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Spatial distribution of microbial community composition along a steep slope plot of the Loess Plateau

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ABSTRACT

Spatial heterogeneity of soil microbes introduces great uncertainty to our understanding of microbe-mediated soil carbon cycling, yet was few studied on sloping lands. Along a steep-slope grassland (35°) on the Chinese Loess Plateau, soils of 0–10 cm were sampled in 2016 at three slope positions (upper, middle and bottom) to determine microbial community composition (by Illumina Hiseq sequencing) and function (enzymes involved in carbon cycling, the *in situ* soil respiration and temperature sensitivity). The bacterial alpha-diversity were greater at middle- and bottom- than at upper slope position, while fungal alpha-diversity varied little across slope positions. The bacterial phylum Proteobacteria was 9.7% and 19.4% lower but Acidobacteria was 36.5% and 41.3% greater at bottom- than at upper- and middle- slope positions. The fungal community transitioned from being Basidiomycota-dominant (relative abundance of 46.8%) at upper slope position to Zygomycota-dominant (relative abundance of 36.5%) at bottom slope position. The β-D-glucosidase activity generally declined down the slope while β-D-xylosidase and cellobiohydrolase activities hiked at middle slope position. All the enzyme activities were suppressed at bottom slope position. Soil respiration increased by 49.1% ($P < 0.05$) while temperature sensitivity decreased by 13.2% ($P < 0.05$) down the slope. Both bacterial richness (OTU) and diversity (Shannon diversity index) positively correlated with soil respiration. The copiotrophic groups (Acidobacteria and Zygomycota) negatively and oligotrophic groups (Proteobacteria and Basidiomycota) positively correlated with temperature sensitivity of soil respiration. Our findings revealed divergent responses of soil bacterial and fungal communities along the slope and highlighted the importance of microbial information in predicting the spatial variability of soil respiration in hillslope ecosystems.

1. Introduction

Soil microorganisms are a main component of the terrestrial biosphere and play key role in mineralization and sequestration of soil organic carbon (SOC), which regulates soil CO_2 flux (Schimel and Schaeffer, 2012; Six et al., 2006; Trivedi et al., 2016). The spatial heterogeneity of soil microbes poses great challenge to accurately estimating CO_2 flux in global carbon (C) cycling (Singh et al., 2010; Wagg et al., 2014). So far, the heterogeneity of soil microbes has been extensively studied in forest (Chen et al., 2016; Churchland et al., 2013; Li et al., 2015), grassland (Budge et al., 2011; Chen et al., 2017; Li et al., 2017a) and farmland (Dungait et al., 2013; Helgason et al., 2014; Xiao et al., 2017b), but less in hillslope ecosystems. Actually, more than 60% of the global land area are slopes with gradients > 8° (Berhe and Kleber, 2013). On sloping lands, soil microbial communities and the microbe-mediated C cycling processes are regulated by water erosion (Huang et al., 2013; Li et al., 2015) through soil water and substrate differentiation (Hu et al., 2016; Wang et al., 2017b). This further brings about considerable uncertainties when estimating soil respiration at global scale (Davidson et al., 2006; Xu and Qi, 2001).

For a certain soil, the microbial community composition and functioning are generally controlled by soil microclimate (Yuste et al., 2014; Yuste et al., 2011; Zhang et al., 2005), substrate quantity and quality (Chen et al., 2016; Fierer et al., 2003; Heitkötter et al., 2017), as well as plant growth and root activity (Hu et al., 2010; Li et al., 2017b; Singh et al., 2010). Soil water and substrate distribution on sloping lands are

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very likely to experience evident changes even over short distance (Du et al., 2015; Helgason et al., 2014; Li et al., 2015), mostly as a result of erosion-induced water and material transport and redistribution (Hu et al., 2016; Wang et al., 2017b; Wang et al., 2017c). Soil water directly alters physical environment for soil organisms and their accessibility to substrate (Jassal et al., 2008; Suseela et al., 2011) and indirectly affects soil microbes by changing the input of plant C into the rhizosphere (Bardgett et al., 2008; Singh et al., 2010). Soils at lower part of a slope tend to have relatively better soil water condition due to more inflow and less outflow (Wang et al., 2017b), as well greater water holding capacity (Wei et al., 2014). The available substrates are also likely to be redistributed by water erosion through selective erosion and deposition processes of light/fine particles along slopes (Lal and Pimentel, 2008; Polyakov and Lal, 2008), namely depleting SOC-rich soil fractions from upper part of the slope and depositing them at lower part (Hu et al., 2013; Wang et al., 2017b). The varying soil water and substrate conditions along the slope can further lead to distinctive vegetation coverage, above- and below-ground plant biomass on different topographic positions (Wang et al., 2015; Xu and Wan, 2008), which in turn generates a variety of substrates for different microbial communities through fresh C supply (Fuchslueger et al., 2014; Li et al., 2017a).

In this study, spatial variations in microbial diversity, community composition and enzyme activity at upper, middle and bottom slope positions on the sloping grassland were investigated. In addition, soil respiration, soil temperature and soil moisture were *in situ* measured for three years. The objectives were to 1) characterize the spatial variation of microbial diversity, community composition and enzyme activities along the steep slope; 2) identify the influential environmental factors of soil microbial community; and 3) explore potential links between microbial diversity, community composition, enzyme activities and soil respiration on the eroding slope. We hypothesized that 1) microbial diversity, abundance and activity would increase down slope due to greater soil water and substrate availability; 2) the deposition of soil water and substrate would result in increased soil respiration and decreased Q_{10} downslope.

2. Materials and methods

2.1. Study site

This study was conducted on a ridge slope in Wangdonggou watershed (35°13′N–35°16′N, 107°40′E–107° 42′E; elevation 946–1226 m; area 8.3 km^2), which is located on the southern Loess Plateau in the middle reaches of the Yellow River, northern China (Fig. 1a). Soils in this region have been heavily weathered with low SOC (Guo et al., 2012), thus highly erodible with poor cohension. Regional soil erosion, average annual soil erosion rate is 50–200 t ha^{-1} (Fu et al., 2005; Xiao et al., 2017a), has greatly reduced crop yield and altered regional hydrologic regimes (Zhang et al., 2015; Zhu et al., 2014), resulting in fragmented terrain (Wang et al., 2017b). In general, sloping land and gullies account for two thirds of the studied Wangdonggou watershed (Fig. 1b), with about 60% of the slopes in length < 60 m and more than 41.2% of the slopes with gradient > 25° (Li and Su, 1991). The region has a mean temperature of 9.4 °C (1957–2016). The average annual precipitation is 560 mm, 60% of which falls between July and September. Average annual sunshine duration is 2330 h, annual total radiation is 484 kJ cm^{-2}, and average frost-free period is 171 days. The meteorological data were provided by the State Key Agro-Ecological Experimental Station established in 1984 in Changwu County. According to the American soil classification system, the studied soil is a uniform loam of loess deposits belonging to Calcic Cambisols, which originate from parent material of calcareous loess.

