Variations in sand physiochemical properties and bacterial communities along an altitude gradient in the Taklimakan Desert

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Abstract

The Taklimakan Desert is the largest desert in China and the second-largest mobile desert in the world. It is characterized by an increasing altitude gradient from north to south. In this study, a total of 48 sand samples were collected in the Taklimakan Desert, and variations in physicochemical parameters and bacterial communities in the samples and the correlation between them were explored. The bacterial community was characterized using 16S rRNA gene sequencing. The obtained taxonomic data revealed significant differences in the relative abundance of bacterial communities and populations among the samples. The predominant phyla were Actinobacteria, Firmicutes, Proteobacteria, and Bacteroidetes. The abundance of Actinobacteria increased gradually while that of Firmicutes decreased gradually with the increase in altitude. At the genus level, the abundance of Bacillus showed a gradual decrease while that of unclassified Micrococcaceae showed a gradual increase. Altitude and pH were the primary factors that shaped the bacterial communities in the desert. Besides, Ca2+ and P were also significantly correlated with the abundance of bacterial communities. The indicator taxa were significant differences in the surface and the subsurface samples.

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Originality-Significance Statement

The Taklimakan Desert is the largest desert in China and the second-largest mobile desert in the world. The detailed microbial ecology of the Taklimakan Desert has been poorly investigated to date. Therefore, a comprehensive investigation is necessary for the taxonomic diversity of bacterial communities in the Taklimakan Desert. This work investigated the physicochemical parameters and bacterial communities of 48 sand samples along to altitude gradient. The obtained taxonomic data revealed significant differences in the relative abundance of bacterial communities and populations among the samples. Altitude and pH were the primary factors that shaped the bacterial communities in the desert. Studying bacterial diversity and community assembly processes along an altitude gradient are necessary for deeply understanding the fundamental ecological processes in desert ecosystems.

Summary

The Taklimakan Desert is the largest desert in China and the second-largest mobile desert in the world. It is characterized by an increasing altitude gradient from north to south. In this study, a total of 48 sand samples were collected in the Taklimakan Desert, and variations in physicochemical parameters and bacterial communities in the samples and the correlation between them were explored. The bacterial community was characterized using 16S rRNA gene sequencing. The obtained taxonomic data revealed significant differences in the relative abundance of bacterial communities and populations among the samples. The predominant phyla were Actinobacteria, Firmicutes, Proteobacteria, and Bacteroidetes. The abundance of Actinobacteria increased gradually while that of Firmicutes decreased gradually with the increase in altitude. At the genus level, the abundance of *Bacillus* showed a gradual decrease while that of unclassified *Micrococcaceae* showed a gradual increase. Altitude and pH were the primary factors that shaped the bacterial communities in the desert. Besides, Ca^{2+} and P were also significantly correlated with the abundance of bacterial communities. The indicator taxa were significant differences in the surface and the subsurface samples.

Keywords: Taklimakan Desert, pH, altitude, bacterial community, physiochemical property

Introduction

Desert is the largest terrestrial ecosystem on earth, which is sensitive to human activity and climatic change (Laity, 2009). The common features of desert, such as extreme drought, strong ultraviolet radiation, and dramatic temperature fluctuations, limit the survival of plants and animals in this extreme environment (Sul et al., 2013). Thus, microorganisms become the dominant component of the desert ecosystem (Pointing et al., 2012).

The different desert habitats shaped the diverse microorganism colonization. Cyanobacteria showed the highest abundance in the biological soil crusts of deserts (Nagy et al., 2005; Zhang et al., 2016a; Arocha-Garza et al., 2017; Mogul et al., 2017; Sun et al., 2018). Actinobacteria was the dominant bacteria in the hyper-arid core in the Atacama Desert (Crits-Christoph et al., 2013). Many previous studies focused on the microbial community composition and assembly in the desert. However, there is no consensus of opinions about which environment factor is the main driver for the microbial community assembly on deserts. For example, Zhang et al. (2019) found that salinity was the key determinant of microbial community assembly in the Gurbantunggut Desert. Crits-Christoph et al. (2013) emphasized that water and salt contents were the main factors shaping soil microbiome in the Atacama Desert. Several previous studies indicated that moisture influenced the microbial community structures, assembly, and colonization of the Namib Desert (Warren-Rhodes et al., 2013; Stomeo et al., 2013; Valverde et al., 2015). Additionally, the results from the Namib Desert showed that soil chemistry and stochasticity affected the bacterial community assembly and xeric stress adjusted the variations of community function (Scola et al., 2018). The inconsistent responses probably came from the environmental heterogeneity of different deserts.

