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Comparison of cyanobacterial communities in temperate deserts: A cue for artificial inoculation of biological soil crusts

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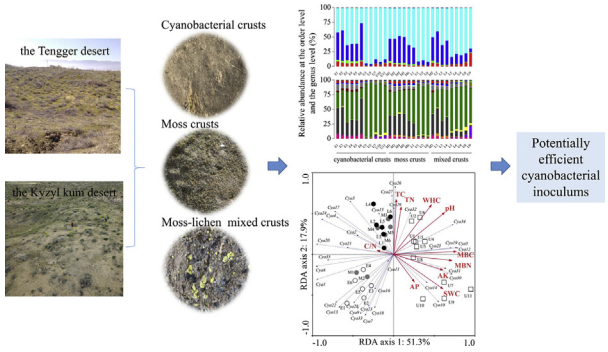
HIGHLIGHTS

- Cyanobacteria in BSCs were compared between deserts with distinct rainfall patterns.
- *M. vaginatus* predominated all the crusts in both temperate deserts.
- Cyanobacterial absolute abundance was lower in better-developed BSCs.
- BSC type and/or geographic location significantly affected Shannon diversity.
- *M. vaginatus*, *Wilmottia*, *Mastigocladopsis* and *Chroococcidiopsis* are potential efficient inoculums.

GRAPHICAL ABSTRACT



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ABSTRACT

The topsoil cyanobacteria in biological soil crusts (BSCs) play a vital role in stabilizing soil surface of disturbed habitats in water and nutrient-poor ecosystems. Currently, artificial inoculation of BSCs is considered as an effective approach to restore habitats and accelerate ecosystem regeneration. Understanding the character of cyanobacterial communities is the necessary prerequisite to explore the artificial inoculation of BSCs. For this reason, cyanobacterial communities in BSCs were compared between two mid-latitute temperate deserts with distinct precipitation patterns. The results showed that *Oscillatoriales* and *Nostocales* dominated crusts in the Tengger desert with majority of rainfall in summer and early autumn while *Oscillatoriales* dominated crusts in the Kyzyl kum desert with more rainfall in winter and early spring. Moreover, filamentous *Microcoleus vaginatus* overwhelmingly dominated all the crusts in both deserts with *Mastigocladopsis* sp. and *Chroococcidiopsis* spp. as the dominant heterocystous cyanobacteria. Of note, genus *Wilmottia* kept a relative stable and high abundance in both deserts. The top two abundantly shared cyanobacteria (> 1% of total sequences) were *M. vaginatus* and *Mastigocladopsis* sp. in both deserts, while 16 genera with significant variances were found between the two deserts ($P<0.05$). Total variations of cyanobacterial communities across the deserts were largely explained by a combination of biotic factors (microbial biomass C and N) and abiotic factors (soil pH, soil water content, soil water holding capacity, and soil available potassium). Compared to better-developed crusts, cyanobacterial abundance was higher in cyanobacterial crusts. BSC type and/or geographic location significantly affected cyanobacterial Shannon diversity without significantly influencing species richness. Our data suggest that the basic and major groups (e.g. *M. vaginatus*, *Wilmottia* spp.,

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Mastigocladopsis sp., and *Chroococcidiopsis* spp.), and the abundantly shared phylotypes which showed significant difference in cyanobacterial communities between deserts, should be focused on to further explore the artificial inoculation of BSCs in temperate drylands.

1. Introduction

Arid desert ecosystems are commonly vulnerable to disturbance due to the limitation of nutrient and soil water availability (Austin et al., 2004; Li et al., 2007). However, microorganisms (e.g. bacteria and fungi) can inhabit a wide range of niches and play an important ecological role in supporting other organisms in extreme environments, and therefore, they are very likely to contribute to ecosystems resilience to disturbance (Ives and Carpenter, 2007). Cyanobacteria, the major components in desert biological soil crusts (BSCs, also biocrusts) communities, can survive and grow rapidly in water and nutrient-poor desert soils. They are critical in maintaining soil stability and nutrient cycles (Belnap, 1995; Yeager et al., 2007; Hagemann et al., 2015; Zhang et al., 2016; Muñoz-Martín et al., 2019). As they can combine soil particles through secreting polysaccharide and reduce soil erosion (Eldridge and Greene, 1994; Belnap et al., 2001), largely determine the photosynthetic capacity of BSCs (Beymer and Klopatek, 1991; Ohad et al., 2010), and contribute to soil fertility of the ecosystems they reside (Wang et al., 2016a), currently, using cyanobacteria to artificially inoculate BSCs against wind erosion is considered as an effective approach to restore habitats and accelerate ecosystem regeneration (Bowker, 2007; Rossi et al., 2017; Muñoz-Rojas et al., 2018; Zhao et al., 2019).

Cyanobacterial assemblages in BSCs were traditionally detected by cultivation-dependent methods and strain isolation attempts with microscopic observations (Lange et al., 1992). Recent molecular methods enabled the researchers to greatly move the field forward in a variety of localities (Garcia-Pichel et al., 2001; Flechtner et al., 2002; Gundlapally and Garcia-Pichel, 2006; Li et al., 2013; Hagemann et al., 2015; Zhang et al., 2016; Pushkareva et al., 2018; Muñoz-Martín et al., 2019). Cyanobacterial community in BSCs was shaped frequently by several major environmental parameters. In arid and semiarid regions of warm climates, genus *Microcoleus* was the major components of BSC community (Büdel et al., 2016), while the family of *Leptolyngbyaceae* were found to be dominant in Western Europe and Artic BSCs (Pushkareva et al., 2015; Williams et al., 2016). As for cyanobacterial community composition, two major strains of *Microcoleus* in BSCs showed distinct response to ambient temperature. Strain *M. vaginatus* was more abundant in colder environments while strain *M. steenstrupii* was more abundant in warmer environments (Garcia-Pichel et al., 2013). Fernandes et al. (2018) demonstrated *Scytonema* sp. was most sensitive to precipitation patterns while *M. vaginatus* was most resilient.

