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Divergent taxonomic and functional responses of microbial communities to field simulation of aeolian soil erosion and deposition

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Abstract

Aeolian soil erosion and deposition have worldwide impacts on agriculture, air quality and public health. However, ecosystem responses to soil erosion and deposition remain largely unclear in regard to microorganisms, which are the crucial drivers of biogeochemical cycles. Using integrated metagenomics technologies, we analysed microbial communities subjected to simulated soil erosion and deposition in a semiarid grassland of Inner Mongolia, China. As expected, soil total organic carbon and plant coverage were decreased by soil erosion, and soil dissolved organic carbon (DOC) was increased by soil deposition, demonstrating that field simulation was reliable. Soil microbial communities were altered ($p < .039$) by both soil erosion and deposition, with dramatic increase in *Cyanobacteria* related to increased stability in soil aggregates. *amyA* genes encoding α-amylases were specifically increased ($p = .01$) by soil deposition and positively correlated ($p = .02$) to DOC, which likely explained changes in DOC. Surprisingly, most of microbial functional genes associated with carbon, nitrogen, phosphorus and potassium cycling were decreased or unaltered by both erosion and deposition, probably arising from acceleration of organic matter mineralization. These divergent responses support the necessity to include microbial components in evaluating ecological consequences. Furthermore, Mantel tests showed strong, significant correlations between soil nutrients and functional structure but not taxonomic structure, demonstrating close relevance of microbial function traits to nutrient cycling.

Keywords: 16S rRNA sequencing, functional traits, GEOCHIP 5.0, microbial community, soile deposition, wind erosion

1 INTRODUCTION

Aeolian soil erosion, exacerbated by anthropogenic perturbations, has become one of the most alarming processes of land degradation and desertification (Burri & Graf, 2009; Okin, Mahowald, Chadwick, & Artaxo, 2004; Quinton, Govers, Van Oost, & Bardgett, 2010; Saxton, Chandler, & Schillinger, 2001). Dust storms can affect large areas by long-distance aeolian soil transport, which leads to considerable loss of economic and environmental benefits (McTainsh & Strong, 2007). Adverse effects of soil erosion on land productivity and carbon cycling have been extensively analysed (Gregorich, Greer, Anderson, & Liang, 1998; Harper, Gilkes, Hill, & Carter, 2010; Lal, 2005; Li et al., 2005; Nordstrom & Hotta, 2004; Quinton et al., 2010; Zhao, Zhou, Zhang, & Zhao, 2006). Reductions in net primary productivity, vegetation coverage and effective rooting depth caused by soil erosion have been well documented (Li, Okin, Alvarez, & Epstein, 2007, 2008; Munson, Belnap, & Okin, 2011), in addition to heavy loss of soil organic carbon (SOC) (Quinton et al., 2010; Yan, Wang, Wang, Zhang, & Patel, 2005). There are other accompanying changes such as increase in soil temperature caused by changes in soil reflectance properties (Lal, 2003), and decrease in available water capacity. In sharp contrast, dust deposition can act as a potential fertilizer because dust often carries the most labile organic fractions of soil (Van Pelt & Zobeck, 2007), which leads to changes of ecosystem functioning in deposited sites.

When winds carry away soil, microbes in the soil ride along like hitchhikers. Given that biological particles may account for up to 25% of atmospheric aerosols (Jaenicke, 2005), the relative abundance of airborne microbes is estimated to range from 10^4 to 10^6 cells/m^3 (Bowers, McLetchie, Knight, & Fierer, 2011). Microbial exposure in air is associated with incidences of disease in crops, livestock, and humans (Barberán et al., 2015). As microbes have been increasingly recognized as key players in mediating soil biogeochemical cycling (Falkowski, Fenchel, & Delong, 2008), it is of great interest to understand how aeolian soil erosion and deposition affect microbial community structure and function. However, to a large extent this knowledge has remained elusive, mainly due to the difficulty in simulating aeolian processes as well as dissecting highly complex microbial communities (Gans, Wolinsky, & Dunbar, 2005). To address this deficiency, here we adopt both high-throughput MiSeq sequencing of 16S rRNA gene amplicons to analyse microbial taxonomy, and a microarray-based tool (GEOCHIP 5.0) to analyse microbial functional genes. GeoChip has been successfully used in a wide range of habitats (Ding et al., 2015; Hazen et al., 2010; He et al., 2007; Yergeau et al., 2012; Yue et al., 2015). Direct comparisons between GeoChip and metagenomics shotgun sequencing technologies revealed similar results (Hazen et al., 2010; Mason et al., 2012; Xue et al., 2016; Yan et al., 2015), but GeoChip has an advantage in quantitative measurements with comparable accuracy to real-time PCR (Tiquia et al., 2004; Yergeau, Kang, He, Zhou, & Kowalchuk, 2007).

This study was conducted in a semiarid grassland of Duolun County located in southeastern Inner Mongolia, China, which had experienced substantial improper land use such as overgrazing and consequently modest to heavy aeolian soil erosion (Hoffmann, Funk, Reiche, & Li, 2011; Hoffmann, Funk, Wieland, Li, & Sommer, 2008; Reiche et al., 2012). In 1999, the total degraded area of the steppe in the Xilin River basin, wherein our study site was located, was estimated to be 7,689.3 km^2, accounting for 72% of the total basin (Tong, Wu, Yong, Yang, & Yong, 2004). Therefore, there is a critical need to evaluate the effect of soil erosion and deposition on this grassland.