The Taklimakan Desert is about 1130 kilometers long from east to west, 400 kilometers wide from north to south, covering an area of 337,600 Km^2. The terrain is high in the southwest and low in the northeast,

with altitudes ranging from 780 m to 1500 m. The detailed microbial ecology of the Taklimakan Desert has been poorly investigated to date. An et al. (2013) investigated the bacterial diversity at the edge of the Taklimakan Desert. Yu et al. (2015) isolated 52 ionizing radiation-tolerant bacteria strains from this desert. Several prior studies identified some novel cultivable bacteria in the Taklimakan Desert (Zhang et al., 2010; Liu et al., 2010; An et al., 2010; Liu et al., 2011). Therefore, a comprehensive investigation is necessary for the taxonomic diversity of bacterial communities in the Taklimakan Desert.

The altitudinal gradient is considered a natural test to evaluate the response of the microbial community to environmental change (Körner, 2007; Siles and Margesin, 2017). Previous studies indicated that the altitudinal gradient might lead to different effects on microbial community population and composition in different ecosystems (Manzoni et al., 2012; Serna-Chavez et al., 2013). The large altitude scales might involve different climatic regions, which is complex to investigate the correlation of microbial community along the altitudinal gradient (Ren et al., 2018). Thus, it may be easier to understand the correlation between altitude gradient and microbial community composition on the same climate conditions. Understanding the response of altitude gradient to the microbial community was important for better understanding the adaptability of microorganisms in the desert ecosystem.

The aims of the present study were to (1) evaluate the variations of physicochemical properties and bacterial communities in the sand of the Taklimakan Desert, (2) reveal how altitude and sand property influence the structure of bacterial communities, and (3) understand the specificity and adaptation of bacterial communities in the Taklimakan Desert.

Experimental procedures

Sites description and samples collection

The Taklimakan Desert is located in the northwest of China, specifically, in the southern region of Xinjiang province and the center of the Tarim Basin. The desert covers an area of 337,600 Km^2 and 85% of the surface is occupied by active dunes (Yang et al., 2016). It is the largest desert in China, and the second-largest mobile desert in the world. The annual mean temperature ranges from 9.9 to 12.6 °C, annual precipitation ranges from 17.4 to 66.3 mm, and the potential evaporation range from 2,100 to 3,400 mm. It belongs to the extremely arid temperate continental climate (Zhu, 1964; Zhu et al., 1981). In this study, the free of vegetation and human activity areas were selected as sampling sites. A total of 48 sand samples along a north-south transect were collected with sterile sampling bags from 8 sites in the Taklimakan Desert in September 2018 (Fig. 1). At least three surface (0-5 cm, S) and subsurface (50 cm, Su) sand samples were separately collected at each sampling site. All the samples were transported to the laboratory within one week at a low temperature and then stored at -20°C. The detailed information of the samples is provided in Table S1.

Measurement of the sand physicochemical property

Sand pH was determined using a pH meter (PT-10, Sartorius, Göttingen, Germany). Sand electrical conductivity (EC) was measured using a conductivity meter (DDSJ-308A, Leici, Shanghai, China). The water content (WC) was calculated based on the moisture difference value. The contents of total carbon (TC), total nitrogen (TN), and total organic carbon (TOC) were detected using an element analyzer (Elementar Vario-EL, Germany). Concentrations of total phosphorus (P), vanadium (V), yttrium (Y), zirconium (Zr), titanium (Ti), manganum (Mn), zinc (Zn), chlorine (Cl) were measured using the wavelength dispersive X-ray fluorescence spectrometer (AXIOS; PANalytical B.V., Netherlands) (Liu et al., 2016; Liang et al., 2019). The content of Cl^- was measured by silver nitrate titration method. The contents of Na^+, Mg^{2+}, Ca^{2+}were determined by atomic absorption spectrophotometry.

DNA extraction and PCR amplification

Total DNA of the sand samples was extracted using the soil DNA extraction kit (Qiagen, Hilden, Germany) according to its manual. The total DNA concentration was detected by 1% agarose gel electrophoresis and a NanoDrop 2000, and 10 ng DNA templates were used for PCR amplification. The 16S rRNA genes (V3-V4)

were amplified using the universal bacterial primers 338F-806R. PCR amplification system was composed of 5× FastPfu Buffer (4 μL), 2.5mM dNTPs (2 μL), 5 μM forward primer (0.8 μL), 5 μM reverse primer (0.8 μL), FastPfu polymerase (0.4 μL), BSA (0.2 μL), DNA template (10 ng), and by adding ddH_20 to 20 μL. PCR reaction cycling was composed of an initial denaturation at 94°C for 5 min, followed by 30 cycles of denaturation at 95°C for 30 s, annealing at 95°C for 30 s, elongation at 72°C for 45 s, and final elongation at 72 for 10 min.

