Soil prokaryotic community structure and co-occurrence patterns on the fragmented Chinese Loess Plateau: Effects of topographic units of a soil eroding catena

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A B S T R A C T

Soil prokaryotes composition and diversity are the key to uncovering the mechanisms that drive variations in soil biogeochemical processes. Soil erosion is a primary factor that affects the spatial distribution of the soil prokaryotic community, but how soil prokaryotes in soil-eroding catena respond to environmental factors related to topography remains largely unclear. In this study, topsoils were sampled from three typical erosion geomorphic units (autonomous, transitional and depositional zones) in 2018 to identify the soil prokaryotic community and interactions among the species on the Chinese Loess Plateau. The alpha-diversity was greater but the beta-diversity was lower in the autonomous and transitional zones than in the depositional zone. Gammaproteobacteria and Bacteroidetes were 73% and 68% lower in the autonomous and transitional zones than in the depositional zone. In addition, Deltaproteobacteria, Acidobacteria, Firmicutes, Actinobacteria, Chloroflexi, Gemmatimonadetes and Nitrospirae were significantly higher in the autonomous and transitional zones. A less clustered network and fewer co-occurrences within the prokaryotic community and functional groups of processes were found in the depositional zone than in the autonomous and transitional zones. The alpha-diversity index was significantly negatively correlated with clay particles, soil water content, soil organic carbon (SOC), and ratio of SOC and nitrogen (C/N) but positively correlated with total nitrogen (TN). The higher relative abundances of copiotrophic groups (including Gammaproteobacteria, Bacteroidetes, etc.) in the depositional zone was mainly due to the increased SOC caused by the deposition of SOC-rich clay. Reassembly of the soil physico-chemistry characteristics among the topographic units significantly altered the soil prokaryotic community along the soil-eroding catena.

1. Introduction

Soil prokaryotes are important for functioning of terrestrial ecosystems by influencing carbon storage and nutrient recycling (Allison and Goulden, 2017; de Carvalho et al., 2016; Takriti et al., 2018). While soil prokaryotes are sensitive indicators of changes in environmental properties (Griffiths and Philippot, 2013), previous studies showed that soil prokaryotes are cosmopolitan and that their patterns are mainly driven by environmental factors. For example, several studies highlighted that particle size (Sessitsch et al., 2001), organic carbon (SOC) (Goldfarb et al., 2011), cation exchange capacity (Mapelli et al., 2018), and nutrient availability (Fierer et al., 2007) significantly influenced soil prokaryotes community structure and interactions among species. Therefore, systematically investigate the effects of physico-chemical factors on soil prokaryotes community structure and interactions among species are essential are needed to understand activity of microbial processes and microbial ecology.

A soil-eroding catena, which has been systematically studied by Lei et al. (2000), is a chain that is mainly characterized by the transport and output of erosion materials with an energy link and an interrelated,

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orderly evolving erosive form. In fact, the effect of the topography on soil-eroding catena is apparent (Hook and Burke, 2000; Seibert et al., 2007), with redistribution of the water, nutrient elements (carbon, nitrogen etc.) and soil particles along topographic units (Khomo et al., 2013; Hu and Kuhn, 2014). To date, the influences of soil-eroding catena on physiochemical properties at different topographies has been extensively studied (Khomo et al., 2013; Sun et al., 2014, 2015; Wang et al., 2017b). Several studies have suggested the topography controls the reception and (re)distribution of radiation, water and sediments over the land surface, influencing soil erosion (Seibert et al., 2007; Gabarron-Galeote et al., 2013; Sun et al., 2014). Some studies showed eroding slopes and depositional plots differentiate soil microbial diversity (Xiao et al., 2017), communities structure (Du et al., 2020; Sun et al., 2018), and microbial activity, such as metabolic coefficient (Mohammadi et al., 2017), greenhouse gas emission (Sun et al., 2018; Wiaux et al., 2014) and enzyme activities (Sun et al. 2018). Nevertheless, very few studies have taken the effects of topographic units (topographically defined as autonomous, transitional and depositional zones, Fig. 1) on soil-eroding catena into consideration when addressing the potential variation of the soil prokaryotic community composition and their co-occurrence patterns.

The Chinese Loess Plateau (6.4×10^5 km^2) is a semi-arid region and is considered to be one of the most severely eroded areas (mean soil loss rate: 2860 t km^{-2} year^{-1}); the Chinese Loess Plateau is characterized by an extremely complex soil-eroding catena (Wang et al., 2017b). Inevitably varied soil-eroding catena are found on the Loess Plateau, which are the result of changing erosion processes with different of hydrodynamic conditions. The southern gully region of the Loess Plateau has three typical topographic units, including autonomous, transitional and depositional zones. The effects of complex topography on soil physiochemical characteristics, such as SOC, nitrogen (TN) and soil water content distribution, on the Loess Plateau have been well documented (Sun et al., 2015; Yang et al., 2017; Wang et al., 2018). Systematic investigations of the soil prokaryotic properties are beneficial to deepen the comprehending of the effects of spatial differentiation on soil erosion and, in particular, to explore this effect on a complex topography under a whole soil-eroding catena. However, such studies on the fragmented southern Loess Plateau are still limited. We hypothesized that the topography of the soil-eroding catena would affect the soil prokaryotic community structure, interactions and functions due to the different clay, water and SOC content. Therefore, this study aimed to explore (1) the changes in the soil prokaryotic community, interactions and functions; (2) the altered keystone species; and (3) the factors influencing the changes in the prokaryotic properties among the topographic units of a whole soil-eroding catena.

2. Materials and methods

2.1. Study site

The study area is located in the Wangdonggou watershed, Shaanxi Province, China (Fig. 1). Soil is loam, clay content is 22%, annual mean precipitation is 568 mm, air temperature is 9.1 °C, frost-free period is 194 days, and potential evapotranspiration is 967 mm (Huang et al., 2003). The topography of the watershed is complex, including autonomous, transitional and depositional zones, with the gully density at 2.78 km km^{-2} (Wang et al., 2017b). Variations in topographic units and changes in land uses have fragmented the Chinese Loess Plateau into a complex combination of autonomous, transitional and depositional zones with cropland, orchard and wasteland. The study watershed was 6.3 km^2, the total length of main gully was 4.97 km, and total length of transect was about 1.6 km. In this watershed, the autonomous, transitional and depositional zones area covers about 1/3 of the total area, respectively (Fig. 1).

