

# Divergent responses of soil bacterial communities in erosion-deposition plots on the Loess Plateau

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## ABSTRACT

Soil erosion and deposition occur widely from regional to global scales and have profound impacts on ecological services and sustainability. Despite their crucial roles in biogeochemical cycles, the responses of soil bacterial communities to soil erosion and deposition remain largely unclear. In this study, a field simulation experiment was conducted to examine variation in soil bacterial communities across eroding slopes and depositional zones with three slope gradients (5°, 10° and 20°) on the Loess Plateau of China (2015–2017). The results showed that soil physicochemical properties were altered by redistribution of runoff and sediment across eroding slopes and depositional zones. Soil bacterial alpha diversity was higher in the depositional zones of both 10° and 20° slopes compared with the 5° reference slopes but no markedly difference was found between eroding slopes and reference slopes. By contrast, bacterial community structure differed between eroding slopes and reference slopes but not between depositional zones and reference slopes. Differentiation of bacterial communities between eroding slopes and depositional zones increased with increasing slope gradients. The bacterial network was greater and more complex within depositional zone than eroding slope, indicating more extensive bacterial interactions and greater community stability potential. Erosion- and deposition-induced redistribution of soil moisture, soil organic matter, available P, and available K were the key determinants of variation in bacterial community structure. Our findings demonstrate the contrasting effects of soil erosion and deposition on soil bacterial communities, which should be given further attention across eroding landscapes.

## 1. Introduction

Soil erosion, a serious eco-environmental problem exacerbated by anthropogenic perturbations, is the most widespread form of land degradation (Lal, 2003; Pimentel et al., 1995). Globally, ~75 Gt of soil is redistributed by erosion per year, of which 70–90% is deposited in various low-lying areas (Stallard, 1998). In general, soil erosion breaks down aggregates and selectively transports fine or light particles and labile organic fractions (Lal, 2003; Muller-Nedebeck et al., 2016), which deteriorates soil structure and results in soil organic carbon loss (Berhe and Kleber, 2013). In contrast, depending on temporal surface runoff and sediment, deposition increases nutrients and wetness, reduces aeration and potentially alters pH and redox conditions, which contribute to the storage and stability of carbon and nitrogen in the soil (Berhe et al., 2018; Berhe and Torn, 2016). These variations in local hydrologic, pedologic and microclimatic conditions can profoundly

impact productivity and stability of soil ecosystems (Gregorich et al., 1998; Kirkels et al., 2014; Yue et al., 2016).

Soil microbes (especially bacteria) are ubiquitous and abundant in soil ecosystems and act as biogeochemical engineers of the earth's biosphere (Bardgett and van der Putten, 2014). Soil microbial communities perform crucial roles in ecosystem functions, including organic matter transformation and decomposition, as well as nutrient and carbon cycling (Allison and Goulden, 2017; Takriti et al., 2018). As reported, soil microbes can contribute considerably to soil organic matter, and microbial anabolism can exert critical control over soil organic carbon stabilization in the global carbon cycle (Liang et al., 2017). Soil bacterial communities are influenced by their soil habitats, and changes in the soil environment can drive dramatic responses in bacterial communities (Griffiths and Philippot, 2013). Since erosion causes soil loss while deposition increases soil resource availability, and both processes probably lead to shifts in bacterial functional groups,

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taxonomic diversity, and community structure (Banerjee et al., 2016). Additionally, soil erosion and deposition can induce soil spatial heterogeneity that may alter bacterial interactions and co-occurrence patterns. Previous studies performed by Mabuhay et al. (2004) and Helgason et al. (2014) have separately investigated the responses of bacterial communities to soil erosion or deposition; and Xiao et al. (2017) demonstrated that erosion homogenizes bacterial communities along eroding slopes. However, the effects of soil erosion and deposition on bacterial communities have not been comprehensively investigated. Moreover, the response characteristics of bacterial community structure and co-occurrence patterns during soil erosion and deposition processes have been largely ignored.

The Loess Plateau of China, covering 640,000 km<sup>2</sup> and featuring numerous loess hills and gullies, is one of the most eroded regions in the world. The complex terrain, intense storms, and anthropogenic disturbances including deforestation, overgrazing and intensive agricultural practices have accelerated the erosion of this inherently highly erodible soil (Shi and Shao, 2000), producing an erosion modulus of 100–20,000 t km<sup>-2</sup> year<sup>-1</sup> (Fu, 2010). In this region, slopes ranging from 8° to 35° are found to account for 45.5% of the total land area and responsible for 82% of the total soil loss. Slopes < 5° cover 43.2% of the total land area and have a lower erosion rate of < 100 t km<sup>-2</sup> y<sup>-1</sup> (Fu, 2010; Fu et al., 2011). Recently, the effects of soil erosion and deposition on soil physicochemical properties have been reported (Rousk et al., 2010). Given the variation in soil physicochemical properties with soil erosion and deposition, we hypothesized that soil bacterial communities may display prominent responses to soil erosion and deposition on the Loess Plateau.

In the present study, a field experiment simulating soil erosion and deposition was conducted on the Loess Plateau from 2015 to 2017. Using high-throughput sequencing, we aimed to (1) assess the effects of soil erosion and deposition on bacterial alpha diversity, community structure and co-occurrence patterns, and (2) determine the influences of soil physicochemical properties and slope gradients on the divergence of bacterial communities during soil erosion and deposition processes.

## 2. Materials & methods

### 2.1. Site description and experimental design

The study site was located at Changwu State Key Agro-Ecological Experimental Station (35°13' N, 107°40' E, 1220 m a.s.l.) in Changwu County, Shaanxi Province, China, which is a typical eroded gully of the south Loess Plateau (Fig. 1a). This site is characterized by heavy rainstorms during hot summer and cold dry weather in winter. The mean annual precipitation is 560 mm, 60% of which occurs from July to September, and the mean annual air temperature is 9.4 °C (according to meteorological data provided by the State Key Agro-Ecological Experimental Station). The soil at the site is loam (Cumulic Haplustoll; the USDA Soil Taxonomy System) developed from loess deposits.

In April 2014, based on local eroding landscape pattern, east-facing erosion-deposition plots were constructed adjacent to each other with three replicates (Fig. 1b–d), including eroding slopes (500 cm long × 100 cm wide × 200 cm deep) of three different slope gradients of 5°, 10° and 20°, each connected with a depositional zone (100 cm long × 100 cm wide × 200 cm deep). A fourth replicate was built for each slope gradient to specifically collect runoff and sediment during individual rainfall events. The plots for collecting runoff and sediment were marked by the yellow dotted lines (Fig. 1b, c). Although there was only one replicate to monitor soil erosional responses, the consistently increasing runoff and sediment with steeper slope gradient over the 39 rainfall events during the three years of experimental period (Table S5) repeatedly confirmed the controlling effects of slope gradients to soil erosion and deposition processes. Therefore, we consider such experimental settings adequately served our purpose to focus on the responses

of soil bacterial communities to slope-scale soil redistribution during erosion and deposition. Moreover, given the prevalently gentle gradient and lower erosion rate (Wang et al., 2017a) in this study area, 5° eroding slopes were set as reference slopes.

The experimental soil was collected from upper 200 cm of the farmland (wheat-corn rotation) in 10 cm increments, and refilled to the erosion-deposition plots layer by layer to form a 200 cm deep profile (Fig. 1d). Each layer of the refilled soil profile was compacted lightly to form the bulk density corresponding to that of the original layer of farmland profile (Table S1). When refilling the soils, roots and plant residuals were removed as often did in previous studies (Huang et al., 2014; Wu et al., 2018a), to help exclude the additional heterogeneity in initial soil conditions of our experiment. The moisture of soil from each layer was modified to ca. 13%. During plot construction, although all the soils were inevitably disturbed when mixing soil, removing visible roots and plant residuals, and refilling soil in erosion-deposition plots, such soil preparation can help us to focus on the responses of soil bacterial communities to erosion and deposition, rather than involving all the relevant factors.

Each erosion-deposition plot was isolated by concrete wall at four sides (the measuring sizes of the concrete wall have shown in Fig. 1c, d), leaving the bottom of each plot unsealed but freely open to enable downward water infiltration (Fig. 1b, d). To exclusively focus on the possible impacts of erosional soil redistribution on soil microbial communities, no crops were planted on eroding slopes or depositional zones, and weeds were manually cleared during the experiment period to eliminate any possible effects from vegetation.

### 2.2. Runoff and sediment collection, soil sampling and physicochemical analyses

To collect runoff suspension, a cylindrical steel tank with an inner diameter of 40 cm and a height of 40 cm was set up for each monitored plot (Fig. 1b, c), the plots for collecting runoff and sediment were marked by the yellow dotted line). After effective erosion events that measurable runoff suspension was generated, the weight and volume of the suspension were measured immediately. Three 500 mL well-blended suspension subsamples were sampled from each tank to determine the sediment concentration. The sediment yield of each erosion event was determined via multiplying sediment concentration by suspension volume. The runoff volume was the difference between suspension mass and sediment mass (assuming the water density as 1 g mL<sup>-1</sup>, cited from Wu et al. (2018b)). The sum of runoff volume and sediment yield of annual erosion events was the annual runoff volume and annual sediment yield, respectively. Annual sediment yield of per unit area (square kilometer) was the annual erosion rate. Annual erosion event, runoff volume, sediment yield and erosion rate from 2015 to 2017 were summarized and listed in Table 1.

In mid-August 2017 (erosion events concentrated in this period), topsoil (0–5 cm) and subsoil (5–10 cm) samples were collected from the three unmonitored replicates. Five soil cores were randomly collected with an auger (3 cm in diameter) from each reference slope, eroding slope and depositional zone and mixed to form a composite sample. Each composite soil sample was divided into two parts; one part was air-dried to determine soil physicochemical properties, and the other part was preserved at –80 °C for analysis of soil bacterial communities. Moreover, to investigate aggregate size distribution, approximately 300 g of bulk soils was randomly collected from the upper 10 cm on each reference slope, eroding slope and depositional zone by using a cylindrical metal core (5 cm in diameter).