Illumina sequencing and bioinformatics analyses

DNA sequencing was performed on an Illumina Miseq PE300 platform in the Majorbio Bio-Pharm Biotechnology Company (Shanghai, China). Raw reads were quality filtered by the QIIME software package (Caporaso et al., 2010). The reads were clustered into the operational taxonomic units (OTUs) at 97% similarity level. The OTU sequences were annotated by the SILVA database. One-way ANOVA with Tukey's test was performed by SPSS software (version 23.0) to test the environmental factors and α-diversity index differences of different samples. Redundancy analysis (RDA) in the vegan package in R3.6.1 was used to calculate the correlation among the environmental variables and the bacterial communities. Analysis of similarity (ANOSIM) was performed to examine the significance among the groups. The number of permutations was set at 999. Linear discriminant analysis effect size (LEfSe) analysis was employed to identify the significant difference of bacterial community between surface and subsurface samples (Segata et al., 2011). Principal coordinates analysis (PCoA) was used to analyze the bacterial community similarity of surface samples based on the Bray-Curtis distance. Variance partitioning analysis (VPA) was applied in the quantitative evaluation of the individual and common degree of interpretation between variant of environmental factors and bacterial communities using the vegan package in R3.6.1. The correlation between environmental factors and different phyla was shown as heatmaps using the spearman correlation coefficient from surface samples.

Results

Physicochemical characteristics of sand samples

In the surface sand samples, the physicochemical parameters displayed significant differences ($P < 0.05$), except Zn and TC, (Table 1 and Table S2). The pH, altitude, Ca^{2+}, P and Y showed highly significant differences ($P < 0.001$). In the subsurface sand samples, the physicochemical parameters exhibited significant differences ($P< 0.05$) except WC, EC, TN, TOC, Cl^-, Mg^{2+} and Cl, (Table 1 and Table S2). The altitude, P, Ti, Mn, V and Y showed highly significant differences ($P< 0.001$). Overall, the soil pH and altitude significantly decreased from north to south ($P < 0.05$). Furthermore, the physicochemical parameters of surface sand were similar to that of the subsurface sand, except the WC and Y levels which exhibited significant differences between the surface and subsurface samples.

Variations of bacterial communities in the samples

16S rRNA gene sequencing generated a total of 2160932 sequences after quality control. The sequences were classified into 5,195 OTUs at the 97% similarity level. In the surface samples, the Shannon index, Chao index, Simpson index, Sobs index and Ace index of the samples ranged from 0.807 to 3.044, from 151 to 312, from 0.133 to 0.807, from 138 to 278, and from 151 to 319, respectively (Table 2). Shannon and Simpson indices showed significant differences in the surface samples. In the subsurface samples, the Shannon index, Chao index, Simpson index, Sobs index and Ace index of the samples ranged from 0.790 to 4.111, from 158 to 431, from 0.058 to 0.816, from 137 to 335, and from 149 to 427, respectively. All of these indices showed significant differences in the subsurface samples. No significant differences were observed between the surface alpha diversity and that of the subsurface.

Bacterial community composition

The obtained OTUs were assigned to 30 bacteria phyla, 54 classes, 150 orders, 267 families, 509 genera, and 783 species. The predominant phyla (relative abundance >1%) were Actinobacteria (41.8%), Firmicutes (29.3%), Proteobacteria (23.1%) and Bacteroidetes (2.7%) in the surface samples (Fig. 2A). The relative abundance of Firmicutes decreased from 67.9% in the 1S to 4.1% in the 8S. The relative abundance of

Actinobacteria increased from 4.7% in the 1S to 77.7% in the 8S. The abundance of Cyanobacteria (2.0%) was the highest in the 2S. The abundance of Gemmatimonadete (2.2%) and Deinococcus-Thermus (0.90%) were the highest in the 1S. Calditrichaeota only existed in the 6S sample. Dependentiae, Latescibacteria, and Elusimicrobia only existed in the 1S, 2S and 3S samples. Synergistetes only existed in the 2S, 3S and 4S samples. Thermotogae only existed in the 1S, 2S, 3S and 4S samples. The above results suggest that the 1S, 2S, 3S, and 4S samples had higher bacterial community diversity than the 4S, 5S, 6S and 7S samples in the phylum level.