Several studies have assessed the effect of BSC type and geography on microbial communities (Büdel, 2001; Redfield et al., 2002; Bates et al., 2010; Xiao and Veste, 2017; Becerra-Absalón et al., 2019). However, these studies did not look specifically at cyanobacterial populations or just focused on cyanobacteria in single BSC type or single desert. Although cyanobacteria form a substantial component of desert BSC communities, few studies systematicly explored the comparison of crust cyanobacterial community between temperate deserts in mid-latitude. Mid-latitude temperate deserts in Central Asia and China often received less than 200 mm annual precipitation and showed distinct precipitation patterns (Li et al., 2005; Wang et al., 2016b). For instance, about 80% of the precipitation in the Kyzyl kum desert in Uzbekistan falls primarily in winter and early spring while most of the precipitation in the Tengger desert in China falls in summer and early autumn (Wang et al., 2016b; Li et al., 2010). BSCs developed well on top soil once the mobile dunes have been stabilized in these deserts (Li et al., 2005). It is suggested that BSCs are critical components of above ground soil in arid and semi-arid ecosystems, and their loss due to land-use and climate changes will be expected to cause desertification processes by increasing magnitude of aeolian dust production (Rodriguez-Caballero et al., 2018). Knowing the framework of biocrust cyanobacteria in mid-latitute temperate deserts can help selecting the local inoculants to successfully survive and form BSCs to cope with wind erosion. Therefore, we aimed to test the following hypotheses: (a) The same type of BSCs would share cyanobacterial phylotypes despite the obvious difference between deserts, (b) BSC types would affect absolute abundance of cyanobacteria in both temperate deserts, (c) BSC type and geographic location would affect the diversity of cyanobacterial communities at a continental-scale.

2. Materials and methods

2.1. Study site

In this study, 18 BSC samples (E1 to E6, M1 to M6, and L1 to L6) were collected from China and 11 BSC samples (U1 to U11) from Uzbekistan. The sampling sites in China are located in the Shapotou Desert Research and Experimental Station on the southeastern fringe of the Tengger Desert, northern China. All the sampling sites are at least 100-m interval and have the similar sandy soil type. The mean annual air temperature in the southeastern fringe of the Tengger desert is 10.0 °C, and the minimum and maximum temperatures are −25.1 °C in January and 38.1 °C in July. The mean annual precipitation in this area is 186 mm and approximately 80% of the precipitation falls in summer and early autumn (between May and September) (Li et al., 2010). The sampling sites in Uzbekistan are located in the Kyzyl kum desert along the middle and downstream of Amu Darya. The average mean annual precipitation over the Amu Darya Basin is about 170 mm, but the basin is characterized by uneven distribution and quantity of precipitation and average annual precipitation exceeds 1000 mm in the alpine area, only 100 mm in the foothills and adjacent plains. About 80% of the precipitation falls primarily in winter and early spring with a mean temperature as low as −30 °C. It is dry and hot in summer and early autumn, with a mean temperature as high as 30 °C in July (Wang et al., 2016b). All the detailed study sites are listed in Table 1.

2.2. Sampling

The top layers (0–2 cm) of soil samples with crust at least 100 cm away from plants were collected in the end of rainfall season of 2019 (April in the Kyzyl kum desert in Uzbekistan and September in the Tengger desert). Briefly, five soil cores (3.5 cm diameter, 2 cm depth) were sampled in each replicate plot individually using a sterile trowel. The equal amounts of each of the five cores were pooled and thoroughly mixed in the field to form a composite sample. For the convenience of later analysis, crust soils are divided into three types based on their morphological features, namely, cyanobacterial crusts (initial stage of crusts) without macroscopic moss or lichen, moss dominated crusts (hereafter referred to as moss crusts) and moss-lichen mixed crusts (hereafter referred to as mixed crusts). Moss crusts and mixed crusts were acknowledged as better-developed crusts (Muñoz-Martín et al., 2019). For mixed crusts, the proportional coverages of moss ranged from about 40% to 70%, estimated by the point frame method (using a 2.5 cm × 2.5 cm grid with 169 points per 30 cm × 30 cm quadrat) (Magurran, 1988). Each of the soil samples was randomly divided into two subsamples:

Table 1
Locations of the sampling plots.

Plot	Region	Longitude	Latitude	Altitude (m a.s.l)	MAP (mm)	BSC morphotypes
E1	the Tengger desert, Shapotou, China	105.011009	37.464233	1316	180.2[a]	cyanobacterial crusts, light color
E2	the Tengger desert, Shapotou, China	105.011632	37.464165	1316	180.2[a]	cyanobacterial crusts, light color
E3	the Tengger desert, Shapotou, China	105.012039	37.464318	1316	180.2[a]	cyanobacterial crusts, light color
E4	the Tengger desert, Shapotou, China	105.012726	37.464250	1316	180.2[a]	cyanobacterial crusts, light color
E5	the Tengger desert, Shapotou, China	105.013348	37.464267	1316	180.2[a]	cyanobacterial crusts, light color
E6	the Tengger desert, Shapotou, China	105.013777	37.464364	1316	180.2[a]	cyanobacterial crusts, light color
M1	the Tengger desert, Shapotou, China	105.013783	37.471539	1322	180.2[a]	moss dominated crusts
M2	the Tengger desert, Shapotou, China	105.013397	37.472049	1321	180.2[a]	moss- lichen mixed crusts
M3	the Tengger desert, Shapotou, China	105.013247	37.472731	1323	180.2[a]	moss dominated crusts
M4	the Tengger desert, Shapotou, China	105.013762	37.473122	1322	180.2[a]	moss dominated crusts
M5	the Tengger desert, Shapotou, China	105.014062	37.473650	1321	180.2[a]	moss dominated crusts
M6	the Tengger desert, Shapotou, China	105.014513	37.473872	1323	180.2[a]	moss dominated crusts
L1	the Tengger desert, Shapotou, China	104.772466	37.454726	1347	180.2[a]	moss dominated crusts
L2	the Tengger desert, Shapotou, China	104.772166	37.454965	1346	180.2[a]	moss- lichen mixed crusts
L3	the Tengger desert, Shapotou, China	104.772684	37.455226	1347	180.2[a]	moss- lichen mixed crusts
L4	the Tengger desert, Shapotou, China	104.773178	37.455516	1346	180.2[a]	moss- lichen mixed crusts
L5	the Tengger desert, Shapotou, China	104.773629	37.455788	1346	180.2[a]	moss- lichen mixed crusts
L6	the Tengger desert, Shapotou, China	104.774079	37.456061	1346	180.2[a]	moss- lichen mixed crusts
U1	the Kyzyl kum desert, near Bukhara, Uzbekistan	63.749017	40.743386	368	157.1[b]	moss dominated crusts,
U2	the Kyzyl kum desert, near Urgench, Uzbekistan	61.087115	41.751231	62	109.6[b]	moss dominated crusts
U3	the Kyzyl kum desert, near Urgench, Uzbekistan	60.479096	42.306139	145	109.6[b]	cyanobacterial crusts, light color
U4	the Kyzyl kum desert, near Nukus, Uzbekistan	60.479106	42.306201	145	116.9[b]	moss- lichen mixed crusts
U5	the Kyzyl kum desert, near Nukus, Uzbekistan	60.551402	42.517731	99	116.9[b]	cyanobacterial crusts, light color
U6	the Kyzyl kum desert, near Nukus, Uzbekistan	60.551487	42.517742	99	116.9[b]	moss dominated crusts
U7	the Kyzyl kum desert, near Aral sea, Uzbekistan	59.397208	42.629922	69	<120[c]	cyanobacterial crusts, light color
U8	the Kyzyl kum desert, near Aral sea, Uzbekistan	59.397318	42.629809	69	<120[c]	moss- lichen mixed crusts
U9	the Kyzyl kum desert, near Aral sea, Uzbekistan	58.337402	43.794889	57	<120[c]	moss- lichen mixed crusts
U10	the Kyzyl kum desert, near Aral sea, Uzbekistan	58.215135	44.504019	17	<120[c]	cyanobacterial crusts, light color
U11	the Kyzyl kum desert, near Aral sea, Uzbekistan	58.238525	44.310092	68	<120[c]	cyanobacterial crusts, dark color