2.2. Experimental design

A natural steep slope (35°) of 50 m long covered by grass was selected as experimental site (Fig. 1c). Three quadrats of 1 m × 1 m were established on each slope position, with the grass species, herb coverage be surveyed. The grass composition are *Bothriochloa ischaemum* L., *Lespedeza davurica* and *Artemisia gmelinii*, among which the *Bothriochloa ischaemum* L. is the dominant species. The coverage of each soil sampling site are around 50% at upper slope position, 75% at middle slope position and 100% at bottom slope positions. To exclude edge effects, three plots were established in the central position of the slope in 2014. To avoid the influence of slope aspect and differences in original soil properties on soil respiration, all three plots were established on the same slope with similar soil properties and therefore, had the same aspects. Each plot was 20 m × 5 m with the longest side in the direction of the slope gradient. Plots were separated 150 m apart and separated by a brick wall of 15 cm in height, 40 cm in depth and 6 cm in thickness to prevent the inflow of runoff outside the plots and the outflow of runoff inside the plots. Each plot was divided into three parts: upper slope position (2.5–7.5 m), middle slope position (7.5–12.5 m), and bottom slope position (12.5–17.5 m). In March 2014, three polyethylene soil collars were placed on each slope position (20 cm in diameter and 12 cm in height) deep to 10 cm to *in situ* collect the soil respiration data. To representatively cover the targeted slope position, the polyethylene collars at each slope position were at least 50 cm apart from each other.

2.3. Measurements of soil respiration, soil temperature and soil moisture

During the three years of observation period (2014, 2015 and 2016), soil respiration rates (R_s) were measured every seven days between 9:00 am and 11:00 am (Iqbal et al., 2009), by mounting a soil CO_2 flux system (a portable chamber of 20 cm in diameter, Li-8100, Lincoln, NE, USA) onto the polyethylene collars (Jiang et al., 2015; Wang et al., 2017a). At the same time with the soil respiration measurement, soil temperature (using a Li-Cor thermocouple probe) and soil moisture (using a Theta Probe ML2X with an HH2 moisture meter) at 10 cm depth were also measured in three directions (0°, 120° and 240°), each 10 cm away from the collar.

2.4. Soil sampling and soil chemical analysis

Three composite soil samples were taken at each part of the plot (upper, middle and bottom slope positions). Each composite soil sample consisted of three subsamples collected randomly at topsoil (0–10 cm), using a soil auger of 3 cm in diameter on October 1 of 2016. Each composite soil sample was then passed through a 2.0-mm sieve and divided into three subsamples: one part stored at −80 °C for DNA extraction, a second part stored at 4 °C and at field moisture for less than 4 days to measure soil enzyme activities, soil microbial biomass carbon content (SMBC), soil dissolved organic carbon (DOC) and soil nitrate (NO_3-N) and ammonium (NH_4-N) nitrogen content. The third part of the soil sample was air dried and then crushed to pass through a 0.15 mm sieve to measure SOC and soil total nitrogen content (TN). The SOC was determined using the K_2CrO_7-H_2SO_4 oxidation method (Sparks et al., 1996). To measure DOC content, the field-moist soil samples (equivalent to 15 g oven-dried soil) were extracted with 60 ml of 0.5 M K_2SO_4 (soil to solution ratio 1:4) for 1 h. After centrifuged at 4000 rpm for 25 min, the supernatant was filtered through a 0.45 mm membrane filter and measured in a Total Organic Carbon Analyzer (TOC-VCPH, Shimadzu, Japan) (Fujii et al., 2011; Vance et al., 1987). The soil nitrate (NO_3-N) and ammonium (NH_4-N) nitrogen were extracted with KCl (1 mol L^{-1}) and determined by colorimetry using a Bran & Luebbe II AutoAnalyser (Fernández-Escobar et al., 2009). Soil pH was determined with a digital pH meter (Woonsocket, RI, USA) using a soil-to-water ratio of 1:2.5(w/v).

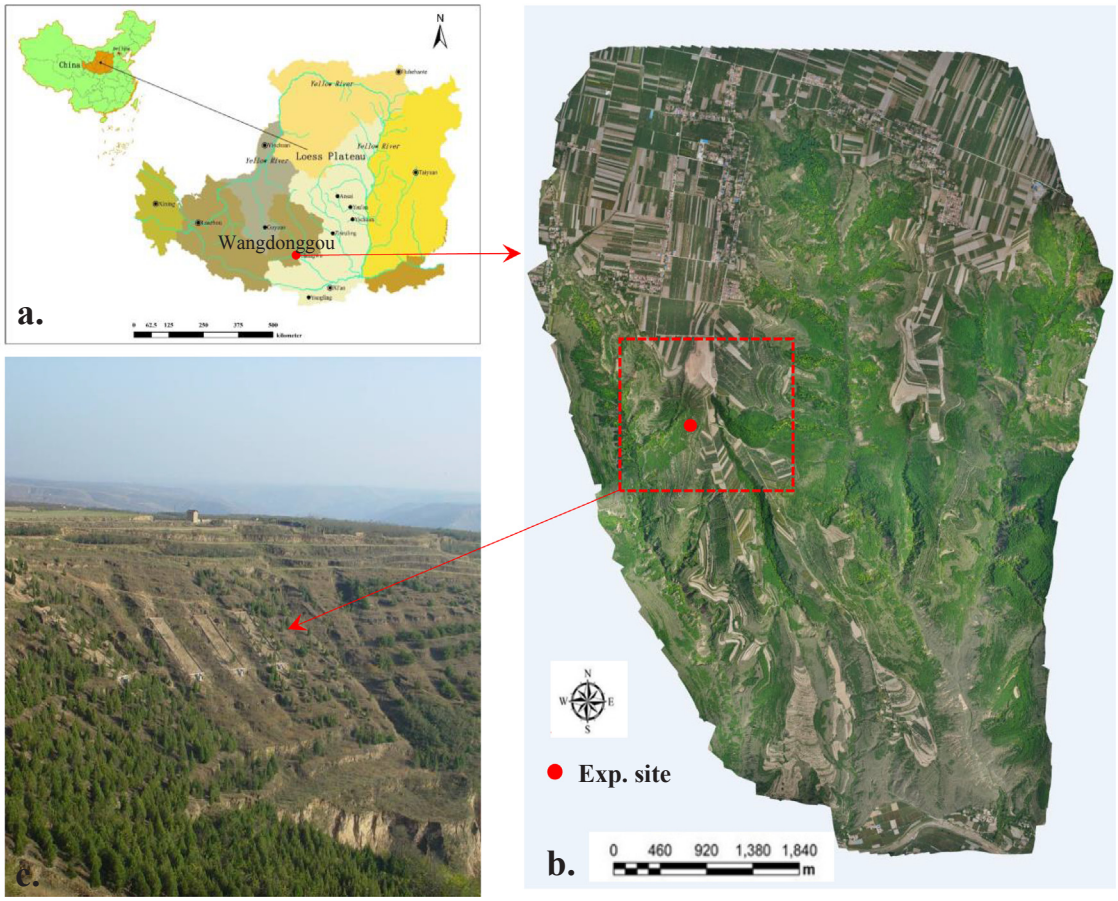

Fig. 1. The location of the experimental site in the Loess Plateau, China (a.) Wang et al. (2017a), the satellite aerial photography of the Wangdonggou small watershed (b.) and the studied slope (c.)

Table 1
Soil biochemical properties at three slope positions.