To obtain the gravimetric moisture content, soil samples were oven-dried at 105 °C for 12 h to achieve constant weight. The particle size distribution was determined using a MS-200 laser particle size analyzer (Malvern Instruments, Worcestershire, UK) and soil bulk density was analyzed using the cutting ring method (Grossman and Reinsch, 2002). The total N, soil organic matter, and available P were measured by the

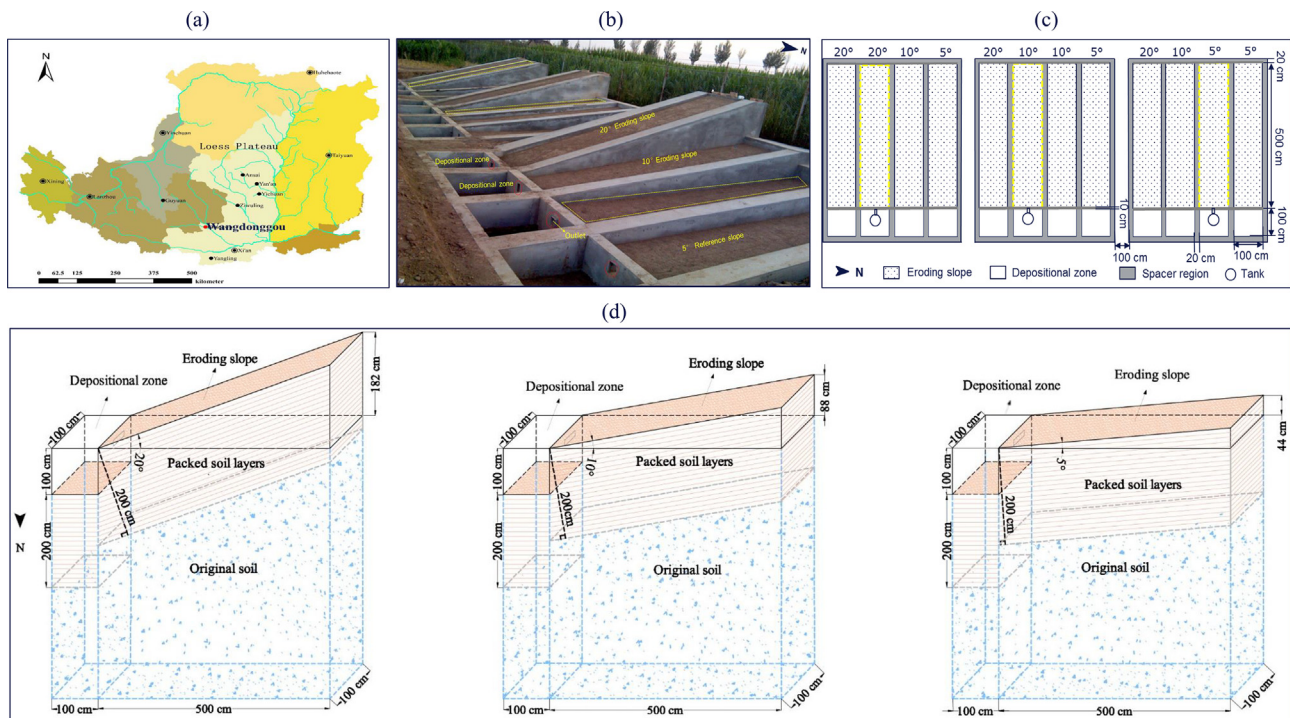


Fig. 1. Location of the study (a, cited from Wang et al. (2016)), photograph of field experimental settings (b) and layout of experimental settings (c) and detailed design on profiles (d) of eroding slopes and depositional zones across three slope gradients.

Kjeldahl (1883) method, the dichromate oxidation method (Walkley and Black, 1934) and the bicarbonate extraction method (Olsen and Watanabe, 1957), respectively. Soil pH (soil:water = 1:2.5, w/w) and available K were analyzed as described by Bao (2000). Soil NO<sub>3</sub>-N and NH<sub>4</sub>-N were extracted 2 M KCl (1:10 ratio) at 200 rpm for 1 h, and then were determined using an Auto Analyzer III continuous flow instrument (Bran+Luebbe GmbH, Germany). Soil dissolved organic carbon was measured by a multi N/C 3100 TOC/TN analyzer (Analytik Jena, Jena, Germany). Water-stable aggregate classes were determined according to Yoder (1936) by fractionating approximately 50 g of soil into three classes, including > 0.25 mm, 0.053–0.25 mm and < 0.053 mm.

### 2.3. DNA extraction, sequencing and data processing

Total genomic DNA was isolated from 0.50 g of each soil sample using a FastDNA SPIN Kit (MP Biochemicals, Solon, OH, USA) following the manufacturer's instructions. The primer pair 515F (5'-GTGCCAGC MGCCGCGGTAA-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3') were applied for amplification of the V4 region of the 16S rRNA gene according to the method of Evans et al. (2014). Sequencing libraries were generated and sequenced on an Illumina HiSeq 2500 platform

(Illumina, Inc., San Diego, USA).

Raw sequences were processed with QIIME (Caporaso et al., 2010), and chimera were detected using UCHIME (Edgar et al., 2011). After quality filtering and removal of chimeric sequences, all remaining high-quality sequences were clustered into operational taxonomic units (OTUs) with a 97% sequence identity threshold using UPARSE (Edgar, 2013). Taxonomic data were assigned to each sequence using mothur and the SILVA SSU rRNA database (Quast et al., 2013). The original sequence data are available at the NCBI with accession number PRJNA562740.

### 2.4. Statistical analyses

All analyses were conducted with R version 3.3.3 (R Core Team, 2017). One-way analysis of variance (ANOVA) was performed to detect differences in soil physicochemical properties, bacterial alpha diversity and the relative abundances of major bacterial phyla between reference slopes and eroding slopes, depositional zones across different slope gradients. Relationships between the relative abundances of major bacterial phyla and soil physicochemical properties were analyzed using Pearson correlations. Based on pairwise Bray-Curtis and Unifrac

**Table 1**  
Erosional responses for the three different slope gradients in 2015–2017.

Year	Rainfall (mm)	Erosion event	Slope gradient (°)	Runoff volume (m <sup>3</sup> )	Sediment yield (kg)	Erosion rate (t km <sup>-2</sup> yr <sup>-1</sup> )
2015	520	13	5 (reference)	0.14	5	1050
			10	0.24	24	4827
			20	0.43	44	8754
2016	524	10	5 (reference)	0.27	14	2824
			10	0.58	45	8939
			20	0.58	48	9624
2017	560	16	5 (reference)	0.23	2	423
			10	0.30	13	2549
			20	0.34	16	3159

Note: annual erosion event is the combined occurrence of runoff generation and sediment deposition per year.

dissimilarities, nonmetric multidimensional scaling (NMDS) performed by “metaMDS” in the vegan package was used to identify variation in soil bacterial communities across different slope gradients. Three non-parametric multivariate statistical methods in the vegan package, i.e., analysis of similarities (ANOSIM), permutational multivariate analysis of variance (PERMANOVA) and multiple response permutation procedure (MRPP), were employed to test the effects of erosion and deposition on soil bacterial communities. To analyze relationships between soil bacterial communities and soil physicochemical properties, redundancy analysis (RDA) was conducted using “rda” in the vegan package.

Co-occurrence networks were built for eroding slopes and depositional zones following an approach similar to that used by Barberan et al. (2012). OTUs with occurrence in at least 80% of all samples and at least 50 reads were selected. Pearson correlations of these OTUs with coefficients ( $\rho$ ) > 0.8 and  $P$ -values < 0.01 were used to construct co-occurrence networks, and  $P$ -values were adjusted by the Benjamini–Hochberg method. Erdős–Rényi random networks were also constructed with the number of nodes and edges equal to the actual networks. Various indices (e.g., modularity, average degree and clustering coefficient) were calculated to describe overall network topological features. Statistical analyses of eroding and depositional networks with corresponding random networks were performed with igraph and Hmisc packages, and visualization of networks was conducted with Gephi (Bastian et al., 2009).

### 3. Results

#### 3.1. Variation in runoff, sediment, erosion rate and soil physicochemical properties

Runoff, sediment yield, and erosion rate for the three slope gradients during 39 measurable erosion events are listed in Table 1. Runoff increased with slope gradients; slopes of 10° and 20° generated 30–115% and 48–207% more runoff than the 5° reference slopes, respectively. Similarly, the annual sediment yield of 10° and 20° slopes was 243–550% and 221–780% more than that of reference slopes, respectively. Erosion rate increased with increasing slope gradients; the most severe erosion occurred on 20° slopes, with erosion rate ranging from 3159 to 9624 t km<sup>-2</sup> year<sup>-1</sup> (Table 1).

No matter in topsoil and subsoil, the soil moisture, soil organic matter, dissolved organic carbon, NO<sub>3</sub>-N, available P and available K in the depositional zones of 10° and 20° slopes were higher than that on the reference slopes (Table 2,  $P$  < 0.05). However, only soil organic matter and dissolved organic carbon in topsoil and soil moisture in subsoil decreased on eroding slopes of 10° and 20° slopes compared to the reference slopes (Table 2,  $P$  < 0.05). In particular, soil moisture, dissolved organic carbon, available P, and available K in both topsoil and subsoil of depositional zones increased with increasing slope gradients. Soil pH was lower in depositional zones than on reference slopes in two soil layers ( $P$  < 0.05, Table 2). Moreover, most soil physicochemical properties in two soil layers differed significantly between eroding slopes and depositional zones (Table S2).

