

Differentiation of microbial activity and functional diversity between various biocrust elements in a heterogeneous crustal community



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ABSTRACT

Biological soil crusts (BSCs) dominate the interspace between sparse vegetation in arid and cold environments worldwide and fulfill diverse ecosystem functions. Natural BSCs are usually classified as a series of stepwise successional stages along with a gradual improvement of biological properties and micro-environmental conditions. However, the effects of spatial heterogeneity on the ecological traits of BSCs remain largely unknown, especially in the microbial scenario. In this study, three adjacent biocrust elements with different successional levels (cyanobacterial, lichen, and moss crusts) were collected from a continuous and heterogeneous crustal community at small scale (centimetre level) in the Gurbantünggüt Desert, aiming to distinguish the alteration of microbial distribution and functional traits among them. The catabolic fingerprint of sole-carbon induced respiration was measured by MicroResp™ respiration system to calculate the functional diversity indices. Ribosomal copy numbers of different soil microbes (bacteria, fungi, and phototrophs), as a proxy for microbial relative abundance, were analysed through quantitative PCR methods. We also evaluated the related physicochemical parameters. The results show evidences that the microbial abundances and functional traits associated with each biocrust element are inconsistent with its successional level. Although higher microbial activities and more benign soil conditions (increased soil moisture and organic matter) were still found in well-developed moss crust, higher microbial abundances (except fungi) and enhanced functional diversity were observed in less-developed cyanobacterial crust. Spatial heterogeneity due to the jigsaw-like pattern of various biocrust elements partly affects microbial performances in BSCs. More studies focusing on quantitatively measuring spatial arrangement of biocrust elements are needed to clarify the mechanisms underlying to functional differentiation in crustal communities.

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1. Introduction

Biological soil crusts (BSCs) are delicate soil aggregates that contain an abundance of highly specialized microorganisms, including heterotrophic bacteria, cyanobacteria, microalgae, fungi, lichens, liverworts, and mosses (Belnap, 2003; Eldridge, 1993). As a sub-ecosystem sensitive to anthropogenic disturbance and environmental constraints, BSCs in deserts link sand particles by the microbial filaments and microbial-secreted extracellular substances to form biological layers at the topsoil (Belnap and Eldridge, 2001; Hu et al., 2003). They involve multiple trophic levels creating food webs as well as complexly diverse ecosystem functions, and play crucial roles in the processes of moisture retention, nutrient cycling, soil fertilization, and land stabilization

(Bowker et al., 2010a; Darby et al., 2007; Shepherd et al., 2002). Due to their special properties, BSCs possess high resistances to ambient stresses and low requirements of source inputs (e.g., water, nutrients), and are capable to survive in those harsh habitats where the natural conditions poorly support the growth of high plants (Garcia-Pichel, 2002). They even compose up to 70% of the total living coverage in some regions and constitute the dominant landscape element at the interspaces between sparse vegetation in arid and cold environments worldwide (Belnap, 2003; Belnap and Eldridge, 2001).

In desert ecosystems, the primary succession of BSCs is generally considered to begin with the colonization of cyanobacteria (such as *Microcoleus* sp. and *Scytonema* sp.) and some heterotrophic microbes on bare soil to form the initial crust, once the soil surface start to be stabilized (Belnap, 2003; Belnap and Eldridge, 2001; Kidron et al., 2008; Shepherd et al., 2002). As a result of the accumulation of nutrient (cyanobacterial nitrogen fixation and photosynthesis), as well as the improvement of microhabitats (e.g., the enhancement of moisture availability), more eukaryotic algae and various lichen/moss species germinate and establish in this crustal community (Kidron et al.,

Abbreviations: BSCs, Biological Soil Crusts; CLPP, Community Level Physiological Profiles; SIR, Substrate-induced Respirations; FDI, Functional Diversity Index; *H'*, Shannon-wiener index; *D*, Simpson index; *PIE*, Hurlbert's inter-specific encounter index.

