



# Bacterial contributions of bio-crusts and litter crusts to nutrient cycling in the Mu Us Sandy Land

Xiaozhen Liu<sup>a</sup>, Yu Liu<sup>a</sup>, Lei Zhang<sup>a</sup>, Rui Yin<sup>a,c</sup>, Gao-Lin Wu<sup>a,b,d,\*</sup>

<sup>a</sup> State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, College of Life Sciences, Northwest A & F University, Yangling, Shaanxi 712100, China

<sup>b</sup> School of Agriculture, Ningxia University, Yinchuan, Ningxia 750021, China

<sup>c</sup> Helmholtz-Centre for Environmental Research-UFZ, Department of Community Ecology, Theodor-Lieser-Strasse 4, 06110 Halle (Saale), Germany

<sup>d</sup> CAS Center for Excellence in Quaternary Science and Global Change, Xi'an 710061, China

## ARTICLE INFO

### Keywords:

Bacterial communities  
Bio-crusts  
Litter crusts  
Nutrient cycling  
Sandy land restoration

## ABSTRACT

Desertification has become an important issue for the sustainable development of human society at global scale and has led to the changes in soil properties and vegetation cover. Biocrusts and litter crusts play roles in improving the soil microhabitat of sandy ecosystems. Soil microbial communities mediate ecosystem functions in various ecosystems, e.g., soil biogeochemical processes. However, limited information is available about how the underlying processes of bio-crusts/litter crusts restoration are driven by soil bacterial communities in sandy land. Here, we investigated the changes in soil bacteria from three groups (sandy land, bio-crusts, and litter crusts) and three soil layers (0–2 cm, 2–5 cm, 5–10 cm) with nine replicates each collected in July 2019 utilized high-throughput pyrosequencing of the V4-V5 rRNA gene region. Most soil nutrients (SOM, AP, AK, and TN) and enzyme activities (BG and DHA) had differences among the three groups and three soil layers. OTU richness and diversity of bacteria were positively correlated with most soil variables. The constructed co-occurrence networks between soil variables and bacterial communities, and within bacterial communities showed that bacterial taxa had closer relationships with all soil variables in crusts than sandy land and varied among the three sand groups (sandy land, bio-crusts, and litter crusts). The result showed that the composition of bacterial community was regulated mainly by soil variables and crust types. Compared with sandy land, more predictors in nutrient cycling were found in crust types. They played major roles in nutrient cycling in desert ecosystem restoration on the basis of random forest modeling. Our findings indicate some bacterial taxa may played the predominant roles in connecting with soil variables and other bacterial taxa across crusts types, and litter crusts and bio-crusts drive the nutrient cycling by mediating the restoration of bacterial taxa in sandy ecosystems.

## 1. Introduction

Land desertification poses a great threat to all types of ecosystems, it can damage ecosystem's basic functions and services to sustain life, causes the losses in soil nutrients, the decline in soil potential productivity, and the reduction in vegetation (D'Odorico et al., 2013). Arid and semiarid areas are among the most susceptible to land desertification, however, they covered approximately one-third of the earth's land and have been expanding rapidly, this is due to climate change and human activities, such as overcultivation, overgrazing, and urbanization (Asner et al., 2003; Sivakumar et al., 2005; Gao et al., 2017). With the increase of the world population and deterioration of living environment,

desertification has becoming one of a major issue for the in human societies at global scale (D'Odorico et al., 2013). For instance, according to The Desertification and Sandification Sate of China, China had a desert area of 2.6 million square kilometers, and another 1.7 million square kilometers of sandy area in 2014, which covers about 27.2% and 17.9% of the country's land, respectively (State Forestry Administration, 2015). The Mu Us Sandy Land, which is located in central north of China, is the region with high risks of desertification in arid Asia (Wang et al., 2017). In 1999, the Grain for Green Program was launched by Chinese government with aims to halt soil erosion and improve the ecological environment (i.e. the losses of soil fertility and the decrease of vegetation coverage). It is the largest ongoing revegetation project in

\* Corresponding author at: State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Northwest A & F University, NO. 26 Xinong Road, Yangling, Shaanxi Province 712100, China.

E-mail address: [wugaolin@nwsuaf.edu.cn](mailto:wugaolin@nwsuaf.edu.cn) (G.-L. Wu).

<https://doi.org/10.1016/j.catena.2020.105090>

Received 9 September 2020; Received in revised form 14 November 2020; Accepted 28 November 2020

Available online 19 December 2020

0341-8162/© 2020 Elsevier B.V. All rights reserved.

China and also one of the largest conservation projects in the world. This project converted croplands into grasslands or shrubs and increased vegetation coverage from 31.6% in 1999 to 59.6% in 2013 on the Loess Plateau (Chen et al., 2015b; Uchida et al., 2005). Meanwhile, apart from the “Grain for Green” Program, several other initiatives have been carried out to restore soil fertility and alter the sand surface to control desertification in sand areas, such as mechanical sand barriers (Bo et al., 2015) and afforestation (Zeng et al., 2008). These initiatives enhanced development of bio-crusts and litter crusts on the Loess Plateau, either directly or as a result of a general improvement of environmental conditions. Better environmental conditions, including appropriate humidity and temperature, promote the development of bio-crusts and litter crusts in the Mu Us Sandy Land (Liu et al., 2019b).

Biological soil crusts (bio-crusts), which are composed of cyanobacteria, lichens, mosses, fungi, and other nonvascular photoautotrophs, are typical for dryland ecosystems worldwide and represent an essential functional component of the pedosphere. Bio-crusts can stabilize soil, increase soil fertility, impact hydrologic cycles, alter soil organic matter content, and provide a home for belowground organisms (Reed et al., 2019; Torres-Cruz et al., 2018). Litter crusts are defined as the cohesiveness of the soil surface shaped by litter and soil and forms a hard shell by the mixing of sand and litter organisms in the wind - water erosion crisscross zone. Bio-crusts and litter crusts play crucial roles in improving microhabitat conditions, forming soil organic matter, affecting hydrological processes, and soil bacterial communities in sandy lands during restoration (Jia et al., 2018; Leloup et al., 2018; Liu et al., 2019b).

In this context, soil variables are most important factors to impact microbial communities, such as soil pH, soil texture and, available nutrients (Chen et al., 2015a; Fierer and Jackson, 2006). On the contrary, microbial communities are important indicators of rehabilitated ecosystems (Banning et al., 2011) and drive the Earth's biogeochemical cycles (Falkowski et al., 2008). Soil bacterial communities represent the greatest biodiversity reservoir and greatly affect ecosystem functions and services (Falkowski et al., 2008; Wagg et al., 2014). An enhanced appreciation of the connection between environment and microbial ecology, in the last decade, has led to many studies focused on the distribution of soil microbial communities (Karimi et al., 2018), the influence of microbial diversity on plant community (Jiao et al., 2019) and multifunctionality of terrestrial ecosystem (Delgado-Baquerizo et al., 2016; Falkowski et al., 2008; Jiao et al., 2019; Karimi et al., 2018). However, limited information is available about the response of bacterial communities on soil variables in natural desert ecosystems. Moreover, each microbe may play a different functional role in complex microbial ecosystem (Li et al., 2019). Experimental evidence suggested that the bacterial communities at phylum level are similar in the two sample types. The relative abundance of several genera has considerably differences at the genus level (Jakobsen et al., 2019). However, the foundational role of the bacterial genera in regulating key ecosystem processes (i.e. nutrient cycling) of litter crusts and bio-crusts in the sandy ecosystem is lacking. Thus, we must expand our insight into the functions of the microorganisms, particularly bacteria genera, in the bio-crusts and litter crusts in the restoring sand ecosystem.

The present study aims to (1) elucidate the variations in soil quality and bacterial communities coupled with the soil quality of bio-crusts and litter crusts, (2) explore the correlations between the soil bacterial taxa and soil variables and the bacterial taxa among themselves in the bio-crusts and litter crusts networks, (3) identify the contributions of the annotated bacterial taxa to nutrient cycling during ecosystem restoration. To achieve these aims, we used high-throughput pyrosequencing of the V4-V5 rRNA gene region to compare the variations of bacterial communities in relation to soil variables, their co-occurrence networks, and their contributions to the soil functioning (nutrient cycling) in bio-crusts and litter crusts of restoring sandy ecosystems.

## 2. Materials and methods

### 2.1. Study sites and sample collection

The study was carried out in the eastern part of the Mu Us Sandy Land ecosystem (110°21' –110°23'E, 38°46'–38°51'N; 1080–1270 m Altitude), located in Shenmu County at the northern of Shanxi Province, China. This region, as the most arid area in Asia, is one of the largest dune areas in the north of China (Wang et al., 2017). Psammophytic shrubs and herbaceous plants are mainly dominant plant species in this study site (Jia et al., 2018). According to our previous studies, bio-crusts and litter crusts, as two major contributors, covered about 40% and 30% of the Mu Us Sandy Land, respectively (Jia et al., 2018). To compare the effects of bio-crusts and litter crusts on the surface microhabitats of the sandy land, three sites (sandy land, bio-crusts, litter crusts) with similar environmental conditions in terms of underlying subsoil, microtopography, and soil hydrology, were selected and the distance between them was above 500 m apart. Sand samples were collected in July 2019 from sampling sites covered by bio-crusts and litter crusts, respectively. After removing the litter horizon, nine replicate sites were randomly selected above 10 m apart and three sand layers (0–2 cm, 2–5 cm, 5–10 cm). Each replicate was mixed with five sand cores by a zigzag pattern (Liu et al., 2019a). In total, 81 soil samples = 3 sites (sandy land, bio-crusts, litter crusts) × 3 depths (0–2 cm, 2–5 cm, 5–10 cm) × 9 replicates were obtained, and all the sand samples were taken to the laboratory on ice within 24 h. A small part of each sample (~2 g) for the DNA analysis was transported to the company (Novogene, Beijing, China) on ice. Another part was sieved (~2 mm) for the analysis of soil properties. The rest was stored at –80 °C.