The content of soil aggregates > 0.25 mm was greater while the fractions of 0.053–0.25 mm and < 0.053 mm were less on eroding slopes than that on reference slopes ( $P$  < 0.05, Table S4). Furthermore, when compared with reference slopes, the fraction of 0.053–0.25 mm increased in depositional zones, but the fractions of > 0.25 mm and < 0.053 mm barely changed ( $P$  < 0.05, Table S4).

#### 3.2. Soil bacterial alpha diversity and community composition

We obtained 2,004,193 high-quality sequences (95.9% of the total 2,089,387) from 16S rRNA gene sequencing for all soil samples (54,872 to 83,679 sequences per sample); on average, 4717 OTUs were identified for each sample. All detected OTUs were classified into 63 bacterial

phyla. The three most abundant phyla of two soil layers were Proteobacteria, Actinobacteria and Acidobacteria, jointly accounting for 62.2% of all bacteria (Fig. 2a, b). Other less abundant phyla were Gemmatimonadetes, Chloroflexi, Planctomycetes, Bacteroidetes, Nitrospirae, Cyanobacteria and Firmicutes (Fig. 2a, b). The relative abundances of bacterial phyla varied at eroding slopes and depositional zones when compared with the reference slopes. In topsoil, Proteobacteria, the most abundant phylum, was less abundant on eroding slopes than on reference slopes (Fig. 2a,  $P$  < 0.05). By contrast, Nitrospirae, which accounted for only a small proportion of total bacteria, showed markedly increased abundance on eroding slopes in subsoil (Fig. 2b,  $P$  < 0.05).

The relative abundances of main bacterial phyla were correlated with soil physicochemical properties (Table 3). The relative abundances of Actinobacteria, Bacteroidetes and Cyanobacteria were negatively correlated with soil moisture, while Acidobacteria, Gemmatimonadetes, Chloroflexi and Nitrospirae were positively correlated with soil moisture ( $P$  < 0.05). The relative abundance of Actinobacteria had positive relationship with dissolved organic carbon, whereas Nitrospirae was negatively correlated with organic matter and dissolved organic carbon ( $P$  < 0.05). Furthermore, particles of different sizes also had significant effects on these bacterial phyla (Table 3).

The Shannon index was calculated as a metric of soil bacterial alpha diversity (Fig. 2c, d). There was no significant difference in Shannon diversity between eroding slopes and reference slopes in two soil layers (Fig. 2c, d). However, the depositional zones hold higher Shannon diversity than the reference slopes, but the significance merely existed in subsoil. Compared with eroding slopes, the depositional zones harbored more diverse bacteria, and these differences increased with increasing slope gradient, resulting in the significantly higher Shannon diversity on 20° slopes in both topsoil and subsoil (Fig. 2c, d;  $P$  < 0.05).

#### 3.3. Soil bacterial community structure

NMDS using both Bray-Curtis and UniFrac distances showed that the bacterial community structure on eroding slopes was distinct from that on reference slopes. However, the bacterial community structure in the corresponding depositional zones was similar to that of reference slopes (Fig. 3). Further, ANOSIM, PERMANOVA and MRPP verified that the bacterial community structure on eroding slopes was significantly different from that of reference slopes, unlike depositional zones (Table S3). For both eroding slopes and depositional zones, there were no marked differences in the bacterial community structure between 10° and 20° slopes. Eroding slopes and depositional zones of 10° slopes supported distinct bacterial communities based on Bray-Curtis distance, while differences for the 20° slopes were observed based on both Bray-Curtis and UniFrac distances (Table S3). In addition, soil bacterial community structure clearly differed between topsoil and subsoil based on Bray-Curtis distance (ANOSIM:  $R$  = 0.389,  $P$  < 0.001; PERMANOVA:  $R^2$  = 0.219,  $P$  < 0.001; MRPP:  $R$  = 0.095,  $P$  < 0.001) and UniFrac distance (ANOSIM:  $R$  = 0.215,  $P$  < 0.001; PERMANOVA:  $R^2$  = 0.077,  $P$  < 0.001; MRPP:  $R$  = 0.021,  $P$  < 0.001).

Redundancy analysis revealed that soil moisture, organic matter, available P and available K were the main environmental predictors controlling bacterial community structure, collectively accounting for 34.2% of total community variation (Fig. 4). Soil moisture explained the largest proportion (11.1%) of total community variation, while organic matter, available P and available K explained 7.6%, 6.1% and 9.4% of the variation, respectively.

#### 3.4. Bacterial co-occurrence networks

Based on strong and significant correlations, bacterial co-occurrence networks were constructed for eroding slopes and depositional zones. The eroding network included 145 nodes and 523 edges, and the depositional network consisted of 153 nodes and 632 edges (Fig. 5a, b).

**Table 2**  
Soil physicochemical properties of reference slopes, eroding slopes and depositional zones across three different slope gradients.

Soil properties	Depth (cm)	5° slope (Reference)	10° slope		20° slope	
			Eroding	Depositional	Eroding	Depositional
Moisture (%)	0–5	4.99 ± 0.71Aa	4.98 ± 0.47A	9.82 ± 0.52b	4.31 ± 0.31A	11.45 ± 0.17c
	5–10	14.77 ± 0.29Ba	15.05 ± 0.12B	16.04 ± 0.44ab	13.89 ± 0.40A	16.63 ± 0.93b
pH	0–5	8.43 ± 0.01ABb	8.46 ± 0.01B	8.17 ± 0.03a	8.40 ± 0.03A	8.13 ± 0.09a
	5–10	8.53 ± 0.05Ab	8.54 ± 0.03A	8.16 ± 0.05a	8.49 ± 0.03A	8.15 ± 0.05a
Soil organic matter (g·kg <sup>-1</sup> )	0–5	18.63 ± 0.09Ba	18.45 ± 1.09AB	21.96 ± 0.88b	16.57 ± 0.83A	22.78 ± 0.88b
	5–10	13.94 ± 0.71Aa	16.52 ± 1.01A	19.44 ± 0.42b	15.91 ± 0.76A	19.20 ± 0.48b
Dissolved organic carbon (mg·kg <sup>-1</sup> )	0–5	56.38 ± 4.17Ba	55.47 ± 3.93AB	110.12 ± 6.04b	45.11 ± 4.49A	131.89 ± 9.35b
	5–10	30.62 ± 1.92Aa	41.66 ± 5.30B	37.72 ± 6.06ab	33.54 ± 2.29A	50.87 ± 7.11b
Total N (g·kg <sup>-1</sup> )	0–5	0.82 ± 0.04Aa	0.80 ± 0.01A	0.90 ± 0.07a	0.82 ± 0.05A	0.93 ± 0.02a
	5–10	0.77 ± 0.01Aa	0.75 ± 0.01A	0.77 ± 0.04a	0.80 ± 0.05A	0.85 ± 0.04a
NO <sub>3</sub> -N (mg·kg <sup>-1</sup> )	0–5	9.52 ± 0.36Aa	9.67 ± 0.23A	18.17 ± 1.63b	9.30 ± 0.46A	41.70 ± 5.59c
	5–10	4.95 ± 0.84Aa	4.67 ± 0.54A	4.86 ± 0.27a	6.20 ± 0.37A	14.72 ± 2.13b
NH <sub>4</sub> -N (mg·kg <sup>-1</sup> )	0–5	3.85 ± 0.88Aa	3.26 ± 0.54A	3.47 ± 0.27a	4.21 ± 0.87A	4.78 ± 1.12a
	5–10	4.39 ± 0.25Aa	4.75 ± 2.58A	4.26 ± 0.32a	4.83 ± 2.26A	3.98 ± 0.12a
Available P (mg·kg <sup>-1</sup> )	0–5	8.52 ± 0.57Aa	11.57 ± 0.15B	10.82 ± 0.06b	16.03 ± 0.40C	11.57 ± 0.24b
	5–10	6.73 ± 0.08Ca	5.58 ± 0.08A	8.45 ± 0.26b	6.33 ± 0.18B	9.78 ± 0.13c
Available K (mg·kg <sup>-1</sup> )	0–5	237.47 ± 8.95Ba	200.67 ± 2.40A	317.37 ± 5.71b	230.07 ± 3.41B	342.43 ± 2.24c
	5–10	163.27 ± 0.68Aa	160.50 ± 5.35A	234.97 ± 1.75b	183.07 ± 6.07A	300.80 ± 4.01c
Clay (%)	0–5	26.79 ± 0.81Aa	26.35 ± 2.37A	26.61 ± 1.25a	25.65 ± 2.21A	27.17 ± 1.18a
	5–10	29.91 ± 1.27Aa	30.32 ± 1.39A	30.41 ± 0.85a	29.59 ± 1.43A	29.06 ± 1.95a
Silt (%)	0–5	65.82 ± 0.56Aa	65.87 ± 1.18A	65.32 ± 0.90a	66.07 ± 0.69A	65.22 ± 2.11a
	5–10	63.23 ± 0.97Aa	64.42 ± 1.74A	64.19 ± 1.02a	64.05 ± 1.48A	64.22 ± 1.04a
Sand (%)	0–5	7.39 ± 0.94Aa	7.78 ± 1.19A	8.08 ± 0.36a	8.28 ± 1.55A	7.61 ± 1.60a
	5–10	6.86 ± 0.70Aa	5.26 ± 1.09A	5.40 ± 0.83a	6.36 ± 0.26A	6.72 ± 0.92a

Note: different capital and lowercase letters indicate significant differences between reference slopes and eroding slopes, depositional zones at  $P < 0.05$ , ANOVA, respectively.