We hypothesize that microbial taxonomic and functional structure would be inversely altered by aeolian soil erosion and deposition based on the concomitant changes in plant, soil and functional process variables. As soil erosion and deposition are known to alter soil carbon profiles, particularly labile carbon, we hypothesize that various microbial functional genes, particularly those associated with labile carbon utilization, would be changed as a functional response.

2 MATERIALS AND METHODS

2.1 Site description and experimental design

This study was carried out in a field site of the Duolun Restoration Ecology Experimentation and Demonstration Station (42°2′N, 116°17′E; 1,324 m asl) located in Inner Mongolia, China. This site is a typical temperate semiarid grassland with a temperate monsoon climate (Chen et al., 2014). The mean annual precipitation is about 380 mm and the mean annual temperature is 2.1°C. The soil type is Haplic Calcisol (FAO). Soil texture is sandy loam with 71.9% sand, 15.6% silt and 12.5% clay. The grassland is dominated by a typical steppe vegetation such as *Stipa krylovii*, *Agropyron cristatum*, *Artemisia frigida*, *Cleistogenes squarrosa* and *Potentilla acaulis*. Average plant heights are 20–40 cm, and plant coverages are 40%–60%.

In spring of 2010, five replicates for each of six groups of control, soil erosion, soil deposition, sheep grazing, soil erosion plus sheep grazing, soil deposition plus sheep grazing were set up with a random block design (Fig. S1). Each plot is a square with the size of 4 m length × 4 m width, with a 2.5-m buffer zone in between plots. We used PVC boards protruding 10 cm above ground each plot to prevent the disturbance of natural wind direction influence and deposited soil from adjacent plots. The background value survey showed that soil temperature, moisture, nutrient contents and vegetation variables were similar across plots at the time of experimental set-up. In this study, we collected 15 soil samples from control, soil erosion and soil deposition plots to focus on soil erosion and deposition effects.

We carried simulated wind erosion and soil deposition manipulations in early May 2010 and 2011, the early growing season when soil was not protected by snow cover or vegetation cover and consequently wind erosion was

rampant in this grassland (Li, Zhao, Zhang, Zhang, & Shirato, 2004). We blew off a 1.5–3.0 cm layer of topsoil from soil eroded plots using a wind fire extinguisher (Taining Machinery Ltd. Co., Taizhou, Jiangsu, CN) (Fig. S1). We used a cloth bag to collect soils blown off from five eroded sites, evenly blended and divided them into five portions. Then we wore rubber gloves and evenly distributed the soil to the surface of the deposited plots. The eroded and deposited soil depths were estimated as modest yearly erosional and depositional intensities in Inner Mongolia grasslands (Zhao, Yi, et al., 2006).

2.2 Sample collection and geochemical analyses

To manifest the lasting effect of wind erosion and deposition on the grassland ecosystem, soil samples were not collected until the middle of August, 2012, when plant variables could easily be measured. At each plot, 4 soil cores of 0–10 cm depth were randomly taken using an auger (5 cm diameter) and mixed to obtain a composite sample. After passing through a 1 mm sieve and removing visible roots and stones by hand, samples were kept on ice during transport to the laboratory. Subsamples for microbial analysis were stored at −80°C, and other subsamples for geophysical and geochemical analyses were air-dried.

To measure soil particle-size distribution, 1 g soil was treated with 40% H_2O_2 before dispersal with sodium hexametaphosphate and sonication. The particle-size distribution of soils samples was then determined using a laser particle-size analyser (LS13320, Beckman Coulter, Inc., Brea, CA, USA), which measured volume per cent of particles classes from 0.04 to 2,000 μm in diameter. Soil texture was assessed from the percentage of clay (<2 μm), silt (2–50 μm), and sand (50–2,000 μm) following the taxonomy of the U.S. Department of Agriculture. Dv (volume fractal dimension of soil particles) (Tyler & Wheatcraft, 1992) was used for characterizing soil particle-size distribution.

Gravimetric soil moisture was measured after oven-drying at 105°C for 12 hr. Soil temperature at a depth of 10 cm was determined using a thermocouple probe connected to an Automated Soil CO_2 Flux System (LI-8100, LI-COR, Lincoln, NE, USA) when sampling. Dissolved inorganic nitrogen (DIN), NH_4^+–N and NO_3^-–N were extracted from 10 g fresh soil with 50 ml 2 M KCl, and measured with a Discrete Auto Analyzer (SmartChem 200, WestCo Scientific Instruments Inc., Italy). Soil pH was measured using a PB-10 basic pH meter (Sartorius AG, Göttingen, Germany) after mixing soil with water at the 1:2.5 ratio (w/v) and settling for 30 min. Total organic carbon (TOC) and total nitrogen (TN) were measured using a solid combustion method at the temperature of 960°C in a combustion tube (Yeomans & Bremner, 1991) with an elemental analyser Elementar vario MACRO CUBE (Elementar Co., Hanau, Germany).

Microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) were measured by a fumigation–extraction method (Brookes et al., 1985) with a

total organic carbon analyser Elementar vario TOC (Elementar Co.). The differences in extractable carbon and nitrogen contents between fumigated and unfumigated subsamples were calculated using conversion factors of 0.45 and 0.54, respectively. The organic carbon in unfumigated soil extracts was deemed as dissolved organic carbon (DOC).