Soil properties	Upper	Middle	Bottom
SOC/g kg^{-1}	7.48 ± 0.42 c	9.93 ± 0.75 b	12.35 ± 0.31 a
DOC/mg kg^{-1}	66.9 ± 1.0 c	169.3 ± 0.4 a	119.2 ± 7.6 b
SMBC/mg kg^{-1}	107.9 ± 0.73 c	259.7 ± 2.63 a	189.3 ± 11.69 b
N_{min}/mg kg^{-1}	3.11 ± 0.12 a	3.72 ± 0.45 a	3.75 ± 0.10 a
pH	8.11 ± 0.05 a	8.09 ± 0.04 a	8.08 ± 0.01 a
Root/t ha^{-1}	1.33 ± 0.07 b	1.50 ± 0.07 b	1.85 ± 0.05 a
BX/nmol $g^{-1}h^{-1}$	3.55 ± 0.42 b	6.79 ± 0.55 a	4.96 ± 0.58 b
BG/nmol $g^{-1}h^{-1}$	28.40 ± 2.45 a	18.41 ± 0.37 b	16.00 ± 1.32 b
CB/nmol $g^{-1}h^{-1}$	1.30 ± 0.38 b	2.57 ± 0.15 a	1.96 ± 0.03 ab

Note: SOC is soil organic carbon; DOC is soil dissolved organic carbon; SMBC is soil microbial biomass carbon; N_{min} denote soil mineral nitrogen content; Root is the fine root biomass (< 2 mm); BX is short for β-D-xylosidase; BG is β-D-glucosidase; CB is cellobiohydrolase; Different letters in a row indicate significant difference at $P < 0.05$, and values are means of three replicates ± SE ($n = 3$).

2.5. Soil biological analysis

The soil microbial biomass carbon content (SMBC) was determined by chloroform fumigation-extraction method (Luo et al., 2015; Vance et al., 1987), using a Total Organic Carbon Analyzer (TOC-VCPH, Shimadzu, Japan). Biomass C was calculated with a scale factor of 0.45 (Wu et al., 1990). Three specific enzyme activities involved in soil carbon cycling were assayed in this study: β-D-xylosidase (BX), β-D-glucosidase (BG) and cellobiohydrolase (CB). Fluorometric substrates linked to 4-MUB-β-D-xyloside, 4-MUB-β-D-glucoside and 4-MUB-cellobioside from Sigma (St Louis, MO, USA) were used for the hydrolytic enzyme assays. Enzymes assays were performed as described by previous report (Deforest, 2009) with slight modifications of the buffer concentrations due to the alkalinity of the soil in this experiment (pH = 8.09). The activities of soil enzymes were calculated using standard equations on a per gram dry soil basis (Bell et al., 2013; German et al., 2011) and expressed in unit of nmol $g^{-1}h^{-1}$. In addition, roots, from the same samples with microbes, were separated from soils by soaking in water and gentle washing over a 0.25 mm mesh. Wet roots were oven dried at 60 °C for 48 h to a constant weight (Wang et al., 2017a).

2.6. DNA extraction and Illumina HiSeq high-throughput sequencing

Total genome DNA was extracted using CTAB/SDS method. DNA concentration and purity was monitored on 1% agarose gels. According to the concentration, DNA was diluted to 1 ng/μL using sterile water. The 515F (5′-GTGCCAGCMGCCGCGGTAA-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′) were designed to amplify the hypervariable V4 region of the 16S rRNA gene from the bacteria; and the fungal ITS1 genes were amplified using primers 1737F (5′-TCCGTAGGTGAACCTGCGG-3′) and 2043R (5′-GCTGCGTTCTTCATCGATGC-3′) (Caporaso and Gordon, 2011). Mix same volume of 1X loading buffer (constrained SYB green) with PCR products and operate electrophoresis on 2% agarose gel for detection. Samples with bright main strip between 400 and 450 bp were chosen for further experiments. PCR products was mixed in equidensity ratios. Then, mixture PCR products was purified with Qiagen Gel Extraction Kit (Qiagen, Germany). Sequencing libraries were generated using TruSeq® DNA PCR-Free Sample Preparation Kit

Table 2
Diversity indices at 97% sequence similarity of 16S and ITS rRNA genes calculated based on 80,208 and 66,221 sequences per sample of bacterial and fungal communities.

Diversity indices		Upper	Middle	Bottom
OTUs	Bacterial 16S	4385 ± 58 b	4729 ± 79 a	4784 ± 94 a
	Fungal ITS	662 ± 29 a	588 ± 157 a	867 ± 78 a
Chao1	Bacterial 16S	4318.7 ± 71.7 b	4664.5 ± 75.5 a	4784.9 ± 92.1 a
	Fungal ITS	684.0 ± 25.5 a	663.6 ± 175.8 a	904.1 ± 101.0 a
ACE	Bacterial 16S	4416.9 ± 73.8 b	4774.8 ± 95.3 a	4871.9 ± 93.7 a
	Fungal ITS	700.1 ± 36.4 a	701.8 ± 173.3 a	928.5 ± 102.9 a
Shannon	Bacterial 16S	9.64 ± 0.07 b	9.87 ± 0.04 a	10.01 ± 0.04 a
	Fungal ITS	4.76 ± 0.43 a	4.45 ± 1.37 a	5.61 ± 0.24 a

Note: Chao1 is short for Chao1 estimator of richness, ACE is short for ACE estimator of richness and Shannon is short for the Shannon diversity index; Values with different letters in a row mean significant difference at $P < 0.05$, values are means of three replicates ± SE ($n = 3$).

(Illumina, USA) following manufacturer's recommendations and index codes were added. The library quality was assessed in the Qubit® 2.0 Fluorometer (Thermo Scientific) and Agilent Bioanalyzer 2100 system. Sequencing was conducted on an Illumina HiSeq 2500 platform (Illumina Corporation, San Diego, USA) and 250 bp paired-end reads were generated. Approximately 80,208 high-quality prokaryotic sequences per sample with average length of approximately 253 bp, and 66,221 high-quality eukaryotic sequences per sample with average length of approximately 239 bp were produced.

2.7. Processing of sequencing data

All sequence reads were merged using FLASH (Magoč and Salzberg, 2011) and assigned to each sample according to their barcodes. Sequences with ≥97% similarity were clustered into operational taxonomic units (OTUs). The aligned 16S rRNA gene sequences were used for a chimera check using the Uchime algorithm (Edgar et al., 2011). Taxonomy was assigned using the Ribosomal Database Project classifier (Wang et al., 2007). Each sample was rarefied to the same number of reads (80,208 and 66,221 sequences). Sequence analysis was performed by UPARSE software package using the UPARSE-OTU and UPARSE-OTUref algorithms (Edgar, 2013). Alpha-diversity indices including Chao1 estimator of richness, abundance-based coverage estimator (ACE) and Shannon's diversity index were generated based on the obtained OTUs. The number of OTUs and Shannon diversity index of microbial community were used to estimate species richness and diversity of microbial community. The high-throughput sequencing data are available in the NCBI Sequence Read Archive (SRA) database (Accession numbers SUB2982447 and SUB2559665).

2.8. Statistical analysis

A univariate exponential function model was used to represent the relationship between soil respiration and soil temperature (Davidson et al., 1998):

$$y = \beta_0 e^{\beta 1 T} \quad (1)$$

where y is the measured soil respiration rate (μmol m^{-2} s^{-1}), T is the measured soil temperature (°C) at a certain soil depth.

The temperature sensitivity of soil respiration (Q_{10}) was calculated as following (Xu and Qi, 2001):

$$Q_{10} = e^{10\beta 1} \quad (2)$$

where β_1 is calculated by Eq. (1).

A one-way analysis of variation (ANOVA) and a least significant difference (LSD) multiple comparison ($P < 0.05$) were used to assess the significance of the slope position effects on the soil biochemical properties, microbial properties, soil respiration and Q_{10} (mean ± SD, $n = 3$). ADONIS analysis on OTUs was conducted to identity similarity of microbial community diversity found between different samples. Pearson correlation analysis and redundancy analysis (RDA) using Monte Carlo permutation (999 repetitions) were used to test the relationships between the microbial groups and environmental variables. The data sets were analyzed prior to the RDA using detrended correspondence analyses to confirm that the gradient lengths fit a linear model. Analysis of ADONIS and RDA were conducted by the R software package v.3.2.3. The statistical analysis was performed using SPSS 20.0 software for Windows (SPSS Inc., Chicago, USA). The figures were generated using Sigmaplot 12.5 software (Systat Software Inc., San Jose, CA, USA).