Major nodes in eroding and depositional networks belonged to Proteobacteria, Actinobacteria and Acidobacteria. Proteobacteria and Actinobacteria were more connected in the depositional network, whereas Gemmatimonadetes, Nitrospirae and Firmicutes had more connections in the eroding network (Fig. 5c).

Network topological features were used to describe the inter-relationships among bacterial species in the networks and to compare the eroding and depositional networks with their identically sized Erdős-Rényi random networks (Table 4). The modularity values of the eroding and depositional networks were 0.643 and 0.533, respectively. Modularity, clustering coefficient and average path length values for the two networks were higher than these of their respective random networks. This indicated that both eroding and depositional networks exhibited prominent ‘small-world’ modularity and a hierarchy of topological features. Modularity, average path length and network diameter values were greater for the eroding network, while clustering coefficient, average degree and density were higher for the depositional network (Table 4).

## 4. Discussion

### 4.1. Both erosion and deposition induce changes in soil physicochemical properties

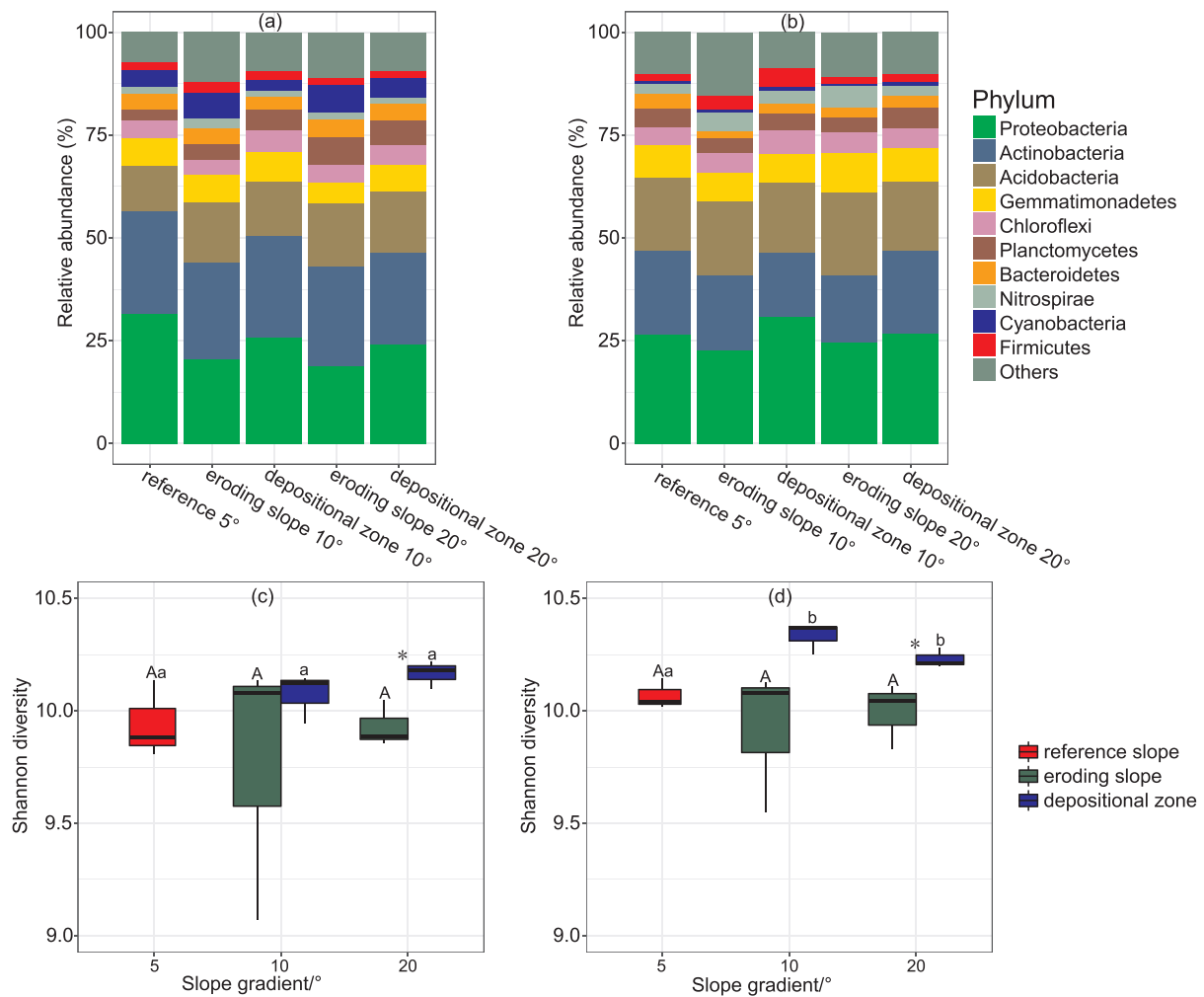
Compared with the reference slopes, the greater soil nutrients (C, N, P) in the depositional zones and the according decrease of organic matter and dissolved organic carbon on the eroding slopes clearly demonstrated the erosion- and deposition-induced spatial variation of soil physicochemical properties over 3 years. This variation mainly resulted from the substantial loss of runoff and sediment from the eroding slopes to the depositional zones (Table 1). Light organic matter and more labile fractions are prone to migrate with runoff and sediment (Nie et al.,

2016), which consequently led to the depletion of soil nutrients on eroding slopes and the enrichment in the lower-lying depositional zones (Table 2).

When compared with the reference slopes, soil nutrients were increasingly depleted or enriched with increasing slope gradients (Table 2). This result could be attributed to the fact that more runoff and sediment were generated with the increase of slope gradient (Table 1), therefore more nutrient loss occurred on eroding slopes via binding with finer particles (El Kateb et al., 2013; Mahmoodabadi and Sajjadi, 2016), which consequently produced more available concentration of nutrients in the depositional zones. Furthermore, the increasing loss of runoff and sediment from slope 10° to 20° caused a growing divergence in soil conditions between the eroding slopes and depositional zones (Tables 1 and S2), further highlighting the enlarging effects of slope gradient on spatial differentiation of soil moisture and nutrients. Similar patterns were also observed by Wang et al. (2017b) that erosion-induced spatial differentiation of soil moisture and soil organic carbon were less pronounced on gentler slopes than on steeper slopes.

### 4.2. Contrasting responses of soil bacterial communities to erosion and deposition

Using high-throughput sequencing, we found that bacterial alpha diversity in depositional zones was higher than on reference slopes in two soil layers after 3 years of erosion (Fig. 2c, d). The substantial environmental disturbance in microbial habitats, induced by deposition, might be responsible for this result. **The temporal deposition of runoff and sediment can promote the creation of additional niches, accelerate the colonization by new soil-dwelling bacterial species and reduce competitive dominance effects;** thus, deposition could result in high bacterial diversity following complex community reassembly processes



**Fig. 2.** The relative abundances of main bacterial phyla from reference slopes, eroding slopes and deposition zones across three different slope gradients in 0–5 cm (a) and 5–10 cm (b), and the Shannon diversity of soil bacterial communities in 0–5 cm (c) and 5–10 cm (d). Different uppercase and lowercase letters indicate significant differences between reference slopes and eroding slopes, depositional zones at  $P < 0.05$ , ANOVA, respectively. Asterisks represent significant differences between eroding slopes and depositional zones at  $P < 0.05$ , Student's t-tests.

**Table 3**  
Pearson correlations between the relative abundances of main phyla and soil physicochemical properties.

Phylum	Moisture	pH	Soil organic matter	Dissolved organic carbon	Total N	NO <sub>3</sub> -N	NH <sub>4</sub> -N	Available P	Available K	Clay	Silt	Sand
Proteobacteria	0.30	-0.26	0.13	-0.06	0.07	-0.10	-0.14	<b>-0.44</b>	0.15	0.31	-0.26	-0.24
Actinobacteria	<b>-0.66</b>	-0.02	0.25	<b>0.43</b>	0.33	0.30	-0.15	<b>0.55</b>	0.34	<b>-0.63</b>	<b>0.38</b>	<b>0.64</b>
Acidobacteria	<b>0.47</b>	0.16	<b>-0.39</b>	-0.33	<b>-0.40</b>	-0.22	0.27	-0.32	<b>-0.36</b>	<b>0.41</b>	-0.30	<b>-0.36</b>
Gemmatimonadetes	<b>0.49</b>	0.12	-0.26	-0.21	-0.08	-0.19	-0.07	<b>-0.55</b>	-0.18	<b>0.49</b>	<b>-0.50</b>	-0.28
Chloroflexi	<b>0.38</b>	<b>-0.41</b>	0.23	0.14	0.02	0.07	0.35	-0.18	0.24	0.22	-0.21	-0.15
Planctomycetes	-0.10	-0.32	0.15	0.27	0.24	<b>0.40</b>	0.26	<b>0.51</b>	0.33	-0.27	0.18	0.26
Bacteroidetes	<b>-0.56</b>	-0.10	0.12	0.26	<b>0.44</b>	0.32	-0.21	<b>0.61</b>	0.30	<b>-0.40</b>	0.17	<b>0.49</b>
Nitrospirae	<b>0.41</b>	<b>0.40</b>	<b>-0.44</b>	<b>-0.46</b>	<b>-0.46</b>	<b>-0.44</b>	<b>0.39</b>	<b>-0.58</b>	<b>-0.55</b>	<b>0.48</b>	-0.32	<b>-0.46</b>
Cyanobacteria	<b>-0.60</b>	0.00	0.21	0.21	0.22	0.24	-0.07	<b>0.57</b>	0.15	<b>-0.54</b>	<b>0.40</b>	<b>0.47</b>
Firmicutes	0.24	-0.13	0.15	-0.15	-0.18	-0.21	-0.28	-0.17	-0.10	0.24	0.09	<b>-0.48</b>

Bold values indicate significant at  $P < 0.05$ .