A 1-m^2 frame with 100 equally distributed grids was placed at the centre of each plot of the permanent quadrat above the canopy to measure plant species richness and coverage. The plant species richness was the number of plant species identified in the quadrat. Plant coverage was visually estimated in the quadrat.

2.3 Soil DNA preparation and experiments

Genomic DNA of each soil microbial community was extracted from 5 g soil sample by a freeze-grinding procedure as described previously (Zhou, Bruns, & Tiedje, 1996). Then crude DNA was purified by phenol extraction and low melting agarose gel electrophoresis. DNA quality was determined by absorbance ratios of A260/280 nm and A260/230 nm using a NanoDrop ND-1000 Spectrophotometer (NanoDrop Technologies Inc., Wilmington, DE, USA). DNA quantity was determined by PicoGreen using a FLUOstar Optima plate reader (BMG Labtech, Jena, Germany).

2.4 Illumina MiSeq sequencing and data processing

High-throughput sequencing of 16S rRNA gene amplicons with an Illumina MiSeq (Illumina, San Diego, CA, USA) was used for microbial taxonomy profiling. The V4 region of the 16S rRNA genes was amplified with the primer pair 515F and 806R (5′-GTGCCAGCMGCCGCGGTAA-3′ and 5′-GGACTACHVGGGTWTCTAAT-3′). A sequential round of PCR was used to combine Illumina adapter sequences with barcodes to all amplified products. The MiSeq 500-cycles kit was used for 2 × 150 bp paired-end sequencing on a MiSeq instrument (Illumina).

We processed raw sequence data on the Galaxy platform with a number of software tools. First, we evaluated the quality of raw sequence data with FastQC (www.bioinformatics.babraham.ac.uk/projects/fastqc/). Then, we carried out demultiplexing to remove PhiX sequences, and we sorted sequences to the appropriate samples based on their barcodes, allowing for 1 or 2 mismatches. We performed quality trimming with Btrim (Kong, 2011). We merged paired-end reads into full length sequences with FLASH (Magoč & Salzberg, 2011). We removed sequences less than 200 bp or containing ambiguous bases. We discarded chimeric sequences based on prediction by UCHIME (Edgar, Haas, Clemente, Quince, & Knight, 2011) with the Greengenes database. We generated OTUs with Uclust (Edgar, 2010) at the 97% similarity level and obtained OTUs after removing OTUs appearing in no more than three of the five replicates to ensure data reproducibility. We assigned taxonomic annotation of individual OTU according to representative sequences using RDP's 16S Classifier (Wang, Garrity, Tiedje, & Cole, 2007).

2.5 GeoChip hybridization and data processing

GEOCHIP 5.0 was used for functional gene profiling and carried out as previously described (Yang et al., 2014). Briefly, 2 μg DNA was labelled with Cy-3 dye by random priming and purified with a QIAquick purification kit (Qiagen, Valencia, CA, USA). After drying in a SpeedVac (ThermoSavant, Milford, MA, USA) for 45 min at 45°C, labelled DNA was rehydrated with 27.5 μl DI water and then hybridization solution was added. A total of 120 μl hybridization solution was loaded onto the gasket slide and hybridized for 20–22 hr at 67°C. GeoChip was imaged (NimbleGen MS 200 microarray scanner) as a Multi-TIFF. The signal intensity of each spot on the microarray was then quantified with the AGILENT FEATURE EXTRACTION program and loaded onto the GeoChip data analysis pipeline (ieg.ou.edu/microarray/) and used to indicate relative abundance of functional genes.

Data normalization and analyses of raw data were described previously (Yang et al., 2014). The threshold of signal-to-noise ratio (SNR = [signal mean-background intensity]/background standard deviation) of GeoChip was determined by thermophile probes, serving as negative controls for the grassland environment, in that less than 5% of all thermophile probes were detected. We also removed genes detected in no more than three of five biological replicates and then logarithmically transformed the values, followed by normalization of the signal intensity of each spot by dividing by total abundance.

2.6 Statistical analyses

Differences of microbial taxonomic and functional structure were examined by three dissimilarity tests of MRPP (multiple response permutation procedure), ANOSIM (analysis of similarities) and Adonis (permutational multivariate analysis of variance) based on the Bray–Curtis distance, using the GeoChip data analysis pipeline (ieg.ou.edu/microarray/). The α-diversity was calculated by Shannon and Simpson indices. Significant differences of relative abundance in the taxonomy or functional gene between the treatments and control were analysed by two-tailed *t* tests based on two-sample equal variances or one-way ANOVA. The response ratio analysis was used to calculate the ratio of mean value in the treatments to that in the control sites. Pearson correlation coefficients were calculated to determine correlations between microbial parameters (e.g., α-diversity or the relative abundance of functional genes) and selected environmental variables or correlations between the relative abundance of functional genes. The detrended correspondence analysis (DCA) was used to examine microbial taxonomic and functional structure. Simple and partial Mantel tests based on Bray–Curtis and Euclidean distance were used to examine the relationships between individual environmental variables and microbial communities. Phylogenetic NRI values were used to quantify phylogenetic structure. These three analyses were performed using functions in the vegan and picante packages in R (v. 3.1.2.).