3. Results

3.1. Soil biochemical variables among slope positions

The SOC was 24.7% ($P < 0.05$) and 39.4% ($P < 0.05$) greater at middle and bottom slope positions than at upper slope position (7.5 g kg^{-1} dry soil). The DOC at middle slope position (169.3 mg kg^{-1}) was 60.5% ($P < 0.05$) and 43.9% ($P < 0.05$) greater than that of upper and bottom slope positions. The soil mineral nitrogen content varied little among slope positions, ranging from of 3.11 to 3.75 mg kg^{-1} dry soil. The root biomass at bottom slope position (1.85 t ha^{-1}) was 39.6% and 29.7% greater than at upper and middle slope positions ($P < 0.05$), with no significant difference between upper and middle slope positions. The soil pH of all soil samples ranged from 8.01 to 8.17, which, however, showed no significant difference among slope positions ($P > 0.05$) (Table 1).

Along the slope, SMBC at middle and bottom slope positions were 140.7% ($P < 0.05$) and 75.5% ($P < 0.05$) higher than at upper slope position (107.9 mg kg^{-1}). The BX activity at the middle slope position (6.79 nmol $g^{-1}h^{-1}$) was 91.2% ($P < 0.05$) and 37.0% ($P < 0.05$) greater than at upper and bottom slope positions, with no significant difference between upper and bottom slope positions. The CB activity was 77.5% greater ($P < 0.05$) at middle than at upper slope position (2.57 *vs.* 1.30 nmol $g^{-1}h^{-1}$), while that of bottom slope position fell in between them. The BG activity was 54.3% ($P < 0.05$) and 77.5% ($P < 0.05$) greater at upper slope position (28.40 nmol $g^{-1}h^{-1}$) than at middle and bottom slope positions, with no significant difference between middle and bottom slope positions (Table 1).

3.2. Microbial properties along the slope

In total, 721,871 and 595,992 high-quality sequences were obtained with an average of 80,208 and 66,221 sequences per sample for bacterial 16S gene and fungal ITS gene from all 9 samples. After OTUs clustering at 97% sequence identity, 8603 and 2038 OTUs remained for bacterial and fungal community. As shown in Table 2, both richness (OTUs) and diversity (Shannon diversity index) of bacterial 16S gene

Table 3
Relative abundances of soil bacterial communities affected by slope positions at phylum, class, order, family and genus levels.

Bacterial 16S	Upper	Middle	Bottom
Phylum			
Proteobacteria	36.46 ± 1.83 a	37.48 ± 0.31 a	31.40 ± 0.25 b
Acidobacteria	13.63 ± 1.75 b	13.16 ± 0.46 b	18.60 ± 0.63 a
Actinobacteria	20.08 ± 2.17 a	21.43 ± 1.06 a	21.27 ± 0.67 a
Gemmatimonadetes	10.35 ± 0.40 a	10.43 ± 0.38 a	7.76 ± 0.16 b
Planctomycetes	2.86 ± 0.88 a	2.34 ± 0.19 a	3.68 ± 0.33 a
Nitrospira	3.60 ± 0.08 a	2.75 ± 0.45 a	2.84 ± 0.08 a
Chloroflexi	3.57 ± 0.40 ab	3.22 ± 0.05 b	4.28 ± 0.23 a
Bacteroidetes	2.63 ± 0.20 a	3.00 ± 0.27 a	2.71 ± 0.17 a
Verrucomicrobia	1.78 ± 0.47 a	1.53 ± 0.12 a	1.97 ± 0.09 a
Firmicutes	0.94 ± 0.16 a	1.00 ± 0.10 a	0.88 ± 0.05 a
Class			
unidentified_Acidobacteria	10.61 ± 1.83 b	9.94 ± 0.41 b	15.48 ± 0.46 a
Alphaproteobacteria	12.96 ± 1.25 a	12.74 ± 0.37 a	11.13 ± 0.11 a
Betaproteobacteria	11.76 ± 0.73 a	11.07 ± 0.53 a	8.78 ± 0.37 b
Thermoleophilia	8.89 ± 1.92 a	10.57 ± 0.80 a	9.51 ± 0.22 a
unidentified_Gemmatimonadetes	10.35 ± 0.40 a	10.43 ± 0.38 a	7.76 ± 0.16 b
Deltaproteobacteria	8.35 ± 0.30 b	9.20 ± 0.24 a	7.70 ± 0.09 b
unidentified_Actinobacteria	5.24 ± 0.66 a	5.57 ± 0.22 a	5.83 ± 0.40 a
Nitrospira	3.60 ± 0.08 a	2.75 ± 0.45 a	2.84 ± 0.08 a
Gammaproteobacteria	3.26 ± 0.39 b	4.31 ± 0.23 a	3.66 ± 0.07 ab
Acidimicrobiia	3.50 ± 0.16 a	3.00 ± 0.10 b	2.89 ± 0.00 b
Order			
Subgroup_6	5.54 ± 1.04 b	5.01 ± 0.22 b	8.21 ± 0.33 a
Gemmatimonadales	8.82 ± 0.60 a	8.42 ± 0.45 a	6.19 ± 0.19 b
Nitrosomonadales	7.80 ± 0.68 a	7.19 ± 0.37 a	5.30 ± 0.23 b
Solirubrobacterales	5.01 ± 0.88 a	6.00 ± 0.36 a	5.40 ± 0.19 a
Sphingomonadales	4.90 ± 0.57 a	4.21 ± 0.17 ab	3.62 ± 0.13 b
Subgroup_4	3.11 ± 0.60 b	2.82 ± 0.23 b	4.69 ± 0.28 a
Gaiellales	3.87 ± 1.09 a	4.57 ± 0.55 a	4.10 ± 0.07 a
Nitrospirales	3.60 ± 0.08 a	2.75 ± 0.45 a	2.84 ± 0.08 a
Myxococcales	3.64 ± 0.16 b	4.49 ± 0.11 a	3.65 ± 0.06 b
Rhodospirillales	3.68 ± 0.39 b	6.23 ± 0.28 a	4.45 ± 0.10 b
Family			
Gemmatimonadaceae	8.82 ± 0.60 a	8.42 ± 0.45 a	6.19 ± 0.19 b
Nitrosomonadaceae	7.80 ± 0.68 a	7.19 ± 0.37 a	5.30 ± 0.23 b
0319-6A21	3.36 ± 0.11 a	2.37 ± 0.45 b	2.49 ± 0.08 ab
RB41	2.57 ± 0.50 b	2.28 ± 0.20 b	3.83 ± 0.25 a
Sphingomonadaceae	2.86 ± 0.36 a	2.46 ± 0.09 a	2.18 ± 0.14 a
Planctomycetaceae	1.41 ± 0.40 ab	1.17 ± 0.06 b	2.18 ± 0.13 a
Gaiellaceae	2.00 ± 0.50 a	2.29 ± 0.31 a	2.03 ± 0.01 a
Chitinophagaceae	1.59 ± 0.20 a	1.49 ± 0.12 a	1.56 ± 0.09 a
Haliangiaceae	1.47 ± 0.04 b	1.81 ± 0.10 a	1.41 ± 0.03 b
Rhodospirillaceae	1.25 ± 0.18 b	1.73 ± 0.06 a	1.38 ± 0.03 ab
Genus			
Sphingomonas	2.75 ± 0.34 a	2.36 ± 0.09 a	2.10 ± 0.14 a
Gaiella	2.00 ± 0.50 a	2.29 ± 0.31 a	2.03 ± 0.01 a
Haliangium	1.47 ± 0.04 b	1.81 ± 0.10 a	1.41 ± 0.03 b
Solirubrobacter	1.26 ± 0.31 a	1.68 ± 0.10 a	1.55 ± 0.09 a
Blastococcus	0.73 ± 0.19 a	0.87 ± 0.06 a	1.00 ± 0.13 a
Blastocatella	0.36 ± 0.07 b	0.34 ± 0.02 b	0.57 ± 0.03 a
Candidatus_Entotheonella	0.62 ± 0.13 a	0.77 ± 0.09 a	0.88 ± 0.03 a
Rubrobacter	0.54 ± 0.10 b	0.65 ± 0.08 ab	0.85 ± 0.05 a
Bacillus	0.26 ± 0.05 a	0.27 ± 0.02 a	0.26 ± 0.02 a
Microvirga	0.58 ± 0.14 a	0.60 ± 0.04 a	0.61 ± 0.04 a