[a] Referenced from Li et al., 2007.
[b] Referenced from White et al., 2014.
[c] Referenced from Nezlina et al., 2005.

one soil subsample (approximately 50 g) was preserved in an ice box and then taken back to the laboratory, immediately passed through a 0.4-mm sieve to remove stones and plant debris, homogenized thoroughly and stored at −70 °C for the subsequent molecular analyses, and the other subsample was divided into two parts: the first part was stored at 4 °C for measurement of microbial biomass C and N, while the residual soil was air dried for physicochemical properties analysis.

2.3. Soil properties

Soil pH was measured in a 1:2.5 (*w*/*v*) aqueous solution. Soil water content was determined by gravimetric method. Soil water holding capacity was measured by the cutting-ring method. Soil total N was determined using Kjeldahl's method (Kjeltec™ 2300, Denmark) and soil organic C was analyzed using the H_2SO_4–$K_2Cr_2O_7$ oxidation method (Nelson and Sommers, 1982). Soil microbial biomass C (MBC) and microbial biomass N (MBN) was determined using a fumigation-extraction method (Brookes et al., 1985; Vance et al., 1987). Soil available P and available K were extracted by the Olsen method (Olsen et al., 1954).

2.4. DNA extraction and 16S rRNA gene sequencing

Genomic DNA was isolated from 0.5 g of each soil sample using the PowerSoil DNA isolation kit (Mobio Laboratories, Carlsbad, CA) according to the manufacturer's instructions. The obtained DNA was quantified and examined for purity with NanoDrop 2000c (Thermo-Fisher Scientific). PCR was carried out using the primer pairs CYA359F and CYA781R (a/b) (Nübel et al., 1997) to amplify the V3–V4 regions of the cyanobacterial 16S rRNA gene. The PCR conditions were as follows: initial denaturation at 95 °C for 2 min, followed by 25 cycles of denaturation at 95 °C for 30 s, annealing at 55 °C for 30 s, extension at 72 °C for 45 s, and a final extension at 72 °C for 10 min. For high-throughput sequencing, the barcode sequences were unique to each sample and PCR reactions were performed in triplicate. Amplicons were extracted from 2% agarose gels and purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA) according to the manufacturer's instructions and quantified using QuantiFluor™-ST (Promega, USA). Purified amplicons were pooled in equimolar ratios and paired-end sequenced on an Illumina HiSeq 2500 platform (BMK Technology Co., Ltd., Peking) according to the standard protocols.

2.5. Real-time PCR

Real-time PCR (qPCR) was performed to determine the variance of cyanobacterial copies between the deserts in China and Uzbekistan. We used the CYA359F and CYA781R (a/b) primer sets for quantifying the total cyanobacteria. Ten-fold serial dilutions of a known copy number of linearized plasmids containing cyanobacterial 16S rRNA gene fragment were subjected to qPCR assay in triplicate to generate an external standard curve. The 20-μL PCR reaction mixtures contained 10 μL of TB Green® Premix (Takara Bio, China), 0.5 μL each of 10 μmol/L forward and reverse primers, 1 μL of DNA template (diluted to 10 ng/μL in advance), and 8 μL of sterile and DNA-free water. The reaction was conducted on a Stratagene Mx3000P Real-time PCR system (Stratagene, Agilent Technologies Inc., USA) using the following program: 95 °C for 1 min followed by 40 cycles at 95 °C for 30 s, annealing at 55 °C for 30 s and extension at 72 °C for 30 s. The melting curve was obtained to confirm that the amplified products were of the appropriate size. For each soil sample, the qPCR reactions were repeated three times.

2.6. Bioinformatics analysis

After sequencing, the original data were sorted into valid reads complying with the following rules: each pyrosequencing read containing a primer sequence should have no ambiguous bases and match the

primer and one of the barcode sequences used. To obtain reads of high quality for the down-stream analysis, raw reads were assembled by FLASH version 1.2.11 (Magoč and Salzberg, 2011), then the assembled reads were filtered by Trimmomatic version 0.33 (Bolger et al., 2014), and reads of less than 200 bp in length or with a quality score < 25 were eliminated by UCHIME version 8.1 (Edgar et al., 2011). The denoised and chimera-checked reads were grouped into operational taxonomic units (OTUs) using the UPARSE algorithm (Edgar, 2013). Taxonomic identification was performed by running through the USEARCH global alignment (Edgar, 2010) against the NCBI 16S rRNA gene database.

Alpha diversity indices (richness, Good's coverage, Chao1 and Shannon's diversity index) were calculated using QIIME (Caporaso et al., 2010). Cyanobacterial community comparisons between different deserts were performed using Metastats (White et al., 2009) to detect the differentially abundant taxonomic groups. A *P*-value significance threshold of 0.05 was employed.