3 RESULTS

3.1 Environmental variables

Changes of environmental variables by soil erosion and deposition were dissimilar (Table S1), but consistent with several observations elsewhere (Li et al., 2007; Quinton et al., 2010; Van Pelt & Zobeck, 2007; Yan et al., 2005). Specifically, aeolian erosion increased soil temperature for 0.80°C at the marginally significant level (p = .07), but decreased soil total organic carbon (TOC) from 15.80 to 14.10 g/kg soil (p = .08) and plant coverage from 53.29% to 36.38% (p = .06). Soil deposition increased (p = .03) soil dissolved organic carbon (DOC) from 74.13 to 123.46 mg/kg soil, albeit TOC remained unaltered. Other edaphic properties such as water content, pH, total nitrogen (TN), NH_4^+, NO_3^- and plant richness remained largely unchanged. In contrast, the functional process of soil respiration was sensitive to environmental disturbance, as it was decreased by aeolian erosion but increased by soil deposition (p < .05). Microbial biomass, measured by microbial biomass carbon and nitrogen, was similar across all plots (Table S1).

3.2 Overall responses of microbial taxonomic structures

A total of 439,058 good-quality 16S rRNA gene sequences were generated by high-throughput sequencing. After resampling sequences with 16,875 sequences per sample, 5,998 OTUs were generated at the 97% similarity level. Among them, 42.2% of OTUs were undescribed (i.e., unrepresented in the reference sequence database) (see Section 2 for details; rarefaction curves are shown in Fig. S2). The detrended correspondence analysis (DCA) showed that microbial communities were well separated into three groups of soil erosion, control and soil deposition (Figure 1a), which was further verified by three nonparametric dissimilarity tests showing significant differences among those groups (Table S2).

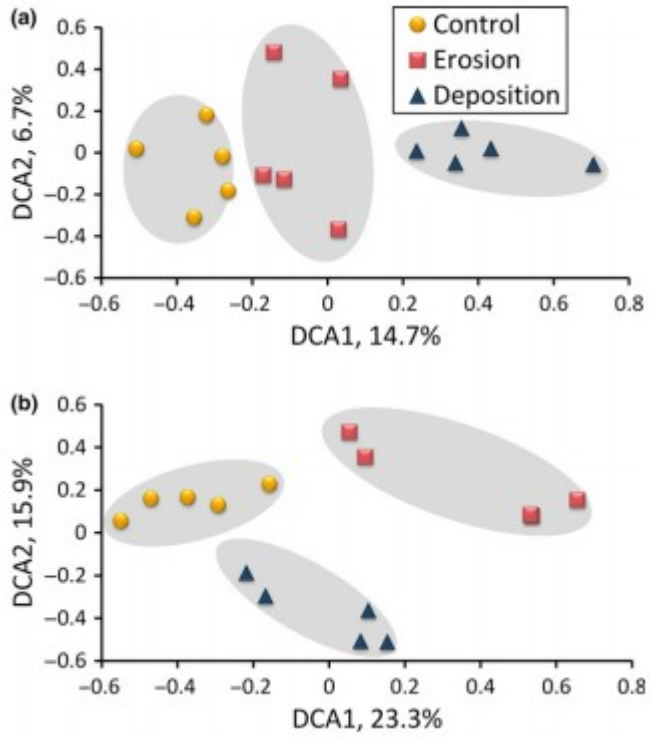

FIGURE 1 The detrended correspondence analysis (DCA) of (a) taxonomic structure and (b) functional structure. The values of axes 1 and 2 are percentages of community variation attributed to the corresponding axis.

The taxonomic α-diversity, based on Shannon and Simpson indices of OTU data, remained unchanged by soil erosion and deposition (Table S3). However, phylogenetic NRI (Net Relatedness Index) values of microbial communities, used to measure phylogenetic clustering (Webb, Ackerly, McPeek, & Donoghue, 2002), were larger than 2 in both eroded and deposited samples and higher than their controls (Table S4), suggestive of environmental filtering by stress (Goberna, Navarro-Cano, Valiente-Banuet, Garcia, & Verdu, 2014).

3.3 Bacterial taxon groups

Actinobacteria (29.9%), *Acidobacteria* (24.5%) and *Proteobacteria* (17.8%) were the most abundant phyla in soil samples, amounting to more than 70% of total OTUs (Figure 2a). Among them, only *Actinobacteria* was altered by soil deposition at the marginally significant level ($p < .10$) (Figure 2b). However, a closer examination showed that certain subgroups of *Acidobacteria* and *Proteobacteria* were also changed. For example, *Gp1 and Gp3*, known to be abundant in soil (Naether et al., 2012), were decreased by 54.9% and 25.0%, respectively, at the eroded site but unchanged at the deposited site. *Gp16* was increased by 33.7% at the eroded site and 29.0% at the deposited site (Fig. S3).