### 2.2. Sand characters and enzyme activities

Sand organic matter (SOM) were measured by potassium dichromate colorimetric method (Nelson and Sommers, 1982); total phosphorus (TP), and available phosphorus (AP) were determined by molybdenum anti-colorimetric method (Olsen and Sommers, 1982); total nitrogen (TN) was determined with the Kjeldahl method (Bremner and Mulvaney, 1996); total potassium (TK), and available potassium (AK) were determined with Flame photometry as described previously (Page et al., 1982).  $\beta$ -glucosidase (BG), dehydrogenase (DHA), Urease (UA), alkaline phosphatase (ALP), and acid phosphatase (ACP) were measured by the methods described in Tabatabai, 1994 (Tabatabai, 1994; Taylor et al., 2002). Briefly, BG activity was determined as the amount of p-nitrophenol (PNP) released; ALP and ACP were determined by p-nitrophenol (PNP) released at pH 11 and 6.5, respectively. UA was measured by the determination of ammonia released. DHA was determined as the amount of the TPF released (Taylor et al., 2002). All the samples were determined using three replicates. The selected parameters reflect either resource pools (SOM, TN, TP, AP, TK) in biogeochemical cycles or important processes regulating availability of these pools (BG, DHA, UA, ALP, ACP). Such as, the important ecosystem processes related to the cycling of carbon (SOM, BG and DHA), nitrogen (TN and UA), phosphorus (AP, TP, ALP, and ACP), and potassium (AK and TK) (Jiao et al., 2019; Jing et al., 2015).

### 2.3. DNA extraction and 16S rRNA gene sequencing

Genomic DNA from each sand sample was extracted from 1 g sand using the OMEGA soil DNA Kit (Omega Bio-Tek, Inc., Norcross, GA, USA) based on the manufacturer's instructions. To assess the bacterial communities, the V4–V5 region of the bacterial 16S rRNA gene was amplified with the primers: 515F (5' – GTGCCAGCMGCCGCGGTAA – 3')/907R (5' – CCGTCAATTCCTTTGAGTTT – 3'). The purified PCR products were pooled and sequenced on the Illumina HiSeq (300 ~ bp paired-end reads) platform (Novogene, Beijing, China).

## 2.4. Data analysis

The acquired sequences were processed to remove low - quality sequences using the QIIME pipeline (Caporaso et al., 2011). The remaining sequences were classified into operational taxonomic units (OTUs) with 97% sequence similarity by the UPARSE pipeline (Edgar, 2013). OTU richness, Chao1 index, Shannon index, ACE index, and Simpson index were calculated by the OTU table in QIIME (Caporaso et al., 2010). The changes in soil nutrients, enzyme activities, and bacterial communities, as well as the relative abundance of the microbial phyla among three soil groups (sandy land, bio-crusts, and litter crusts) and three soil layers (0–2 cm, 2–5 cm, and 5–10 cm), were conducted based on one-way ANOVAs with Tukey's tests by GraphPad Prism version 8.0.2 (GraphPad Inc. San Diego, CA, USA). The normality of data and the equality of variance were tested. If the data did not meet normality or homogeneity, non-parametric Kruskal-Wallis analyses were used. Redundancy analysis (RDA) was performed to visualize the influence of soil variables on bacterial community composition in R package "vegan" (Oksanen et al., 2013).

The co-occurrence networks were constructed for bio-crusts and litter crusts based on significant correlations between bacterial genera and all of the soil nutrients (Pearson's correlation,  $p$ .thres = 0.05,  $r$ .thres = 0.6), and among the bacterial genera themselves (Pearson's correlation,  $p$ .thres = 0.05,  $r$ .thres = 0.8), which were visualized by R packages 'igraph' (Hartmann et al., 2015; Qian et al., 2018). In the co-occurrence networks, each node represents one bacterial genus and each edge represents a significant correlation between two nodes. A set of metrics: number of edges (Num. edges), average. degree, average. path. length, diameter, and modularity were calculated to estimate network topological features. Num. edges represent the number of edges. To identify the major statistically significant bacterial predictors

for sand nutrient cycling, a Random Forest (RF) modeling was performed with the forest (5000 trees) using the "random Forest" package (Archer, 2016). The model significance was computed by the R package "A3" (Fortmann-Roe, 2013). A total of 35 classified microbial phyla and 143 annotated genera from 6 predictors at the phylum level were selected in the Random Forest modeling. Percentage increases in the mean squared error (MSE) was used to estimate the importance of variables. All statistical analyses were performed by GraphPad Prism 8.02 or R software (v3.6.3; <https://www.r-project.org/>).

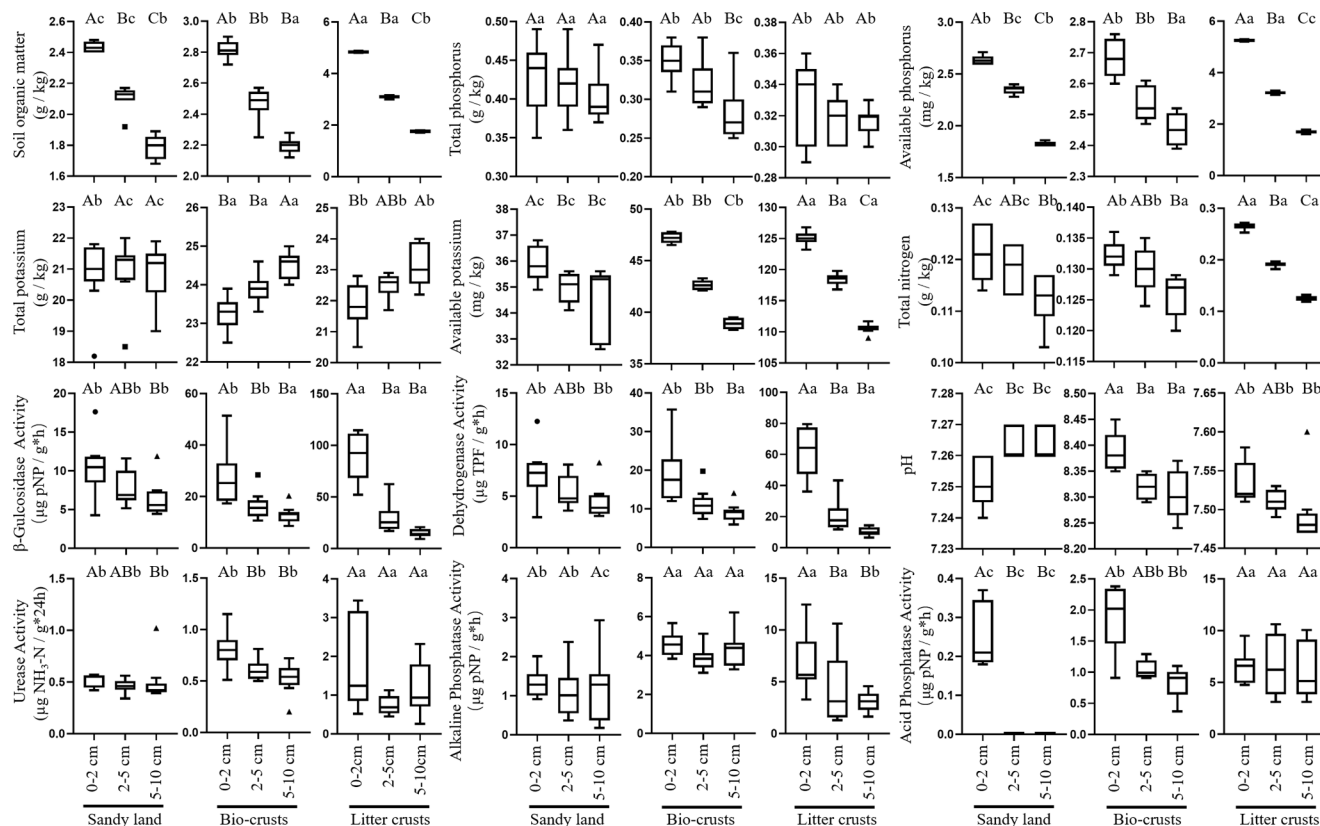
## 3. Results

### 3.1. Variation in sand nutrients and enzyme activities

Soil nutrients and enzyme activities typically differed among three soil groups and three sand layers, most of which were significant differences. Litter crusts had significantly higher SOM, TN, AP, AK, BG, DHA, UA, and ACP than those in the sandy land and the bio-crusts in surface soil (0–2 cm and 2–5 cm); TK, SOM, TK, AK, TN, ALP, ACP were significantly higher in the bio-crusts than those in the sandy land in the surface soil (0–2 cm and 2–5 cm). SOM, AP, AK, BG, and DHA were highest in the topsoil (0–2 cm) of the bio-crusts and litter crusts. (Fig. 1). These results indicated that both litter crusts and bio-crusts improved the sand soil quality compared with sandy land, and litter crusts had more significant improvement in sandy soil quality than bio-crusts, especially, in the surface of the sand layer. The statistical information listed in Table S1.

### 3.2. Variation in sandy bacterial community

In total, 6,865,683 high-quality sequences were classified into



**Fig. 1.** Variation in soil properties and enzyme activities ( $n = 9$ ) among three soil groups (sandy land, biocrusts, and litter crusts) and three soil layers (0–2 cm, 2–5 cm, and 5–10 cm). Different lowercase letters indicate significant difference among three soil group in the same soil layer ( $p < 0.05$ ), and different uppercase letters indicate significant difference among three soil layers in the same soil group ( $p < 0.05$ ). Error bars indicate standard deviation.