(Violle et al., 2010; Zhang et al., 2018). Meanwhile, enrichment of soil nutrients in depositional zones provided greater resource availability, which can also increase bacterial diversity (Critschioph et al., 2013; Tiemann and Billings, 2011). Furthermore, soil moisture plays an importance role in soil nutrient diffusion, and this could affect nutrient supply to bacterial communities (Wang et al., 2018), especially in arid and semiarid areas (Maestre et al., 2015). Hence, soil moisture significantly impacted soil bacterial communities (Fig. 4), and the higher moisture content in depositional zones likely contributed to increased

bacterial alpha diversity, which was consistent with the observed positive correlation between soil moisture and Shannon diversity ( $R^2 = 0.42$ ,  $P < 0.05$ ). However, soil bacterial alpha diversity on eroding slopes was not significantly different from that on reference slopes in both topsoil and subsoil (Fig. 2c, d). This result may be partly attributed to the resistance or functional redundancy of soil microorganisms to environmental disturbance that helps to maintain stable community diversity (Griffiths and Philippot, 2013; Guo et al., 2018). Furthermore, compared with the reference slopes, the similar low soil

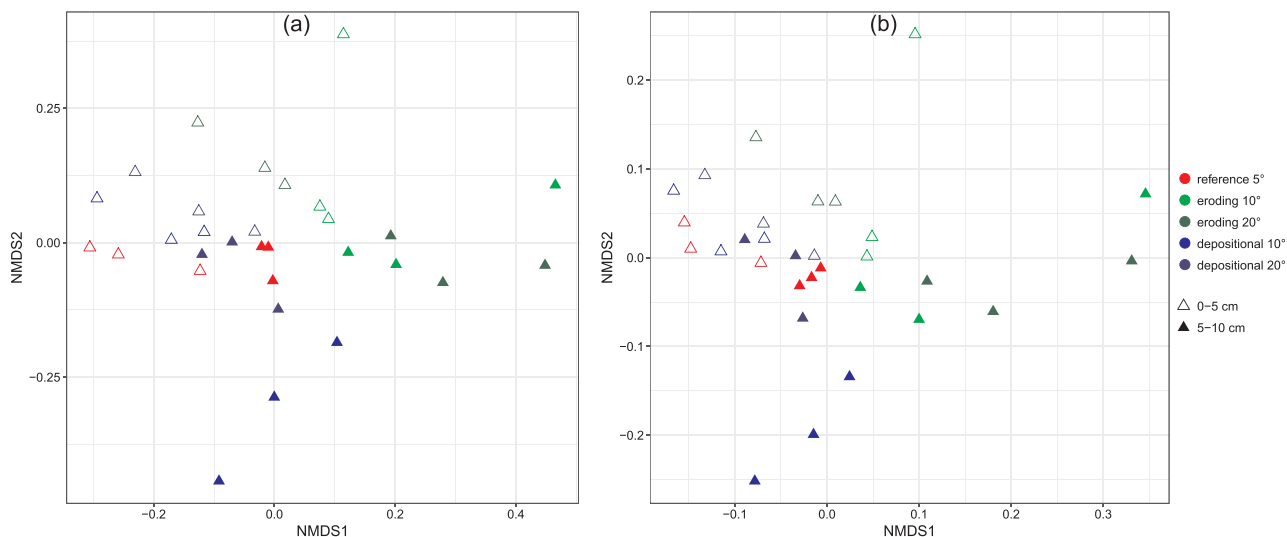


Fig. 3. NMDS of soil bacterial communities across three different slope gradients in two soil layers based on Bray-Curtis (a) and UniFrac (b) distances.

moisture (Table 2) may also constrain the change of alpha diversity in two soil layers of eroding slopes.

In contrast to alpha diversity, soil bacterial community structure of eroding slopes was significantly different from that of reference slopes (Fig. 3 and Table S3), which might be attributed to the erosion-induced disturbance. In the erosion process, the splashing and collision of raindrops, shear forces of runoff and material detachment and dramatic changes in hydrology can result in complex, patchy and variable soil environmental heterogeneity on eroding slopes (Xiao et al., 2018). Soil aggregates broken up by runoff shear force, exposed bacteria into air without aggregates protection and decreased the available substrate supplied for bacteria, and thus caused harms to the growth and proliferation of bacterial communities (Li et al., 2015; Wei et al., 2016). Significantly, the pattern that higher coarse aggregates > 0.25 mm

presented on eroding slopes while the fractions of 0.053–0.25 mm and < 0.053 mm were less (Table S4) than that on reference slopes, suggested that the spatial distribution of different sizes aggregates was altered by selective erosion processes (Liu et al., 2018). Because of soil aggregates serving as the microhabitats of bacterial communities (Bach et al., 2018), the changes in soil aggregates might contribute to the shift of bacterial community on eroding slopes. Besides, the decreased substrates (soil organic matter and dissolved organic carbon) on eroding slopes (Table 2) probably constrained the metabolism of bacteria and induced the selection of specific populations which can better adapt to nutrient-limited conditions (Daebeler et al., 2014; Hartmann et al., 2017). The RDA results confirmed the importance of substrate supply in regulating bacterial communities (Fig. 4). Eventually, the combination of erosion-induced changes in soil aggregates and the reduction of

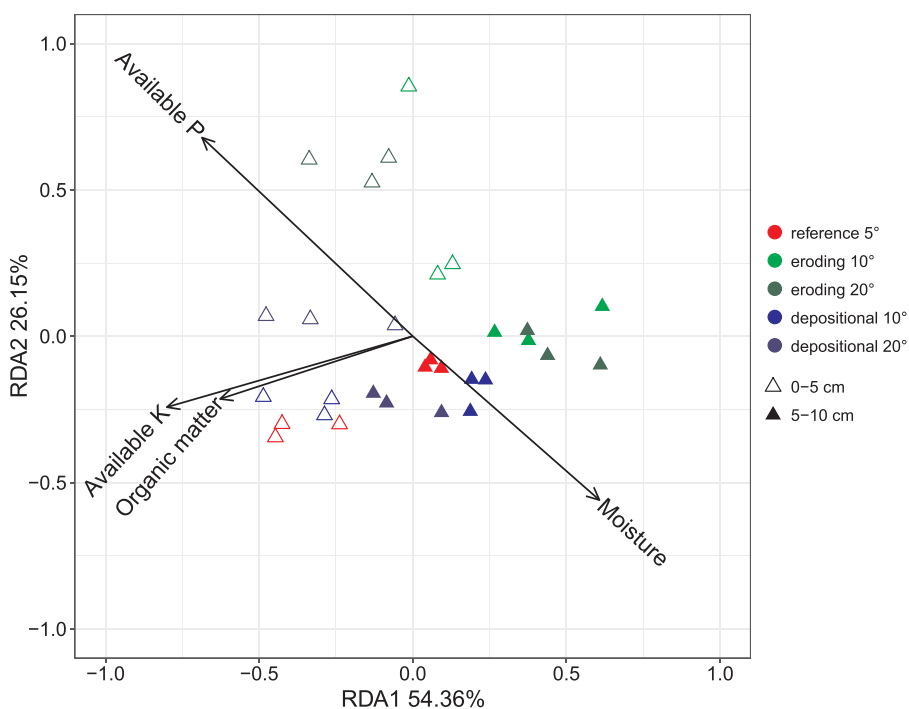
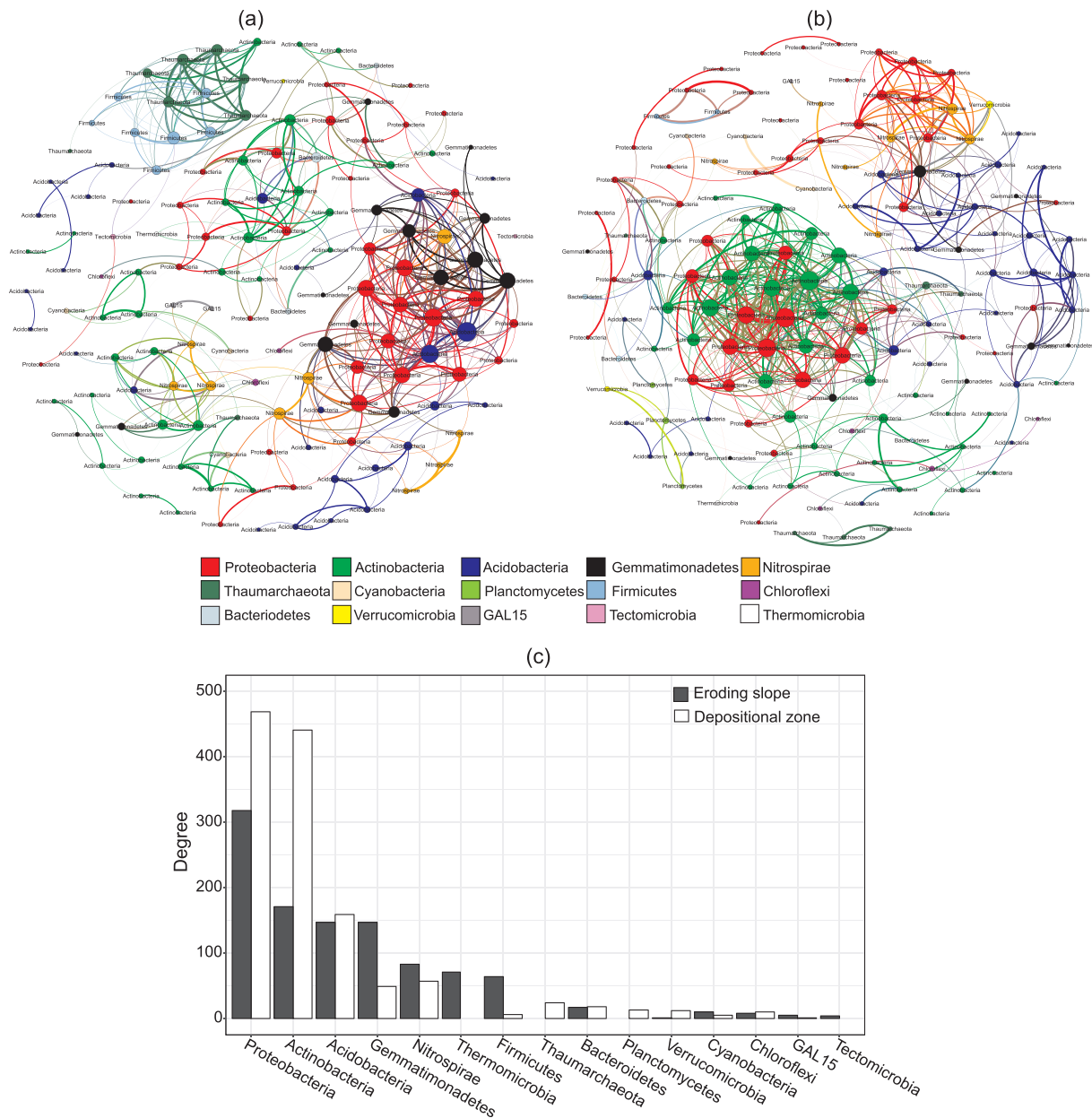