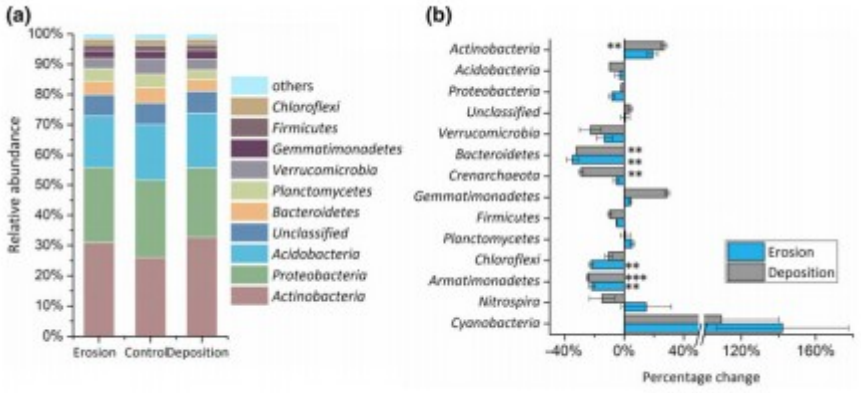

FIGURE 2 (a) Relative abundances of microbial phyla with erosion and deposition; (b) per cent changes in relative abundances of microbial phyla with erosion and deposition. Asterisk indicates significant differences. $^{**}p < .05$; $^{***}p < .01$

We examined *Cyanobacteria*, which was often observed at eroded sites (Fierer et al., 2012). Strikingly, we found that *Cyanobacteria* substantially increased by 142.2% at the eroded site, and 109.4% at the deposited site (Figure 2b). In addition, we identified a number of OTUs belonging to *Mesorhizobium, Bradyrhizobium, Opitutus, Chitinophaga, Rhizobium, Solirubrobacter* and *Rhodoplanes* in soil erosion and deposition samples, which were also commonly detected in soil dust (Barberán et al., 2015).

3.4 Overall responses of microbial functional structures

DCA (Figure 1b) and dissimilarity tests (Table S2) with 28,952 functional genes detected by GeoChip showed that microbial functional structures were distinct for soil erosion, control and soil deposition groups. Functional α-diversities, based on the Shannon and Simpson indices of GeoChip data, were higher in soil erosion and deposition samples than control samples ($p < .05$) (Table S3), which could also be attributed to niche differentiation by environmental filtering (Cardinale, 2011). Those findings in soil deposition samples were somewhat unexpected as soil DOC was increased by 66.5% (Table S1), owing to the potential fertilization effect by soil deposition (Van Pelt & Zobeck, 2007).

3.5 Functional genes associated with carbon cycling

Most of the microbial functional genes associated with carbon fixation were decreased ($p < .05$) or remained unchanged in relative abundance at eroded and deposited sites (Fig. S4). In particular, there were decreases in genes associated with dicarboxylate/4-hydroxybutyrate and reductive tricarboxylic acid cycles, including 4-hydroxybutyryl-CoA dehydratase and *frdA*.

Most of the bacterial carbon degradation genes were decreased ($p < .05$) or remained unchanged by soil erosion (Figure 3), which were consistent with a decrease in soil respiration (Table S1). Decreased genes included those associated with labile carbon degradation (e.g., *apu*, *cda*, glucoamylase,

isopullulanase, *pulA*, pectate_lyase, pectinase, *pme*, *rgh* and *rgl*) and recalcitrant carbon degradation (e.g., *camDCBA*, endochitinase and cutinase). However, a large number of bacterial carbon degradation genes were also decreased ($p < .05$) or remained unchanged by soil deposition (Figure 3). Notably, there was a striking exception in *amyA* encoding α-amylases, which amounted to 29.0% of the relative abundance of bacterial genes associated with carbon degradation. It was specifically increased ($p = .01$) by 18.6% at the deposited site, but unchanged at the eroded site (Figure 3).

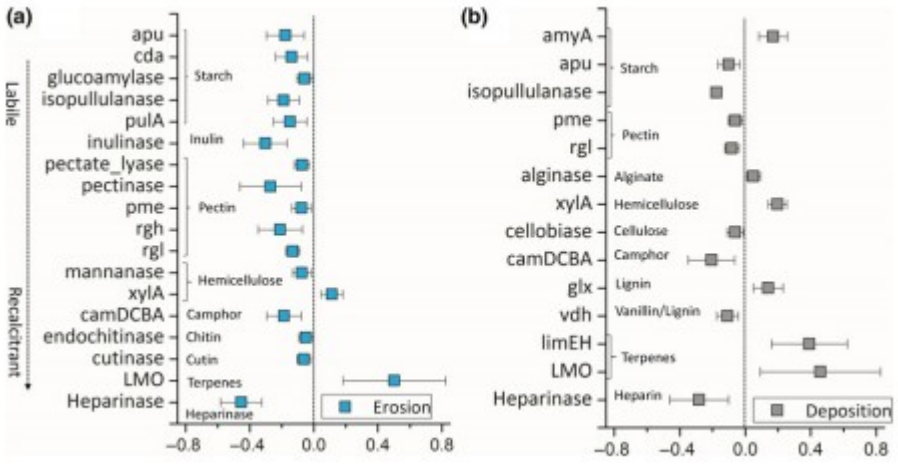

FIGURE 3 The response ratio analysis to detect changes of bacterial carbon degradation genes by (a) soil erosion and (b) soil deposition. Only significant changes at the confidence level of 0.90 are shown