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2010). When the dense lichens or mosses dominate crust surface, BSCs succeed to lichen or moss crusts (Lan et al., 2015). As the later successional stages of BSCs, moss crusts develop and succeed from either cyanobacterial crust or lichen crust, and lichen crusts always from cyanobacterial crust (Eldridge and Greene, 1994; Lan et al., 2011). Whereas, lichen crust is often absent in many cases, and cyanobacterial crust may also not develop into lichen or moss crusts due to the semi-equilibrium with ambient stresses, which are able to prevent the succession of crustal communities at a certain crust type (Kidron et al., 2010; Li et al., 2013). This successional process has been increasingly investigated on a wide range of attributions like species composition (Gundlapally and Garcia-Pichel, 2006; Hu and Liu, 2003; Kidron et al., 2010), carbon and nitrogen turnover (Brankatschk et al., 2013; Kidron et al., 2015b; Tighe et al., 2012), hydrological dynamics (Colica et al., 2014; Fischer et al., 2014), and soil properties (Dümig et al., 2014; Hu and Liu, 2003; Lan et al., 2013). According to these empirical parameters, natural BSCs are usually identified and classified as several distinct successional stages (Lan et al., 2013; Zaady et al., 2010). The dominant phototrophic species that contribute greatly to the morphological traits of BSCs are widely used to designate the stages as cyanobacterial/algal crust, lichen crust, or moss crust, respectively. Early-stage BSCs enhance soil fertility and improve microhabitats for the later succession (Belnap and Gardner, 1993), so that “less-developed” cyanobacterial crust is commonly considered to be large poorer than “well-developed” lichen and moss crusts in multiple properties. Previous studies have demonstrated that the development of BSCs is usually associated with the enhancement of ecosystem functioning in soil fertilizing (Belnap, 2002; Brankatschk et al., 2013). This differentiation in the level of ecological functions among successional stages also involves other vital nutrient-cycling processes performed by heterotrophic microbes (e.g., bacteria, fungi), which act as decomposers or primary consumers in the community (Bates and Garcia-Pichel, 2009; Zaady et al., 2010). The biomass and composition of the decomposers/consumers have been observed to shift (Gundlapally and Garcia-Pichel, 2006; Yu et al., 2012), consistent with the utilization rates of organic sources and soil enzyme activities among BSC stages (Belnap and Eldridge, 2001; Yu et al., 2012).

Despite substantial studies focused on the alteration and succession of BSCs, the morphological heterogeneity, resulting from different ratio and spatial distribution of various crusts which are assembled within a continuous crustal community at small scale, is still largely overlooked. Actually, the spatial pattern of most BSC stages at the micro-landscape scale (from *cm* level to *m* level) is highly mottled and patchy (Bowker et al., 2013), such that diverse well-developed patches (lichen and/or moss crusts) are usually surrounded by less-developed interpatch (i.e., cyanobacterial and/or algal crusts which fill the interspace among patches, see details in Fig. 1). Regardless of the bare sandy substrates outside the crustal community, these mature patch and relatively poor interpatch form an intact crustal community, and we call them “biocrust elements” hereafter in this study. Since the distribution of soil microbes follows the source availability (moisture, organic matter, nutrients, etc.) (Fischer et al., 2014; Kidron and Vonshak, 2012; Schlesinger and Pilmanis, 1998), it can be assumed that the aforementioned organisms in BSCs persist more in those well-developed patches than less-developed cyanobacterial interpatch. Then, given diverse organic substances secreted by microorganisms and their distinct taxonomical composition among biocrust elements (Gundlapally and Garcia-Pichel, 2006; Hu et al., 2003; Zaady et al., 2010), we hypothesize that patch-interpatch configuration of the crustal microcosm creates an asymmetrical pattern of activity and functional diversity between mature patches and poor interpatch, comparing to their different successional levels. Previous literatures have presented some evidences on the causality between the spatial configuration of visible cryptogams in BSCs (i.e., lichen and moss species) and the levels of ecosystem functions (Bowker et al., 2013; Fischer et al., 2014, 2012; Maestre et al., 2005). However, to our knowledge, a little attention has been paid to the nature of soil microbes in adjacent biocrust elements collected from a patchy pattern of the