2.7. Statistical analysis

Analysis of variance was carried out using the SPSS version 16.0 (SPSS Inc., Chicago, IL, USA). Student's *t*-test was conducted to compare pairwise community dissimilarities between the Tengger desert and the Kyzyl kum desert. One-way ANOVA was used to determine significant community differences between BSC types at $P < 0.05$. Two-way ANOVA was used to determine the effects of BSC types and/or the geographic locations on cyanobacterial diversity (Shannon index) and richness (ACE). Data normality and equality of error variances were checked by Shapiro-Wilk test and Levene's test separately before two-way ANOVA analysis. The influence of edaphic factors on the distribution of the cyanobacterial phylotypes was analyzed by ordination analysis conducted in CANOCO for Windows, version 4.5 (ter Braak and Smilauer, 2002).

2.8. Nucleotide sequence accession numbers

The sequencing data were deposited into the Sequence Read Archive (SRA) of NCBI under accession numbers SRR11485336-SRR11485364. All the representative sequences for shared OTUs between BSC types were deposited in GenBank under accession numbers MT366972-MT366990.

3. Results

3.1. Evaluation of 16S rDNA high-throughput sequencing

In this work, 584,217 high-quality trimmed reads with average lengths ranged from 379 to 387 bp were retrieved from 29 DNA samples, of which 570,955 reads (97.73%) belonged to cyanobacteria, confirming the specificity of the primer set. At 97% sequence similarity, the 16S rRNA gene sequences were grouped into 76 cyanobacterial OTUs when noncyanobacterial reads were removed. Rarefaction analysis was used to detect the sampling effort and compare microbial richness between different samples (Fig. A.1). All the samples were near to saturation as the curves approached a plateau level after 5000 reads sampled, indicating the sequencing effort was sufficient to detect most cyanobacterial diversity presented at each sampling site. The results revealed that the sample L5 and U8 was the richest in the Tengger desert and the Kyzyl kum desert, respectively. As shown in Table A.1 and Fig. 1, among three BSC types, moss crusts showed the highest Shannon indices in the Tengger desert while moss-lichen mixed crusts did in the Kyzyl kum desert. The communities showed a higher alpha diversity in the Tengger desert than in the Kyzyl kum desert estimated by Shannon and Simpson indices although a marginal non-significant difference ($P = 0.076$) shown in mixed crusts between two deserts. But no significant differences were found in ACE richness between two deserts.

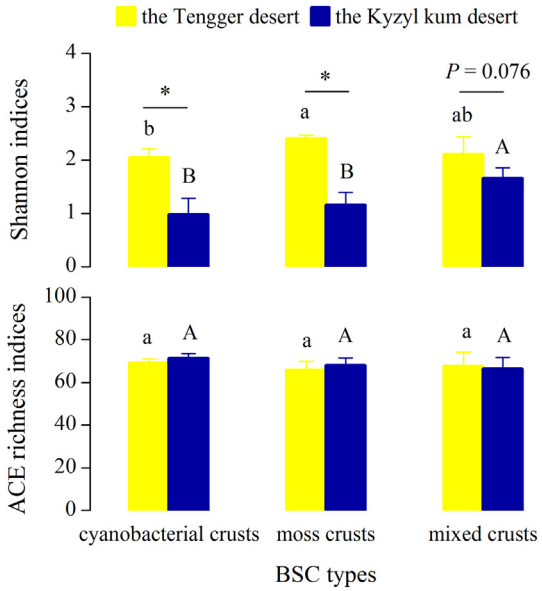

Fig. 1. Shannon diversity indices and ACE richness indices of different BSC types in the Tengger desert and the Kyzyl kum desert. Error bars show the standard errors of the means ($n = 3$ for moss- and mixed crusts in the Kyzyl kum desert, $n = 5$ and 6 for cyanobacterial crusts in the Kyzyl kum desert and the Tengger desert, respectively, and $n = 6$ for moss crusts in the Tengger desert). Different letters indicate significant differences at $P < 0.05$.

3.2. Comparision of cyanobacterial communities between the two deserts

The cyanobacterial communities in all crusts from the Tengger desert were dominated by *Oscillatoriales* (25.8–63.3%, mean 48.2% in cyanobacterial crusts, 47.4–66.7%, mean 55.2% in moss crusts, and 39.7–83.3%, mean 61.5% in mixed crusts) and *Nostocales* (25.6–63.3%, mean 40.9% in cyanobacterial crusts, 28.4–45.9%, mean 38.1% in moss crusts, and 12.3–52.9%, mean 32.7% in mixed crusts), while *Oscillatoriales* overwhelmingly dominated cyanobacterial communities in the Kyzyl kum desert crusts (mean 91.4%, 90.8%, and 75.6% in cyanobacterial crusts, moss crusts, and mixed crusts, respectively) (Fig. 2-A). *Microcoleus* was the most dominant genus in both deserts, accounting for 58.2% of total sequences in all crusts (mean 36.4% and 86.6 in cyanobacterial crusts, mean 44.5% and 85.3% in moss crusts, and mean 51.6% and 67.6 in mixed crusts, respectively in the Tengger desert and the Kyzyl kum desert), followed by *Mastigocladopsis* (20.9%), *Wilmottia* (5.4%) and *Chroococcidiopsis* (2.8%). A small proportion of unclassified cyanobacteria (approximately 0.3%) were also found (Fig. 2-B).

To determine the spatial variability of cyanobacteria taxa, we performed a pairwise comparison using Metastats analysis between the two deserts. At order level, *Nostocales* showed significant differences in all types of BSCs, *Synechococcales*, *Oscillatoriales* and *Chroococcales* showed in both cyanobacterial crusts and moss crusts, while *Chroococcidiopsidales* only showed in cyanobacterial crusts, between the two deserts. Metastats identified 16 genera with significant variances such as *Microcoleus* and *Chroococcidiopsis* in cyanobacterial crusts and moss crusts, while *Leptolyngbya*, *Mastigocladopsis*, and *Scytonema* in all types of BSCs between the two deserts (Table A.2).