Note: Values with different letters in a row mean significant difference at $P < 0.05$, values are means of three replicates ± SE ($n = 3$).

were significantly greater at middle and bottom slope positions than at upper slope position ($P < 0.05$), while that of fungal ITS gene had no significant difference across slope positions ($P > 0.05$). The ADONIS analysis revealed similarity of bacterial community structure among slope positions but distinct fungal community structure between upper and bottom slope positions ($r^2 = 0.34$, $P < 0.05$).

The dominant phyla for bacterial community across the samples were Proteobacteria, Actinobacteria, Acidobacteria and Gemmatimonadetes, representing 80.7% of the bacterial reads (Table 3, Fig. 2a). At the phylum level, a few significant differences were observed among slope positions, such as Proteobacteria at bottom slope position (relative abundance of 31.4%) was 9.7% and 19.4% lower than that at upper (relative abundance of 36.5%) and middle (relative abundance of 37.5%) slope positions ($P < 0.05$). In contrast, the phylum Acidobacteria did oppositely (Table 3, Fig. 2a), which was 36.5% and 41.3% greater at bottom- (relative abundance of 18.6%) than at upper- (relative abundance of 13.6%) and middle- (relative abundance of 13.2%) slope positions ($P < 0.05$). The relative abundances of Actinobacteria were numerically equivalent among slope positions, ranging from 20.1% to 21.4%. Over 88 bacterial classes were detected, among them unidentified_Acidobacteria, Alphaproteobacteria, Betaproteobacteria were highly detected in all of the soils (Table 3, Fig. 2b). The class unidentified_Acidobacteria within phylum Acidobacteria was significantly greater at bottom- (relative abundance

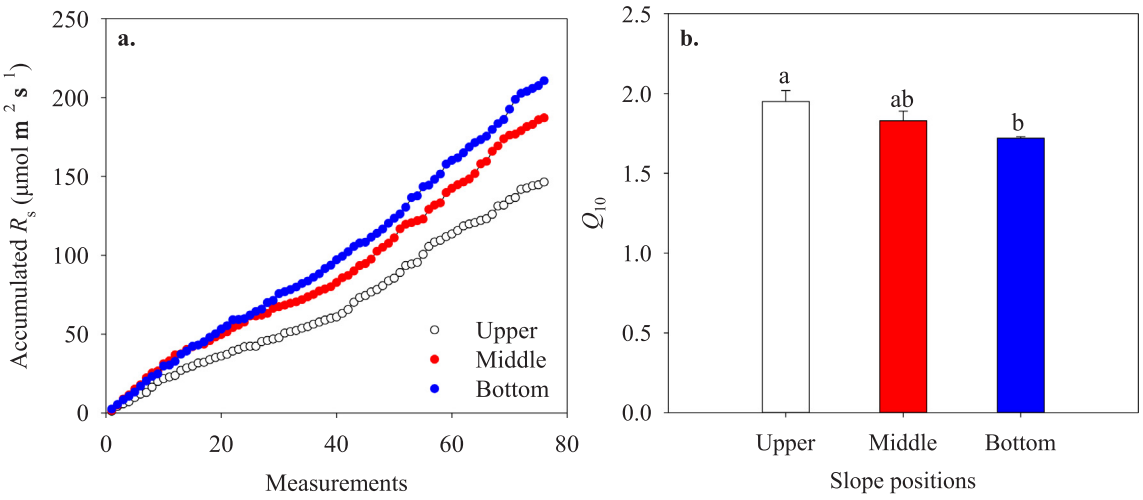

Fig. 2. Dynamics of accumulated soil respiration rate (a.) and Q_{10} (b.) at upper, middle and bottom slope positions.

of 15.5%) than at upper- (relative abundance of 10.6%) and middle- (relative abundance of 9.9%) slope positions (by 31.5% and 35.8%, $P < 0.05$). However, class Betaproteobacteria did oppositely (by 25.3% and 20.7%).

The fungal phylum Basidiomycota was predominant at upper and middle slope positions with abundances of 46.8% and 45.6%, and decreased to 10.9% at bottom slope position. In contrast, the phylum of Zygomycota, with the abundances of 4.7% and 11.3% at upper and middle slope positions, significantly increased to 36.5% at bottom slope position (Table 4, Fig. 2c). The relative abundances of Ascomycota showed no significant difference among slope positions. Taxonomical classification at the class level revealed that the relative abundances of class Incertae_sedis_Zygomycota (mainly order Mortierellales, Table 4) were significantly greater at bottom slope position (relative abundance of 36.5%) than at upper and middle slope positions (relative abundances of 4.7% and 11.3%). In contrast, the relative abundance of class Agaricomycetes (mainly order Agaricales) was significantly lower at bottom slope position (relative abundance of 10.2%) than at upper and middle slope positions (Table 4: relative abundances of 46.2% and 45.3%, Fig. 2d).

3.3. Soil respiration and Q_{10} among slope positions

Soil temperature varied little among slope positions (Table 5, $P > 0.05$). The soil moisture (%WFPS) was greater at bottom- (29.0% on average) than at upper- (25.2% on average, $P < 0.05$) and middle- (26.3% on average, $P < 0.05$) slope positions (Table 5). During the observation period, the accumulated soil respiration rates (R_s) showed the order of upper < middle < bottom slope positions (Fig. 3a). The average R_s at middle and bottom slope positions were 21.8%–36.2% and 38.2%–65.8% greater than at upper slope position over the study years. After averaging three years, the annually mean soil respiration at middle (2.17 μmol m^{-2} s^{-1}) and bottom (2.65 μmol m^{-2} s^{-1}) slope positions were 20.0% ($P < 0.05$) and 49.1% ($P < 0.05$) greater than that at upper slope position (1.81 μmol m^{-2} s^{-1}) (Table 5). Furthermore, the inter-positions spatial variation of both soil water and nutrients not only affected soil respiration but also changed the Q_{10}. With the three years' data set, mean Q_{10} at middle and bottom slope positions were 6.1% ($P > 0.05$) and 13.2% ($P < 0.05$) lower than that at upper slope position [(1.83 ± 0.06 and 1.72 ± 0.01) *vs.* 1.95 ± 0.07] (Fig. 3b).