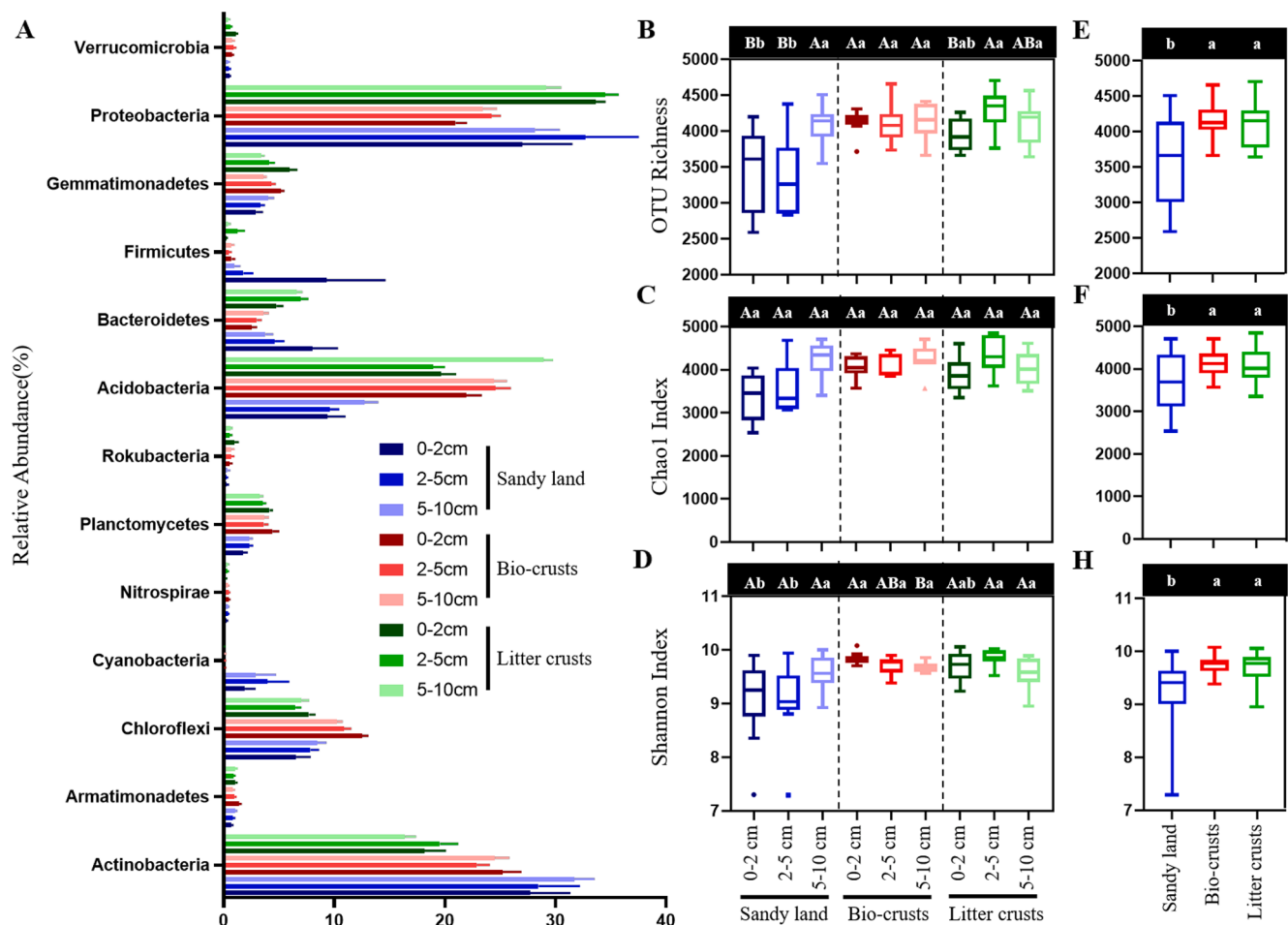
14,560 operational taxonomic units (OTUs) after the 97% sequence similarity cutoff across 81 sand samples (Table S2). The OTU richness in biocrust and the litter crusts were significantly greater than this in the sandy land in the surface soil (0–2 cm and 2–5 cm) (Fig. 2B and Table S3). Bacterial OTU were primarily classified into the 66 microbial phyla, and the most dominant bacterial phyla were the phyla Proteobacteria (28.2%), Actinobacteria (23.86%), Acidobacteria (18.92%) (Fig. 2A, and Table S4). 39.57% OUT were classified into the 707 genera, the most dominant identified genera were Sphingomonas (2.4%) and Nocardioides (2.2%), respectively belonging to the Proteobacteria, and Actinobacteria phyla (Table S5). For most of the bacterial phyla and genera, relative abundance of the phyla or genera bacteria significantly different among three sand groups ( $P > 0.05$ ) (Table S4, Table S5). The Shannon index of bacterial community diversity in the litter crusts and bio-crusts were significantly higher than this in sandy land in the surface soil (0–2 cm and 2–5 cm). The bacterial communities clearly differed among three soil groups (Fig. 2E, F, H and Table S3).

### 3.3. Co-occurrence patterns of soil bacterial communities

Redundancy analysis (RDA) was performed to investigate the influence of soil variables on bacterial community among three sand groups and three sand layers. We found that soil variables well explain dynamic

changes of bacterial communities at the phylum level or genus level. However, the correlations are not alike between the level of bacterial phylum and genus (Fig. 3 and Table S6). For instance, AK was the most important variable for litter crusts bacterial community at genus level, whereas, SOM, AP, TN, DHA, GB, and UA were more important at the genus than at the phylum level (Fig. 3 and Table S6). Furthermore, the co-occurrence networks were constructed for three sand groups to investigate the correlations between the bacterial genera and soil nutrients (Fig. 4A and Table S7). The network structure was distinct, the bio-crusts network had more edges (34) than sandy land network (33) and litter crusts network had more than two times (2.71) as many edges as found in bio-crusts. There is the highest average degree in the litter crusts and higher average degree in the bio-crusts network than these in the sandy land network. These showed that most soil nutrients had closer relationships with bacterial genera in the litter crusts than in the bio-crusts and sandy land.

Given the interactions between bacterial taxa, we constructed co-occurrence networks to explore the interactions between the bacterial genera with each other in three sand groups, respectively (Fig. 4B and Table S8). Diverse topological characteristics were observed. The modularity indices were 0.881, 0.587, and 0.892 in the sandy land, bio-crusts, and litter crusts network, respectively. These values (The modularity indices  $> 0.4$  show that the network has a modular



**Fig. 2.** Variation in the microbial communities among three sand groups (sandy land, biocrusts, and litter crusts). (A) Relative abundances of the microbial taxa annotated ( $>1\%$  of total community) at the phylum level; Difference in OTU richness (B), Chao1 index (C), Shannon index (D) of the microbial community ( $n = 9$ ) among three soil groups (sandy land, biocrusts, and litter crusts) and three soil layers (0–2 cm, 2–5 cm, and 5–10 cm). Difference in OTU richness (E), Chao1 index (F), Shannon index (H) of the microbial community ( $n = 27$ ) among three soil groups. Color of blue, red, green represent sandy land, biocrusts, and litter crusts, respectively. Different lowercase letters indicate significant difference among three soil layer ( $p < 0.05$ ), and different uppercase letters indicate significant difference among three soil layers in the same soil group ( $p < 0.05$ ). Error bars indicate standard deviation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



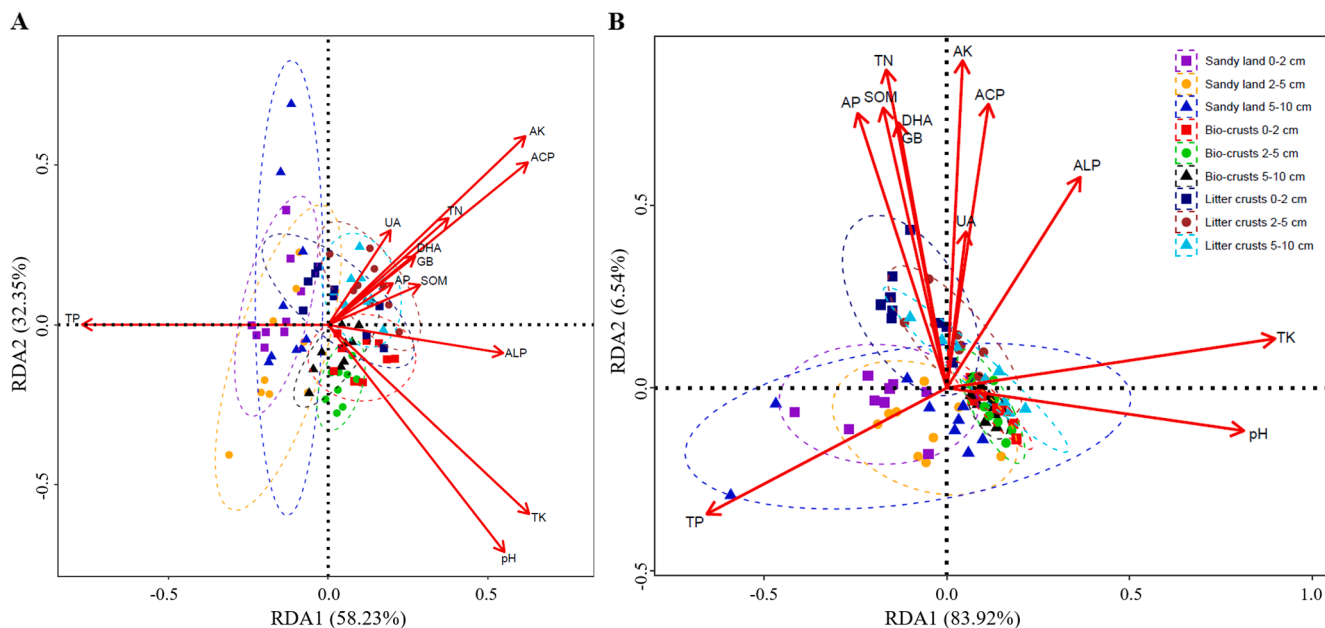


Fig. 3. Redundancy analysis (RDA) for identifying the influence of soil nutrients and enzyme activities on bacterial community composition at the phylum level (A) or the genus level (B). Dashed ellipses represent nine treatments; Arrows represent the soil variables associated with bacterial community composition.