The abundant OTUs (> 0.1% of total sequences) shared by BSCs were checked in three BSC types. As shown in Table 2, five OTUs were shared by all types of BSCs. Among these, the OTUs related to *Oscillatoriales* were the most abundant (47.57% of the total number of sequences), and *Nostocales* accounted for 21.12%. One abundant OTU belonging to *Oscillatoriales* (3.13%) was shared only by all cyanobacterial crusts and moss crusts. Five abundant OTUs were shared only by both moss crusts and mixed crusts, and they belonged to *Chroococcidiopsidales* and *Oscillatoriales* (1.63% and 3.56%, respectively). The abundant OTUs

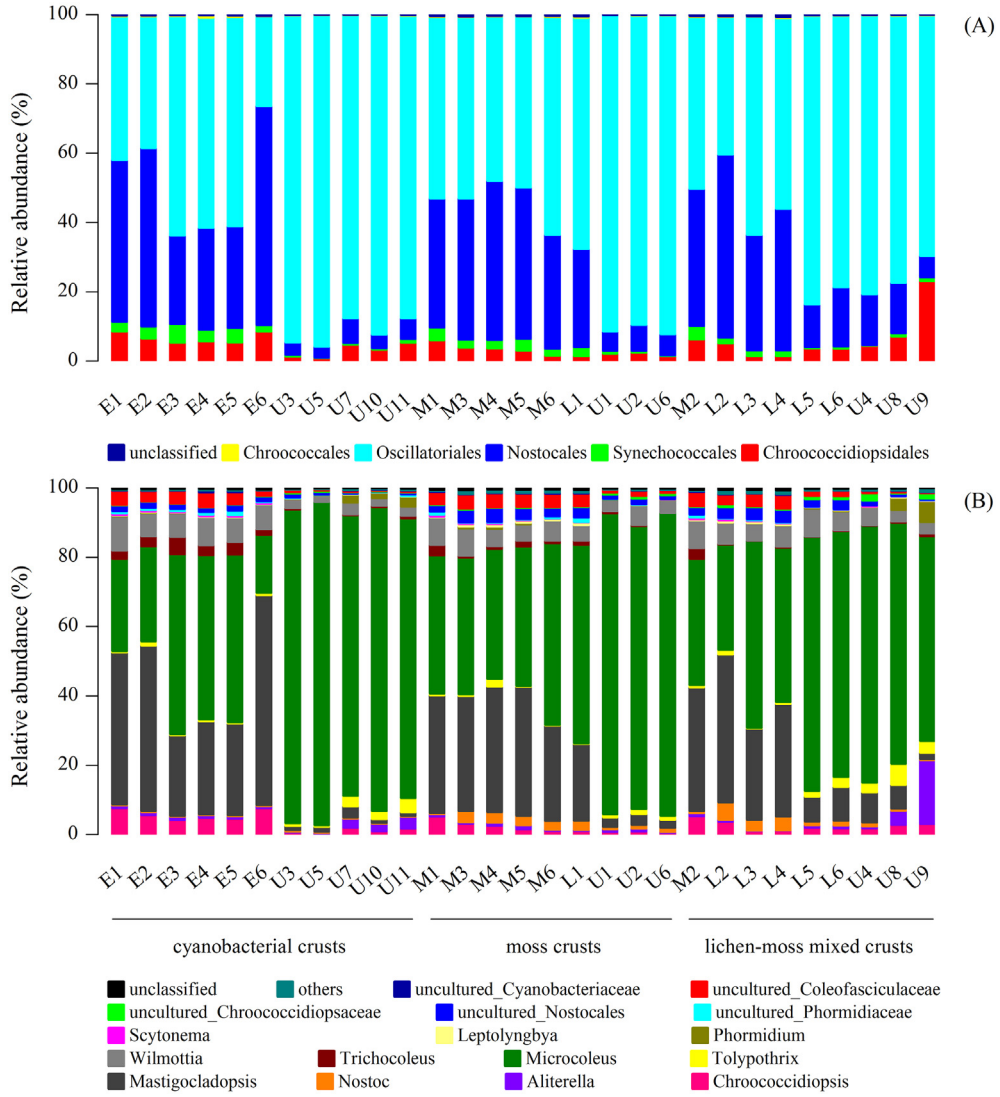

Fig. 2. Cyanobacterial community composition at the order level (A) and the genus level (B) based on 97% similarity. 'Others' indicate the low abundant genus of *Chlorogloea*, *Nodosilinea*, *Phormidesmis*, *Oculatella*, *Loriellopsis*, *Crinalium*, *Tychonema* and unclutured_*Oscillatoriales*. Samples E1 to E6, M1 to M6, L1 to L6 were collected from the Tengger desert and U1 to U11 were sampled in the Kyzyl kum desert.

uniquely shared by all moss crusts were affiliated with *Nostocales* (0.76%) and *Oscillatoriales* (2.26%), while one abundant OTU belonging to *Oscillatoriales* (11.09% of the total number of sequences) was uniquely shared by all mixed crusts. However, no OTUs were shared uniquely by all cyanobacterial crusts. Among all the shared OTUs, the OTU affiliating with *Microcoleus vaginatus* (44.17%) was the most abundant in both deserts, followed by OTUs affiliating with *Mastigocladopsis* sp. (19.58%) and *Microcoleus* sp. (11.09%).

3.3. Absolute abundance of cyanobacteria in BSC communities

In this study, cyanobacterial abundance was higher in cyanobacterial crusts than in better-developed BSCs. As shown in Fig. 3, total cyanobacterial 16S rDNA copies was highest in initial cyanobacterial crusts with average values of 2.97×10^{10} and 3.16×10^{10} in the Tengger desert and the Kyzyl kum desert respectively, followed by mixed crusts (average of 8.04×10^{8} and 3.29×10^{9} respectively in the Tengger desert and the Kyzyl kum desert). While cyanobacterial abundance was the lowest in moss crusts, and the average values were 8.72×10^{7} and 8.67×10^{8} respectively in the Tengger desert and the Kyzyl kum desert. Moreover, the copies were one order of magnitude higher in mixed crusts than in moss crusts, although there was no significant difference. Interestingly, no significant difference was found in the same BSC types between different deserts by Student's *t*-test.

3.4. The relationship between cyanobacterial community variation and edaphic properties

Redundancy analysis (RDA) was used to explore the effect of edaphic properties on cyanobacterial communities. Edaphic characteristics of the two deserts were demonstrated in Table A.3. Initial detrended correspondence analysis suggested a lineal character of the data response to the sample origin (the lengths of gradients were < 3). Therefore, the multivariate redundancy analysis (RDA) was used. Monte Carlo permutation tests were conducted using 499 random permutations. The subsequent forward-selection procedure ranked the environmental variables according to their importance and significance for the distribution of the cyanobacterial phylotypes. The triplots diagram (Fig. 4) showed that the cyanobacterial communities were distinct at each site included in this study. Samples from the Tengger desert were obviously located on the left of Axis 1, while samples from the Kyzyl kum desert on the right. Samples within a site were more similar than samples between sites,

Table 2
The list of cyanobacterial 16S rRNA gene sequences shared by BSC morphotypes sampled from the Tengger desert, China, and the Kyzyl kum desert, Uzbekistan. Data were assessed on the basis of the abundant OTUs (the relative abundance was over 0.1% in total number of sequences).