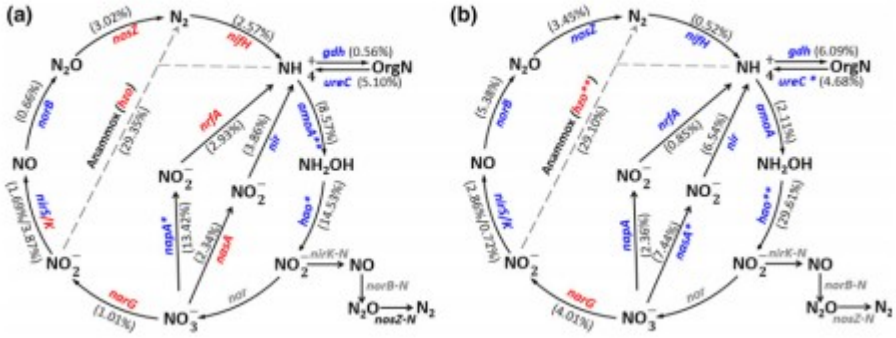

FIGURE 4 The fold change of nitrogen cycle genes by (a) soil erosion and (b) soil deposition. The percentage of each gene indicates the extent of fold change, with red and blue colours representing increase and decrease, respectively. The percentage was calculated by relative abundance of each gene at the eroded or deposited site divided by the control. Asterisk indicates significant differences. *$p < .05$; **$p < .01$

Thirteen of nineteen archaeal genes associated with carbon degradation decreased in relative abundances at the eroded site (Fig. S5a). Archaeal *amyA* genes increased by 14.9% at the deposited site, whereas most of other archaeal genes decreased or remained unaltered (Fig. S5b). In

comparison, changes of fungal genes were more disparate, with 12 decreased and 10 increased genes at the eroded site, and 7 decreased and 6 increased genes at the deposited site ($p < .05$) (Fig. S5c,d).

3.6 Functional genes associated with nitrogen, phosphorus and potassium cycling

Almost all of functional genes associated with nitrogen cycling decreased ($p < .05$) or remained unaltered at both eroded and deposited sites (Figure 4), which held true across bacteria, archaea and fungi (Table S5). Specifically, nitrification genes (*amoA* and *hao*) decreased by 8.6%–14.5% at the eroded site, and ammonification gene (*ureC*) decreased by 4.7% at the deposited site.

GeoChip has three gene families associated with phosphorus cycling. The relative abundance of polyphosphate kinase (*ppk*) associated with polyphosphate synthesis remained unchanged, but phytase genes associated with phytic acid hydrolysis and exopolyphosphatase (*ppx*) genes associated with polyphosphate degradation decreased at the deposited site (Fig. S6). Similarly, *kdpA, ktrBD, kup* and *trkGH*, all of which were associated with potassium transport, decreased at the deposited site (Fig. S7).

3.7 Environmental variables linking to taxonomic or functional traits

Mantel tests showed that soil temperature was correlated ($p < .05$) with taxonomic structure at the species and phylum levels, and pH was correlated at the genus, family, order and class levels (Table 1). Consistently, the Pearson correlation analysis showed that soil pH was positively correlated ($r = .51$, $p = .05$) with microbial taxonomic diversity (Fig. S8). In contrast, total nitrogen and total organic carbon were correlated with functional genes at the family, subcategory or category level, revealing close linkages between soil geochemical variables and functional genes (Table 1). Plant species richness was also correlated with functional genes at the probe level. We also found that *amyA* was positively correlated with DOC ($r = .59$, $p = .02$) (Figure 5a), which further established a linkage between soil nutrient and the functional gene. In addition, *nifH* was positively correlated with TN ($r = .62$, $p = .01$) (Figure 5b).

TABLE 1 Effects of environmental variables on microbial taxonomic and functional structure by simple and partial Mantel tests

			Simple		Partial	
			r	*p*-Value	*r*	*p*-Value
Taxonomic structure	Phylum	*T*	.299	**.011**[a]	.301	**.013**
		pH	.181	.090	.183	.092
	Class	pH	.299	**.016**	.284	**.026**
	Order	pH	.322	**.013**	.306	**.023**
	Family	pH	.349	**.007**	.334	**.019**
	Genus	pH	.371	**.009**	.357	**.010**
	Species	*T*	.299	**.009**	.301	**.007**
		pH	.181	.120	.183	.099
Functional structure	Category[b]	Water content	.246	.077	.252	.067
		TN	.294	**.020**	.300	**.026**
	Subcategory 1	TOC	.168	.093	.139	.128
		TN	.255	**.042**	.233	**.050**
	Subcategory 2	TOC	.222	**.037**	.183	.080
		TN	.267	**.023**	.225	.056
	Gene	TOC	.155	.110	.050	.276
		TN	.249	**.029**	.124	.176
	Probe	Plant species richness	.240	**.034**	.240	**.039**

T, temperature; TOC, total organic carbon; TN, total nitrogen.

[a]Values of significance at $p < .05$ are shown in bold.

[b]Classification of functional genes. Probes are sequences targeting the same gene but derived from different microbial taxa. Category, subcategory 1 and subcategory 2 are different levels of gene classification based on functions as detailed in He et al. (2007).

