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Recovery of microbial community structure of biological soil crusts in successional stages of Shapotou desert revegetation, northwest China

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ABSTRACT

Microbial community structure of biological soil crusts (BSCs) in successional stages of Shapotou desert revegetation, northwest China, was assessed using Illumina MiSeq sequencing. Bacterial diversity and richness were highest after 15 years, while those of fungi increased along a chronosequence of stabilized dunes. Hierarchical clustering and principal coordinate analysis showed significant differences in bacterial communities between biocrusts and physical crusts, whereas fungal communities clustered into four groups. Each age of BSCs exhibited the same dominant phyla at different proportions. The recovery time for bacteria was more than 15 years, whereas that for fungi ranged from decades to centuries, indicating that fungal richness might be a potential indicator for predicting the degree of BSC recovery.

Biological soil crusts (BSCs) constitute one of the most important landscapes (Belnap and Eldridge, 2003), having critical roles in semi-arid and arid ecosystems (Eldridge and Greene, 1994; Li, 2012; Weber et al., 2016). In general, BSCs encounter the main successional stages in desert ecosystem: mobile sand, physical crust, algal, lichen, and moss crust (Lan et al., 2012; Liu et al., 2006). Recent estimates suggest that the recovery time of cyanobacterial soil crusts is 15–50 years, whereas that of soil lichens range from decades to centuries (Pointing and Belnap, 2012). However, there is no information about when the microbial community structure can reach a stable state in the recovery process of BSCs in desert ecosystems. Bacteria and fungi are the major microorganisms in BSCs (Bates et al., 2010; Gundlapally and Garcia-Pichel, 2006). During the BSC successional process, microbial species composition and community structure significantly change (Gundlapally and Garcia-Pichel, 2006; Moquin et al., 2012; Zhang et al., 2016). Most of the research on prokaryotic diversity of BSCs has mainly focused on cyanobacteria-dominated biocrusts in arid and semi-arid regions (Abed et al., 2010; Garcia-Pichel et al., 2001; Nagy et al., 2005; Steven et al., 2013; Yeager et al., 2004). Recent studies on the bacterial community structure of bryophyte or lichen-dominated crusts have indicated that lichen-associated communities encompass wide taxonomically diverse bacteria (Bates et al., 2011; Cardinale et al., 2008; Maier et al., 2014). However, studies on fungal diversity during BSC development in desert zones are relatively few (Abed et al., 2013; Grishkan et al., 2015). Thus, what are the changes in microbial community composition and function in different successional stages of BSCs? In addition, what is the effect of these changes on the recovery process of BSCs in desert revegetation in temperate zones?

To answer these questions, we selected BSCs in Shapotou restored vegetation, located on the southeast fringe of Tengger Desert, northwest China. The unirrigated vegetation system was established in 1956 and extended in 1964, 1973, 1981, and later on by planting shrubs (Li et al., 2007b; Liu et al., 2006). In the revegetation area, BSCs varied with the ages of restored vegetation enclosures, and bacteria and fungi were selected to study the BSC microbial community. We hypothesized that the BSC microbial community structure reaches a steady state after a certain developmental period, and is of particular importance to vegetation stability and soil properties during the successional stages of revegetation in desert ecosystems. We sampled BSCs at the revegetation established in 1964, 1981, 1987, 2000, and 2010 in November 2015, and named them according to fixed-sand time as 51 YR (51-year-old revegetation), 34 YR, 28 YR, 15 YR, and 5 YR, respectively. Mobile sand (MS) was employed as a control (Fig. S1).

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In each revegetation, five crust cores (3.5-cm diameter) in each plot (Fig. S1D) were sampled individually using a sterile trowel to separate crusts from underlying soil. One sample comprised six plots, yielding a mixture of 30 cores. Triplicate samples were collected from each revegetation, transported to the laboratory, immediately crumbled to pieces, sieved (1 mm) to remove stones and plant roots, homogenized thoroughly, and stored at −70 °C for subsequent analyses. Soil DNA extraction, PCR, and sequencing are described in Supplementary methods. The raw sequence data were processed using Trimmomatic software. Quality filtering, chimera identifications, and operational taxonomic unit (OTU) clustering (>97% similarity) were performed using USEARCH (version 7.1 http://drive5.com/uparse/). The sampling methods, experimental protocols, and data-handling procedures are described in Supplementary methods. The sequences obtained were deposited into NCBI Sequence Read Archive database under accession number SRA483274.