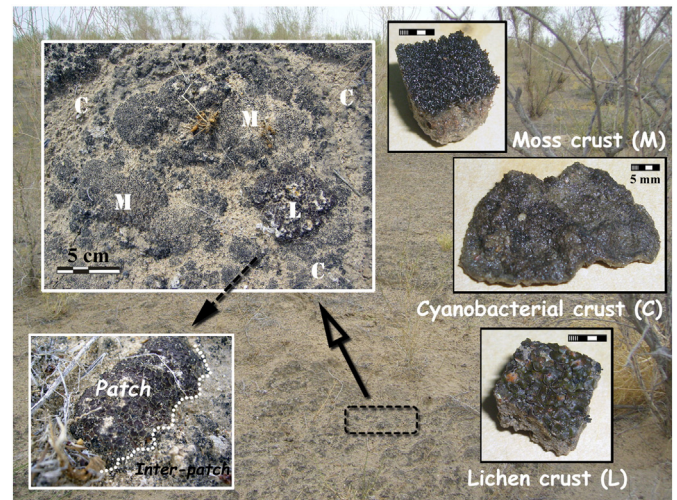


Fig. 1. Various elements of the crustal community, cyanobacterial crust (C), lichen crust (L) and moss crust (M), and the patch-interpatch heterogeneous distribution at small scale.

crustal community. When various biocrust elements distribute heterogeneously at a fine scale (*cm* level), do they interact with each other and change the performance of soil microbes on ecological functions and its diversity significantly?

In this study, we intended to focus on the catabolic processes in carbon cycling by employing community-level physiological profile analyses (CLPP, MicroResp™ respiration system) to evaluate the functional activity and diversity of soil microorganisms persisting in various adjoining biocrust elements of a continuous crustal community. CLPP analysis offers a flexible way to clarify the substrate specific response of microbial community to different carbon sources with a gradient of structural complexity (Brackin et al., 2013; Campbell et al., 2003). The catabolic fingerprint of CLPP to some degree reflects the functional differentiation among the biocrust elements. The field sampling was conducted in several small parallel plots which were built up by a single crustal whole with three biocrust elements in each. This scale level can facilitate the observation of differentiation owing to soil microbial activity. Bare sandy soil is excluded from the scope of spatial pattern in this study. Microbial ribosomal copy numbers, as a proxy for microbial relative abundance, were also measured, together with physicochemical parameters of soil properties.

2. Material and methods

2.1. Study site and crust sampling

The study site is located in the western area of the Gurbantünggüt Desert (45°17' N, 86°47' E, 410 m a.s.l., Fig. S1), which is the biggest semi-fixed desert in China (Su et al., 2012). The desert is situated in the center of the Junggar basin, Xinjiang. The annual mean temperature is 6–10 °C, while the maximum temperature is over 40 °C (Chen et al., 2007). The annual mean precipitation of this arid region is approximately 80 mm, and precipitation usually falls during spring and winter. Snow covers the ground for 100–160 d·a⁻¹ during winter (Liu et al., 2013), and the snowmelt in late March is an important source of moisture for BSC development. By contrast, the annual average evaporation and active cumulative temperature (≥ 10 °C) reach 2606 mm and 3500 °C, respectively (Zhang et al., 2007). The dominant shrubs and sub-shrubs in the study field include *Ephedra distachya*, *Calligonum leucocladum*, *Artemisia arenaria*, and *Seriphidium terrae-albae*; BSCs cover the space between plants (Chen et al., 2007).

Crust sampling was performed in August 2011, on a large gently sloping sandy land, in an area of around 150 m × 400 m in open field

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