Fig. 4. RDA of soil bacterial communities across three different slope gradients in two soil layers. Only significant soil physicochemical properties, including moisture, soil organic matter, available K and available P are shown ( $P < 0.05$ ).



**Fig. 5.** Bacterial co-occurrence networks of eroding slopes (a) and depositional zones (b), and the distribution of degree of connectivity at the taxonomic level of phylum (c). A connection denotes a significant correlation (Pearson’s  $\rho > 0.8$ ,  $P < 0.01$ ), and a node represents an operational taxonomic unit (97% sequence identify threshold, OTU). The size of each node is proportional to the degree of connectivity, and the thickness of each connection between two nodes is proportional to the values of Pearson's correlation coefficient.

**Table 4**  
Topological features of co-occurrence networks constructed for soil bacterial communities of eroding slopes and depositional zones (corresponding to Fig. 5).

Network metrics	Eroding network	Depositional network
<b>Empirical networks</b>		
Modularity (MD)	0.643	0.533
Clustering coefficient (CC)	0.602	0.615
Average path length (APL)	3.275	3.065
Network diameter (ND)	10	9
Average degree (AD)	7.214	8.261
Graph density (GD)	0.050	0.054
<b>Random networks</b>		
MD ± SD	0.297 ± 0.015	0.275 ± 0.015
CC ± SD	0.050 ± 0.006	0.053 ± 0.005
APL ± SD	2.721 ± 0.011	2.601 ± 0.008

substrate may be responsible for the changes in bacterial community structure on eroding slopes. Nevertheless, though depositional zones experienced remarkable soil physicochemical changes, we did not observe any significant difference in bacterial community structure between depositional zones and reference slopes (Fig. 3 and Table S3). This is probably because a greater supply of water and nutrients in depositional zones (Table 2), providing more opportunities for different species to interact with each other, could strengthen the stability of bacterial community to resist the changes of environmental perturbation (Ghoul and Mitri, 2016; Wang et al., 2018). Moreover, in accordance with previous study (Chu et al., 2016), the bacterial community structure between topsoil and subsoil was significantly different.

Depositional zones supported more diverse bacterial communities than eroding slopes (Fig. 2c, d). The deposition of runoff and sediment created more favorable (high moisture and enriched nutrient content)



and heterogeneous soil conditions, which could stimulate higher microbial diversity than eroding slopes (Banerjee et al., 2016). Furthermore, increased slope gradient strengthened the differences in bacterial communities between eroding slopes and depositional zones (Fig. 2c, d; Fig. 3 and Table S3). The steeper slope gradients reinforced more runoff and sediment migration (Table 1) and enhanced the differences in the soil environment between eroding slopes and depositional zones (Table S2). Following the concept of bacterial communities depending on soil resources (Banerjee et al., 2016), the largest variation of soil condition at the steeper slope 20° resulted in the significant differences of soil bacterial alpha diversity and community structure between its eroding slopes and depositional zones (Figs. 2c, d; 3 and Table S3). Our results suggested that environmental heterogeneity induced by erosion and deposition can exert critical control on spatial distribution of bacterial communities on the Loess Plateau.

#### 4.3. Distinct effects of erosion and deposition on bacterial co-occurrence network patterns

Co-occurrence networks were built to explore the network characteristics and relationships of soil bacterial species, which may provide new insights into the biological effects of soil erosion and deposition (Barberan et al., 2012). Bacterial species in both eroding and depositional networks clustered tightly and non-randomly rather than by chance (Fig. 5a, b). The compositions of eroding and depositional networks were distinct, which may reflect the different roles of environmental filtering in bacterial community composition in specific erosion- and deposition-induced soil conditions (Faust and Raes, 2012). Compared with eroding network, the predominant distributions and correlations of Proteobacteria and Actinobacteria in depositional networks (Fig. 5a–c) indicated that these bacterial groups may feed on similar nutrient pools and share other functional traits in depositional zones. Hence, they may form competitive and/or cooperative relationships that play fundamental ecological roles related to community structure assembly and stability during deposition process.

Since the relative abundances of main bacterial phyla were significantly correlated with soil physicochemical factors (Table 3), soil nutrients between eroding slopes and depositional zones could contribute to the differentiation of bacterial co-occurrence (Mapelli et al., 2018). Actinobacteria are ubiquitous and generally considered as saprophytic microorganisms that can degrade soil organic carbon and play a vital role in carbon cycle (Guo et al., 2019). In our study, Actinobacteria were found significantly and positively correlated with dissolved organic carbon (Table 3), and thus the significant increase of dissolved organic carbon in depositional zones may contribute to the dominance of Actinobacteria in the depositional network. Correspondingly, Nitrospirae, usually living in oligotrophic environment (Geyer and Barrett, 2019), were enriched in eroding network. This may be partly attributed to the depletion of soil organic matter and dissolved organic carbon on eroding slopes (Table 3). The differential enrichment of these bacterial species in eroding and depositional networks may generate contrasting topologies, and thus biogeochemical functions.

Eroding and depositional networks exhibited different topological features (Table 4), suggesting that soil erosion and deposition altered bacterial co-occurrence patterns. Modularity values of > 0.4 indicate a modular structure for both eroding and depositional networks of soil bacterial communities, and the eroding network was more modular than the depositional network (Table 4). Modularity, a metric of non-random connections among nodes in a given module (Faust et al., 2012), can reflect environmental adaption of soil microbes in ecology. Bacterial species within modules have similar ecological functions; hence, modules can be interpreted as niches (Faust et al., 2012), and a higher modularity may imply that more diverse but fragmented niches exist on eroding slopes. By contrast, limited but larger modules in depositional zones may form robust functional clusters, which could strengthen information communication and accelerate energy and

material flow among modules (Tao et al., 2018).

The modular feature was also confirmed by the higher clustering coefficient in the depositional network (Table 4), suggested that more connections among bacterial species may enhance modular functions and thus the entire bacterial network (Faust and Raes, 2012). The average path length was shorter in the depositional network (Table 4), which suggested that the network may respond to environmental disturbance rapidly through efficient information transfer pathways. We compared overall network characteristics and found that the depositional network was larger (more nodes and edges) and more complex (larger average degree of connectivity) than the eroding network. The more favored soil environment (high moisture and enriched nutrient content; Table 2) in depositional zones may support increased network complexity, resulting in enhanced community stability and nutrient transfer efficiency (Wang et al., 2018). However, the simpler networks on eroding slopes may have fewer bacterial connections and be vulnerable to soil disturbance, which could have a negative impact on ecological functions within eroding habitats.

## 5. Conclusions

In the 3-year field simulation experiment, soil erosion and deposition had contrasting effects on bacterial communities. Soil erosion altered bacterial community structure rather than alpha diversity, whereas deposition increased bacterial alpha diversity but did not alter community structure. Increasing slope gradients enlarged the differences in both bacterial alpha diversity and community structure between eroding slopes and depositional zones. Erosion- and deposition-induced soil moisture, soil organic matter, available P and available K were the key drivers of variation in bacterial community structure. The depositional network was larger and more complex than the eroding network, which is indicative of higher resource transfer potential and community stability in depositional zones. Taken together, these findings provide new insights into the effects of soil erosion and deposition on bacterial communities, which have implications for the understanding of the relationships between soil erosion/deposition and biodiversity. Future studies are necessary to assess the effects of soil erosion and deposition on active bacterial communities via RNA-based sequencing.

## Declaration of Competing Interest

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

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2019.113995>.