Accession numbers of OTUs	Highest match/accession number Highest cultured match/accession number	% similarity	Order	% in the total	Shared by BSCs
MT366972	Uncultured cyanobacterium clone CNY_03000/JQ402599 *Chroococcidiopsis*_SAG_2023/AJ344552	100 99	*Chroococcidiopsidales*	1.63	moss crusts, moss-lichen mixed crusts
MT366973	Uncultured *Phormidium* sp. clone OTU_37/MF527175 *Wilmottia murrayi* ACKU584/MN473878	100 98	*Oscillatoriales*	1.03	moss crusts, moss-lichen mixed crusts
MT366974	Uncultured *Microcoleus* sp. clone OTU_16/MF527155 *Microcoleus steenstrupii* clone 177-4B/AF355392	100 99	*Oscillatoriales*	0.57	moss crusts
MT366975	Uncultured *Microcoleus* sp. clone OTU_28/MF527166 -	100	*Oscillatoriales*	0.41	moss crusts
MT366976	Uncultured *Microcoleus* sp. clone OTU_1/MF527140 *Microcoleus vaginatus* CJI-U2-KK1/EF654062	100 100	*Oscillatoriales*	44.17	cyanobacterial crusts, moss crusts, moss-lichen mixed crusts
MT366977	Uncultured cyanobacterium clone CNY_02877/JQ402510 *Microcoleus steenstrupii* HSN002/MK487685	100 100	*Oscillatoriales*	1.58	cyanobacterial crusts, moss crusts, moss-lichen mixed crusts
MT366978	Uncultured Microcoleus sp. clone OTU_24/MF527162 *Microcoleus steenstrupii* clone 129–1/AJ871979	100 97	*Oscillatoriales*	0.70	moss crusts, moss-lichen mixed crusts
MT366979	Uncultured Nostoc sp. clone OTU_39/MF527177 *Nostoc* cf. *indistinguendum* FI5-VF4/MH427693	100 100	*Nostocales*	0.26	moss crusts
MT366980	Uncultured cyanobacterium clone BkfYyyy800/KC463672 -	100	*Oscillatoriales*	0.66	moss crusts, moss-lichen mixed crusts
MT366981	Uncultured cyanobacterium clone C55/KT715236 *Ramsaria avicennae* SM S12C clone cl3/MF348316	100 96	*Oscillatoriales*	0.26	moss crusts
MT366982	Uncultured cyanobacterium clone M74/KT715429 *Mastigocladopsis* sp. CCG2/ DQ235802	100 99	*Nostocales*	19.58	cyanobacterial crusts, moss crusts, moss-lichen mixed crusts
MT366983	Uncultured *Microcoleus* sp. clone OTU_5/MF527144 *Microcoleus* sp. W1S8/LN880059	100 100	*Oscillatoriales*	11.09	moss-lichen mixed crusts
MT366984	Uncultured cyanobacterium clone CNY_02835/JQ402478 -	100	*Nostocales*	0.22	moss crusts
MT366985	Uncultured cyanobacterium clone spt54/KF841531 *Microcoleus steenstrupii* clone 141–2/AJ871981	100 98	*Oscillatoriales*	3.13	cyanobacterial crusts, moss crusts
MT366986	Uncultured cyanobacterium clone G8/KT715349 *Nostoc* cf. *lichenoides* JT1-VF7/MH427698	100 100	*Nostocales*	0.28	moss crusts
MT366987	Uncultured cyanobacterium clone CNY_03147/JQ402709 *Tolypothrix distorta* ACT712 clone 5/MK247973	100 100	*Nostocales*	1.54	cyanobacterial crusts, moss crusts, moss-lichen mixed crusts
MT366988	Uncultured *Microcoleus* sp. clone OTU_9/MF527148 *Microcoleus steenstrupii* SON59/KC999631	100 100	*Oscillatoriales*	1.17	moss crusts, moss-lichen mixed crusts
MT366989	Uncultured cyanobacterium clone CNY_02822/JQ402468 *Microcoleus steenstrupii* clone 177-7A/AF355395	99 98	*Oscillatoriales*	1.02	moss crusts
MT366990	Uncultured cyanobacterium clone M65/KT715420 *Pycnacronema arboriculum* 41PC/MF581657	100 99	*Oscillatoriales*	1.82	cyanobacterial crusts, moss crusts, moss-lichen mixed crusts

which is similar to the previous research (Nagy et al., 2005), indicating that the geographic locations significantly affect the composition of the cyanobacterial community. Sites near the Aral sea location of the Kyzyl kum desert in Uzbekistan were demonstrated to harbor especially distinct assemblages of cyanobacteria, and the most dissimilar cyanobacterial communities were observed in samples U7, U8, U9, U10, and U11, locations characterized by extremely uneven distribution and quantity of precipitation (Wang et al., 2016b). Edaphic context within each site corresponded to differences in cyanobacterial community structure. The edaphic factors most correlated with this result were determined by Monte Carlo Permutation test (Table A.4). Soil pH, soil water content (SWC), soil water holding capacity (WHC), soil available potassium (AK), soil microbial biomass carbon (MBC), and soil microbial biomass nitrogen (MBN) had significant effects on the distribution of the cyanobacterial phylotypes in the Tengger desert and the Kyzyl kum desert. Among these, the biotic factors MBC and MBN were the first two prominent factors, followed by abiotic factors pH, SWC, WHC, and AK. The ordination indicated that species Cya5, Cya10, Cya12, Cya14, Cya19, Cya25, Cya30, Cya31 and Cya34 relatively preferred the microorganisms-rich soil conditions with high soil MBC and MBN, and species Cya1, Cya2, Cya3, Cya4, Cya8, Cya15, Cya17, Cya20, Cya21, Cya24 and Cya35 preferred the soil conditions with low rate of soil carbon turnover (relatively high C/N). Moreover, Cya13, Cya16, Cya29, and Cya30 were positively related to the variation of soil water content (SWC).