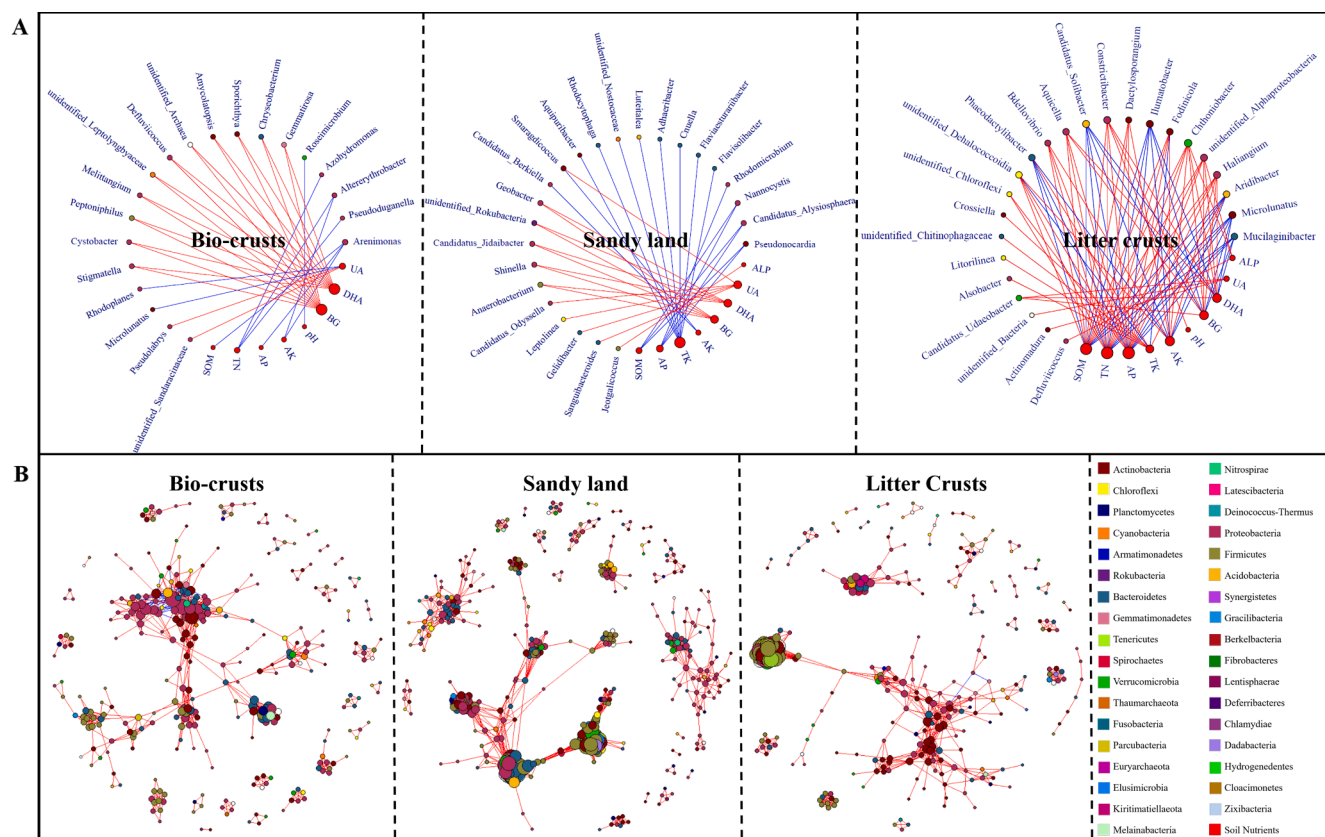


Fig. 4. Co-occurrence networks of soil bacterial communities in the sandy land, biocrusts, and litter crusts. The color of nodes represent bacterial genera and soil variables (red nodes represent soil variables, the other color nodes represent bacterial genera). (A) The correlations between the soil variables and bacterial taxa. (B) The correlations among the bacterial taxa themselves. Red edges represent positive correlation, blue edges represent the negative correlation. SOM, sand organic matter; TK, total potassium; AK, available potassium; TP, total phosphorus; AP, available phosphorus; TN, total nitrogen; UA, urease activity; GB,  $\beta$ -glucosidase activity; DHA, dehydrogenase activity; ALP, alkaline phosphatase activity; ACP, acid phosphatase activity. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

structure) mean these networks had a modular structure. The highest average degree in the sandy land network than these in the litter crusts and bio-crusts networks. There were 975 edges and 94.26% positive correlations identified as co-occurrences in the bio-crusts and 1,787 edges and 99.89% positive correlations in the litter crusts. In sum, bacterial co-occurrence patterns were distinctly different between the bio-crusts and litter crusts.

### 3.4. The potential contributions of bacterial taxa to sand nutrient cycling

The contributions of bacterial communities to sand functionings were evaluated by Random Forest (RF) modeling. We uncovered the potential major bacterial drivers of sand nutrient cycling in the crust types by RF analysis, including 35 microbial phyla. We discovered that 9 bacteria phyla were the most important predictors to nutrient cycling in the bio-crusts and litter crusts (Fig. 5A). Planctomycetes, Cyanobacteria, Armatimonadetes, Rokubacteria, Nitrospirae, Latescibacteria,

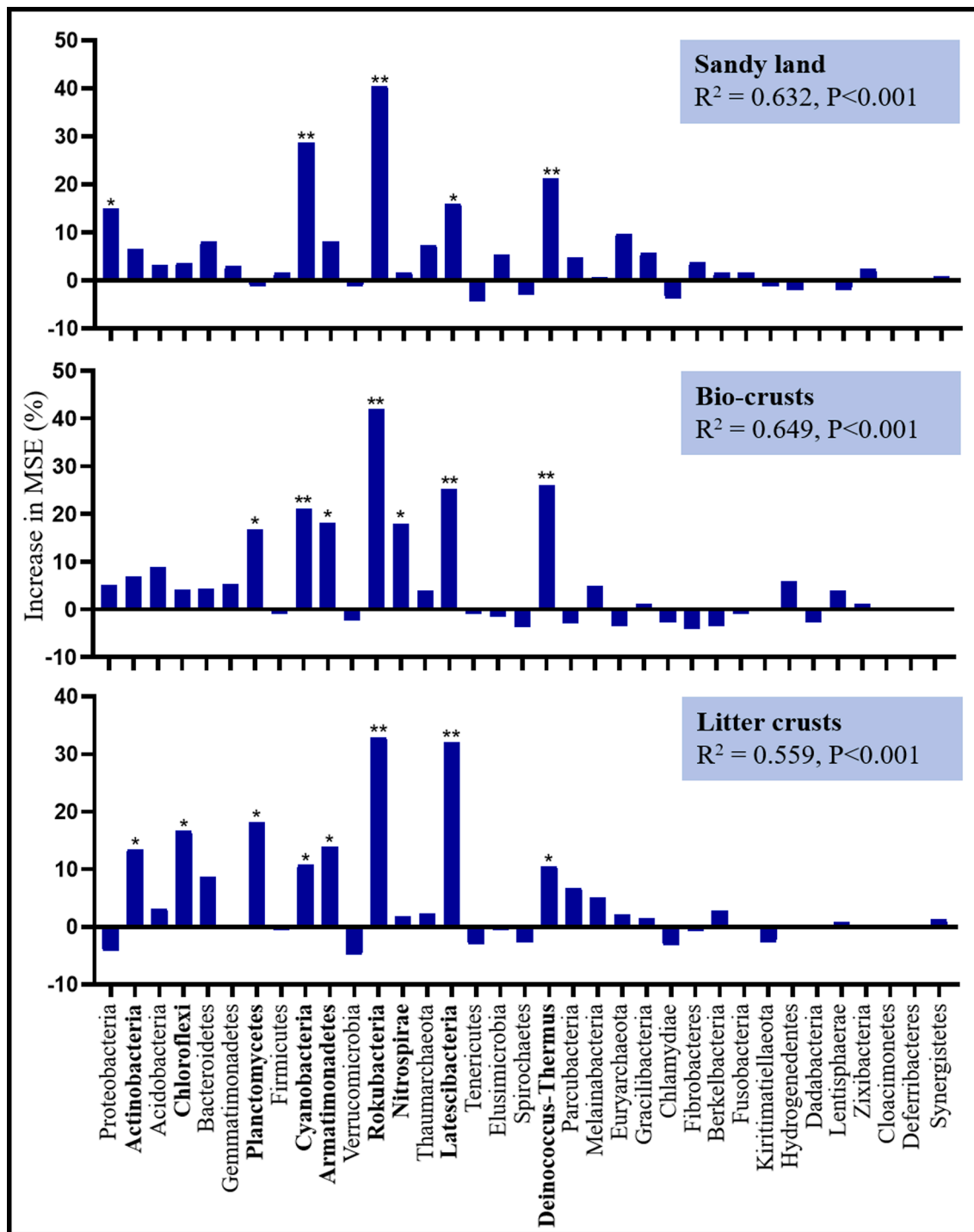


Fig. 5. Random forest (RF) shows all annotated microbial drivers at the phyla level for sand nutrient cycling in sandy land, biocrusts, and litter crusts, respectively. MSE is the mean square error. MSE% values represent the importance of these predictors. Higher MSE% values mean more important predictors. The significance of the model was estimated by the R package “A3”. \*, P < 0.05; \*\*, P < 0.01.