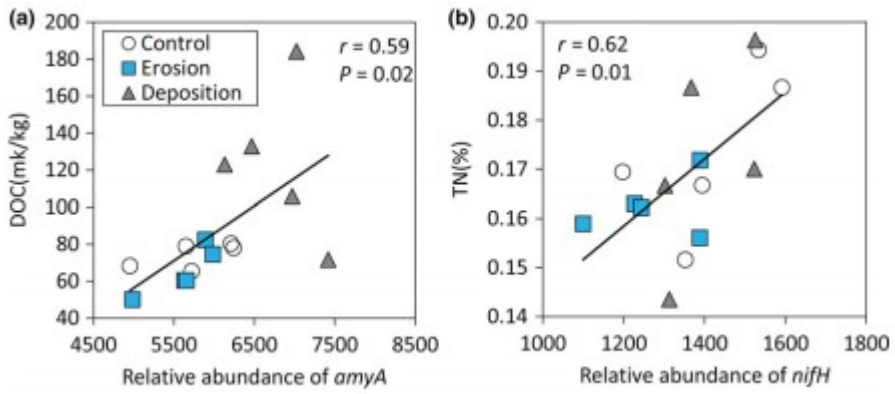

FIGURE 5 Pearson correlations between (a) relative abundance of *amyA* and DOC; and (b) relative abundance of *nifH* and TN. DOC, dissolved organic carbon; TN, total nitrogen

4 DISCUSSION

The yearly estimate for aeolian soil erosion is 549 million ha (Lal, 2003). With an estimated mobilization of 0.5 ± 0.15 Pg of carbon, 23–42 Tg of nitrogen and 14.6–26.4 Tg of phosphorus per year, aeolian erosion is considered to be one of the most widespread forms of soil degradation (Quinton et al., 2010; Zhang et al., 2014). Therefore, it has solicited substantial attention to assess its impact on ecosystems and soil biogeochemical cycling. However, despite a number of studies to simulate wind erosion (Chepil & Milne, 1939; Gardner et al., 2012; Gerety & Slingerland, 1983; Gillette, 1978; Goossens & Offer,

1990; Logie, 1981), none has carried out fixed-site sampling to analyse soil microbial communities. The decreases in TOC and plant coverage at eroded sites and the increase in DOC at deposited sites (Table S1) were similar to previous observations (Li et al., 2007; Quinton et al., 2010; Van Pelt & Zobeck, 2007; Yan et al., 2005). Therefore, this field simulation appeared to be reliable. However, TOC did not increase with deposition, which might be ascribed to several possibilities. Soil respiration was significantly increased (Table S1), which can reduce TOC. Alternatively, TOC can be utilized by plants. As some of plant parameters are difficult to measure (e.g., root growth), we cannot estimate the influence of plants to TOC. There are also technical issues to be considered. For example, we have used a 1 mm sieve to remove visible plant roots and rocks from bulk soil, which inevitably remove big soil aggregates that might have different carbon profiles from fine dusts (Sessitsch, Weilharter, Gerzabek, Kirchmann, & Kandeler, 2001).

Both taxonomic and functional structures of microbial communities were altered ($p < .05$) by soil erosion and deposition (Figure 1), suggesting that they were sensitive to environmental changes. Distinct microbial community changes in taxonomic or functional structure have been documented in grassland soils when exposed to changes in temperature, elevated CO_2 or grazing, which can be attributed to vegetation or soil geochemical variables (He et al., 2012; Sheik et al., 2011; Yang et al., 2013). However, a simple explanation of our result is that soil microbial communities exhibit a depth distribution function; that is, microbial biomass generally decreases and community structure varies with soil depth (Fierer, Schimel, & Holden, 2003). As surface soil was transferred from the eroded plots to the deposited plots, microbial communities were inevitably altered. Intriguingly, neither plant nor microbial community have recovered 15 months after soil transfer, indicative of lasting effects of soil erosion and deposition on grassland ecosystems. In accordance, we found that environmental filtering/selection, regarded as a fundamental process in shaping microbial communities (Hanson, Fuhrman, Horner-Devine, & Martiny, 2012), appeared to be an important driver for community changes by soil erosion and deposition (Table 1).

Although total microbial biomass remained similar across all of soil samples (Table S1), soil erosion and deposition increased *Actinobacteria* and *Cyanobacteria*, and erosion decreased *r-Proteobacteria* (Figures 2 and S3). Consistently, desert soils, where soil erosion is rampant, were rich in *Actinobacteria* and *Cyanobacteria*, but had fewer *r-Proteobacteria* than other microbial biomes (Fierer et al., 2012). *Cyanobacteria* comprises a key component of soil to stabilizing aggregates that increase soil's resistance to aeolian erosion, as filamentous *Cyanobacteria* and exopolysaccharides play vital roles in binding fine particles to each other in soil (Belnap & Gillette, 1998; Eldridge & Leys, 2003; Zhang, Wang, Wang, Yang, & Zhang, 2006). Intriguingly, similar degrees of aggregates were detected across treatments (Table S1), which were at odds with previous studies of breakdown of soil aggregates by wind erosion (Lal, 2003; Zhao, Yi, et al., 2006). Although we

could not exclude the possibility that breakdown of aggregates mainly occurred in large particles, which were sieved out by 1 mm sieves during soil sampling, it was also likely that the increase in *Cyanobacteria* in erosion and deposition plots was sufficient to restore the degree of soil aggregates.

The decrease in many microbial carbon degradation genes at the eroded site (Figure 3a) indicates the limitation of functional potentials in carbon degradation, which is conducible to the decrease in soil respiration (Table S1). In contrast, the increase in soil respiration at the deposited site is likely contributed by enhancement of functional potentials in degrading labile carbon substrate (e.g., *amyA*; Figure 3b), triggered by the increase in soil DOC (Table S1). However, the decrease in many microbial carbon degradation genes at the deposited site might be attributed to observed effects of environmental filtering/selection (Tables S3 and S4).