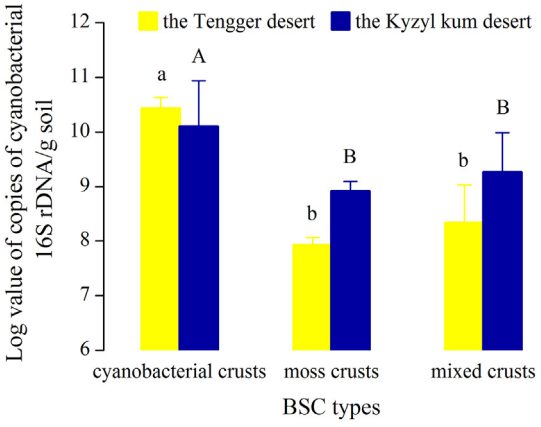

Fig. 3. Absolute abundance of cyanobacteria (copies of 16S RNA genes per gram of dry weight of soil) in BSCs quantified by qPCR. Error bars show the standard errors of the means (n = 3 for moss- and mixed crusts in the Kyzyl kum desert, n = 5 and 6 for cyanobacterial crusts in the Kyzyl kum desert and the Tengger desert, respectively, and n = 6 for moss crusts in the Tengger desert). Different letters indicate significant differences at $P < 0.05$.

3.5. Influence of BSC type and geographic location on cyanobacterial communities

After data normality and equality of error variances were checked by Shapiro-Wilk test and Levene's test respectively, two-way ANOVA

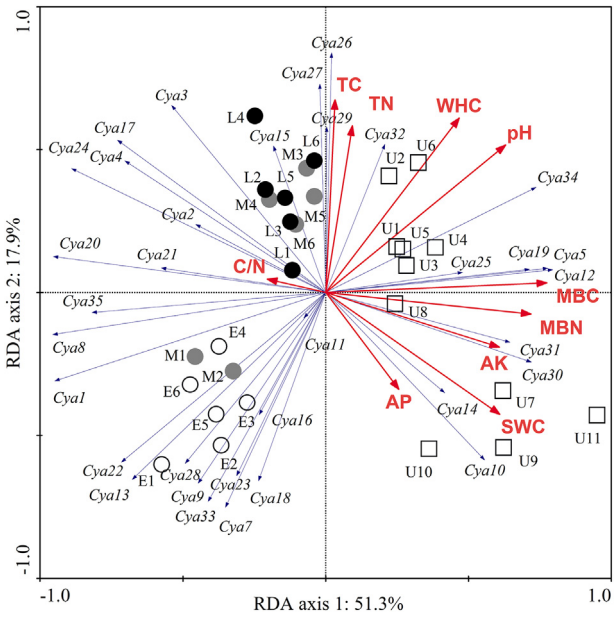

Fig. 4. Diagram of a Redundancy analysis (RDA) on cyanobacterial communities with environmental variables in the Tengger desert and the Kyzyl kum desert. Soil properties are represented by total soil carbon (TC), total soil nitrogen (TN), the ratio of soil carbon and soil nitrogen (C/N), soil water content (SWC), soil water holding capacity (WHC), soil acidity and alkalinity (pH), soil available phosphorus (AP), soil available potassium (AK), soil microbial biomass carbon (MBC), and soil microbial biomass nitrogen (MBN). The significance (according to the Monte Carlo permutation test) of all canonical axes was $P = 0.0020$, which means that the environmental factors have a significant influence on the distribution of the cyanobacterial phylotypes at species level. The first two axes explained 53.8% and 16.1% of the total variation respectively. Cya means species. Cya1, Cya12 and Cya13, *Chroococcidiopsis* spp.; Cya2, Cya3, Cya4, Cya21, Cya22, Cya23, and Cya33, *Microcoleus* spp.; Cya5, uncultured_*Chroococcidiopsaceae* spp.; Cya6, uncultured_*Coleofasciculaceae* spp.; Cya7, uncultured_*Cyanobacteriaceae* spp.; Cya8, *Scytonema* spp.; Cya9, uncultured_*Phormidiaceae* spp.; Cya10, *Aliterella* spp.; Cya11, *Chlorogloea* spp.; Cya14, *Crinalium* spp.; Cya15, *Cyanobacterium* spp.; Cya16, *Trichocoleus* spp.; Cya17 and Cya18, *Oculatella* spp.; Cya19, *Loriellopsis* spp.; Cya20, *Mastigocladopsis* sp.; Cya24 and Cya32, *Microcoleus steenstrupii*; Cya25, *Nodosilinea* spp.; Cya26 and Cya27, *Nostoc* spp.; Cya28, *Phormidesmis* spp.; Cya29, *Phormidium* spp.; Cya30, *Leptolyngbya* spp.; Cya31, *Tolypothrix* spp.; Cya34, *Microcoleus vaginatus*; Cya35, *Wilmottia* spp. Squares represent samples in the Kyzyl kum desert and circles represent samples in the Tengger desert. Circles filling in blank represent E site samples, light grey ones represent M site samples and dark grey ones represent L site samples.

analysis was performed. The Shannon index and ACE richness index showed distinct different response patterns to BSC type and geographic location, as demonstrated in Table 3, BSC type and/or geographic location significantly affected cyanobacterial Shannon diversity, while species richness was not influenced by BSC type and/or BSC geographic location.

4. Discussion

To find the best suitable cyanobacteria strains for inoculation against wind erosion is a critical challenge. Previous works focused on cyanbacteria with high growth rate and crust-forming capacity (e.g. *Oscillatoria* sp., *Nostoc* sp. or *Scytonema* sp.), compatibility with the environment and impacts on soil fertility (e.g. *M. vaginatus* and native N-fixing species) (Acea et al., 2003; Fattahi et al., 2020; Román et al., 2018). However, little attention has been paid to species selection on the basis of the framework of cyanobacterial communities in BSCs. In fact, only a minority of the cyanobacterial species found is responsible for natural BSC formation and many others are very likely opportunistic (Büdel et al., 2016), indicating the possibility that the basic and major cyanobacterial groups can induce BSC formation.