## References

- Allison, S.D., Goulden, M.L., 2017. Consequences of drought tolerance traits for microbial decomposition in the DEMENT model. *Soil Biol. Biochem.* 107, 104–113. <https://doi.org/10.1016/j.soilbio.2017.01.001>.
- Bach, E.M., Williams, R.J., Hargreaves, S.K., Yang, F., Hofmocker, K.S., 2018. Greatest soil microbial diversity found in micro-habitats. *Soil Biol. Biochem.* 118, 217–226. <https://doi.org/10.1016/j.soilbio.2017.12.018>.
- Banerjee, S., Kirkby, C.A., Schmutter, D., Bissett, A., Kirkegaard, J.A., Richardson, A.E.,

2016. 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. <https://doi.org/10.1016/j.soilbio.2016.03.017>.
- Bao, S.D., 2000. *Soil and Agricultural Chemistry Analysis*. Agriculture Publication, Beijing.
- Barberan, 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. <https://doi.org/10.1038/ismej.2011.119>.
- Bardgett, R.D., van der Putten, W.H., 2014. Belowground biodiversity and ecosystem functioning. *Nature* 515 (7528), 505–511. <https://doi.org/10.1038/nature13855>.
- Bastian, M., Heymann, S., Jacomy, M., 2009. Gephi: an open source software for exploring and manipulating networks. *International AAAI Conference on Weblogs and Social Media*.
- Berhe, A.A., Barnes, R.T., Six, J., Marinspiotta, E., 2018. Role of soil erosion in biogeochemical cycling of essential elements: carbon, nitrogen, and phosphorus. *Annu. Rev. Earth. Pl. Sc.* 46 (1). <https://doi.org/10.1146/annurev-earth-082517-010018>.
- Berhe, A.A., Kleber, M., 2013. Erosion, deposition, and the persistence of soil organic matter: mechanistic considerations and problems with terminology. *Earth. Surf. Proc. Land.* 38 (8), 908–912. <https://doi.org/10.1002/esp.3408>.
- Berhe, A.A., Torn, M.S., 2016. Erosional redistribution of topsoil controls soil nitrogen dynamics. *Biogeochemistry* 132 (1–2), 37–54. <https://doi.org/10.1007/s10533-016-0286-5>.
- 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.L., 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., Yatsunenok, T., Zaneveld, J., Knight, R., 2010. QIIME allows analysis of high-throughput community sequencing data. *Nat. Methods* 7 (5), 335–336. <https://doi.org/10.1038/nmeth.f.303>.
- Chu, H.Y., Sun, H.B., Tripathi, B.M., Adams, J.M., Huang, R., Zhang, Y.J., Shi, Y., 2016. Bacterial community dissimilarity between the surface and subsurface soils equals horizontal differences over several kilometers in the western Tibetan Plateau. *Environ. Microbiol.* 18 (5), 1523–1533. <https://doi.org/10.1111/1462-2920.13236>.
- Critchfield, A., Robinson, C.K., Barnum, T., Fricke, W.F., Davila, A.F., Jedynek, B., McKay, C.P., Diruggiero, J., 2013. Colonization patterns of soil microbial communities in the Atacama Desert. 28–28. *Microbiome* 1 (1). <https://doi.org/10.1186/2049-2618-1-28>.
- Daebeler, A., Bodelier, P.L., Yan, Z., Hefting, M.M., Jia, Z., Laanbroek, H.J., 2014. Interactions between Thaumarchaea, Nitrospira and methanotrophs modulate autotrophic nitrification in volcanic grassland soil. *ISME J.* 8 (12), 2397–2410. <https://doi.org/10.1038/ismej.2014.81>.
- Edgar, R.C., 2013. UPARSE: highly accurate OTU sequences from microbial amplicon reads. *Nat. Methods* 10 (10), 996–998. <https://doi.org/10.1038/nmeth.2604>.
- Edgar, R.C., Haas, B.J., Clemente, J.C., Quince, C., Knight, R., 2011. UCHIME improves sensitivity and speed of chimera detection. *Bioinformatics* 27 (16), 2194–2200. <https://doi.org/10.1093/bioinformatics/btr381>.
- El Kateb, H., Zhang, H., Zhang, P., Mosandl, R., 2013. Soil erosion and surface runoff on different vegetation covers and slope gradients: a field experiment in Southern Shaanxi Province, China. *Catena* 105, 1–10. <https://doi.org/10.1016/j.catena.2012.12.012>.
- Evans, C.C., LePard, K.J., Kwak, J.W., Stancukas, M.C., Laskowski, S., Dougherty, J., Moulton, L., Glawe, A., Wang, Y., Leone, V., Antonopoulos, D.A., Smith, D., Chang, E.B., Ciancio, M.J., 2014. Exercise prevents weight gain and alters the gut microbiota in a mouse model of high fat diet-induced obesity. *Plos One* 9 (3). <https://doi.org/10.1371/journal.pone.0092193>.
- Faust, K., Raes, J., 2012. Microbial interactions: from networks to models. *Nat. Rev. Microbiol.* 10 (8), 538–550. <https://doi.org/10.1038/nrmicro2832>.
- Faust, K., Sathirapongsasuti, J.F., Izard, J., Segata, N., Gevers, D., Raes, J., Huttenhower, C., 2012. Microbial co-occurrence relationships in the human microbiome. *PLoS Comp. Biol.* 8 (7). <https://doi.org/10.1371/journal.pcbi.1002606>.
- Fu, B.J., 2010. Soil erosion and its control in the Loess Plateau of China. *Soil Use Manage.* 5 (2), 76–82. <https://doi.org/10.1111/j.1475-2743.1989.tb00765.x>.
- Fu, B.J., Liu, Y., Lü, Y.H., He, C.S., Zeng, Y., Wu, B.F., 2011. Assessing the soil erosion control service of ecosystems change in the Loess Plateau of China. *Ecol. Complex.* 8 (4), 284–293. <https://doi.org/10.1016/j.ecocom.2011.07.003>.
- Geyer, K.M., Barrett, J.E., 2019. Unimodal productivity-diversity relationships among bacterial communities in a simple polar soil ecosystem. *Environ. Microbiol.* 21 (7), 2523–2532. <https://doi.org/10.1111/1462-2920.14639>.
- Ghoul, M., Mitri, S., 2016. The ecology and evolution of microbial competition. *Trends Microbiol.* 24 (10), 833–845. <https://doi.org/10.1016/j.tim.2016.06.011>.
- Gregorich, E.G., Greer, K.J., Anderson, D.W., Liang, B.C., 1998. Carbon distribution and losses: erosion and deposition effects. *Soil Till. Res.* 47 (3), 291–302. [https://doi.org/10.1016/S0167-1987\(98\)00117-2](https://doi.org/10.1016/S0167-1987(98)00117-2).
- Griffiths, B.S., Philippot, L., 2013. Insights into the resistance and resilience of the soil microbial community. *FEMS Microbiol. Rev.* 37 (2), 112–129. <https://doi.org/10.1111/j.1574-6976.2012.00343.x>.
- Grossman, R.B., Reinsch, T.G., 2002. Bulk density and linear extensibility. In: Dane, J.H., Topp, G.C. (Eds.), *Methods of Soil Analysis, Part 4, SSSA Book Series 5. SSSA, Madison, WI, USA*, pp. 201–225. <https://doi.org/10.2136/sssabookser5.4.c9>.
- Guo, Y.Q., Chen, X.T., Wu, Y.Y., Zhang, L., Cheng, J.M., Wei, G.H., Lin, Y.B., 2018. Natural revegetation of a semiarid habitat alters taxonomic and functional diversity of soil microbial communities. *Sci. Total Environ.* 635, 598–606. <https://doi.org/10.1016/j.scitotenv.2018.04.171>.
- Guo, Y.Q., Hou, L.J., Zhang, Z.Y., Zhang, J.L., Cheng, J.M., Wei, G.H., Lin, Y.B., 2019. Soil microbial diversity during 30 years of grassland restoration on the Loess Plateau, China: tight linkages with plant diversity. *Land Degrad. Dev.* 30 (10), 1172–1182. <https://doi.org/10.1002/ldr.3300>.
- Hartmann, M., Brunner, I., Hagedorn, F., Bardgett, R.D., Stierli, B., Herzog, C., Chen, X., Zingg, A., Graf-Pannatier, E., Rigling, A., Frey, B., 2017. A decade of irrigation transforms the soil microbiome of a semi-arid pine forest. *Mol. Ecol.* 26 (4), 1190–1206. <https://doi.org/10.1111/mec.13995>.
- Helgason, B.L., Kongschuh, H.J., Bedard-Haughn, A., VandenBygaart, A.J., 2014. Microbial distribution in an eroded landscape: buried horizons support abundant and unique communities. *Agr. Ecosyst. Environ.* 196, 94–102. <https://doi.org/10.1016/j.agee.2014.06.029>.
- Huang, J.Q., Li, Z.W., Nie, X.D., Zhang, J.C., Tang, Z.H., Ma, W.M., Yu, W., Zeng, G.M., 2014. Microbial responses to soil rewetting in erosional and depositional environments in relation to the organic carbon dynamics. *Geomorphology* 204, 256–264. <https://doi.org/10.1016/j.geomorph.2013.08.010>.
- Shi, H., Shao, M.A., 2000. Soil and water loss from the Loess Plateau in China. *J. Arid Environ.* 45 (1), 9–20. <https://doi.org/10.1006/jare.1999.0618>.
- Kirkels, F., Cammeraat, L.H., Kuhn, N.J., 2014. The fate of soil organic carbon upon erosion, transport and deposition in agricultural landscapes—a review of different concepts. *Geomorphology* 226, 94–105. <https://doi.org/10.1016/j.geomorph.2014.07.023>.
- Kjeldahl, J., 1883. Neue methode zur bestimmung des stickstoffs in organischen körnern. *Anal. Bioanal. Chem.* 22, 366–382. <https://doi.org/10.1007/BF01338151>.
- Lal, R., 2003. Soil erosion and the global carbon budget. *Environ. Int.* 29 (4), 437–450. [https://doi.org/10.1016/S0160-4120\(02\)00192-7](https://doi.org/10.1016/S0160-4120(02)00192-7).
- Li, Z.W., Xiao, H.B., Tang, Z.H., Huang, J.Q., Nie, X.D., Huang, B., Ma, W.M., Lu, Y.M., Zeng, G.M., 2015. Microbial responses to erosion-induced soil physico-chemical property changes in the hilly red soil region of southern China. *Eur. J. Soil. Biol.* 71, 37–44. <https://doi.org/10.1016/j.ejsobi.2015.10.003>.
- Liang, C., Schimel, J.P., Jastrow, J.D., 2017. The importance of anabolism in microbial control over soil carbon storage. *Nat. Microbiol.* 2 (8). <https://doi.org/10.1038/nmicrobiol.2017.105>.
- Liu, L., Li, Z.W., Chang, X.F., Nie, X.D., Liu, C., Xiao, H.B., Wang, D.Y., 2018. Relationships of the hydraulic flow characteristics with the transport of soil organic carbon and sediment loss in the Loess Plateau. *Soil Till. Res.* 175, 291–301. <https://doi.org/10.1016/j.still.2017.09.011>.
- Mabuyah, J.A., Nakagoshi, N., Isagi, Y., 2004. Influence of erosion on soil microbial biomass, abundance and community diversity. *Land Degrad. Dev.* 15 (2), 183–195. <https://doi.org/10.1002/ldr.607>.
- Maestre, F.T., Delgado-Baquerizo, M., Jeffries, T.C., Eldridge, D.J., Ochoa, V., Gozalo, B., Luis Quero, J., Garcia-Gomez, M., Gallardo, A., Ulrich, W., Bowker, M.A., Arredondo, T., Barraza-Zepeda, C., Bran, D., Florentino, A., Gaitan, J., Gutierrez, J.R., Huber-Sannwald, E., Jankju, M., Mau, R.L., Miriti, M., Naseri, K., Ospina, A., Stavi, I., Wang, D., Woods, N.N., Yuan, X., Zaady, E., Singh, B.K., 2015. Increasing aridity reduces soil microbial diversity and abundance in global drylands. *Proc. Natl. Acad. Sci. U. S. A.* 112 (51), 15684–15689. <https://doi.org/10.1073/pnas.1516684112>.
- Mahmoodabadi, M., Sajjadi, S.A., 2016. Effects of rain intensity, slope gradient and particle size distribution on the relative contributions of splash and wash loads to rain-induced erosion. *Geomorphology* 253, 159–167. <https://doi.org/10.1016/j.geomorph.2015.10.010>.
- Mapelli, F., Marasco, R., Fusi, M., Scaglia, B., Tsiamis, G., Rolli, E., Fodelianakis, S., Bourtzi, K., Ventura, S., Tambone, F., Adani, F., Borin, S., Daffonchio, D., 2018. The stage of soil development modulates rhizosphere effect along a High Arctic desert chronosequence. *ISME J.* <https://doi.org/10.1038/s41396-017-0026-4>.
- Muller-Nedebeck, D., Chivenge, P., Chaplot, V., 2016. Selective organic carbon losses from soils by sheet erosion and main controls. *Earth. Surf. Proc. Land.* 41 (10), 1399–1408. <https://doi.org/10.1002/esp.3916>.
- Nie, X.J., Zhang, J.H., Cheng, J.X., Gao, H., Guan, Z.M., 2016. Effect of soil redistribution on various organic carbons in a water- and tillage-eroded soil. *Soil Till. Res.* 155, 1–8. <https://doi.org/10.1016/j.still.2015.07.003>.
- Olsen, S.R., Watanabe, F.S., 1957. A method to determine a phosphorus maximum for soils as measured by the Langmuir isotherm. *Soil Sci. Soc. Am. J.* 21, 144–149. <https://doi.org/10.2136/sssaj1957.03615995002100020004x>.
- Pimentel, D., Harvey, C., Resosudarmo, P., Sinclair, K., Kurz, D., McNair, M., Crist, S., Shpritz, L., Fitton, L., Saffouri, R., 1995. Environmental and economic costs of soil erosion and conservation benefits. *Science* 267 (5201), 1117–1123. <https://doi.org/10.1126/science.267.5201.1117>.
- Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., Gloeckner, F.O., 2013. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucl. Acids Res.* 41 (D1), D590–D596. <https://doi.org/10.1093/nar/gks1219>.
- Core Team, R., 2017. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- 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 (10), 1340–1351. <https://doi.org/10.1038/ismej.2010.58>.
- Stallard, R.F., 1998. Terrestrial sedimentation and the carbon cycle: coupling weathering and erosion to carbon burial. *Global Biogeochem. Cy.* 12 (2), 231–257. <https://doi.org/10.1029/98gb00741>.
- Takriti, M., Wild, B., Schneck, J., Mooshammer, M., Knoltsch, A., Lashchinskiy, N., Eloy Alves, R.J., Gentsch, N., Gittel, A., Mikutta, R., Wanek, W., Richter, A., 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. <https://doi.org/10.1016/j.soilbio.2018.02.022>.
- Tao, J.M., Meng, D.L., Qin, C., Liu, X.D., Liang, Y.L., Xiao, Y.H., Liu, Z.H., Gu, Y.B., Li, J., Yin, H.Q., 2018. Integrated network analysis reveals the importance of microbial interactions for maize growth. *Appl. Microbiol. Biotechnol.* 102 (8), 3805–3818.