Deinococcus-Thermus were predictors in bio-crusts and Actinobacteria, Chloroflexi, Planctomycetes, Cyanobacteria, Armatimonadetes, Rokubacteria, Latescibacteria, and Deinococcus-Thermus were predictors in litter crusts. Furtherly, 143 annotated genera from the Actinobacteria, Planctomycetes, Chloroflexi, Armatimonadetes, Deinococcus-Thermus, Nitrospirae were selected to identify the major predictors at the genus level (Table S5). Compare to sandy land, more predictors were found in the bio-crusts and litter crusts. We observed 22 and 20 predictors to nutrient cycling in bio-crusts and litter crusts, respectively (Fig. 6). *Blastococcus*, *Couchioplanes*, *Crossiella*, *Geodermatophilus*, *Actinoplanes*, *Parviterribacter*, *Marmoricola*, *Rhizocola*, *Tepidisphaera*, and *Fimbriglobus* are the same predictors to the nutrient cycling between the bio-crusts and litter crusts. Most of the predictors were distinct between bio-

crusts and litter crusts not only at the phylum level but also at the genus level and the particular bacterial consortium made important contributions to soil functionings.

#### 4. Discussion

##### 4.1. Influence of crusts on sand characters and bacterial communities

Bio-crusts and litter crusts improved sand surface microhabitats, including soil properties and hydrological processes, and caused the development of soil fertility (Ferrenberg et al., 2018; Liu et al., 2019b). Our study showed that most sand nutrients, enzyme activities, and the diversity of soil bacteria communities increased markedly during the

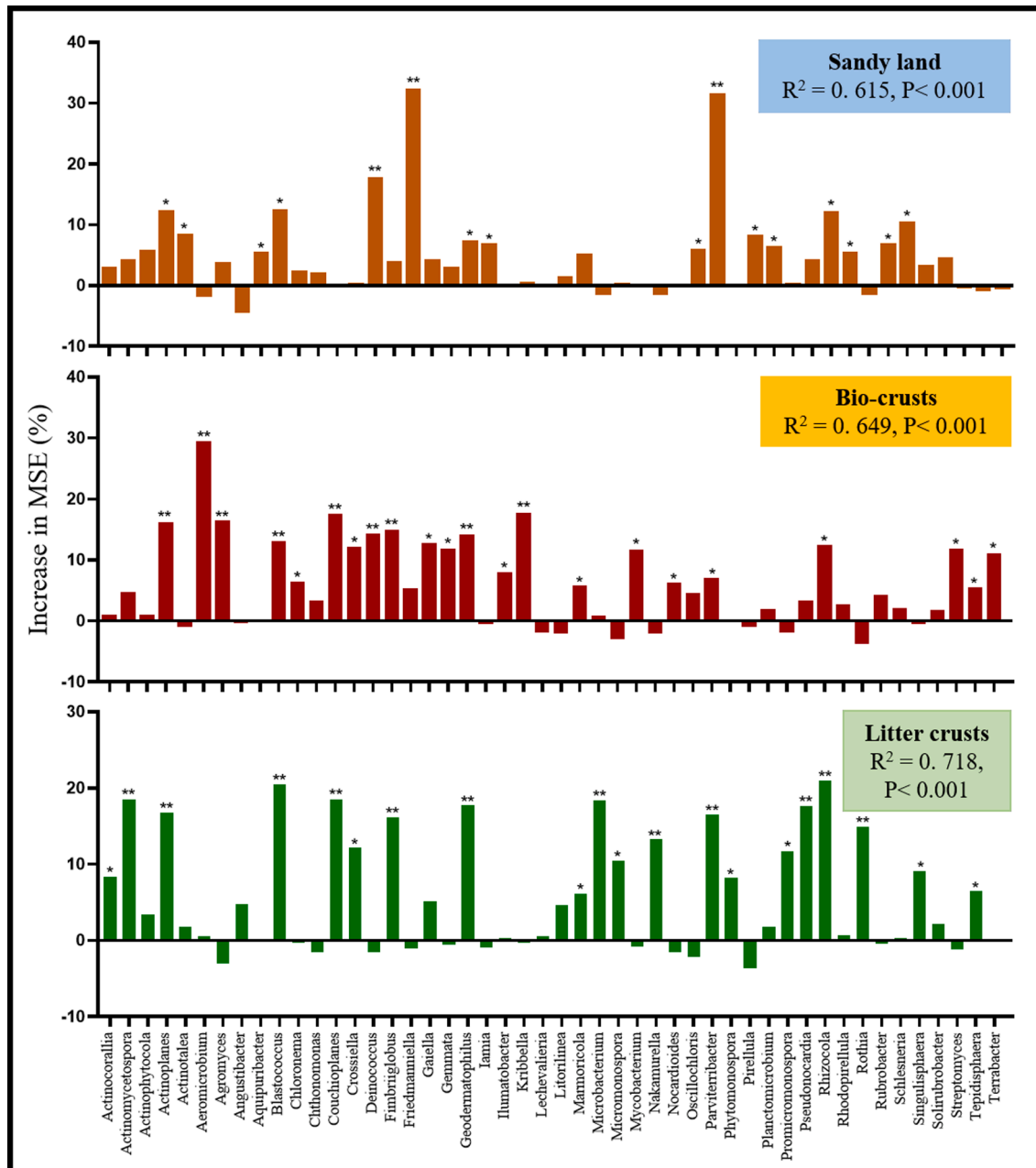


Fig. 6. Random forest (RF) shows all potential drivers (MSE% values > 5%) of the phyla Actinobacteria, Planctomycetes, Chloroflexi, Armatimonadetes, Deinococcus-Thermus, Nitrospirae at the genus level for sand nutrient cycling in the sandy land, biocrusts and litter crusts, respectively. Color of orange, red and green represent the sandy land, biocrusts and litter crusts, respectively. MSE is the mean square error. MSE% values represent the importance of these predictors. Higher MSE% values mean more important predictors. The significance of the model was estimated by the R package “A3”. \*, P < 0.05; \*\*, P < 0.01. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

development of bio-crusts and litter crusts. This finding indicated that these crusts have a positive effect on sandy ecosystem restoration.

In this study, litter crusts enhanced most sand nutrients and enzyme activities compared with bio-crusts. This result is consistent with previous study that litter crusts significantly increase soil organic matter than those in bio-crusts (Liu et al., 2019b). This condition can be apparently and partially due to many substrates for decomposition provided from the litter crusts, thereby elucidating the improvement of soil quality in sandy litter crusts. Soil quality determined the nature of vegetation series and the achievement of ecological restoration (Putten et al., 2013). Previous studies indicated that the diversity of bacteria typically increases with ecosystem restoration. The richness and diversity of bacterial communities in the litter crusts and bio-crusts were significantly higher than in the sandy land. This condition is attributed to the opportunities for the interactions of different species among themselves are provided by the improved soil quality (Liu et al., 2019a). These crusts can provide favorable environment for vegetation species formation via improving soil surface microhabitats of sandy land in the wind-water erosion crisscross region. Moreover, most soil nutrients contents and enzyme activities were greatest in topsoil, as shown in previous results (Liu et al., 2018). These differences in soil properties may have an influence on the soil microorganisms. The diversity of bacteria was higher in the deep layer (5–10 cm) than in the other layers in sandy land. This finding is inconsistent with studies that the diversity of bacterial communities commonly decreases with increasing soil depth (Jiao et al., 2018a). This result may be due to the specific environmental conditions of sandy land, including the high air temperature, low soil humidity, and abundant solar radiation in surface soil (Liu et al., 2018).

#### 4.2. Influence of litter crusts and bio-crusts on co-occurrence networks

Many studies have reported that the co-occurrence patterns of complex ecological interactions that form bacterial communities can demonstrate the interactions of soil variables and bacterial taxa. These patterns are generally used to evaluate the information on community interactions in natural habitats. In our co-occurrence networks, the interactions of soil variables and bacterial genera were complicated in the litter crusts network. This result may be related to the accumulation of soil nutrients and enzyme activities that contributed to the bacterial community activity. The bio-crusts and litter crusts networks were significantly different at the genus level, which may be due to their heterogeneity in response to the soil properties and different habitats.

