soil Biol. Biochem.* 121, 212–220.
- Tedersoo, L., 2017. Correspondence: Analytical flaws in a continental-scale forest soil microbial diversity study. *Nat. Commun.* 8, 15572.
- Tiemann, L.K., Billings, S.A., 2011. Changes in variability of soil moisture alter microbial community C and N resource use. *Soil Biol. Biochem.* 43, 1837–1847.

- Torsvik, V.L., Goksy, J., Daae, F.L.J.A., 1990. High diversity in DNA of soil bacteria. *Appl. Environ. Microbiol. Reports* 56, 782–787.
- Treseder, K.K., 2008. Nitrogen additions and microbial biomass: a meta-analysis of ecosystem studies. *Ecol. Lett.* 11, 1111–1120.
- Van Bruggen, A.H.C., Semenov, A.M., 2000. In search of biological indicators for soil health and disease suppression. *Appl. Soil Ecol.* 15, 13–24.
- Van Der Heijden, M.G.A., Bardgett, R.D., van Straalen, N.M., 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol. Lett.* 11, 296–310.
- Van Oost, K., et al., 2007. The impact of agricultural soil erosion on the global carbon cycle. *Science* 318, 626–629.
- Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. *Soil Biol. Biochem.* 19, 703–707.
- Veresoglou, S.D., Halley, J.M., Rillig, M.C., 2015. Extinction risk of soil biota. *Nat. Commun.* 6, 9862.
- Wagg, C., Bender, S.F., Widmer, F., van der Heijden, M.G.A., 2014. Soil biodiversity and soil community composition determine ecosystem multifunctionality. *PNAS* 111, 5266–5270.
- Wang, X., Cammeraat, E.L.H., Cerli, C., Kalbitz, K., 2014. Soil aggregation and the stabilization of organic carbon as affected by erosion and deposition. *Soil Biol. Biochem.* 72, 55–65.
- Wang, S., Wang, X.B., Han, X.G., Deng, Y., 2018. Higher precipitation strengthens the microbial interactions in semi-arid grassland soils. *Glob. Ecol. Biogeogr.* 27, 570–580.
- Wortman, S.E., Drijber, R.A., Francis, C.A., Lindquist, J.L., 2013. Arable weeds, cover crops, and tillage drive soil microbial community composition in organic cropping systems. *Appl. Soil Ecol.* 72, 232–241.
- Wu, J., Joergensen, R.G., Pommerening, B., Chaussod, R., Brookes, P.C., 1990. Measurement of soil microbial biomass C by fumigation-extraction—an automated procedure. *Soil Biol. Biochem.* 22, 1167–1169.
- Xu, M.X., Li, Q., Wilson, G., 2016. Degradation of soil physicochemical quality by ephemeral gully erosion on sloping cropland of the hilly Loess Plateau, China. *Soil Tillage Res.* 155, 9–18.
- Xu, X., Zhou, Y., Ruan, H.H., Luo, Y.Q., Wang, J.S., 2010. Temperature sensitivity increases with soil organic carbon recalcitrance along an elevational gradient in the Wuyi Mountains, China. *Soil Biol. Biochem.* 42, 1811–1815.
- Xue, L., et al., 2020. Long term effects of management practice intensification on soil microbial community structure and co-occurrence network in a non-timber plantation. *For. Ecol. Manage.* 459, 117805.
- Yuan, M.M., et al., 2021. Climate warming enhances microbial network complexity and stability. *Nat. Clim. Change* 11, 343–348.
- Zhang, X.M., et al., 2018. Effect of intermediate disturbance on soil microbial functional diversity depends on the amount of effective resources. *Environ. Microbiol.* 20, 3862–3875.
- Zhang, Y., Peng, B.Z., Gao, X., Yang, H., 2004. Degradation of soil properties due to erosion on sloping land in southern Jiangsu Province, China. *Pedosphere* 14, 17–26.
- Zhao, C.S., et al., 2020. Comparing the Effects of Biochar and Straw Amendment on Soil Carbon Pools and Bacterial Community Structure in Degraded Soil. *J. Soil Sci. Plant Nutrition* 20, 751–760.
- Zhou, J.Z., Deng, Y., Luo, F., He, Z.L., Yang, Y.F., 2011. Phylogenetic Molecular Ecological Network of Soil Microbial Communities in Response to Elevated CO₂. *Mbio* 2, e00122–e211.
- Zhou, J.Z., et al., 2016. Temperature mediates continental-scale diversity of microbes in forest soils. *Nat. Commun.* 7, 12083.
- Zinn, Y.L., Lal, R., Resck, D.V.S., 2011. Eucalypt plantation effects on organic carbon and aggregation of three different-textured soils in Brazil. *Soil Res.* 49 (7), 614–624.