After processing, 18 libraries of bacterial 16S rRNA and eukaryotic ITS rRNA genes were respectively constructed. The numbers of OTUs detected in each sample of different ages were 1197–2307 for bacteria and 156–441 for fungi (Table S1). Alpha diversity analysis revealed the microbial richness and diversity. Rarefaction analysis showed a higher bacterial diversity in 15 YR, when compared with that in 5 YR and MS (Figs. S2A and B); however, fungal diversities increased with fixed-sand time (Figs. S2C and D). Community richness estimation using ACE and Chao revealed a similar trend as that of community diversity, which was further supported by Shannon's index (Table S1). Thus, 15 YR is an important marker for bacteria, with both diversities and richness reaching the highest level. Conversely, while fungal diversities also increased, the richness improved in 51 YR. This is consistent with studies reporting on recovery of soil properties and processes after sand-binding, with annual soil properties recovery rates being higher in 0–14-year revegetated sites than those in the oldest revegetated sites (43–50 years) (Li et al., 2007a, b), suggesting that the BSC bacterial community recovered quickly during the fastest soil properties recovery phase, while the fungal recovery was longer, similar to soil texture and nutrients recovery. Further investigation is needed to determine the time required for fungi to reach the maximum abundance and confirm the relationship between successional stages of BSCs and fungal richness.

Hierarchical clustering and phylogenetic community composition analyses at genus level (Fig. 1) showed that BSCs clustered into two and four groups for bacterial and fungal communities,