Soil microbes may be related to the soil properties and among themselves through various mechanisms (Ma et al., 2016). In this study, we found that the bacterial networks were distinct among the three sample groups. Bacterial genera had more connections with each other in the litter crusts network (num. edges = 1787) than in the bio-crusts network (num. edges = 975). More positive correlations identified as co-occurrences were found in the litter crusts (99.89%) than in the bio-crusts (94.26%). Dominant positive correlations illustrate that most bacterial genera may share similar ecological niches or synergistically operate in the litter crusts environment, which is consistent with other microbial networks (Aschenbrenner et al., 2017; Zhang et al., 2018). The bacterial taxa enriched in the litter crusts might benefit from sufficient soil nutrients, thereby enabling them to take up the leading ecological niches in the interaction network. In litter crusts network, the most important genera, including *Romboutsia*, *Paeniclostridium*, and *Mogibacterium* belong to the phyla Firmicutes. The lowest relative abundance of these genera and the most important roles were observed. Our study showed that the relative abundance of bacterial taxa is not directly related to ecosystem function, consistent with sulfate reducer *Desulfosporosinus* with the low (0.006%) abundance managed the majority of soil SO<sub>4</sub> reduction (Pester et al., 2010). It is known that members of the Firmicutes have ability to degrade cellulose in the litter. But, the highest relative abundance of the Firmicutes were observed in the sandy land probably because the much phenotypic variation of its

members enables these organisms to live in various environments (Lawson et al., 1993), and many members with spore-forming ability are able to endure harsh environmental conditions (Zhuang et al., 2010). However, negative correlations (5.74%), which show co-exclusion between the two bacterial genera, were rarer than positive ones in the bio-crusts network. The number of negative links was higher than in the litter crusts network, probably due to a more competitive connection between bacterial genera in the bio-crusts. More negative correlations were found between *Gaiella* and other genera, for instance, *Gaiella* and *Hydrocarboniphaga*, *Microvirga*, or *Belnapia*. *Gemmatimonas*, *Hydrocarboniphaga*, *Microvirga*, and *Belnapia* were the important genera in the bio-crust network. Compared with the sandy land, the highest relative abundance of the *Gaiella* and lower abundance of the *Hydrocarboniphaga*, *Microvirga*, or *Belnapia* were found in the bio-crusts. *Gaiella* is chemoorganotrophic and had the ability to utilize organic acids, amino acids, and some sugars as single carbon sources but not utilize hydrocarbons as carbon (Albuquerque et al., 2018). *Hydrocarboniphaga*, *Microvirga*, or *Belnapia* belong to the Proteobacteria, these members were facultative and aerobic bacteria and can utilize various organic substrates (Slezak et al., 2017). Most organisms contain or produce small amounts of hydrocarbon, such as, the fermentation of many bacteria in the soil and the decomposition of plants. *Hydrocarboniphaga* active in hydrocarbon degradation (Palleroni et al., 2004) and *Microvirga* can degrade some hydrocarbon (i.e. Tween 20, D-sorbitol, adonitol, and alpha-iso-leucine) as carbon and nitrogen sources (Veyisoglu et al., 2016). This observation may be because the accumulation of hydrocarbons has an opposite effect on the growth of *Gaiella* and *Hydrocarboniphaga* or *Gaiella* and *Microvirga* in bio-crusts. These results may indicate the preferences of specific bacteria for soil crust types and substrates.

#### 4.3. Bacterial community predictors of sandy nutrient cycling

Plant and microbial diversity drive terrestrial ecosystem multifunctionality (Delgado-Baquerizo et al., 2016). Recent research provides evidence that microbial communities play pivotal roles in driving soil nutrient cycling in reforested ecosystems (Jiao et al., 2018b). Our results showed that the members of the predictors varied with the crust types in sandy land. Nitrospirae was the important and unique predictor to the nutrient cycling in the bio-crusts likely due to its diverse metabolism. Most of its genera are aerobic chemolithotrophs, including nitrifiers, dissimilatory sulfate reducers, and magnetotactic forms (Garrity et al., 2001). Nitrospirae is an extensive nitrite-oxidizing bacterial taxa and plays a major role in the soil nitrogen cycle. In our study, Nitrospirae showed the highest relative abundance in the bio-crusts, and had a slight higher content of TN and UA compared with in sandy land, which participate in nitrogen cycle. This result showed that the nitrogen-cycling bacterial group was crucial in the development of the bio-crusts, and the soil conditions in the bio-crusts were enhanced with long-term crust restoration in the sandy land. Actinobacteria and Chloroflexi are the important and unique predictors to the nutrient cycling in the litter crusts. This condition is probably because Actinobacteria, as an excellent indicator of soil biological activity, metabolize cellulose, lignin, and other complex polymers, mediate the decomposition of organic matter in ecosystems, and influence the nutrient cycling in the soil (Kirby, 2005). The relative abundance of Actinobacteria accounted for the high proportion across the three groups with their capacity to colonize bare soil (Suela Silva et al., 2013). However, their decrease with the increase in soil nutrients agrees with the study that Actinobacteridae are more abundant in patches without vegetation than in shrubs (Hortal et al., 2013). Actinobacteria play a beneficial role in the soil by providing protection against abiotic stresses and enhancing plant nutrition acquisition (Shi et al., 2019). Chloroflexi can offer energy through photosynthesis, degradation of plant-derived compounds, and organic matter decomposition (Wang et al., 2018). Previous study showed that it was negatively correlated with TN and organic carbon in



the litter crusts (Lozano et al., 2014) and the relative abundance of Chloroflexi decreased with the development of soil (Brown and Jumpponen, 2014). These findings are consistent with our study that showed the lowest relative abundance of Chloroflexi and the highest content of TN and organic matter, and its relative abundance is indirectly correlated with soil nutrients and enzyme activities. Actinobacteria and Chloroflexi are pivotal in predicting the cycling of sand nutrients under the litter crusts. Our experimental results reveal the distinct contributions of bacterial taxa to soil functions (multi-nutrient cycling) in bio-crusts and litter crusts in sandy lands.

Increasing attentions in manipulating host-microbiome interactions by adding bacteria in a range of systems should focus on a fine scale to analyze the relationships between the microbial populations and soil functioning under natural conditions. However, most studies have focused on the microbial indicator at the phylum level or class level of bacteria. In our study, we aimed to determine the predictors of nutrient cycling at the genus level. Our results indicated that approximately 31% of predictors (10) were the same between the bio-crusts and litter crusts at genus level, and they were more connected with other bacterial genera in the co-occurrence networks. Hence, they may affect the soil ecosystem functioning by contributing to nutrient cycling in the crust types of ecosystem restoration. The unique bacterial predictors' groups in the bio-crusts or litter crusts with these bacterial consortiums can play important roles in nutrient cycling in different habitats. This finding is consistent with the study of distinct microbial communities that can exhibit distinct responses in different habitats (Wagner et al., 2016). The number of bacterial predictors were more in the crusts than in the sandy land. This result suggested the importance of soil bacterial communities in impacting ecosystem functioning (multiple nutrient cycling) during the development of the bio-crusts and litter crusts in sandy land. Our results showed particular bacterial consortium play important roles in predicting soil nutrient cycling in sandy ecosystem restoration. In a microbial ecosystem, the identification of the key microbial populations is often associated with the occurrence and abundance of species in local habitat (Mei et al., 2016). Therefore, the important drivers at the genus level with litter crusts and bio-crusts contribute to the applications of the key microbial driver in ecosystem restoration. These observations indicate bacteria participate in the biogeochemical cycling of multi-nutrients in the litter crusts and bio-crusts and the importance of investigating distinct responses contributed to sand nutrient cycling in the sandy ecosystem restoration. These studies enrich our knowledge on crusts and bacterial communities in restoring sandy land.

## 5. Conclusions

Soil bacterial communities represent important variables for predicting nutrients cycling of restoration trajectories, thereby affecting belowground ecological restoration. In this study, the bacterial communities showed increased diversity and varied composition and structure in the crust types compared with the sandy land. The diversity and OUT richness were positively correlated with soil nutrients (except TP) in surface soil (0–2 cm and 2–5 cm). Litter crusts network had closer relationships between the soil bacterial taxa and soil nutrients and more positive correlations among themselves than in the bio-crusts network. The bacterial drivers play the most important roles in mediating sand nutrient cycling in the crust types of ecosystem restoration. These findings increase our understanding of the complex interactions between bacterial communities and crust types during the ecosystem recovery. The distinct response strategies of particular bacterial groups at the genus level can be important for the comprehensive understanding of the belowground microcosms with litter crusts and bio-crusts in the surface sand. Our study provides a new perspective that the exploration of the specific functions of particular bacterial consortiums in nutrient cycling is crucial to their applications in pivotal ecosystem functioning. Future work should be conducted to isolate the most important drivers of the bacterial taxa. Bacterial inoculants may promote soil bacterial

functioning in nutrient cycling and may be potentially implemented as an approach for increasing soil fertility in degraded lands or agricultural lands.

## Declaration of Competing Interest

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

## Acknowledgements

We thank the editors and anonymous reviewers for their constructive comments and suggestions. This study was funded by projects of the National Natural Science Foundation of China (NSFC 41722107, 41930755), Natural Science Basic Research Program of Shaanxi (2020JQ-275), the Fundamental Research Funds for the Central Universities (2452019187, 2452018086), the Youth Talent Plan Foundation of Northwest A & F University (2452018025) and the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB40000000).

## Authors' contributions

G.L.W conceived the idea and designed the study; X.L., Y.L. and L.Z. performed the experiment and collected the data; X.L. analyzed the data; X.L. and G.L.W led the writing of the manuscript with the help of R.Y. All authors contributed critically to the draft and gave final approval for publication.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.catena.2020.105090>.