In the subsurface samples, the dominated bacterial phyla (relative abundance >1%) were Actinobacteria, Firmicutes, Proteobacteria, Bacteroidetes, Chloroflexi, Gemmatimonadete, Fusobacteria, and Acidobacteria (Fig. S1A). The relative abundance of Firmicutes decreased from 61.6% in the 1Su to 4.4% in the 8Su. The relative abundance of Actinobacteria increased from 5.7% in the 1Su to 75.4% in the 8Su. Dependentiae only existed in the 2Su samples. WPS-2 only existed in the 4Su samples. Entotheonellaeota only existed in the subsurface samples than surface samples.

At the genus level, the predominated genera in the samples were unclassified*Micrococcaceae* (36.6%), *Bacillus* (24.3%),*Sphingomonas* (4.1%), unclassified *Burkholderiaceae*(2.8%), *Escherichia-Shigella* (2.5%), *Acinetobacter*(2.5%), *Microbacterium* (1.8%),*Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium* (1.5%), and*Methylobacterium* (1.5%) (Fig. 2B). Besides, the relative abundance of *Bacillus* gradually decreased from north to south. The abundance of unclassified *Micrococcaceae* and*Sphingomonas* gradually increased from north to south. The abundance of *Gilliamella* (14.9%) and *Snodgrassella*(10.7%) were significant higher in the 4S sample than those of other samples. The abundance of*Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium* (6.3%) was the highest in the 3S sample. Each sampling site has its unique genus. For example, *Glycomyces* , *Constrictibacter* ,*Sulfurifustis,* and *Erysipelotrichaceae* _UCG-003 only existed in the 1S sample. *Candidatus_Saccharimonas* and*Promicromonospora* only existed in the 2S sample.*Megamonas* , *Acholeplasma* and *Perlucidibaca* only existed in the 3S sample. *Thermovirga* ,*Prochlorococcus* _MIT9313, *Succiniclasticum* ,*Shuttleworthia* , *Rosenbergiella* , *Aminobacterium, Barnesiella,* and *Rhizobacter* only existed in the 4S sample. Norank *Calditrichaceae* and UBA1819 only existed in the 5S sample.*Granulicella* and *Candidatus_Riegeria* only existed in the 6S sample. Additionally, *Pseudorhodoplanes* , norank JG30-KF-CM66 and *Novosphingobium* only existed in the 1S, 2S, 3S, and 4S samples.

In the subsurface samples, the dominated bacteria were unclassified*Micrococcaceae* (32.1%), *Bacillus* (28.8%),*Sphingomonas* (3.8%), unclassified *Burkholderiaceae*(3.6%), *Escherichia-Shigella* (2.6%), *Acinetobacter*(2.9%), *Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium*(2.0%), *Microbacterium* (1.7%), *Methylobacterium* (1.6%) and *Streptomyces* (1.4%) (Fig. 2B). Compared with the surface samples, the dominant communities in the 4Su sample were distinctly different from those in the 4S sample (Fig. 2B and Fig. S1B).*Streptomyces* , *Brevundimonas* , *Pseudomonas* , norank*Beijerinckiaceae* , *Bacteroides* , *Aeromonas* ,*Stenotrophomonas* , *Lactobacillus* , *Fusobacterium,* and*Bradyrhizobium* abundances in the 4Su sample were significantly higher than those in the other samples. The abundance of unclassified*Micrococcaceae* was significantly lower than that in the 2Su (0.3%) and 4Sub (0.7%) samples than the 2S (27.2%) and 4S (25.2%) samples. The abundance of*Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium* (9.8%) was the highest in the 1Su sample.

The correlation between bacterial communities and physicochemical characteristics

PCoA showed that the PC 1 axis and PC 2 axis explained 70.19% and 15.96% the difference of bacterial communities in the samples, respectively (Fig. 3A). The bacterial communities in the S1, S2, S3, and S4 were clearly separated from those in the S5, S6, S7 and S8 at PC 1 axis. ANOSIM analysis also supported the PCoA result, suggesting that the bacterial communities in the S1, S2, S3 and S4 were significant (p <0.05) different from those in the S5, S6, S7 and S8 (Fig. 3B). The same result was obtained from Bray Curtis analysis, which showed that the distance of bacterial communities in the S1, S2, S3 and S4 sites were wider than those in the S5, S6, S7 and S8 sites.