Filamentous nonheterocystous cyanobacteria such as *M. vaginatus* and other members of *Microcoleus* are clearly dominant in desert BSC community, and seem to dominate BSC cyanobacterial community worldwide (Büdel et al., 2009; Garcia-Pichel et al., 2013; Muñoz-Martín et al., 2019). In the present study, *M. vaginatus* was the most abundant species in BSCs of both temperate deserts as evidenced by *M. vaginatus* accounting for 17.6% and 77.1% respectively in the Tengger desert and the Kyzyl kum desert. Moreover, genus *Wilmottia* found exclusively in cold and temperate areas of the world (Strunecký et al., 2011; Machado-de-Lima et al., 2017), kept a relative stable and high abundance in both deserts (4.5–10.0% in the Tengger desert and 2.0–5.6% in the Kyzyl kum desert), indicating *Wilmottia* spp. may be the same core nonheterocystous components as *M. vaginatus* in BSCs of both temperate deserts. At the same time, main genera of filamentous nonheterocystous *Synechococcales* have been identified (i.e., *Leptolyngbya*, *Phormidesmis*, *Trichocoleus*, *Nodosilinea*, and *Oculatella*) (Fig. 2-A). The proportions of *Trichocoleus* and *Leptolyngbya* were reported to increase with reducing precipitation, indicating the relative high desiccation tolerance of these strains (Dojani et al., 2014; Patzelt et al., 2014; Hagemann et al., 2015; Muñoz-Martín et al., 2019), however, they were positively correlated with soil water content (SWC) in this study (Fig. 4). *Trichocoleus* showed a very stable abundance in the Tengger desert while *Trichocoleus* and *Leptolyngbya* kept a very low abundance in the Kyzyl kum desert (Fig. 2).

The importance of nitrogen-fixing cyanobacteria in BSCs has been first emphasized by Belnap (1995) and thereafter concerns have been raised about possible global distribution pattern of heterocystous cyanobacteria. *Scytonema*, *Tolypothrix*/*Spirirestis*, and *Nostoc* are the dominant dinitrogen-fixing cyanobacteria typically found in dryland BSCs (Yeager et al., 2007; Büdel et al., 2016). In agreement with that *Mastigocladopsis* was probably the endemic strains (Hagemann et al., 2017; Becerra-Absalón et al., 2019), *Mastigocladopsis* sp. was the most abundant shared heterocystous cyanobacteria in both deserts and showed a very high abundance in the Tengger desert crusts (33.1%) and lower in the Kyzyl kum desert crusts (2.8%), followed by *Tolypothrix*, *Nostoc*, and uncultured_*Nostocales* (Fig. 2). *Chroococcidiopsis* could contribute to dinitrogen fixing in the soils (Bothe et al., 2010) and they have been recently reported in BSCs (Hagemann et al., 2015; Williams et al., 2016; Muñoz-Martín et al., 2019). The relatively high abundance of *Chroococcidiopsis* phylotypes (4.5% and 1.3% in the Tengger desert and the Kyzyl kum desert, respectively) was rather remarkable, contributing BSC dinitrogen-fixation capability to enhance the fertility of local ecosystems.

Crusts at early successional stages usually suffer from nutrient limitations, which restricts the abundance of heterotrophic microbes (Wang et al., 2016a; Maier et al., 2018). Cyanobacteria are major photoautotrophic organisms and pioneer colonizers and they would stimulate the proliferation of other microorganisms (Acea et al., 2001), which is partially supported by the present result and the result from the Gurbantünggüt Desert by Li et al. (2016) that higher photoautotrophic microorganism abundances were observed in less developed cyanobacterial crusts.

More carbon substances can be observed more frequently in mature habitats such as moss crusts and lichen crusts (Li et al., 2016), thus, greater diversity of microbes often occur in the well developed habitats (Grayston et al., 1998). In the present study, the content of soil carbon substances increased in better-developed moss- and mixed crusts

Table 3
Two-way ANOVA analysis of the effect of BSC type and geographic location on cyanobacterial shannon diversity and ACE richness. Blod fonts indicate significant differences at $P < 0.05$.

Factors	Shannon diversity index*			ACE richness index#		
	df	F	*P*	df	F	*P*
BSC type	2	4.843	**0.018**	2	1.797	0.188
location	1	94.605	**0.000**	1	0.389	0.539
BSC type × location	2	6.551	**0.006**	2	0.444	0.647

* indicates coefficients of determination $R^2 = 0.857$. # indicates $R^2 = 0.185$.

(Table A.3), and cyanobacterial communities also showed a higher alpha diversity in better-developed crusts. This result was in accordance with previous studies that sites with vascular plants supported more cyanobacterial phylotypes whereas sites with almost no vascular plants supported less cyanobacterial phylotypes (Bell, 1993; Siegesmund et al., 2008). In the present study, BSC type and/or geographic location significantly affected cyanobacterial alpha diversity, suggesting that BSC type and/or geographic location structured crust cyanobacterial communities. However, species richness was not influenced by BSC types and/or BSC geographic location as evidenced by our finding that no significant differences were found in ACE richness between three BSC types or the same type of BSCs between two deserts (Fig. 1).

5. Conclusions

This study showed that filamentous *M. vaginatus* predominated in BSC cyanobacterial communities of the two temperate deserts with *Mastigocladopsis* sp. and *Chroococcidiopsis* spp. as the dominant heterocystous cyanobacteria. The top two abundantly shared cyanobacteria were *M. vaginatus* and *Mastigocladopsis* sp. in all types of crusts. Furthermore, this study demonstrated lower cyanobacterial abundances in better-developed crusts, indicating cyanobacteria as pioneer colonizers would stimulate the proliferation of other heterotrophic microorganisms. BSC type and/or geographic location significantly affected cyanobacterial Shannon diversity without significantly influencing species richness in case of annual rainfall amount less than 200 mm. As artificial inoculation of BSCs is an important and promising strategy for restoring degraded ecosystems, filamentous nonheterocystous cyanobacteria of *M. vaginatus* and *Wilmottia*, and heterocystous cyanobacteria of *Mastigocladopsis and Chroococcidiopsis*, may be the core ecosystem 'engineers' to form BSCs in both temperate deserts, and then, they would be potential efficient inoculums for inducing BSCs formation. At the same time, the phylotypes showing significant differences between BSC types, should also be focused on to artificial inoculation of BSCs in temperate drylands.

CRediT authorship contribution statement

Jin Wang: Investigation, Methodology, Writing - original draft. **Peng Zhang:** Investigation, Data curation, Software. **Jing-Ting Bao:** Data curation, Software, Writing - review & editing. **Jie-Cai Zhao:** Investigation. **Guang Song:** Investigation. **Hao-Tian Yang:** Investigation. **Lei Huang:** Investigation. **Ming-Zhu He:** Investigation. **Xin-Rong Li:** Conceptualization, Supervision.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.140970.

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