## References

- Albuquerque, L., Rainey, F.A., Costa, M.S., 2018. Gaiella. *Bergey's Manual of Systematics of Archaea and Bacteria*, 1-7. <https://doi.org/10.1002/9781118960608.gbm01469>.
- Archer, E., 2016. rFPermute: Estimate Permutation p-Values for Random Forest Importance Metrics. <https://CRAN.R-project.org/package=rFPermute>.
- Aschenbrenner, I.A., Cernava, T., Erlacher, A., Berg, G., Grube, M., 2017. Differential sharing and distinct co-occurrence networks among spatially close bacterial microbiota of bark, mosses and lichens. *Mol. Ecol.* 26, 2826–2838. <https://doi.org/10.1111/mec.14070>.
- Asner, G.P., Archer, S., Flintheughes, R., Ansley, R.J., Wessman, C.A., 2003. Net changes in regional woody vegetation cover and carbon storage in Texas drylands, 1937–1999. *Global Change Biol.* 9, 316–335. <https://doi.org/10.1046/j.1365-2486.2003.00594.x>.
- Banning, N.C., Gleeson, D.B., Grigg, A.H., Grant, C.D., Andersen, G.L., Brodie, E.L., Murphy, D.V., 2011. Soil microbial community successional patterns during forest ecosystem restoration. *Appl. Environ. Microbiol.* 77, 6158–6164. <https://doi.org/10.1128/AEM.00764-11>.
- Bo, T.L., Ma, P., Zheng, X.J., 2015. Numerical study on the effect of semi-buried straw checkerboard sand barriers belt on the wind speed. *Aeolian Res.* 16, 101–107. <https://doi.org/10.1016/j.aeolia.2014.10.002>.
- Bremner, J.M., Mulvaney, C.S., 1996. Nitrogen-total. In: Page, A.L. (Ed.), *Methods of soil analysis, Part 2. Chemical and Microbiological Properties*, 72. American Society of Agronomy and Soil Science Society of America, Madison, pp. 595–624.
- Brown, S.P., Jumpponen, A., 2014. Contrasting primary successional trajectories of fungi and bacteria in retreating glacier soils. *Mol. Ecol.* 23, 481–497. <https://doi.org/10.1111/mec.12487>.
- Caporaso, J.G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F.D., Costello, E.K., Fierer, N., Pena, A.G., Goodrich, J.K., Gordon, J.I., Huttley, G.A., Kelley, S.T., Knights, D., Koenig, J.E., Ley, R.E., Lozupone, C.A., McDonald, D., Muegge, B.D., Pirrung, M., Reeder, J., Sevinsky, J.R., Turnbaugh, P.J., Walters, W.A., Widmann, J., Yatsunenkov, T., Zaneveld, J., Knight, R., 2010. QIIME allows analysis of high-throughput community sequencing data. *Nat. Methods* 7, 335–336. <https://doi.org/10.1038/nmeth.f.303>.
- 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. *Proc. Natl. Acad. Sci. USA* 108, 4516–4522. <https://doi.org/10.1073/pnas.1000080107>.
- Chen, J., Chen, Z.P., Ai, Y.W., Xiao, J.Y., Pan, D.D., Li, W., Huang, Z.Y., Wang, Y.M., 2015a. Impact of soil composition and electrochemistry on corrosion of rock-cut