RDA analysis showed that the sand physiochemical properties explained 80.25% (RDA1 explained 70.78%

and RDA2 explained 9.47%) the variances of bacterial community at the phylum level (Fig. 4). The sand pH (RDA1 = 96.5%, r^2= 0.38, p = 0.01) and P (RDA1 = 99.8 %, r^2 = 0.38, p =0.019) significantly positively correlated with RDA1, and altitude (RDA1 = 100%, r^2 = 0.50, p = 0.001) and Ca^{2+} (RDA1 = 97.2 %, r^2 = 0.44,p =0.006) significantly negatively correlated with RDA1, indicating that these factors were vital to explain the variations of bacterial community structure. At the OTU level, CCA analysis showed that the similar correlation between the factors and the bacterial communities, namely, pH (r^2 = 0.49, p =0.002) and P (r^2 = 0.37, p =0.035) significantly positively correlated with CCA1, and altitude (r^2 = 0.55, p = 0.001) and Ca^{2+} (r^2= 0.48, p =0.003) significantly negatively correlated with CCA1, suggesting that these factors had a similar important effects on bacterial communities.

VPA analysis showed that both altitude and pH explained 42.7% of the variations bacterial community. Ca^{2+}, altitude and pH explained 50.3% of the variations of the bacterial community. TOC, altitude, and pH explained 46.4% of the variations. EC, altitude, and pH explained 40.4% of the variations (Fig. S2).

The Spearman correlation analysis was evaluated the correlation between different phyla and each of the sand physiochemical properties (Fig. 5). The sand physiochemical properties were divided into two groups. Group 1 included EC, altitude and Ca^{2+}. Group 2 included Cl^-, WC, TOC, Cl, TC, Mg^{2+}, TN, Na^+, V, Zn, Zr, Y, Ti, Mn, pH, and P. Besides, the bacterial phyla were grouped into three clusters. Cluster 1 was significantly positively correlated with altitude and Ca^{2+} but negatively correlated with V, Zn, Zr, Y, Ti, Mn, pH, and P. Cluster 2 was significantly positively correlated with Ca^{2+}, TOC, Cl, Mg^{2+}, Na^+, V, Zr, Y, Ti, Mn, and P, but negatively correlated with Cl^-. Cluster 3 was significantly negatively correlated with EC, altitude, and Ca^{2+}, but positively correlated with TC, TN, V, Zn, Zr, Y, Ti, Mn, pH, and P.

Comparative analysis of taxonomic composition between the surface and subsurface samples

LEfSe analysis was used to reveal the significant different bacteria between the surface and subsurface samples (Fig. 6). In the surface sample, *Pasteurellales* (from order to family), the genus unclassified *Lachnospiraceae* and *Actinobacillus* were significantly enriched. In the subsurface samples, the family*Nitrosomonadaceae* , the genus Ellin6067, *Entotheonellaeota*(from phylum to genus), the family *Paenibacillaceae* , the genus*Dialister,* and TK10 (from class to genus) were significantly enriched.

Discussion

This study was designed to reveal the variations in bacterial community structure and environmental factors and their correlations in the Taklimakan Desert. To date, the bacterial communities in about nine deserts in the world have been explored using 16S rRNA amplicon sequencing, and the results indicate the similar dominant bacterial phyla, i.e., Actinobacteria, Proteobacteria, Bacteroidetes, Firmicutes, Chloroflexi, and Cyanobacteria, though the proportion of each phylum displayed great difference among the deserts (Table 3). Actinobacteria have been documented to play an important role in soil development and the geochemical cycle (Goodfellow et al., 1983; Hill et al., 2011). The Actinobacteria bacteria can form spores to resist extreme conditions and can produce extracellular hydrolytic enzymes to decompose plant and animal residues and complex organic compounds in soils (El-Tarabily et al., 2006; Eisenlord et al., 2010; Miao et al., 2010). Firmicutes also is a representative bacterial phylum of desert microbes (Chanal et al., 2006; Lester et al., 2007; Gommeaux et al., 2010). The Firmicutes bacteria can produce endospores, which contribute to the colonization in arid environment. The abundance of Firmicutes in the Taklimakan Desert was much higher than that in the other deserts (Crits-Christoph et al., 2013; Gunnigle et al., 2017; Sun et al., 2018; Zhang et al., 2019). The dominated Cyanobacteria isolated from deserts such as Mojave Desert, Sonoran Desert, and Tengger Desert (Nagy et al., 2005; Mogul et al., 2017; Sun et al., 2018), which were covered by biocrusts in surface soil. However, the highest abundance of Cyanobacteria was 2% in the Taklimakan Desert. The dominated phyla in the Taklimakan Desert were similar to the Eastern Desert (Köberl et al., 2011). Moreover, although the Chloroflexi and Acidobacteria were the predominated phyla in some deserts, they were the low abundance phyla in the Taklimakan Desert. These results suggested that the common and unique characteristics of the bacterial community in deserts.