As soil organic matter is comprised of organic carbon, nitrogen and phosphorus, enhanced SOC mineralization by soil mobilization could render nitrogen and phosphorus accessible to microbial processes (Jacinthe, Lal, & Kimble, 2002). Therefore, the stability and availability of nitrogen and phosphorus may serve as limiting factors for plant production and plant-derived soil carbon, thus playing a vital role in regulating carbon cycling (Van Groenigen et al., 2006). In addition, many bacteria can use nitrate or nitrite for anaerobic respiration when coupled with degradation of organic compounds, as shown by recent findings that addition of nitrogen to contaminated sediments promotes organic carbon degradation and prevents phosphorus release (Xu et al., 2014). In this study, we found strong, positive correlations between a number of carbon degradation genes and the ammonification gene *ureC* and nitrification gene *amoA* (Table S6). In addition, microbial coupling within nitrogen cycling was notable. For example, *Nir* and *nasA* associated with assimilatory nitrogen reduction were significantly correlated ($r = .56$, $p < .05$), as were denitrification genes *narG* and *nirS* ($r = .67$, $p < .01$) (Fig. S9). The observation of decreased nitrogen cycling genes implicated possible limitation of available nitrogen at eroded and deposited sites (Figure 4) despite little changes in TN (Table S1), as low soil nitrogen availability can constrain the positive ecosystem response to elevated CO_2 (Reich & Hobbie, 2012).

Environmental filtering is a fundamental ecological process that can result in the phylogenetic clustering of microbes (Bryant et al., 2008). We found that NRI values were correlated with TN ($r = .56$, $p = .03$) and $NH4^+$ ($r = .46$, $p = .08$), implying that nitrogen components might be important limiting factors that lead to phylogenetic clustering. Most significantly changed stress genes associated with glucose limitation, nitrogen limitation, phosphate limitation and protein stress were increased by soil erosion or deposition (Fig. S10), which also implicated the environmental stress. Notably, more functionally diverse microbial communities can utilize limited amounts of available nutrients more efficiently through niche differentiation (Cardinale, 2011). Thus, while not directly tested here, the trends in the community structures

and environmental parameters reflect patterns that have been supported by ecological theories of environmental filtering and niche differentiation (Koenig et al., 2011; Sachs, Mueller, Wilcox, & Bull, 2004).

Previous studies have demonstrated the pivotal role of soil pH in shaping microbial communities (Lauber, Hamady, Knight, & Fierer, 2009; Rousk et al., 2010). Our study provided additional evidence by correlating soil pH to microbial communities at different taxonomic levels, as well as the taxonomic diversity (Table 1 and Fig. S8). However, soil pH was not important for the overall functional structure of the microbial communities. Rather, environmental variables representing organic matter quality and quantity, such as plant species richness, total nitrogen and total organic carbon, were correlated with functional structure (Table 1). Together with evidence of positive correlations between *amyA* and DOC, and *nifH* and TN (Figure 5), it appears that nutrient variables have close relevance to functional potentials. This was similar to our recent studies showing strong linkages between functional genes and soil nutrients (Liu et al., 2015; Zhao et al., 2014), and suggested microbial acclimation to environment.

Aeolian transfer is a convenient, swift route for microbial conveyance. This could cause various diseases and allergic reactions, as airborne pathogens can be responsible for the spread of respiratory diseases (Clifton & Peckham, 2010; Eames, Tang, Li, & Wilson, 2009). α-Amylase has been well documented as a strong allergen (Houba, van Run, Doekes, Heederik, & Spithoven, 1997), and a substantial increase in *amyA* gene in relative abundance by soil deposition therein might confer an allergic disease risk. In addition, three *Sphingomonas* OTUs, frequently identified as opportunistic and/or potential plant pathogens (Favet et al., 2013), were present in control and deposited sites but absent from the eroded site (Fig. S11a), which could have a potential risk of pathogen conveyance. At the functional gene level, relative abundance of genes associated with virulence increased ($p = .01$) (Fig. S11b). The most highly increased genes associated with virulence were toxin genes derived from *the genus of vibrio*, the aetiological agent of cholera (Wachsmuth, Blake, & Olsvik, 1994), and the *pilin* gene derived from *Vibrio parahaemolyticus*, which is an important prerequisite for host invasion (O'Boyle & Boyd, 2013). Our DNA-based evidence provides valuable insights for identifying likely associations between aeolian transferred microbes and incidences of diseases, which opens the door for more detailed pathogenic analyses.

In a nutshell, we found that taxonomic and functional traits of microbial communities were altered by soil erosion and deposition. It was surprising to note several lines of evidence showing nutrient constraints by aeolian soil erosion and deposition, underscoring the difficulty in fully anticipating complex responses of microbial communities. These findings are important for elucidating microbe-mediated nutrient cycling as well as incorporating microbial community information in assessing the ecological impact of soil erosion and deposition. However, to further understand grassland microbial

communities, an integrated, comprehensive campaign to monitor the time-series microbial dynamics is needed.

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DATA AVAILABILITY

GeoChip data are available online (www.ncbi.nlm.nih.gov/geo/) with the accession no. GSE67347. MiSeq data are available in NCBI SRA database with the accession no. SRP066059.

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