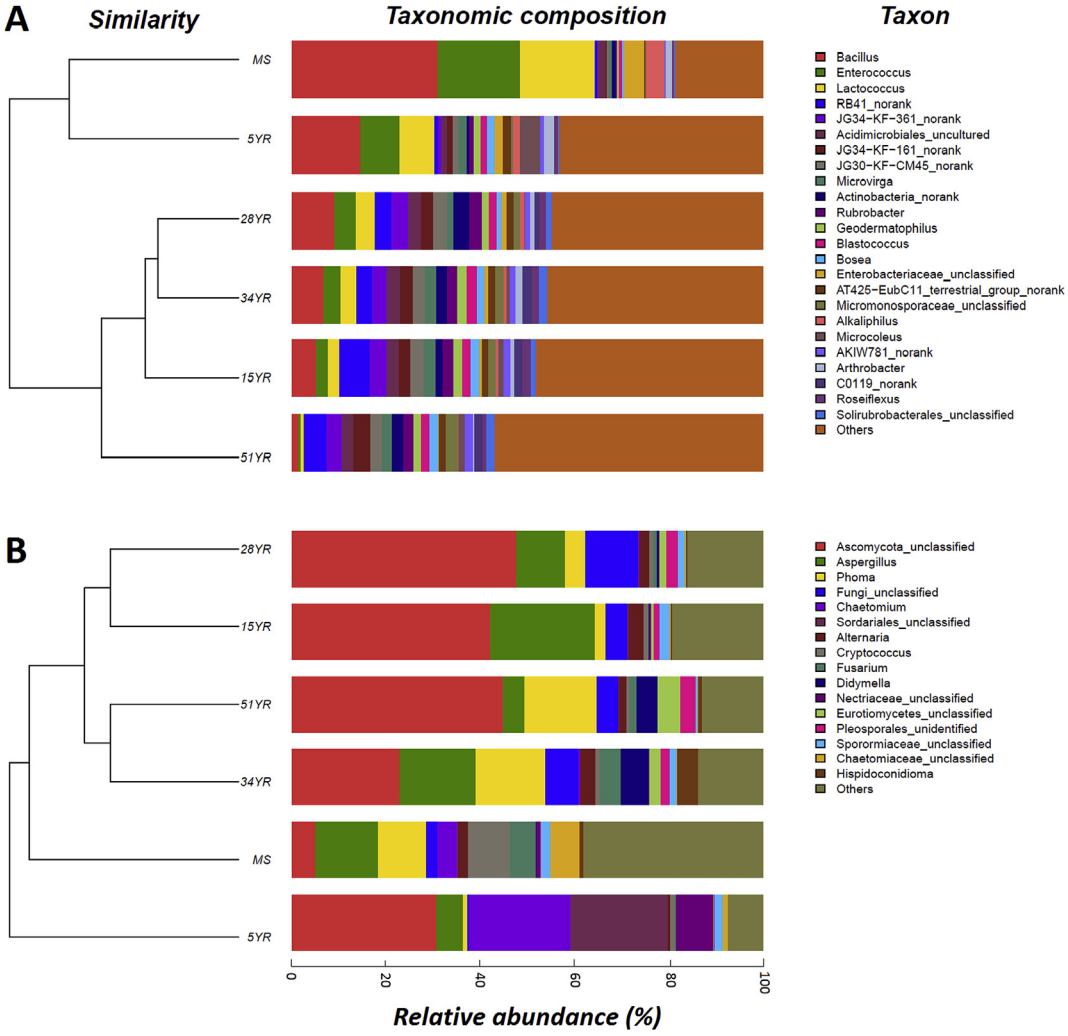

Fig. 1. Hierarchical clustering and phylogenetic community composition of bacteria (A) and fungi (B) at the genus level in BSCs of six different ages. Hierarchical clustering was based on 97% similarity. The sequence percentage of the major bacteria (A) and fungi (B) in taxonomic composition was above 1% in at least one sample. MS, 5 YR, 15 YR, 28 YR, 34 YR, and 51 YR represent mobile sand, 5-, 15-, 28-, 34-, and 51-year-old BSCs, respectively.