Several previous researchers investigated the key factors that shape the desert microbial communities. For

example, Zhang et al. (2019) showed that salinity is the key factor to drive microbial community structure and assembly in the Gurbantunggut Desert. Crits-Christoph et al. (2013) suggested that water content and salinity are the key factor in shaping the microbiome in the Atacama Desert, the driest desert in the world. Scola et al. (2018) proposed that the soil chemistry and stochasticity influenced the bacterial community assembly in the Namib Desert, the oldest desert on the planet. The above results imply the differences in the soil physicochemical properties in different deserts, which in turn drive the succession and adaptation of microbes in the deserts. In the present study, RDA analysis showed that altitude and pH were strong significantly correlated with the bacterial community (Fig. 4). The VPA result indicated that altitude and pH were the main factors shaping bacterial community assembly in the Taklimakan Desert (Fig. S2A).

Many studies showed that the altitude gradient has the effect on soil microbial community (Körner, 2007; Manzoni et al., 2012; Serna-Chavez et al., 2013; Siles and Margesin, 2017). Many environmental factors, such as nitrogen loading, temperature, and UV radiation, vary with altitude elevation, resulting in the variation of the microbial community (Sundqvist et al., 2013; Hayden and Beman, 2016). Our results confirmed that the alpha diversity indices of bacterial communities were significantly different along the altitude gradient in the Taklimakan Desert (Table 2). Similar results were proved by the previous studies (Meng et al., 2013; Ren et al., 2018).

Altitude has a great influence on the distribution of microbial communities. Concerning bacterial community compositions,*Actinobacteria* displayed the highest relative abundance in neutral sands and was significantly negatively correlated with pH (Fig. 5). This result was consistent with the previous studies (Lauber, 2009; Yun et al., 2016). Many studies indicated that pH was the main driver to the Actinobacteria community and diversity in different ecological environments. For example, pH significantly influences the variation of the Actinobacteria community in the Palace Leas hay meadow (Jenkins et al., 2009). The Actinobacteria community in the Tianshan Glacier forelands was also affected by the pH (Zhang et al., 2016b). Our study showed that pH was a crucial environmental factor that affected the Actinobacteria community in the desert ecosystem. Additionally, pH was significantly positively correlated with Firmicute, Nitrospirae, Latescibacteria, Thermotogae, and Synergistetes. This could be explained by the fact that pH can directly affect the diversity of the microbial community by inducing the availability of substrates in soils (Kemmitt et al., 2006). Zhang (2019) and Feeser (2018) reported the EC was the key factor in structuring microbial communities for desert soil. In the present study, EC was nonsignificantly correlated with the bacterial community. This was inconsistent with the result that water content and conductivity had a great effect on bacterial diversity and community than that of temperature in desert stream sediments (Zeglin et al., 2011).

Zhao et al. (2019) reported that Chlorofexi was significantly positively associated with P. Li et al. (2014) showed that the abundance of Chlorofexi was closely related to EC. However, our result indicated that Chlorofexi was not associated with EC or P, but significantly negatively correlated with Ca^{2+} (Fig. 5). The effect of Ca^{2+} on desert microbial community assembly has been reported (Rao et al., 2016), which probably be another key factor for soil bacterial community structure composition (Xia et al., 2016).

The present study further investigated the difference of bacterial communities between the surface and subsurface sand (Fig. 6).*Lachnospiraceae* and *Actinobacillus* were the indicator bacterial taxa in the surface sand. The *Lachnospiraceae* is a common taxon observed in host-associated and sewage effluent samples (Meehan & Beiko, 2014). The *Actinobacillus* usually inhabited in the mucous membranes of humans and animals (Olsen et al., 2005). Obviously, the appearance of these taxa in the surface sand is related to human activity. *Nitrosomonadaceae* , *Ellin* 6067,*Entotheonellaeota* ,*Paenibacillaceae* ,*Dialister,* and TK10 were significantly enriched in the subsurface sand. The limitation of oxygen availability in the subsurface sand selected some anaerobic and microaerobic bacterial taxa, such as the anaerobic*Nitrosomonadaceae* , *Paenibacillaceae,* and*Entotheonella,* which were dominated in the subsurface samples (Fig. 6). *Nitrosomonadaceae* has been reported to be ammonia-oxidizing bacteria (Xia et al., 2005). Studies have investigated the*Entotheonella*bacteria which can produce diverse natural active products (Bhushan et al., 2017). Moreover, the genomic analysis of*Entotheonella* revealed that*Entotheonella* can utilize a variety of carbon sources, fixation of CO_2, anaerobic respiration, and denitrification (Liu et al., 2016). The order *Ellin6067* was reco-

gnized as playing a vital role in the degradation of xenobiotic and other complex organic (Lezcano et al., 2017). The family*Paenibacillaceae* not only secreted chitinase to degrade chitin (Tran et al., 2018) but also can utilize nitrates under anoxic condition through denitrification (Konishi et al., 2017) and degrade the explosives residues in anaerobic treatment (Indest et al., 2017). All these studies showed that the obvious difference of indictor bacteria in the surface and subsurface samples. These results implied that the strong adaptability of bacterial communities to different extreme environments.