2.2. Soil sample collection

We randomly collected the soil samples from autonomous, transitional and depositional zones in October during 2018, the samples site in the transitional zone was apart about 2.0 km form autonomous zone, and the depositional zones was the bottom of the main gully. Totally, we collected 26 samples (cropland: 5 and orchard: 5) in the autonomous zone, 10 samples (cropland: 5 and orchard: 5) in the transitional zone and 6 samples (wasteland) in the depositional zone. For each soil sample (0–10 cm), six soil cores were randomly collected using a soil auger (d = 3 cm) and then mixed to compost sample. The samples were placed in a portable refrigerator for transport to the laboratory. Then, the subsamples were: (1) stored at − 80 °C for analysing the bacteria and fungi composition, and (2) air dried for determining the SOC, TN, Olsen-P, soil texture, and pH.
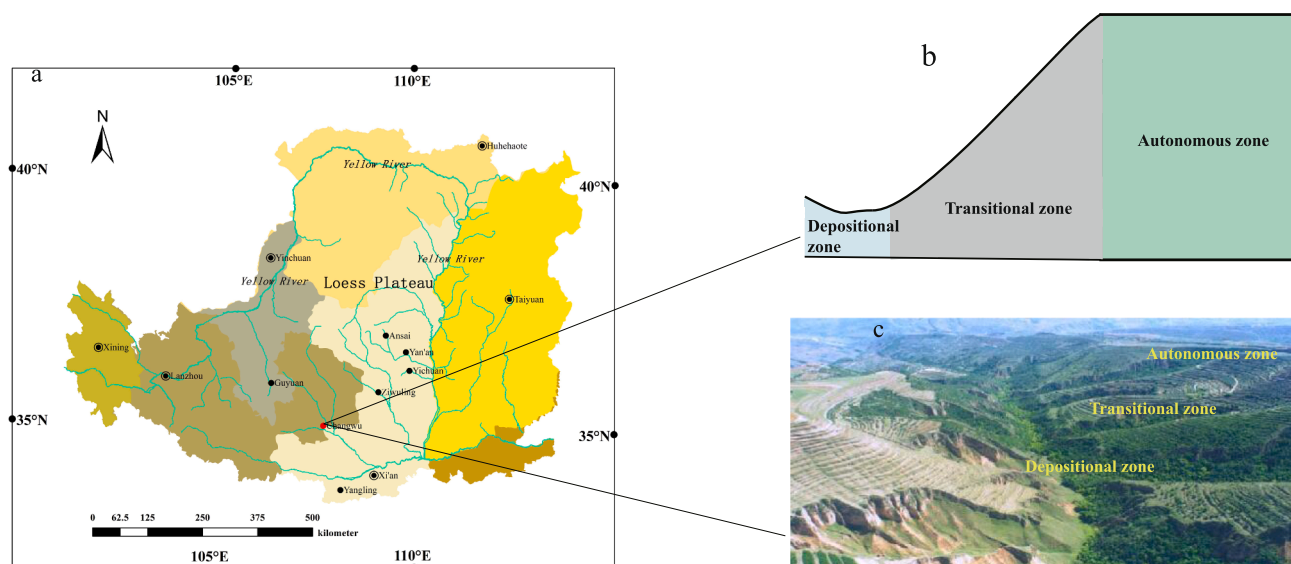

Fig. 1. Information for studies area. a, location of the study area (cited from Wang et al., 2016); b, schematic transects of soil-eroding catenas; c, photo of the study area (cited from Wang et al., 2017b).

2.3. Soil characteristics and microbial community analysis

SOC and total nitrogen (TN) were measured by K_2CrO_7-H_2SO_4 oxidation method and Kjeldahl method, respectively (Fujii et al., 2011; Sparks et al., 1996; Grimshaw et al., 1989). Soil pH was analysed as described by Bao (2000). Olsen-P was determined as described by Olsen and Watanabe (1957). Soil water content was calculated from the weight differences between moist and dry soil samples collected by rings. Soil particle sizes distribution was determined with the laser diffraction particle size analyser (MS2000, Malvern).

We used MoBio Power Soil™ DNA Isolation Kits to extract DNA from the soil, and a Nanodrop spectrophotometer was used to check the quantification and quality. The V4 region of the 16S rRNA gene was amplified using the 515F and 806R primers (Caporaso et al., 2011). Sequencing libraries were generated using TruSeq Rapid PE Cluster Kit (Cat No.PE-402-4001) following manufacturer's recommendations and index codes were added. At last, sequencing was performed using the Illumina HiSeq 2500 platform and 250 bp paired-end reads were generated. As described by Edgar (2013), sequences analysis were performed by Uparse software (Uparse v7.0.1001, http://drive5.com/uparse/). Operational taxonomic units (OTUs) were clustered with sequences ≥ 97% similarity. For each sample, OTU was normalized to the same least sequences (34186) for α-diversity (Chao1, observed species and Shannon index) analyses. FAPROTAX was used to predict the functional groups of processes of the prokaryotes (Louca et al. 2016). The sequence data have been deposited with the NCBI (PRJNA628855, PRJNA636893).

Co-occurrence network analysis was used to investigate the interactions of prokaryotic taxa and functional groups of processes. Genera with mean abundances higher than 0.1% and all functional groups of processes (relative abundances) were selected for Spearman's correlation analysis (igraph and Hmisc packages), and robust if the Spearman's correlation coefficient was > 0.6 and the P-value was < 0.01 (Barberan et al., 2012). Gephi platform was used to visualize the network (Bastian et al., 2009; Newman, 2003, 2006). Values of topological features were evaluated by path length, diameter, degree, density, clustering coefficient and modularity. Genera with the highest mean degree were considered keystone species (Berry and Widder, 2014).

2.4. Statistical analyses

Alpha diversity was calculated with QIIME (Version 1.7.0), and beta-diversity was estimated according to the Bray-Curtis distance between the samples. Canonical correspondence analysis (CCA) was used to evaluate the effects of variables on prokaryotic community structures. The differences in the variables were compared using analysis of variance with ANOVA (IBM SPSS 20.0).

3. Results

3.1. Soil properties

The soil properties markedly differed across the three topographic units (Table 1). SOC, soil water content, clay (<0.002) and C/N were significantly higher but TN and Olsen-P were significantly lower in the depositional zone than the autonomous and transitional zones (Table 1). Compared with that in the autonomous zone (7.80 g kg^{-1}), the SOC was increased by 55% in the depositional zone but decreased by 12% in the transitional zone. Olsen-P was 12% and 32% lower and TN was 22% and 29% lower in the transitional and depositional zones, respectively, than in the autonomous zone. Soil water content was 21% and 31% greater and clay was 43% and 12% greater in the depositional zone than in the other two topographic units.

Table 1

Soil properties of the autonomous, transitional and depositional zones.

Soil properties	Autonomous zone	Transitional zone	Depositional zone
SOC (g kg^{-1})	7.80 ± 0.71b	6.87 ± 0.61c	12.12 ± 1.35a
TN (g kg^{-1})	1.07 ± 0.20a	0.83 ± 0.05b	0.76 ± 1.61b
Olsen − P (mg kg^{-1})	19.09 ± 7.05a	16.81 ± 3.51b	12.95 ± 1.62c
C/N ratios	7.50 ± 2.00b	8.25 ± 1.10a	16.04 ± 1.67c
pH	8.07 ± 0.06a	8.02 ± 0.11a	8.10 ± 0.03a
Soil water (%)	21.89 ± 0.52b	20.09 ± 0.69b	26.40 ± 0.38a
Clay (< 0.002, %)	25.45 ± 2.76b	32.42 ± 2.38a	36.27 ± 1.65a

Note: SOC, Soil organic carbon; TN, Total nitrogen; C/N ratios, SOC/TN ration. Values with different letters in a row mean a significant difference at $p < 0.05$. The values are means of three replicates ± standard deviations.