- slope nets along railway lines in China. *Sci. Rep.* 5, 14939. <https://doi.org/10.1038/srep14939>.
- Chen, Y.P., Wang, K.B., Lin, Y.H., Shi, W.Y., Song, Y., He, X.H., 2015b. Balancing green and grain trade. *Nat. Geosci.* 8, 739–741. <https://doi.org/10.1038/ngeo2544>.
- D'Odorico, P., Bhattachan, A., Davis, K.F., Ravi, S., Runyan, C.W., 2013. Global desertification: drivers and feedbacks. *Adv. Water Resour.* 51, 326–344. <https://doi.org/10.1016/j.advwatres.2012.01.013>.
- Delgado-Baquerizo, M., Maestre, F.T., Reich, P.B., Jeffries, T.C., Gaitan, J.J., Encinar, D., Berdugo, M., Campbell, C.D., Singh, B.K., 2016. Microbial diversity drives multifunctionality in terrestrial ecosystems. *Nat. Commun.* 7, 10541. <https://doi.org/10.1038/ncomms10541>.
- Edgar, R.C., 2013. UPARSE: highly accurate OTU sequences from microbial amplicon reads. *Nat. Methods* 10, 996–998. <https://doi.org/10.1038/nmeth.2604>.
- Falkowski, P.G., Fenchel, T., Delong, E.F., 2008. The microbial engines that drive Earth's biogeochemical cycles. *Science* 320, 1034–1039. <https://doi.org/10.1126/science.1153213>.
- Ferrenberg, S., Faist, A.M., Howell, A., Reed, S.C., 2018. Biocrusts enhance soil fertility and *Bromus tectorum* growth, and interact with warming to influence germination. *Plant Soil* 429, 77–90. <https://doi.org/10.1007/s11104-017-3525-1>.
- Fierer, N., Jackson, R.B., 2006. From the cover: The diversity and biogeography of soil bacterial communities. *Proc. Natl. Acad. Sci. USA* 103. <https://doi.org/10.1073/pnas.0507535103>.
- Fortmann-Roe, S., 2013. Accurate, Adaptable, and Accessible Error Metrics for Predictive. R package version 0.9.2.
- Gao, L.Q., Bowker, M.A., Xu, M.X., Sun, H., Tuo, D.F., Zhao, Y.G., 2017. Biological soil crusts decrease erodibility by modifying inherent soil properties on the Loess Plateau, China. *Soil Biol. Biochem.* 105, 49–58. <https://doi.org/10.1016/j.soilbio.2016.11.009>.
- Garrity, G.M., Holt, J.G., Phylum, B.V.III., 2001. Nitrospirae phy. In: Boone, D.R., Castenholz, R.W., Garrity, G.M. (Eds.), *Bergey's Manual of Systematic Bacteriology*. Springer, New York, NY, pp. 451–464.
- Hartmann, M., Frey, B., Mayer, J., Mader, P., Widmer, F., 2015. Distinct soil microbial diversity under long-term organic and conventional farming. *ISME J.* 9, 1177–1194. <https://doi.org/10.1038/ismej.2014.210>.
- Hortal, S., Bastida, F., Armas, C., Lozano, Y.M., Moreno, J.L., García, C., Pugnaire, F.I., 2013. Soil microbial community under a nurse-plant species changes in composition, biomass and activity as the nurse grows. *Soil Biol. Biochem.* 64, 139–146. <https://doi.org/10.1016/j.soilbio.2013.04.018>.
- Jakobsen, A.M., Bahl, M.I., Buschhardt, T., Hansen, T.B., Al-Soud, W.A., Bregner, A.D., Sorensen, S.J., Nesbakken, T., Aabo, S., 2019. Bacterial community analysis for investigating bacterial transfer from tonsils to the pig carcass. *Int. J. Food Microbiol.* 295, 8–18. <https://doi.org/10.1016/j.ijfoodmicro.2019.02.003>.
- Jia, C., Liu, Y., He, H.H., Miao, H.T., Huang, Z., Zheng, J.Y., Han, F.P., Wu, G.L., 2018. Formation of litter crusts and its multifunctional ecological effects in a desert ecosystem. *Ecosphere* 9, e02196. <https://doi.org/10.1002/ecs20196>.
- Jiao, S., Chen, W.M., Wang, J.L., Du, N.N., Li, Q.P., Wei, G.H., 2018a. Soil microbiomes with distinct assemblies through vertical soil profiles drive the cycling of multiple nutrients in reforested ecosystems. *Microbiome* 6, 146. <https://doi.org/10.1186/s40168-0018-40526-40160>.
- Jiao, S., Chen, W.M., Wang, J.M., Zhang, L., Yang, F., Lin, Y.B., Wei, G.H., 2018b. Plant growth and oil contamination alter the diversity and composition of bacterial communities in agricultural soils across China. *Land Degrad. Dev.* 29, 1660–1671. <https://doi.org/10.1002/ldr.2932>.
- Jiao, S., Du, N.N., Zai, X.Y., Gao, X.E., Chen, W.M., Wei, G.H., 2019. Temporal dynamics of soil bacterial communities and multifunctionality are more sensitive to introduced plants than to microbial additions in a multicontaminated soil. *Land Degrad. Dev.* 30, 852–865. <https://doi.org/10.1002/ldr.3272>.
- Jing, X., Sanders, N.J., Shi, Y., Chu, H.Y., Classen, A.T., Zhao, K., Chen, L.T., Shi, Y., Jiang, Y.X., He, J.S., 2015. The links between ecosystem multifunctionality and above- and belowground biodiversity are mediated by climate. *Nat. Commun.* 6, 8159. <https://doi.org/10.1038/ncomms9159>.
- Karimi, B., Terrat, S., Dequiedt, S., Saby, N.P.A., Horrigue, W., Lelièvre, M., Nowak, V., Jolivet, C., Arruays, D., Wincker, P., Cruaud, C., Bispo, A., Maron, P.A., Prévost-Bouré, N.C., Ranjard, L., 2018. Biogeography of soil bacteria and archaea across France. *Sci. Adv.* 4, eaat1808. <https://doi.org/10.1126/sciadv.aat1808>.
- Kirby, R., 2005. Actinomycetes and lignin degradation. *Adv. Appl. Microbiol.* 58, 125–168. [https://doi.org/10.1016/S0065-2164\(05\)58004-3](https://doi.org/10.1016/S0065-2164(05)58004-3).
- Lawson, P.A., Llop-Perez, p., Hutson, R.A., Hippe, H., Collins, M.D., 1993. Towards a phylogeny of the clostridia based on 16S rRNA sequences. *FEMS Microbiol. Lett.* 87–92. <https://doi.org/10.1111/j.1574-6968.1993.tb06493.x>.
- Leloup, J., Baude, M., Nunan, N., Meriguet, J., Dajoz, I., Le Roux, X., Raynaud, X., 2018. Unravelling the effects of plant species diversity and aboveground litter input on soil bacterial communities. *Geoderma* 317, 1–7. <https://doi.org/10.1016/j.geoderma.2017.12.018>.
- Li, L.Y., Abou-Samra, E., Ning, Z., Zhang, X., Mayne, J., Wang, J., Cheng, K., Walker, K., Stintzi, A., Figeys, D., 2019. An in vitro model maintaining taxon-specific functional activities of the gut microbiome. *Nat. Commun.* 10, 1–11. <https://doi.org/10.1101/616656>.
- Liu, X.K., Lu, R., Du, J., Lyu, Z., Wang, L., Gao, S., Wu, Y., 2018. Evolution of peatlands in the Mu Us Desert, northern China, since the last deglaciation. *J. Geophys. Res. Earth* 123, 252–261. <https://doi.org/10.1002/2017jf004413>.
- Liu, Y., Chen, X.T., Liu, J.X., Liu, T.T., Cheng, J.M., Wei, G.H., Lin, Y.B., 2019a. Temporal and spatial succession and dynamics of soil fungal communities in restored grassland on the Loess Plateau in China. *Land Degrad. Dev.* 30, 1273–1287. <https://doi.org/10.1002/ldr.3289>.
- Liu, Y., Cui, Z., Huang, Z., Miao, H.T., Wu, G.L., 2019b. The influence of litter crusts on soil properties and hydrological processes in a sandy ecosystem. *Hydrol. Earth Syst. Sci.* 23, 2481–2490. <https://doi.org/10.5194/hess-23-2481-2019>.
- Lozano, Y.M., Hortal, S., Armas, C., Pugnaire, F.I., 2014. Interactions among soil, plants, and microorganisms drive secondary succession in a dry environment. *Soil Biol. Biochem.* 78, 298–306. <https://doi.org/10.1016/j.soilbio.2014.08.007>.
- Ma, B., Wang, H.Z., Dsouza, M., Lou, J., He, Y., Dai, Z.M., Brookes, P.C., Xu, J.M., Gilbert, J.A., 2016. Geographic patterns of co-occurrence network topological features for soil microbiota at continental scale in eastern China. *ISME J.* 10, 1891–1901. <https://doi.org/10.1038/ismej.2015.261>.
- Mei, R., Narihiro, T., Nobu, M.K., Kuroda, K., Liu, W.T., 2016. Evaluating digestion efficiency in full-scale anaerobic digesters by identifying active microbial populations through the lens of microbial activity. *Sci. Rep.* 6, 34090. <https://doi.org/10.1038/srep34090>.
- Nelson, D.W., Sommers, L.E., 1982. Total Carbon, Organic Carbon, and Organic Matter. In Page A L, Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties. American Society of Agronomy and Soil Science Society of America, Madison, 9, 539–577.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., et al., 2013. Package 'vegan. *Community Ecology Package 2*, 1–295 <https://CRAN.R-project.org/package=vegan>.
- Olsen, S.R., Sommers, L.E., 1982. Phosphorus. In Page A L, Miller R H, Keeney D R. Methods of Soil Analysis. Part 2. American Society of Agronomy and Soil Science Society of America, Madison, 403–430.
- Page, A.L., Miller, R.H., Keeney, D.R., 1982. Methods of Soil Analysis. 2nd eds. Part 2. Chemical and Microbiological Properties. American Society of Agronomy and Soil Science Society of America, Madison, 539–579.
- Palleroni, N.J., Port, A.M., Chang, H.K., Zylstra, G.J., 2004. Hydrocarboniphaga effusa gen. nov., sp. nov., a novel member of the gamma-Proteobacteria active in alkane and aromatic hydrocarbon degradation. *Int. J. Syst. Evol. Microbiol.* 54, 1203–1207. <https://doi.org/10.1099/ijs.0.03016-0>.
- Pester, M., Bittner, N., Deevong, P., Wagner, M., Loy, A., 2010. A 'rare biosphere' microorganism contributes to sulfate reduction in a peatland. *ISME J.* 4, 1591–1602. <https://doi.org/10.1038/ismej.2010.75>.
- Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T., Kardol, P., Kironomos, J.N., Kulmatiski, A., Schweitzer, J.A., Suding, K.N., Voorde, T.F.J.V., Wardle, D.A., 2013. Plant-soil feedbacks: the past, the present and future challenges. *J. Ecol.* 101, 265–276. <https://doi.org/10.1111/1365-2745.12054>.
- Qian, X., Chen, L., Guo, X.M., He, D., Shi, M.M., Zhang, D.X., 2018. Shifts in community composition and co-occurrence patterns of phyllosphere fungi inhabiting *Mussaenda shikokiana* along an elevation gradient. *Peer J.* 6, e5767. <https://doi.org/10.7717/peerj.5767>.
- Reed, S.C., Delgado-Baquerizo, M., Ferrenberg, S., 2019. Biocrust science and global change. *New Phytol.* 3, 223. <https://doi.org/10.1111/nph.15992>.
- Shi, S.H., Tian, L., Nasir, F., Bahadur, A., Batool, A., Luo, S.S., Yang, F., Wang, Z.C., Tian, C.J., 2019. Response of microbial communities and enzyme activities to amendments in saline-alkaline soils. *Appl. Soil Ecol.* 135, 16–24. <https://doi.org/10.1016/j.apsoil.2018.11.003>.
- Sivakumar, M.V.K., Das, H.P., Brunini, O., 2005. Impacts of present and future climate variability and change on agriculture and forestry in the arid and semi-arid tropics. *Clim. Change* 70, 31–72. <https://doi.org/10.1007/s10584-005-5937-9>.
- Slezak, R., Grzelak, J., Krzystek, L., Ledakowicz, S., 2017. The effect of initial organic load of the kitchen waste on the production of VFA and H<sub>2</sub> in dark fermentation. *Waste Manag* 68, 610–617. <https://doi.org/10.1016/j.wasman.2017.06.024>.
- State Forestry Administration, P.R.C., 2015. The desertification and sandification state of China.
- Suela Silva, M., Naves Sales, A., Teixeira Magalhaes-Guedes, K., Ribeiro Dias, D., Schwan, R.F., 2013. Brazilian cerrado soil Actinobacteria ecology. *Biomed Res. Int.* 2013, 503805. <https://doi.org/10.1155/2013/503805>.
- Tabatabai, M.A., 1994. Soil Enzymes. In: Weaver, R.W., Angle, J.S., Bottomley, P.S. (Eds.), *Methods of Soil Analysis: Microbiological and Biochemical Properties*. Soil Science Society of America, Madison, pp. 775–833. <https://doi.org/10.2136/sssabookser5.2.c37>.
- Taylor, J.P., Wilson, B., Mills, M.S., Burns, R.G., 2002. Comparison of microbial numbers and enzymatic activities in surface soils and subsoils using various techniques. *Soil Biol. Biochem.* 34, 387–401. [https://doi.org/10.1016/S0038-0717\(01\)00199-7](https://doi.org/10.1016/S0038-0717(01)00199-7).
- Torres-Cruz, T.J., Howell, A.J., Reibold, R.H., McHugh, T.A., Eickhoff, M.A., Reed, S.C., 2018. Species-specific nitrogenase activity in lichen-dominated biological soil crusts from the Colorado Plateau, USA. *Plant Soil* 429, 113–125. <https://doi.org/10.1007/s11104-018-3580-2>.
- Uchida, E., Xu, J., Rozelle, S., 2005. Grain for green: cost-effectiveness and sustainability of China's conservation set-aside program. *Land Econ.* 81, 247–264. <https://doi.org/10.3368/le.81.2.247>.
- Veyisoglu, A., Tatar, D., Saygin, H., Inan, K., Cetin, D., Guven, K., Tuncer, M., Sahin, N., 2016. *Microvirga makkahensis* sp. nov., and *Microvirga arabica* sp. nov., isolated from sandy arid soil. *Antonie Van Leeuwenhoek* 109, 287–296. <https://doi.org/10.1007/s10482-015-0631-z>.
- Wagg, C., Bender, S.F., Widmer, F., van der Heijden, M.G., 2014. Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proc. Natl. Acad. Sci. USA* 111, 5266–5270. <https://doi.org/10.1073/pnas.1320054111>.
- Wagner, M.R., Lundberg, D.S., Del Rio, T.G., Tringe, S.G., Dangl, J.L., Mitchell-Olds, T., 2016. Host genotype and age shape the leaf and root microbiomes of a wild perennial plant. *Nat. Commun.* 7, 12151. <https://doi.org/10.1038/ncomms12151>.
- Wang, C., Liu, S.Y., Zhang, Y., Liu, B.Y., He, F., Xu, D., Zhou, Q.H., Wu, Z.B., 2018. Bacterial communities and their predicted functions explain the sediment nitrogen

- changes along with submerged macrophyte restoration. *Microb. Ecol.* 76, 625–636. <https://doi.org/10.1007/s00248-018-1166-4>.
- Wang, X.M., Cheng, H., Li, H., Lou, J.P., Hua, T., Liu, W.B., Jiao, L.L., Ma, W.Y., Li, D.F., Zhu, B.Q., 2017. Key driving forces of desertification in the Mu Us Desert, China. *Sci. Rep.* 7, 3933. <https://doi.org/10.1038/s41598-017-04363-8>.
- Zeng, D.H., Hu, Y.L., Chang, S.X., Fan, Z.P., 2008. Land cover change effects on soil chemical and biological properties after planting Mongolian pine (*Pinus sylvestris* var. *mongolica*) in sandy lands in Keerqin, northeastern China. *Plant Soil* 317, 121–133. <https://doi.org/10.1007/s11104-008-9793-z>.
- Zhang, B.G., Zhang, J., Liu, Y., Shi, P., Wei, G.H., 2018. Co-occurrence patterns of soybean rhizosphere microbiome at a continental scale. *Soil Biol. Biochem.* 118, 178–186. <https://doi.org/10.1016/j.soilbio.2017.12.011>.
- Zhuang, X.L., Han, Z., Bai, Z.H., Zhuang, G.Q., Shim, H., 2010. Progress in decontamination by halophilic microorganisms in saline wastewater and soil. *Environ. Pollut.* 158, 1119–1126. <https://doi.org/10.1016/j.envpol.2010.01.007>.