- <https://doi.org/10.1007/s00253-018-8837-4>.
- 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 (9), 1837–1847. <https://doi.org/10.1016/j.soilbio.2011.04.020>.
- Violle, C., Pu, Z., Jiang, L., 2010. Experimental demonstration of the importance of competition under disturbance. *Proc. Natl. Acad. Sci. U. S. A.* 107 (29), 12925–12929. <https://doi.org/10.1073/pnas.1000699107>.
- Walkley, A., Black, I.A., 1934. An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. *Soil Sci.* 37 (1), 29–38. <https://doi.org/10.1097/00010694-193401000-00003>.
- Wang, R., Wang, Z.Q., Sun, Q.Q., Zhao, M., Du, L.L., Wu, D.F., Li, R.J., Gao, X., Guo, S.L., 2016. Effects of crop types and nitrogen fertilization on temperature sensitivity of soil respiration in the semi-arid Loess Plateau. *Soil Till. Res.* 163, 1–9. <https://doi.org/10.1016/j.still.2016.05.005>.
- Wang, S., Wang, X.B., Han, X.G., Deng, Y., 2018. Higher precipitation strengthens the microbial interactions in semi-arid grassland soils. *Global Ecol. Biogeogr.* 27 (5), 570–580. <https://doi.org/10.1111/geb.12718>.
- Wang, Z.Q., Hu, Y.X., Wang, R., Guo, S.L., Du, L.L., Zhao, M., Yao, Z.H., 2017a. Soil organic carbon on the fragmented Chinese Loess Plateau: combining effects of vegetation types and topographic positions. *Soil Till. Res.* 174, 1–5. <https://doi.org/10.1016/j.still.2017.05.005>.
- Wang, Z.Q., Wang, R., Sun, Q.Q., Du, L.L., Zhao, M., Hu, Y.X., Guo, S.L., 2017b. Soil CO<sub>2</sub> emissions from different slope gradients and positions in the semiarid Loess Plateau of China. *Ecol. Eng.* 105, 231–239. <https://doi.org/10.1016/j.ecoleng.2017.04.050>.
- Wei, S.C., Zhang, X.P., McLaughlin, N.B., Yang, X.M., Liang, A.Z., Jia, S.X., Chen, X.W., 2016. Effect of breakdown and dispersion of soil aggregates by erosion on soil CO<sub>2</sub> emission. *Geoderma* 264, 238–243. <https://doi.org/10.1016/j.geoderma.2015.10.021>.
- Wu, X.L., Wei, Y.J., Wang, J.G., Cai, C.F., Deng, Y.S., Xia, J.W., 2018a. RUSLE erodibility of heavy-textured soils as affected by soil type, erosional degradation, and rainfall intensity: a field simulation. *Land Degrad. Dev.* 29 (3), 408–421. <https://doi.org/10.1002/ldr.2864>.
- Wu, X.L., Wei, Y.J., Wang, J.G., Xia, J.W., Cai, C.F., Wei, Z.Y., 2018b. Effects of soil type and rainfall intensity on sheet erosion processes and sediment characteristics along the climatic gradient in central-south China. *Sci. Total Environ.* 621, 54–66. <https://doi.org/10.1016/j.scitotenv.2017.11.202>.
- Xiao, H.B., Li, Z.W., Chang, X.F., Huang, B., Nie, X.D., Liu, C., Liu, L., Wang, D.Y., Jiang, J.Y., 2018. The mineralization and sequestration of organic carbon in relation to agricultural soil erosion. *Geoderma* 329, 73–81. <https://doi.org/10.1016/j.geoderma.2018.05.018>.
- Xiao, H.B., Li, Z.W., Chang, X.F., Huang, J.Q., Nie, X.D., Liu, C., Liu, L., Wang, D.Y., Dong, Y.T., Jiang, J.Y., 2017. Soil erosion-related dynamics of soil bacterial communities and microbial respiration. *Appl. Soil Ecol.* 119, 205–213. <https://doi.org/10.1016/j.apsoil.2017.06.018>.
- Yoder, R.E., 1936. A direct method of aggregate analysis of soils and a study of the physical nature of erosion losses. *J. Am. Soc. Agron.* 28 (5), 337–351. <https://doi.org/10.2134/agronj1936.00021962002800050001x>.
- Yue, Y., Ni, J.R., Ciais, P., Piao, S.L., Wang, T., Huang, M.T., Borthwick, A.G., Li, T.H., Wang, Y.C., Chappell, A., Van Oost, K., 2016. Lateral transport of soil carbon and land-atmosphere CO<sub>2</sub> flux induced by water erosion in China. *Proc. Natl. Acad. Sci. U. S. A.* 113 (24), 6617–6622. <https://doi.org/10.1073/pnas.1523358113>.
- Zhang, X.M., Johnston, E.R., Barberan, A., Ren, Y., Wang, Z.P., Han, X.G., 2018. Effect of intermediate disturbance on soil microbial functional diversity depends on the amount of effective resources. *Environ. Microbiol.* 20 (10), 3862–3875. <https://doi.org/10.1111/1462-2920.14407>.