In conclusion, our results showed that the abundance of bacterial communities varied significantly along an altitude gradient in Taklimakan Desert. Altitude and pH were the primary factors that determine the structure of bacterial communities. Besides, Ca^{2+} and P were also significantly correlated with the distribution of bacterial communities. At the abundance of Actinobacteria increased gradually while that of Firmicutes decreased gradually with the decrease in altitude gradient. The indicator groups were significant differences in the surface and subsurface sand. Studying bacterial diversity and community assembly processes along an altitude gradient are necessary for deeply understanding the fundamental ecological processes in desert ecosystems.

Author contributions

GZ, GL, TC, and SL planned and designed the research. YL and MW provided help in sampling. JL, GZ, BZ, XY and AK analyzed the data. JL, GZ, YL and WZ conducted the experiments and wrote the manuscript. All authors were involved in revising the manuscript critically.

Conflict of interest

The authors declare that there are no conflicts of interest.

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Fig. 1 The map of sampling sites in the Taklimakan Desert.

Fig. 2 The bacterial communities at the phyla level (A) and genus level (B) in the surface samples. Only the phyla or genera with more than 1% relative abundance in at least one sample are presented.

Fig. 3 PCoA graph (A) and distance box plot (B) showing the significant differences in bacterial communities in the surface sand.

Fig. 4 Redundancy analyses (RDA) result showing the correlation between bacteria community (at the phylum level) and physicochemical parameters. Top 10 phyla and only significantly correlated environmental factors were shown.

Fig. 5 Spearman correlation analyses showing the bacterial phyla that are significant positively/negatively correlated with the sand physicochemical parameters in the surface samples. *0.01 < p [?] 0.05, **0.001 < p [?] 0.01, ***p [?] 0.001.

Fig. 6 Cladogram showing the distribution of bacterial lineages (A) and LDA analysis the influence of abundance on the different effect size (B) in bacterial communities associated with the surface and subsurface samples. Cladogram circles indicate phylogenetic taxa from phylum to genus. LDA scores [?] 2.

Table 1 Physicochemical property of the sand samples.

Samples	Sand factors	Sand factors	Sand factors	Sand factors	Sand factors	Sand factors	Sand factors
	pH	EC (mS/cm)	TN (%)	TOC (%)	Altitude	Na^+ (g/kg)	Ca^{2+} (g/kg)
1S	8.78±0.10a	472.67±46.25ab	0.04±0.005ab	0.80±0.04a	877.00±0.58a	0.31±0.061a	0.02±0.004a
2S	8.53±0.10a	401.67±53.99a	0.03±0.002ab	0.45±0.09b	901.00±2.31b	0.10±0.022b	0.02±0.002a
3S	8.48±0.10a	480.33±11.61ab	0.02±0.002ac	0.79±0.04a	942.33±3.84c	0.10±0.006b	0.03±0.003b
4S	8.74±0.15a	706.33±36.78c	0.03±0.004ac	0.87±0.00a	982.00±1.15d	0.24±0.045a	0.04±0.004c
5S	8.17±0.13b	689.67±37.02c	0.04±0.005b	0.76±0.07a	1046.00±1.00e	0.10±0.033b	0.03±0.003bc
6S	7.99±0.02bc	564.33±56.44abc	0.03±0.003bc	0.73±0.08a	1070.33±1.86f	0.12±0.010b	0.04±0.001c
7S	7.96±0.02bc	609.33±94.51bc	0.03±0.004bc	0.77±0.04a	1082.33±1.20g	0.12±0.008b	0.04±0.001c
8S	7.78±0.10c	577.67±78.36abc	0.02±0.004c	0.72±0.02a	1156.33±1.86h	0.13±0.018b	0.03±0.001bc
1Su	8.56±0.16a	593.67±176.71a	0.035±0.002a	0.68±0.25ab	877.00±0.58a	0.14±0.04a	0.02±0.006a
2Su	8.64±0.09a	701.33±268.24a	0.032±0.005a	0.46±0.16a	901.00±2.31b	0.16±0.04ab	0.02±0.004ab
3Su	8.62±0.28a	551.00±46.29a	0.03±0.003a	0.77±0.05ab	942.33±3.84c	0.11±0.01a	0.03±0.002b
4Su	8.44±0.15ab	769.00±17.90a	0.028±0.004a	0.86±0.08b	982.00±1.15d	0.26±0.06b	0.04±0.002cd
5Su	8.17±0.14b	594.67±56.74a	0.034±0.006a	0.76±0.05ab	1046.00±1.00e	0.09±0.03a	0.03±0.005cd
6Su	8.08±0.02bc	414.67±80.62a	0.03±0.004a	0.84±0.05ab	1070.33±1.86f	0.09±0.02a	0.04±0.004cd
7Su	8.08±0.02c	543.33±123.5a	0.028±0.001a	0.84±0.03ab	1082.33±1.20g	0.16±0ab	0.04±0.002d