3.4. Linking microbial properties to environmental variables and soil respiration

The SOC, DOC, root biomass and soil moisture were selected as environmental variables for RDA of soil bacteria (Fig. 3a), which could explained 71.4% of the soil bacterial community composition variation ($P < 0.05$). The bacterial communities among slope positions were more affected by the first axis, with the first two axes explained 34.01% and 29.50% of the total variation. Root biomass ($r^2 = 0.93$, $P < 0.05$), followed by SOC ($r^2 = 0.78$, $P < 0.05$) and then soil moisture ($r^2 = 0.63$, $P < 0.05$) and DOC ($r^2 = 0.48$, $P > 0.05$) were influential environmental gradients on the spatial distribution of bacterial community composition. The SOC, soil pH, root biomass and soil moisture were selected as environmental variables for RDA of soil fungi (Fig. 3b). Results showed that they could explain 58.0% of the fungal community composition variation ($P > 0.05$), with 27.79% and 20.69% of the total variation explained by the first two axes. Similar to bacterial community, soil moisture ($r^2 = 0.86$, $P < 0.05$), followed by SOC ($r^2 = 0.67$, $P < 0.05$), and then root biomass ($r^2 = 0.60$, $P > 0.05$) and soil pH ($r^2 = 0.35$, $P > 0.05$) were influential environmental gradients on the distribution of fungal community composition among slope positions.

Pearson correlation analysis confirmed the RDA results and further revealed that both bacterial richness and diversity positively correlated with SOC and root biomass. The main abundant bacterial classes that differentiated slope positions, i.e., unidentified_Acidobacteria positively and Betaproteobacteria negatively correlated with SOC, soil moisture and root biomass. The main abundant fungal order Mortierellales positively correlated with root biomass (Table S1). Pearson correlation analysis additionally showed that the SMBC positively correlated with bacterial richness and Gammaproteobacteria, while CB activity positively correlated with Alphaproteobacteria and Betaproteobacteria. Both bacterial richness and diversity positively correlated with soil respiration but only bacterial richness negatively correlated with Q_{10}. Moreover, Q_{10} was positively correlated with bacterial class Alphaproteobacteria and fungal order Agaricales; but negatively correlated with bacterial class unidentified_Acidobacteria and fungal order Mortierellales (Table S2).

4. Discussion

A notable finding from our data was the divergent responses of bacterial and fungal communities along the steep slope (Tables 2–4; Fig. 2), which was likely due to the different physiological properties of bacterial and fungal communities. Specifically, bacterial alpha-diversity

Table 4
Relative abundances of soil fungal communities affected by slope positions at phylum, class, order, family and genus levels.

Fungal ITS	Upper	Middle	Bottom
Phylum			
Basidiomycota	46.83 ± 16.70 a	45.59 ± 24.27 a	10.91 ± 1.35 b
Zygomycota	4.72 ± 1.57 b	11.30 ± 7.78 b	36.47 ± 8.30 a
Ascomycota	14.52 ± 4.83 a	15.23 ± 6.84 a	22.81 ± 7.16 a
Glomeromycota	0.02 ± 0.00 a	0.02 ± 0.01 a	0.02 ± 0.01 a
Chytridiomycota	0.00 ± 0.00 a	0.00 ± 0.00 a	0.01 ± 0.01 a
Others	33.91 ± 13.38 a	27.87 ± 14.37 a	29.77 ± 1.24 a
Class			
Agaricomycetes	46.19 ± 16.72 a	45.34 ± 24.40 a	10.24 ± 1.36 b
Incertae_sedis_Zygomycota	4.72 ± 1.57 b	11.30 ± 7.78 b	36.47 ± 8.30 a
Leotiomycetes	3.30 ± 2.64 a	3.26 ± 1.61 a	6.26 ± 3.02 a
Eurotiomycetes	2.86 ± 1.38 a	2.51 ± 0.97 a	2.77 ± 0.28 a
Dothideomycetes	0.74 ± 0.21 b	1.13 ± 0.60 b	3.92 ± 1.08 a
Pezizomycetes	0.12 ± 0.07 b	0.40 ± 0.18 b	1.63 ± 0.42 a
Saccharomycetes	0.21 ± 0.09 a	0.18 ± 0.09 a	0.07 ± 0.03 a
Geoglossomycetes	0.03 ± 0.03 a	0.29 ± 0.29 a	0.51 ± 0.26 a
Incertae_sedis_Ascomycota	0.01 ± 0.00 b	0.01 ± 0.00 b	0.03 ± 0.01 a
Tremellomycetes	0.48 ± 0.10 a	0.20 ± 0.11 a	0.43 ± 0.01 a
Order			
Agaricales	23.72 ± 11.39 a	6.05 ± 2.83 b	6.53 ± 0.70 b
Mortierellales	4.40 ± 1.66 b	10.43 ± 7.14 b	35.26 ± 7.61 a
Boletales	7.74 ± 6.67 a	2.51 ± 2.44 a	0.07 ± 0.04 a
Sebacinales	0.01 ± 0.00 a	0.12 ± 0.08 a	0.02 ± 0.00 a
Trechisporales	2.96 ± 2.88 a	2.92 ± 2.89 a	0.06 ± 0.00 a
Incertae_sedis_Leotiomycetes	0.39 ± 0.18 a	1.46 ± 1.09 a	3.55 ± 2.59 a
Cantharellales	0.41 ± 0.15 a	0.62 ± 0.26 a	1.92 ± 1.01 a
Pleosporales	0.36 ± 0.04 a	0.75 ± 0.34 a	1.88 ± 0.86 a
Chaetothyriales	1.03 ± 0.94 a	0.21 ± 0.10 a	0.19 ± 0.06 a
Russulales	0.01 ± 0.01 a	0.01 ± 0.01 a	0.00 ± 0.00 a
Family			
Mortierellaceae	4.40 ± 1.66 b	10.43 ± 7.14 b	35.25 ± 7.61 a
Hygrophoraceae	14.77 ± 12.42 a	1.54 ± 1.01 b	1.88 ± 1.78 b
Hydnodontaceae	2.96 ± 2.88 a	2.92 ± 2.89 a	0.06 ± 0.00 a
Incertae_sedis_Leotiomycetes	0.22 ± 0.11 a	0.22 ± 0.22 a	3.25 ± 2.59 a
Incertae_sedis_Agaricales	1.80 ± 1.77 a	0.03 ± 0.02 a	0.11 ± 0.03 a
Clavariaceae	2.02 ± 0.65 a	1.42 ± 0.81 a	2.72 ± 0.85 a
Incertae_sedis_Pleosporales	0.20 ± 0.05 a	0.35 ± 0.19 a	1.20 ± 0.94 a
Herpotrichiellaceae	0.96 ± 0.93 a	0.14 ± 0.07 a	0.12 ± 0.05 a
Stephanosporaceae	0.01 ± 0.01 a	0.01 ± 0.01 a	0.00 ± 0.00 a
Genus			
Mortierella	4.28 ± 1.70 b	10.25 ± 7.17 b	33.33 ± 6.81 a
Camarophyllopsis	1.80 ± 1.77 a	0.02 ± 0.02 a	0.11 ± 0.03 a
Clavaria	1.99 ± 0.66 a	1.40 ± 0.80 a	1.62 ± 0.60 a
Cladosporium	0.31 ± 0.17 b	0.27 ± 0.27 b	1.75 ± 0.34 a
Eremiomyces	0.00 ± 0.00 a	0.01 ± 0.00 a	0.88 ± 0.65 a
Conocybe	0.39 ± 0.14 a	1.01 ± 0.62 a	0.11 ± 0.08 a
Tetracladium	0.12 ± 0.08 b	0.08 ± 0.08 b	0.65 ± 0.24 a
Parasola	0.03 ± 0.02 a	0.00 ± 0.00 a	0.05 ± 0.03 a
Exophiala	0.01 ± 0.00 a	0.01 ± 0.00 a	0.01 ± 0.00 a

Note: Different letters in a row indicate significant difference at $P < 0.05$, and values are means of three replicates ± SE ($n = 3$).

was greater at middle and bottom slope positions than at upper slope position while fungal alpha-diversity was unchanged among slope positions (Table 2). The bacterial community had increased or decreased abundances among slope positions while fungal community had changed dominant species (Tables 3 and 4, Fig. 2). These results provided evidence to reject our first hypothesis.