3.2. Soil prokaryotic diversity and community structure

The topographic units significantly influenced the soil prokaryotic community structure (Fig. 2). Compared with those in the autonomous and transitional zones, the relative abundances of Gammaproteobacteria, Bacteroidetes, and Verrucomicrobia was significantly higher and the relative abundances of Deltaproteobacteria, Acidobacteria, Actinobacteria, Firmicutes, Chloroflexi, Gemmatimonadetes, and Nitrospirae was lower than those in the depositional zone. Prokaryotic alpha-diversity was significantly lower in the depositional zone than in the autonomous and transitional zones, while it exhibited similar values between the autonomous and transitional zones (Table 2).

Furthermore, the prokaryotic community in the depositional zone showed the highest beta-diversity, which indicates a higher dispersion (Fig. 3a). CCA analyses showed soil clay, soil water content, SOC, TN, Olsen-P, C/N, and pH explained 71.21% of the variation, with the first two axes explaining 58.56% and 12.65%, respectively. (Fig. 3b). SOC was the highest ($r^2 = 0.91$, $p < 0.01$), followed by C/N ($r^2 = 0.88$, $p < 0.01$), and then soil clay ($r^2 = 0.79$, $p < 0.01$), soil water content ($r^2 = 0.72$, $p < 0.01$) and TN ($r^2 = 0.26$, $p < 0.05$). The primary phylum were influenced by the soil physico-chemistry properties. Proteobacteria and Bacteroidetes were significantly and positively correlated with clay content, soil water content and C/N, whereas Actinobacteria and Chloroflexi were negatively correlated with them (Table 3). Additionally, at class level, Gammaproteobacteria was positively correlated with clay and SOC, whereas Deltaproteobacteria was negatively correlated with clay and SOC (Table 3).

3.3. Prokaryotic co-occurrence patterns at topographic units

The soil prokaryotes in the depositional zone has less nodes and edges, which indicated more loosely distributed in depositional zone when compared with autonomous and transitional zones (Fig. 4). The network pattern of the depositional zone contained longer characteristic path lengths (2.590) and a higher modularity index (0.535) than that of
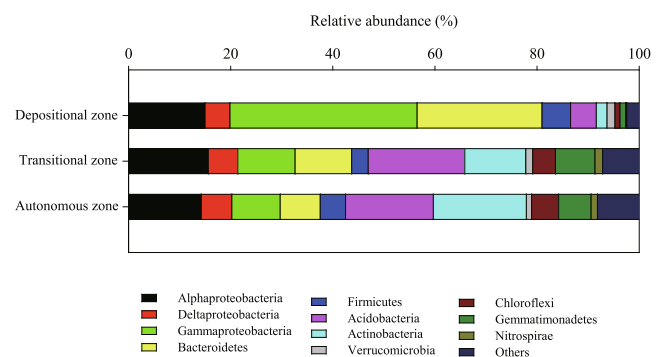

Fig. 2. Taxonomic compositions of the bacterial and fungal communities. Phyla or classes with abundance < 1.0% are summed as "others".

Table 2
Diversity indices in the autonomous, transitional and depositional zones.

Soil properties	Autonomous zone	Transitional zone	Depositional zone
Observed species	3281 ± 273a	3289 ± 139a	2264 ± 161b
Shannon	10.11 ± 0.20a	10.01 ± 0.12a	8.48 ± 0.33b
Simpson	0.998 ± 0.00a	0.998 ± 0.00a	0.988 ± 0.00b
Chao1	3902 ± 419a	3855 ± 302a	2989 ± 200b
ACE	3897 ± 396a	3870 ± 224a	3033 ± 200b

Note: values with different letters in a row mean a significant difference at $p < 0.05$. The values are means of three replicates ± standard deviations.

the autonomous zone (2.231, and 0.429, respectively) and transitional zone (2.356 and 0.482, respectively). The number of co-occurrences was much greater in the autonomous zone than in the transitional and depositional zones. The total correlation edges of the soil prokaryotes were 1666, 1023, and 894 in the autonomous, transitional and depositional zones, respectively. The keystone species were also changed by the topographic units in the eroding landscape (Fig. 4). In the autonomous zone, the soil network was mainly influenced by the phyla Firmicutes, Bacteroidetes, Proteobacteria, and Actinobacteria. In the transitional zone, the soil network was mainly influenced by Bacteroidetes, Firmicutes, and Proteobacteri. However, the soil network was mainly influenced by Bacteroidetes, Proteobacteria, Verrucomicrobia, Proteobacteria, and Oxyphotobacteria in the depositional zone.

Similar to the prokaryotic community co-occurrence patterns in the topographic units, lower links (166), lower mean density (1.430), lower

mean degree (2.721) and higher modularity (0.741) were found in the functional groups of processes network patterns in the depositional zone (Fig. 5). However, in contrast to prokaryotic community co-occurrence, a higher clustering coefficient (0.741) and a shorter path length (1.430) were found in the depositional zone. The key functional groups of processes were also significantly different among the three topographic units. The key functional groups of processes in the autonomous zone included *cyanobacteria, oxygenic photoautotrophy, photoautotrophy, chemoheterotrophy, aerobic nitrite oxidation*, etc. However, *dark hydrogen oxidation, methanogenesis by CO_2 reduction with H_2, hydrogenotrophic methanogenesis, methanogenesis, reductive acetogenesis*, etc., in the transitional zone and *chlorate reducers, knallgas bacteria, nitrogen fixation, nitrate respiration*, etc. in the depositional zone were found in this study (Fig. 5).

3.4. Correlations between soil prokaryotic diversity and keystone species and environmental factors

The alpha-diversity indices were negatively correlated with clay, soil water content, SOC and C/N ratio, whereas they were positively correlated with TN and Olsen-P (Fig. 6). In the autonomous zone, the keystone species were generally positive to clay, pH, TN and Olsen-P but negatively correlated with C/N (Fig. 7). The keystone species in the transitional zone were negatively correlated with clay (except *Alistipes* and *Haliangium*) and Olsen-P but positive to pH, SOC, TN, and C/N (Fig. 7). In the depositional zone, most of the keystone species were
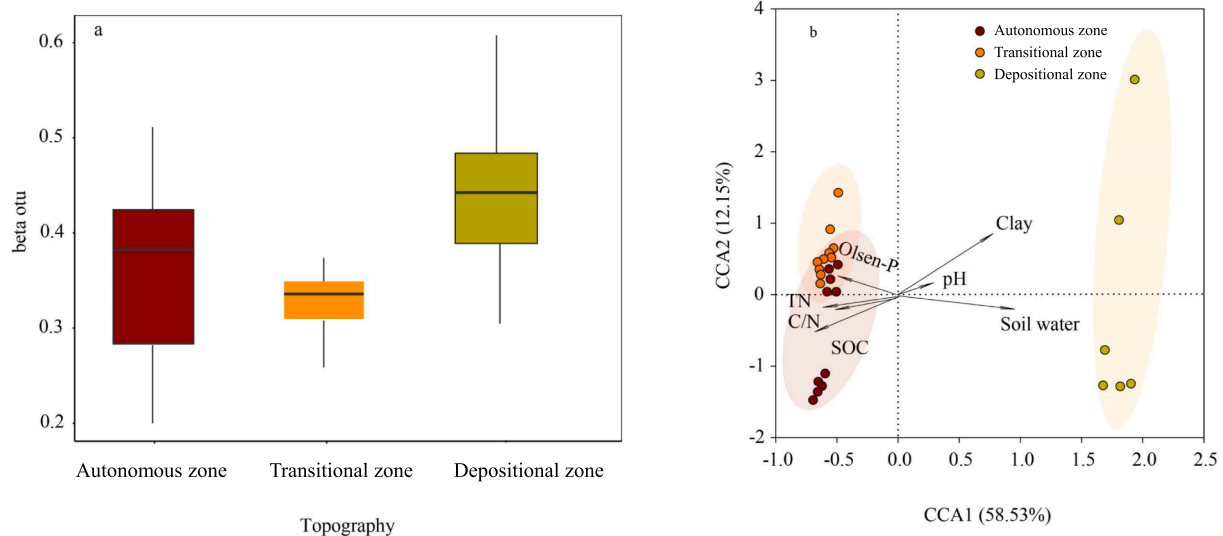