Samples	Sand factors	Sand factors	Sand factors	Sand factors	Sand factors	Sand factors	Sand factors
8Su	7.65±0.08c	727.33±82.63a	0.027±0.005a	0.62±0.04ab	1156.33±1.86h	0.1±0.01a	0.04±0.002cd

Total organic carbon (TOC), total nitrogen (TN). Data are the means ± standard error (SE; n= 3). Different letters indicate significant differences between the sands samples (p <0.05).

Table 2 Statistical comparisons of alpha-diversity between different sand samples.

Sample	Sobs	Shannon	Simpson	Ace	Chao 1	Coverage (%)
1S	247±34a	0.807±0.114a	0.807±0.024a	319±39a	312±40a	99.4
2S	217±44a	1.756±0.534ab	0.468±0.162b	241±50a	241±50a	99.7
3S	248±60a	1.745±0.13ab	0.451±0.088b	305±98a	305±98a	99.5
4S	233±52a	2.094±0.104bc	0.312±0.012bc	258±59a	258±59a	99.7
5S	236±71a	2.616±0.305bc	0.194±0.026c	251±73a	251±73a	99.8
6S	278±71a	3.044±0.489c	0.133±0.032c	297±73a	297±73a	99.7
7S	163±16a	2.012±0.151b	0.273±0.031bc	186±21a	186±21a	99.8
8S	138±13a	1.891±0.092b	0.278±0.02bc	151±13a	151±13a	99.8
1Su	240±17a	1.281±0.233ad	0.664±0.062a	271±14a	275±10ab	99.6
2Su	243±42a	0.79±0.211a	0.816±0.05a	289±47a	302±58b	99.5
3Su	335±16b	1.911±0.466abd	0.463±0.14b	427±17b	431±21c	99.3
4Su	247±20a	4.111±0.65c	0.058±0.043c	287±50a	284±45b	99.7
5Su	200±43ac	2.594±0.325b	0.184±0.041c	210±44ac	212±45ab	99.8
6Su	193±24ac	2.434±0.247bd	0.183±0.031c	215±25ac	219±24ab	99.7
7Su	144±18c	2.144±0.2bd	0.215±0.054c	158±22c	163±21a	99.8
8Su	137±6c	1.904±0.02abd	0.267±0.007bc	149±9c	158±11a	99.8

Data are the means ± standard error (SE; n= 3). Different letters indicate significant differences between the sands samples (p<0.05).

Table 3 The dominant bacterial taxa revealed by 16S rRNA gene sequencing in deserts worldwide.

Desert	**Phylum number**	**Phyla**	**Abundance**	**References**
Taklimakan	30	Actinobacteria Firmicutes Proteobacteria	41.8 29.3 23.1	This study
Badain Jaran	32	Actinobacteria Proteobacteria Bacteroidetes Firmicutes Chloroflexi	35 24 17 7 7	Sun et al., 2018
Tengger	28	Actinobacteria Proteobacteria Cyanobacteria Chloroflexi Bacteroidetes Acidobacteria	29 23 20 8 6 7	Sun et al., 2018

Desert	Phylum number	Phyla	Abundance	References
Mojave	11	Cyanobacteria Proteobacteria Chloroflexi Actinobacteria Bacteroidetes	33 26 12 9.1 6	Mogul et al., 2017
Atacama	13 ([?]1%)	Actinobacteria Acidobacteria Proteobacteria	72-88 4-7 2-9	Crits-Christoph et al., 2013
Thar	12	Actinobacteria Proteobacteria Acidobacteria	39 33 9	Sivakala et al., 2018
Gurbantunggut	10 ([?]1%)	Actinobacteria Proteobacteria Bacteroidetes Chloroflexi Firmicutes	41 24 5 5 6	Zhang et al., 2019
Eastern	18	Proteobacteria Firmicutes Actinobacteria	30 27 11	Köberl et al., 2011
Negev	11([?]1%)	Actinobacteria Proteobacteria Bacteroidetes Chloroflexi	28 31 10 7	Baubin et al., 2019