4.1. Slope positions altered both diversity and composition of bacterial community

The greater bacterial alpha-diversity at middle and bottom slope positions than at upper slope position (Table 2) clearly illustrated the sensitivity of bacterial diversity to spatial variation along the slope. This partly resulted from the more favorable soil water condition (by 4.4% and 15.1%, Table 5) due to water redistribution (Wang et al., 2017c), with determination coefficient of 0.73 between bacterial diversity and soil moisture (Table S1). Such effect was also observed by Yuste et al. (2011), who reported the inability of the bacterial unicellular body form to bridge the air-filled voids under drought condition (Griffin, 1985). On the semiarid steep-slope, soil water affected bacterial diversity not only directly (Jassal et al., 2008; Suseela et al., 2011) but also indirectly via driving substrate redistribution along the slope (Bryan, 2000) and changing the transfer of recently plant-assimilated C to soil bacteria (Bardgett et al., 2008; Singh et al., 2010). This was confirmed by the positive correlations between bacterial alpha-diversity and SOC, root biomass (Table S1). In fact, more bacterial species meet their minimum resource requirements with the resource level increases within certain degree (Banerjee, 2016). RDA results (Fig. 3a) confirmed the importance of soil water and substrate supply (SOC and plant C inputs) in regulating bacterial distribution on the slope.

Contrasting responses of bacterial classes Betaproteobacteria (increased) and unidentified_Acidobacteria (decreased) were observed along the slope (Table 3, Fig. 2a, b). The Betaproteobacteria had negative correlations with SOC, root biomass and soil moisture (Table S1),

Table 5
Mean soil temperature, soil moisture and soil respiration (R_s) at the three slope positions for 2014, 2015 and 2016.

Years	Slope positions	Soil temperature/°C	Soil moisture/% WFPS	R_s/μmol m^{-2} s^{-1}
2014	Upper	20.3 ± 2.9 a	26.6 ± 1.6 b	1.90 ± 0.25 b
	Middle	18.8 ± 3.8 a	27.0 ± 1.9 b	2.72 ± 0.22 ab
	Bottom	20.9 ± 3.7 a	29.3 ± 2.1 a	2.59 ± 0.32 a
2015	Upper	20.2 ± 3.0 a	23.2 ± 1.6 b	1.26 ± 0.12 b
	Middle	19.2 ± 4.4 a	25.2 ± 1.5 ab	1.58 ± 0.19 ab
	Bottom	21.4 ± 4.0 a	28.8 ± 1.6 a	2.09 ± 0.18 a
2016	Upper	20.3 ± 2.7 a	25.7 ± 1.8 b	2.27 ± 0.46 b
	Middle	19.5 ± 4.4 a	26.6 ± 2.0 ab	2.77 ± 0.35 ab
	Bottom	21.6 ± 3.7 a	28.8 ± 1.9 a	3.14 ± 0.37 a
Mean	Upper	20.0 ± 0.6 a	25.2 ± 1.7 b	1.81 ± 0.33 c
	Middle	20.3 ± 0.6 a	26.3 ± 1.9 b	2.36 ± 0.28 b
	Bottom	20.5 ± 0.6 a	29.0 ± 1.9 a	2.61 ± 0.32 a

Note: n = 25 in 2014, n = 24 in 2015 and n = 26 in 2016 for soil temperature, soil moisture and soil respiration; Different letters in a column indicate significant difference among slope positions at $P < 0.05$.

suggesting their oligotrophic nature, while unidentified_Acidobacteria showed positive correlations, implying their copiotrophic nature. This contradicted the common sense (Fierer et al., 2008; Zhang et al., 2016). Possible causes may be related to the optimal pH ranges (4–8) for soil bacterial communities (Rousk et al., 2010). The high soil pH (Table 1) along the slope might be the factor accounting for the abnormal distribution patterns of soil bacterial community due to inhibition of the normal growth of soil bacteria. Another explanation may be the interaction between soil bacteria and soil fungi, between soil microbes and root system through competitive exclusion (Mayfield and Levine, 2010), especially in the loess soil where soil fertility was initially low (Guo et al., 2012). Potential mechanism of such changes in bacterial community composition remains unclear and more researches are needed in the future.

4.2. Slope positions changed the composition but not the diversity of fungal community

Unlike bacterial alpha-diversity, the fungal alpha-diversity was unchanged among slope positions (Table 2), suggesting its resistance to slope positions-induced variation in moisture, root biomass and soil C, N fractions (Table S1). Similar results were observed in another semi-arid soil (Yuste et al., 2011), which considered that the hyphal/mycelial growth form in fungi facilitates them to overcome better the disadvantages of water-poor and/or nutrient-poor conditions than bacteria. However, fungal community composition showed strong sensitivity to spatial variance among slope positions (Table 4, Fig. 2c, d), indicating that the phylotype composition of the fungal communities could adapt accordingly to environmental changes without a general loss in diversity (Yuste et al., 2014). More specifically, the fungal communities changed from being Agaricales-dominant at upper slope position to Mortierellales-dominant at bottom slope position (Table 4, Fig. 2c, d), suggesting that fungal communities transitioned from slow-growing oligotrophic groups (Li et al., 2017b; Sinsabaugh et al., 2005) to fast-growing copiotrophic groups (Chigineva et al., 2009; Wang, 2012). The greater overall contribution of Agaricales to the fungal community composition at upper and middle slope positions than at bottom slope position may be related to their improved metabolic capacities for decomposing lignocellulose (Li et al., 2017b; Sinsabaugh et al., 2005), a major component of organic C in grassland debris. However, the bottom slope position provided a habitat that favored the growth of order Mortierellales due to the large number of newly sequestrated C inputs into soils form plant (Wang et al., 2014), as the fast-growing opportunistic fungi were stimulated by easily accessible C sources (Chigineva et al., 2009). This was confirmed by its positive correlation with root biomass (Table S1). RDA result (Fig. 3b) showed the importance of soil water and SOC in shaping fungal distribution. The extremely significant effect of soil water on fungal community was possibly not only through driving substrate redistribution down slope but also via enhancing plant C inputs to soils (Bardgett et al., 2008; Singh et al., 2010). The soil pH in this study, although being one of the most important influential driving factors for the soil microbial communities (Lauber et al., 2009; Pennanen et al., 1998; Siles and Rosa, 2016), only exerted weak effect on soil fungal community along the slope due to its narrow range among slope positions (Table 1: 8.08–8.11).