Fig. 3. a, Beta diversity; b, ordination plots of the results from the canonical correlation analysis (CCA) to identify relationships between soil microbial and environmental variables.

Table 3
Spearman correlation between phylum or class and soil properties

Phylum	Clay	pH	SOC	TN	Olsen-P	Soil water	C/N
Proteobacteria	0.723*	0.037	0.372	−0.661**	−0.180	0.547**	0.516*
Alphaproteobacteria	0.251	−0.265	−0.085	−0.099	0.304	0.270	−0.132
Deltaproteobacteria	−0.456*	−0.164	−0.254	0.212	0.041	−0.413	−0.096
Gammaproteobacteria	0.669**	0.120	0.458*	−0.709**	−0.338	0.502*	0.654**
Bacteroidetes	0.768**	0.389	0.426*	−0.470*	−0.170	0.481*	0.513*
Firmicutes	−0.088	−0.014	0.372	0.137	−0.100	0.263	0.092
Acidobacteria	−0.169	−0.301	−0.821**	0.227	0.451*	−0.754**	−0.540**
Actinobacteria	−0.726**	−0.142	−0.407	0.765**	0.319	−0.473*	−0.651**
Verrucomicrobia	0.334	0.117	−0.125	−0.382	−0.121	−0.256	0.131
Chloroflexi	−0.787**	−0.223	−0.362	0.517*	0.108	−0.366	−0446*
Gemmatimonadetes	−0.313	−0.095	−0.686**	0.284	0.411	−0.661**	−0.453*
Nitrospirae	−0.304	−0.266	−0.741**	0.203	0.278	−0.683**	−0.444*

Note: * represents significant correlations at the level of $p < 0.05$, ** represents significant correlations at the level of $p < 0.01$.
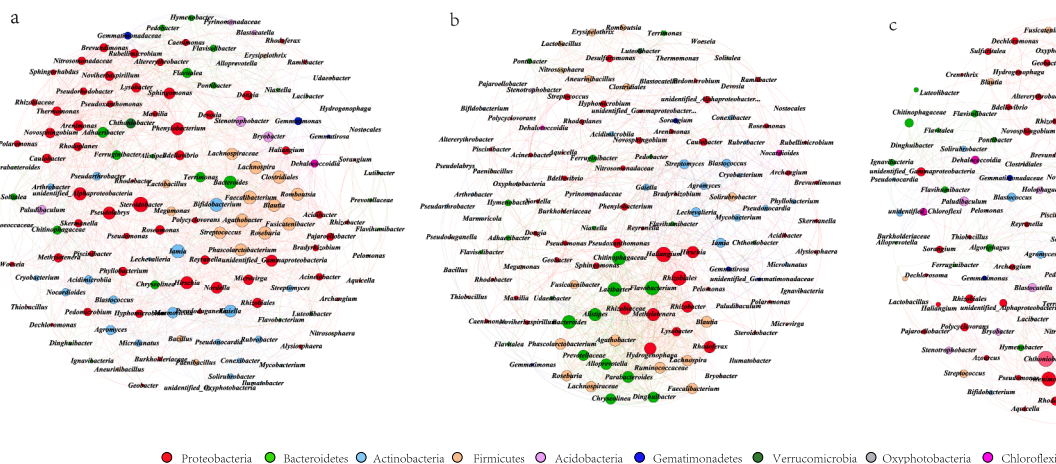
Topography	Node	Links	Path length	Mean density	Modularity	Clustering coefficient	Mean degree
Autonomous zone	140	1666	2.231	0.082	0.429	0.290	11.650
Transitional zone	140	1023	2.356	0.053	0.482	0.243	7.307
Depositional zone	153	894	2.590	0.038	0.535	0.270	5.837

Fig. 4. Soil bacteria co-occurrence networks of autonomous zone (a), transitional zone (b), and depositional zone (c).
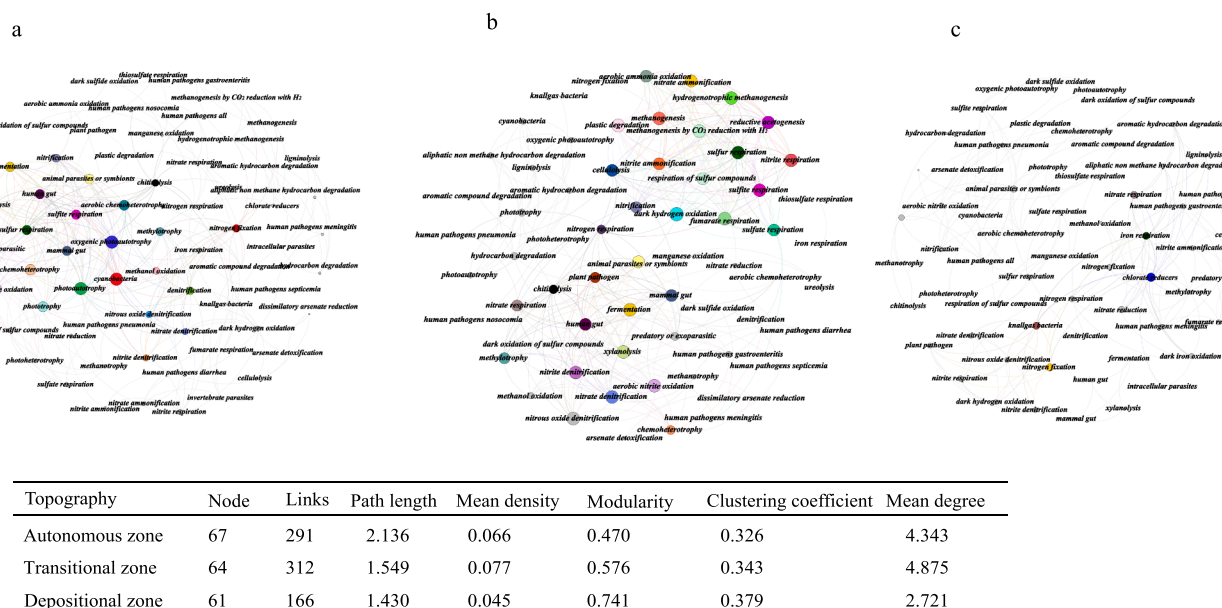
Topography	Node	Links	Path length	Mean density	Modularity	Clustering coefficient	Mean degree
Autonomous zone	67	291	2.136	0.066	0.470	0.326	4.343
Transitional zone	64	312	1.549	0.077	0.576	0.343	4.875
Depositional zone	61	166	1.430	0.045	0.741	0.379	2.721