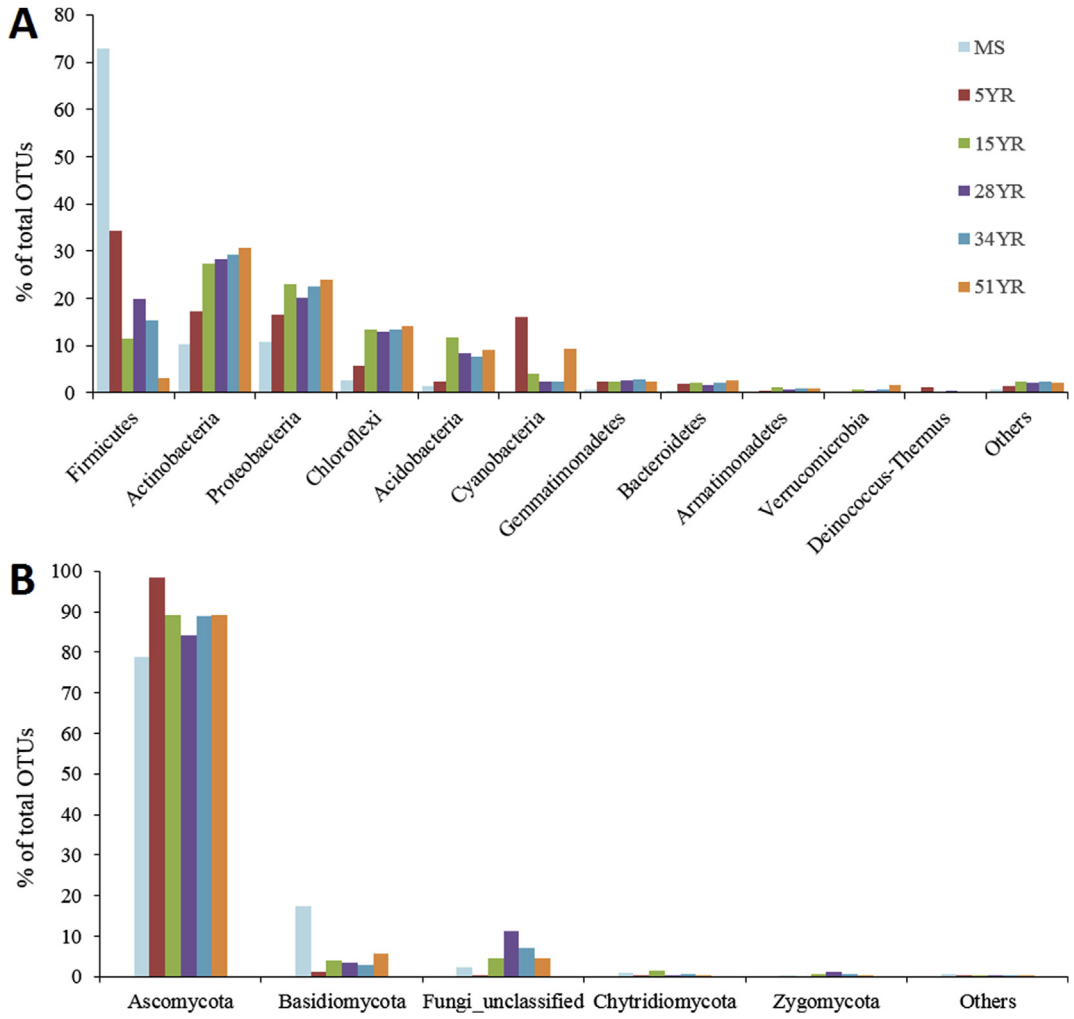

Fig. 2. Abundant phyla (>10% of total OTUs) and low-abundance phyla (>1% of total OTUs) of bacteria (A) and fungi (B) distributed in BSCs of six different ages. Data are defined at 3% OTU genetic distance. MS, 5 YR, 15 YR, 28 YR, 34 YR, and 51 YR represent mobile sand, 5-, 15-, 28-, 34-, and 51-year-old BSCs, respectively.

respectively: Bacteria – short-term (MS and 5 YR, dominated by physical crusts) and long-term (>15-year-old BSCs, dominated by algae, lichen, or moss); fungi – MS, 5 YR, 15YR-28YR, and 34YR-51YR). Principal coordinate analysis (Fig. S3) showed significant differences in bacterial and fungal community compositions among the groups. Metagenome analysis revealed the same dominant phyla at different proportions in each age of BSCs (Fig. 2). Actinobacteria and Proteobacteria were the most dominant bacteria in all biocrusts, except in physical crusts (Firmicutes was the most dominant in MS and 5 YR), followed by Chloroflexi, Acidobacteria, Firmicutes, and Cyanobacteria (Fig. 2A). Actinobacteria and Proteobacteria are usually considered to be copiotrophic, being predominant in high C environments (Fierer et al., 2007). However, these results differ from those reported for other crust types and soils (Moquin et al., 2012; Zhang et al., 2016). Unexpectedly, Actinobacteria and Cyanobacteria were dominant in BSCs of several decades, despite their prevalence in early successional stages and significant roles in initial crust development (Belnap and Lange, 2001). Furthermore, an unusually high proportion of Chloroflexi suggested a general adaptation to arid environments and its importance in the formation and persistence of BSCs in arid zones (Lacap et al., 2011; Wang et al., 2015). Moreover, predominance of Ascomycota in all samples (Fig. 2B) confirming that it is the dominant fungal colonizer in all crusts, regardless of their origin (Abed et al., 2013). The different proportions of dominant phyla altered functions of microbial communities in the successional process of BSCs, which in turn promoted BSC development.

In conclusion, the initial 15 YR was found to be critical for the recovery of microorganisms of BSCs in Tengger Desert revegetation. The recovery time for bacteria was more than 15 years, whereas that for fungi ranged from decades to centuries, indicating that fungi are more sensitive than bacteria. Thus, fungal richness could be a potential indicator for predicting the degree of recovery of BSCs in this zone.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2016.12.030.

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