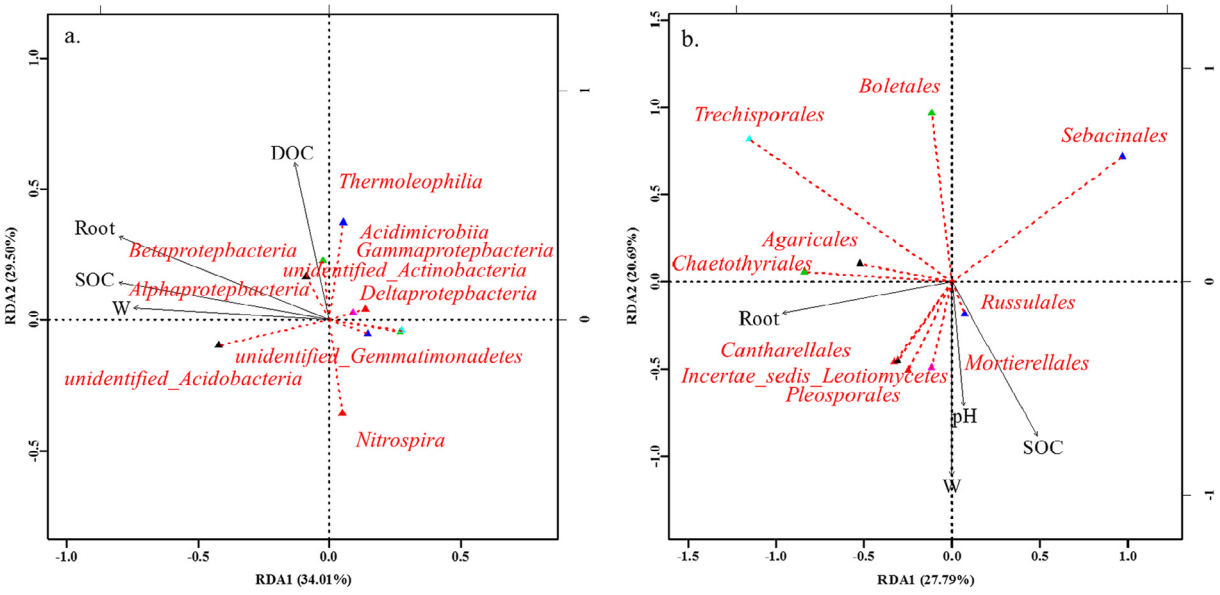

Fig. 3. Ordination plots of the results from the redundancy analysis (RDA) to identify relationships between bacterial (a.) and fungal (b.) populations (red arrows) and environmental variables (black arrows). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.3. Linking microbial community to soil respiration along the slope

In our study, contrasting distribution patterns of soil respiration (increased) and Q_{10} (decreased) were observed down the slope (Table 5), providing evidence to support the second hypothesis. Few taxonomy was observed to be related with soil respiration (Table S2), which may be because the responses of root respiration were more evident than that of microbial respiration. No systematic difference was found in Q_{10} among roots differing in root biomass or root N concentration in previous studies (Atkinson et al., 2007). It is plausible that microbial response to either improved substrate availability or increased plant C inputs drove the observed decrease in Q_{10}. Variation in microbial respiration Q_{10} on the slope could be attributed to shifts in microbial trophic strategy (Bai et al., 2017) and substrate utilization (Schutter and Dick, 2001; Struecker and Joergensen, 2015). Strong correlations between bacterial alpha-diversity and soil respiration (positive), as well Q_{10} (negative) (Table S2) suggested that shifts in microbial diversity may be drivers of carbon mineralization (Tardy et al., 2015). Our result adds to a growing number of studies that confirmed the relevant role of soil microbial communities in soil C balance (Banerjee, 2016; Fuchslueger et al., 2014; Wagg et al., 2014). Moreover, the positive correlation between soil Alphaproteobacteria (oligotrophic) and Q_{10} (Table S2) was likely due to their susceptibility to the recalcitrant C (Preusser et al., 2017). This was confirmed by the positive correlation between Alphaproteobacteria and cellobiohydrolase activity (Table S2). According to the enzyme-activation theory, the substrate of recalcitrant molecular structure was degraded with higher Q_{10} (Bosatta and Ågren, 1999) and *vice versa*. In contrast, the unidentified_Acidobacteria (copiotrophic) had negatively correlation with Q_{10} due to their preference of labile C, which was confirmed by its negative correlation with cellobiohydrolase activity (Table S2). In a similar way, it was likely that the oligotrophic fungal order Agaricales correlated positively with Q_{10} (Table S2) due to its susceptibility to the recalcitrant C (Bastida et al., 2016; Vo et al., 2013), while the copiotrophic fungal order Mortierellales did negatively due to the susceptibility of the fast-growing saprobic fungi to simple soluble C (Li et al., 2017b), which was confirmed by its negative correlation with β-D-glucosidase activity (Table S2).

The shift in microbial community composition (Table 4, Fig. 2c, d) suggested changes in microbial substrate utilization (Li et al., 2017b), which were confirmed by the spatial variation in enzyme activities along the slope (Table 1). In middle slope position, the reduced abundance of order Agaricales (Table 4), increased β-D-xylosidase and cellobiohydrolase activities and decreased β-D-glucosidase activities than in upper slope position (Table 1), indicated changes in microbial utilization C source from recalcitrant C (such as lignocellulose) to more labile C (such as xylose, cellulose and hemicellulose) (Bastida et al., 2016; Du et al., 2010; Stone et al., 2012; Vo et al., 2013). In bottom slope position, the decreased Betaproteobacteria, increased unidentified_Acidobacteria, replacement of Agaricales by Mortierellales and depression of all the enzyme activities suggested a possible functional redundancy in the communities (Banerjee, 2016) and further changes in microbial utilization to simple soluble C (Kjøller et al., 2002). These substrate down slope required declining activation energy for chemical and microbial decomposition (Ball and Virginia, 2014; Bosatta and Ågren, 1999). Therefore, explanation of the decreasing Q_{10} down slope could be the switch of oligotrophic groups to copiotrophic groups and their utilization of C sources. These results revealed that erosional distributions of water and substrate lead to differentiate the microbial utilization of SOC at different slope positions. The divergent responses of enzyme activities also rejected the first hypothesis raised in this study.

5. Conclusions

In the hillslope grassland ecosystem of the Loess Plateau, all the microbial diversity, abundances and enzyme activities had divergent responses to spatial variations in soil water and substrate along the steep slope. More specifically, bacterial diversity was greater at middle and bottom slope positions, while fungal diversity varied little across slope positions. The bacterial community had increased abundance of Acidobacteria and decreased abundance of Proteobacteria at bottom slope position than at upper and middle slope positions; fungal community transitioned from being Agaricales-dominant to being Mortierellales-dominant downslope. The enzyme activities associated with recalcitrant C decomposition declined down slope while that associated with labile C decomposition hiked at middle slope position; all the enzyme activities were suppressed at bottom slope position. Shift in microbial community composition and enzyme activities suggested microbial substrate utilization changed from recalcitrant C to more labile C and then to simple soluble C, resulting in increased soil respiration and decreased Q_{10} down the slope.

Our results highlight the importance of microbial information in understanding the mechanism driving SOC cycling in hillslope ecosystems and assessing the carbon emission effect of soil erosion. Subtle changes in soil water can drive dramatic differentiation in substrate, diversity, structure, composition and activities of microbial community at a small scale along the steep slope. The divergent responses of soil bacterial and fungal communities to spatial variations of water and substrate along the steep slope should be properly taken into account for accurately modelling the soil carbon budget under changing environment in hillslope ecosystems. Otherwise, the soil CO_2 flux estimation would be biased. To further understand soil microbial community composition and function on steep slopes, an integrated monitoring of the spatial-scale microbial dynamics is needed.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.apsoil.2018.06.018.

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