Fig. 5. Soil bacterial function co-occurrence networks of autonomous zone (a), transitional zone (b), and depositional zone (c).
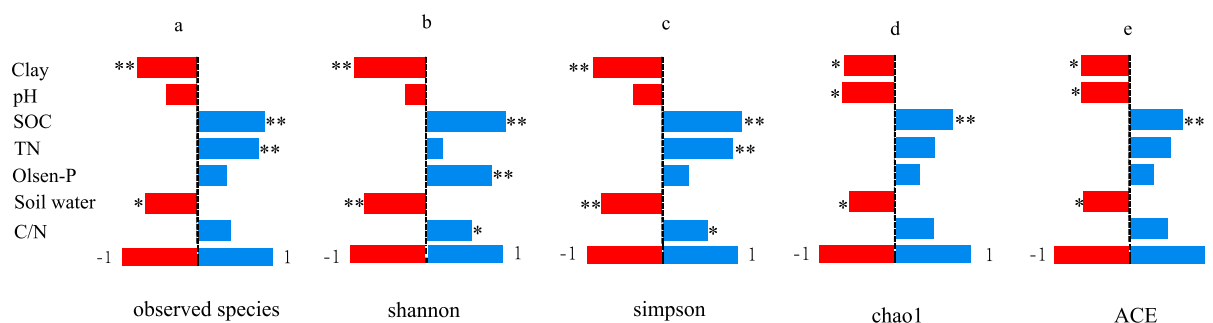

Fig. 6. Correlations between selected soil physico-chemical properties and the bacterial α-diversity in different tomography, and * represent significant correlations at the level of $p < 0.05$, ** represent significant correlations at the level of $p < 0.01$.

Fig. 7. Correlations between selected soil physico-chemical properties and the relative abundance of the hub genus in different tomography, and * represent significant correlations at the level of $p < 0.05$, ** represent significant correlations at the level of $p < 0.01$.
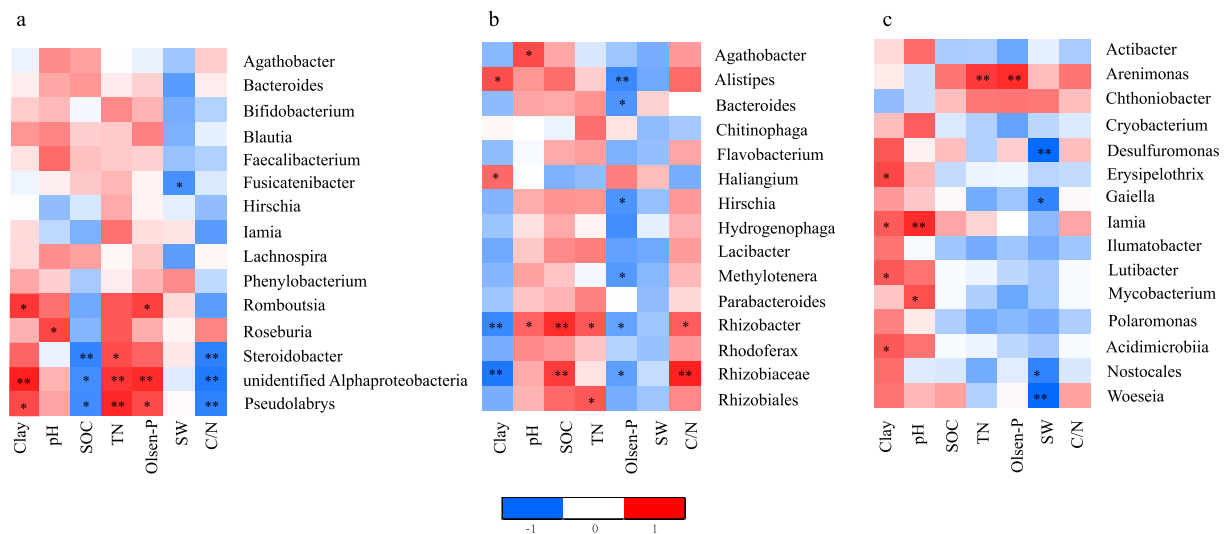
positive to clay, pH, and C/N but negative to Olsen-P, except the *Arenimonas* and *Chothoniobater* (Fig. 7).

4. Discussion

4.1. Soil-eroding catena induced differences in soil properties among topographic units

A continuous increasing trend of clay content, soil water content and SOC and a decreasing trend of TN and Olsen-P values occurred from the autonomous zone to the depositional zone (Table 1). The clay content in the depositional zone was pronouncedly lower than that in the autonomous and transitional zones, similar result has been observed in previous studies who found finer soil textures at downslope positions (Khomo et al., 2011; Bojko and Kabala, 2016). This may be the result of the selective transport of fine particles by runoff (Hu and Kuhn, 2014). In addition, selective deposition not only affects the distribution of eroded soil fractions but also influences other soil properties, such as the spatial patterns of particle-bound substances (SOC, phosphorus, e.g.) and soil climate as a consequence of the altering clay content. In the present study, we found the highest SOC content in the depositional zone (12.12 g kg^{-1}), which may be primarily due to selective erosion from the transitional zone (6.87 g kg^{-1}), which is supported by Nitzsche et al. (2017) who also noted that the accumulation of C (particulate/soluble) transported downslope via erosion can result in higher soil C in depositional areas. This result was different to the Sun et al. (2015), who pointed out that SOC concentrations in the sloping areas and gullies were greater than those on the summits. This may be related to the different management practices in the highland region (cropland in autonomous zone in present study) and hilly region (cropland in gullies in Sun's study). In addition, the higher TN and Olsen-P values in autonomous and transitional zones where distributed with cropland and orchard, were resulted from the higher fertilizer input (160 ~ 300 kg N ha^{-1} and 39 ~ 385 kg P ha^{-1}). The increased soil water content in the depositional zone was determined by the erosion runoff deposition and higher clay content, which increased the water holding capacity (Assi et al., 2019).

4.2. Changes in soil prokaryotic communities among topographic units in soil-eroding catena

A complex topography induced by soil erosion has been incised into the plateau, fragmented as an eroding landscape (Wang et al., 2017b),

but its impact on the soil prokaryotic diversity and community composition is less frequently studied. Deterioration of the soil in the depositional zone significantly decreased the prokaryotic alpha-diversity and increased the beta-diversity when compared with those in the autonomous and transitional zones (Table 2 and Fig. 3a), and similar results were also reported by Hargreaves et al. (2015), who found greater alpha-diversity on summit than that on slope positions. This observation may be primarily due to soil chemical properties. The lower TN and Olsen-P indicate a significant decrease in the substrates and nutrients available for soil prokaryotic growth and development, although with a higher SOC. Second, the higher soil water content in valley could limit the O$_2$ content and diffusion, thus inhibiting aerobic prokaryotes (Cook and Knight, 2003; Manzoni et al., 2012), and previous studies also showed prokaryotes are largely inhibited under water-filled conditions (Seaton et al., 2020). In addition, higher pore connectivity, changed by the higher water content, decreased the prokaryotic diversity (Carson et al., 2010), which is supported by our results, where alpha-diversity was lower in the depositional and transitional zones than in the autonomous zone (Table 2). Microbial diversity was negatively correlated with the clay fraction, which is contrasting to previous results (Naveed et al., 2016; Seaton et al., 2020). These divergent results may be due to the different mineral composition of soil particle size fractions in different study regions, which is known to influence microbial associations with soil particles (Carson et al., 2009). In addition, our study was different to the studies which on the specific erosion- and deposition-plots, such as no differences (Xiao et al., 2017) and contrasts differences (Sun et al., 2018) in bacterial species diversity, this maybe related the research scale (the watershed in present study *vs.* slope in their studies). Contrasting to the variation of alpha-diversity among topographic units, beta-diversity was higher in the depositional zone (Fig. 3), this maybe relate to the higher soil water content (Table 1) which was an important factor for contributing beta-diversity pointed out by Dimitriu and Grayston (2010).

The soil prokaryotic community composition was also altered among the three topographic units. Separate clusters were formed by prokaryotic communities in the depositional zone and the other two topographic units (Fig. 3b). The altered prokaryotic community structure was mainly influenced by the redistribution of SOC, clay content and soil water content caused by selective erosion and sediment transport. The significantly higher abundances of Gammaproteobacteria and Bacteroidetes in the depositional zone were found to be correlated with the higher SOC and lower C/N (Table 3), and these were also in line with previous studies showing that copiotrophic groups (*r*-strategists) prefer

environments where organic C with high quantity and quality (Fierer et al., 2007; Fierer et al., 2012; Goldfarb et al., 2011). Previous studies reported that Actinobacteria have different lifestyles according to the current nutrient conditions (Trivedi et al., 2015; Wang et al., 2017a). In this study, the lower Actinobacteria abundances in the depositional zone soils suggested that they are oligotrophic (Fig. 2). Gemmatimonadetes were significantly decreased in abundances in the depositional zone, which might be due to the higher soil water content, because DeBruyn et al., (2011) has showed Gemmatimonadetes were more adapted to low moisture soil.

In addition to the chemical properties, a stronger relationship between α-diversity and clay (Fig. 6) and a stronger relationship between the dominant phylum and clay (Table 3) was also identified in the present study. These results implicated that the bacterial community composition under the eroded landscapes might be closely related to clay changes, which are the result of the migration of sediments due to erosion. Some previous studies also showed that soil particles inhabited by various microbial species are transported with the overland runoff (Huang et al., 2013), but the specific information about this possibility requires further investigation.

4.3. Soil prokaryotes co-occurrences among topographic units in soil-eroding catena

The distinct compositions of the three topographic units networks indicated the different roles of environmental filtering in prokaryotic community composition in eroding landscapes (Fig. 4). The higher modularity and path length, lower edges and mean density in the transitional and depositional zones indicated that these two topographic units had less complexity of the prokaryotic co-occurrence networks. These findings all indicated that a more stressful environment in which soil prokaryotes coexist was more likely to form in the transitional and depositional zones than in the autonomous zone. Similar results were also found for soil prokaryotic communities that had more interactions and frequent communication in upward-slopes (Liu et al., 2020).

The main reasons for this phenomenon may be as follows. First, the chemically deteriorated soil conditions (except SOC) induced by soil erosion, such as decreased TN and Olsen-P, and increased C/N, can all decrease the complexity of prokaryotic co-occurrence networks. Second, physically deteriorated soil conditions, higher soil water content, decreased redox, and higher clay content cause reductions in the O_2 content and diffusion, which inhibits aerobic prokaryotes, thus decreasing the complexity of prokaryotic co-occurrence networks.

Functional groups of processes networks showed a decreased complexity from the autonomous zone to the transitional zone and then to the depositional zone (Fig. 5), which is similar to the prokaryotic network. This observation was also found in previous studies, which showed environmental factors not only varied by soil microbial networks (Banerjee et al., 2016a; Banerjee et al., 2016b) but also influenced the microbial functional network (Zheng et al., 2019).

In addition, significantly different functional groups of processes were also filtered from the assembly by environmental characteristics among the three topographic units (Fig. 5). The key functional groups of processes were also significantly different among the three topographic units. The autonomous and transitional zone networks showed more key functional groups of processes than the depositional zone networks, and these functional groups of processes were mainly related to N cycling, including *aerobic nitrite oxidation, denitrification, nitrogen fixation, nitrate denitrification, nitrous oxide denitrification*, etc. However, the key functional groups of processes related to carbon cycling in the transitional zone were *methanogenesis by CO_2 reduction with H_2, hydrogenotrophic methanogenesis, methanogenesis*, etc., and some reduction functional groups were identified as the key processes in the depositional zone.

Our study have pointed out the soil prokaryotic properties were influenced by environmental filtering effects under soil eroding catena. Further studies will conduct to explore the directly effects on prokaryotic properties from the runoff and sediment transporting, which aim to deepen understand the effects of dynamic soil-eroding catena on bacteria properties and function in eroding landscape.

5. Conclusion

This study analysed the effects of topographic units on the structure of microbial community composition and co-occurrence patterns under a whole soil-eroding catena on the fragmented Chinese Loess Plateau. Alpha-diversity was greater, beta-diversity was lower, in the autonomous and transitional zones than in the depositional zone. Less clustered networks and fewer co-occurrences within the soil prokaryotic community and functional groups of processes in the depositional zone indicated that the depositional zone was a less diverse and more stressful environment in which soil microbes co-existed. This observation may be a result of the redistribution of soil clay content (<0.002), soil water content, soil organic matter (SOC), nitrogen (TN), and Olsen-P induced by the erosion process in eroding landscapes. Reassembly of soil environment characteristics among the geomorphic units resulted in a significantly varied soil prokaryotic community in the soil-eroding catena. These results shed new light on the effects of the spatial differentiation of a complex topography on soil prokaryotes properties under a whole soil-eroding catena.

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.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2020.105035.

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.

Assi, A.T., Blake, J., Mohtar, R.H., Braudeau, E., 2019. Soil aggregates structure-based approach for quantifying the field capacity, permanent wilting point and available water capacity. Irrig. Sci. 37, 511–522. https://doi.org/10.1007/s00271-019-00630-w.

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, 1805–1816. https://doi.org/10.1111/1462-2920.12986.

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. 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, 343–351. https://doi.org/10.1038/ismej.2011.119.

Bastian, M., Heymann, S., Jacomy, M., 2009. Gephi: an open source software for exploring and manipulating networks. ICWSM 8, 361–362.

Berry, D., Widder, S., 2014. Deciphering microbial interactions and detecting keystone species with co-occurrence networks. Front. Microbiol. 5, 1–14. https://doi.org/10.3389/fmicb.2014.00219.

Bojko, O., Kabala, C., 2016. Transformation of physicochemical soil properties along a mountain slope due to land management and climate changes - A case study from the

Karkonosze Mountains, SW Poland. Catena 140, 43–54. https://doi.org/10.1016/j.catena.2016.01.015.

Caporaso, J.G., Lauber, C.L., Walters, W.A., Berg-Lyons, D., Lozupone, C.A., Turnbaugh, P.J., Fierer, N., Knight, R., 2011. Global patterns of 16S rRNA diversity at a depth of millions of sequences per sample. PNAS 108, 4516–4522. https://doi.org/10.1073/pnas.1000080107.

Carson, J.K., Campbell, L., Rooney, D., Clipson, N., Gleeson, D.B., 2009. Minerals in soil select distinct bacterial communities in their microhabitats. FEMS Microbiol. Ecol. 67, 381–388. https://doi.org/10.1111/j.1574-6941.2008.00645.x.

Carson, J.K., Gonzalez-Quinones, V., Murphy, D.V., Hinz, C., Shaw, J.A., Gleeson, D.B., 2010. Low Pore Connectivity Increases Bacterial Diversity in Soil. Appl. Environ. Microbiol. 76, 3936–3942. https://doi.org/10.1128/aem.03085-09.

Cook, F.J., Knight, J.H., 2003. Oxygen transport to plant roots: Modeling for physical understanding of soil aeration. Soil Sci. Soc. Am. J. 67, 20–31.

de Carvalho, T.S., Jesus, E.D., Barlow, J., Gardner, T.A., Soares, I.C., Tiedje, J.M., Moreira, F.M., 2016. Land use intensification in the humid tropics increased both alpha and beta diversity of soil bacteria. Ecology 97, 2760–2771. https://doi.org/10.1002/ecy.1513.

DeBruyn, J.M., Nixon, L.T., Fawaz, M.N., Johnson, A.M., Radosevich, M., 2011. Global Biogeography and Quantitative Seasonal Dynamics of Gemmatimonadetes in Soil. Appl. Environ. Microbiol. 77, 6295–6300. https://doi.org/10.1128/aem.05005-11.

Dimitriu, P.A., Grayston, S.J., 2010. Relationship between soil properties and patterns of bacterial beta-diversity across reclaimed and natural boreal forest soils. Microb. Ecol. 59, 563–573. https://doi.org/10.1007/s00248-009-9590-0.

Du, L., Wang, R., Gao, X., Hu, Y., Guo, S., 2020. Divergent responses of soil bacterial communities in erosion-deposition plots on the Loess Plateau. Geoderma 358, 113995. https://doi.org/10.1016/j.geoderma.2019.113995.

Fierer, N., Bradford, M.A., Jackson, R.B., 2007. Toward an ecological classification of soil bacteria. Ecology 88, 1354–1364. https://doi.org/10.1890/05-1839.

Fierer, N., Lauber, C.L., Ramirez, K.S., Zaneveld, J., Bradford, M.A., Knight, R., 2012. Comparative metagenomic, phylogenetic and physiological analyses of soil microbial communities across nitrogen gradients. ISME J. 6, 1007–1017. https://doi.org/10.1038/ismej.2011.159.

Fujii, K., Hartono, A., Funakawa, S., Uemura, M., Kosaki, T., 2011. Fluxes of dissolved organic carbon in three tropical secondary forests developed on serpentine and mudstone. Geoderma 163, 119–126. https://doi.org/10.1016/j.geoderma.2011.04.012.

Gabarron-Galeote, M.A., Martinez-Murillo, J.F., Quesada, M.A., Ruiz-Sinoga, J.D., 2013. Seasonal changes in the soil hydrological and erosive response depending on aspect, vegetation type and soil water repellency in different Mediterranean microenvironments. Solid Earth 4, 497–509. https://doi.org/10.5194/se-4-497-2013.

Goldfarb, K.C., Karaoz, U., Hanson, C.A., Santee, C.A., Bradford, M.A., Treseder, K.K., Wallenstein, M.D., Brodie, E.L., 2011. Differential growth responses of soil bacterial taxa to carbon substrates of varying chemical recalcitrance. Front. Microbiol. 2 https://doi.org/10.3389/fmicb.2011.00094.

Griffiths, B.S., Philippot, L., 2013. Insights into the resistance and resilience of the soil microbial community. FEMS Microbiol. Rev. 37, 112–129. https://doi.org/10.1111/j.1574-6976.2012.00343.x.

Grimshaw, H.M., Allen, S.E., Parkinson, J.A., 1989. Nutrient elements. In: Allen, S.E. (Ed.), Chemical Analysis of Ecological Material. Blackwell Scientific. Oxford.

Hargreaves, S.K., Williams, R.J., Hofmockel, K.S., 2015. Environmental filtering of microbial communities in agricultural soil shifts with crop growth. PLoS ONE 10. https://doi.org/10.1371/journal.pone.0134345.

Hook, P.B., Burke, I.C., 2000. Biogeochemistry in a shortgrass landscape: Control by topography, soil texture, and microclimate. Ecology 81, 2686–2703. https://doi.org/10.2307/177334.

Hu, Y., Kuhn, N.J., 2014. Aggregates reduce transport distance of soil organic carbon: are our balances correct? Biogeosciences 11, 6209–6219. https://doi.org/10.5194/bg-11-6209-2014.

Hu, Y., Kuhn, N.J., 2014. Aggregates reduce transport distance of soil organic carbon:are our balances correct? Biogeosciences 11, 6209–6219. https://doi.org/10.5194/bg-11-6209-2014.

Huang, J., Li, Z., Zeng, G., Zhang, J., Li, J., Nie, X., Ma, W., Zhang, X., 2013. Microbial responses to simulated water erosion in relation to organic carbon dynamics on a hilly cropland in subtropical China. Ecol. Eng. 60, 67–75. https://doi.org/10.1016/j.ecoleng.2013.07.040.

Huang, M.B., Shao, M.G., Zhang, L., Li, Y.S., 2003. Water use efficiency and sustainability of different long-term crop rotation systems in the Loess Plateau of China. Soil Tillage Res. 72, 95–104. https://doi.org/10.1016/s0167-1987(03)00065-5.

Khomo, L., Bern, C.R., Hartshorn, A.S., Rogers, K.H., Chadwick, O.A., 2013. Chemical transfers along slowly eroding catenas developed on granitic cratons in southern Africa. Geoderma 202, 192–202. https://doi.org/10.1016/j.geoderma.2013.03.023.

Khomo, L., Hartshorn, A.S., Rogers, K.H., Chadwick, O.A., 2011. Impact of rainfall and topography on the distribution of clays and major cations in granitic catenas of southern Africa. Catena 87, 119–128. https://doi.org/10.1016/j.catena.2011.05.017.

Lei, A.L., Tang K.L., Wang, W.,L,. 2000. Significance and Character of Conception of Soil Erosion Chain. Journal of soil and water conservation, 14, 78-83. DOI:10.13870/j.cnki.stbcxb.2000.03.017.

Liu, Y., Zhang, L.P., Lu, J.K., Chen, W.M., Wei, G.H., Lin, Y.B., 2020. Topography affects the soil conditions and bacterial communities along a restoration gradient on Loess-Plateau. Appl. Soil Ecol. 150, 14. https://doi.org/10.1016/j.apsoil.2019.103471.

Louca, S., Parfrey, L.W., Doebeli, M., 2016. Decoupling function and taxonomy in the global ocean microbiome. Science 353, 1272–1277. https://doi.org/10.1126/science.aaf4507.

Manzoni, S., Schimel, J.P., Porporato, A., 2012. Responses of soil microbial communities to water stress: results from a meta-analysis. Ecology 93, 930–938. https://doi.org/10.1890/11-0026.1.

Mapelli, F., Marasco, R., Fusi, M., Scaglia, B., Tsiamis, G., Rolli, E., Fodelianakis, S., Bourtzis, 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. 12, 1188–1198. https://doi.org/10.1038/s41396-017-0026-4.

Mohammadi, M.F., Jalali, S.G., Kooch, Y., Said-Pullicino, D., 2017. The effect of landform on soil microbial activity and biomass in a Hyrcanian oriental beech stand. Catena 149, 309–317. https://doi.org/10.1016/j.catena.2016.10.006.

Naveed, M., Herath, L., Moldrup, P., Arthur, E., Nicolaisen, M., Norgaard, T., Ferre, T.P.A., de Jonge, L.W., 2016. Spatial variability of microbial richness and diversity and relationships with soil organic carbon, texture and structure across an agricultural field. Appl. Soil Ecol. 103, 44–55. https://doi.org/10.1016/j.apsoil.2016.03.004.

Newman, M.E., 2003. The structure and function of complex networks. SIAM Rew. 45, 167–256. https://doi.org/10.1137/S003614450342480.

Newman, M.E., 2006. Modularity and community structure in networks. P Natl. Acad. Sci. USA 103, 8577–8582. https://doi.org/10.1073/pnas.0601602103.

Nitzsche, K.N., Kaiser, M., Premke, K., Gessler, A., Ellerbrock, R.H., Hoffmann, C., Kleeberg, A., Kayler, Z.E., 2017. Organic matter distribution and retention along transects from hilltop to kettle hole within an agricultural landscape. Biogeochemistry 136, 47–70. https://doi.org/10.1007/s10533-017-0380-3.

Olsen, S.R., Watanabe, F.S., 1957. A method to determine a phosphorus adsorption maximum of soils as measured by the Langmuir isotherm. Soil Sci. Soc. Am. J. 21, 144–149.

Seaton, F.M., George, P.B.L., Lebron, I., Jones, D.L., Creer, S., Robinson, D.A., 2020. Soil textural heterogeneity impacts bacterial but not fungal diversity. Soil Biol. Biochem. 144, 10. https://doi.org/10.1016/j.soilbio.2020.107766.

Seibert, J., Stendahl, J., Sorensen, R., 2007. Topographical influences on soil properties in boreal forests. Geoderma 141, 139–148. https://doi.org/10.1016/j.geoderma.2007.05.013.

Sessitsch, A., Weilharter, A., Gerzabek, M.H., Kirchmann, H., Kandeler, E., 2001. Microbial population structures in soil particle size fractions of a long-term fertilizer field experiment. Appl. Environ. Microbiol. 67, 4215–4224. https://doi.org/10.1128/aem.67.9.4215-4224.2001.

Sparks, D.L., Page, A.L., Helmke, P.A., Loeppert, R.H., Soltanpour, P.N., Johnston, C.T., Sumner, M.E., 1996. Methods of soil analysis. Part 3: Chemical Methods. Soil Science Society of America Inc., Madison, WI.

Sun, Q., Hu, Y., Wang, R., Guo, S., Yao, L., Duan, P., 2018. Spatial distribution of microbial community composition along a steep slope plot of the Loess Plateau. Appl. Soil Ecol. 130, 226–236. https://doi.org/10.1016/j.apsoil.2018.06.018.

Sun, W., Shao, Q., Liu, J., Zhai, J., 2014. Assessing the effects of land use and topography on soil erosion on the Loess Plateau in China. Catena 121, 151–163. https://doi.org/10.1016/j.catena.2014.05.009.

Sun, W.Y., Zhu, H.H., Guo, S.L., 2015. Soil organic carbon as a function of land use and topography on the Loess Plateau of China. Ecol. Eng. 83, 249–257. https://doi.org/10.1016/j.ecoleng.2015.06.030.

Takriti, M., Wild, B., Schnecker, 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.

Trivedi, P., Rochester, I.J., Trivedi, C., Van Nostrand, J.D., Zhou, J., Karunaratne, S., Anderson, I.C., Singh, B.K., 2015. Soil aggregate size mediates the impacts of cropping regimes on soil carbon and microbial communities. Soil Biol. Biochem. 91, 169–181. https://doi.org/10.1016/j.soilbio.2015.08.034.

Wang, Y., Ji, H., Wang, R., Guo, S., Gao, C., 2017a. Impact of root diversity upon coupling between soil C and N accumulation and bacterial community dynamics and activity: Result of a 30 year rotation experiment. Geoderma 292, 87–95. https://doi.org/10.1016/j.geoderma.2017.01.014.

Wang, Y.X., Ran, L.S., Fang, N.F., Shi, Z.H., 2018. Aggregate stability and associated organic carbon and nitrogen as affected by soil erosion and vegetation rehabilitation on the Loess Plateau. Catena 167, 257–265. https://doi.org/10.1016/j.catena.2018.05.005.

Wang, Z., Hu, Y., Wang, R., Guo, S., Du, L., Zhao, M., Yao, Z., 2017b. Soil organic carbon on the fragmented Chinese Loess Plateau: Combining effects of vegetation types and topographic positions. Soil Tillage Res. 174, 1–5. https://doi.org/10.1016/j.still.2017.05.005.

Wang, R., Wang, Z., Sun, Q., Zhao, M., Du, L., Wu, D., Li, R., Gao, X., Guo, S., 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.

Wiaux, F., Vanclooster, M., Cornelis, J.-T., Van Oost, K., 2014. Factors controlling soil organic carbon persistence along an eroding hillslope on the loess belt. Soil Biol. Biochem. 77, 187–196. https://doi.org/10.1016/j.soilbio.2014.05.032.

Xiao, H., Li, Z., Chang, X., Huang, J., Nie, X., Liu, C., Liu, L., Wang, D., Dong, Y., Jiang, J., 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.

Yang, Y., Dou, Y., Liu, D., An, S., 2017. Spatial pattern and heterogeneity of soil moisture
along a transect in a small catchment on the Loess Plateau. J. Hydrol. 550, 466–477.
https://doi.org/10.1016/j.jhydrol.2017.05.026.

Zheng, W., Zhao, Z., Lv, F., Wang, R., Gong, Q., Zhai, B., Wang, Z., Zhao, Z., Li, Z., 2019.
Metagenomic exploration of the interactions between N and P cycling and SOM
turnover in an apple orchard with a cover crop fertilized for 9 years. Biol. Fertil. Soils
55, 365–381. https://doi.org/10.1007/s00374-019-01356-9.