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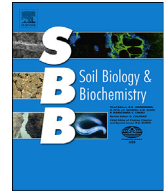

Fungal community assemblages in a high elevation desert environment: Absence of dispersal limitation and edaphic effects in surface soil

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ABSTRACT

Recent studies have shown the significant effects of environmental selection and possible dispersal limitation on soil fungal communities. However, less is known about the role of soil depth in fungal community assemblages, especially under soil environments that are intensely cold, infertile and water-deficient. In Ngari drylands of the Asiatic Plateau, we studied fungal assemblages at two soil depths, using Illumina sequencing of the ITS2 region for fungal identification (0–15 cm as the surface soil and 15–30 cm as the subsurface soil). Fungal diversity in the surface soil was much higher than that in the subsurface soil ($P < 0.001$), and communities differed significantly between the two layers ($P = 0.001$). Neither soil properties nor dispersal limitation could explain variation in the surface-soil fungal community. For the subsurface, by contrast, soil, climate and space explained 27% of variation in fungal community. Collectively, these results point to high dispersal rates and absence of edaphic effects in the surface-soil fungal community assemblage in Ngari drylands. It also suggests that for soil fungi with highly effective dispersal, regional distributions may fit with Bass-Becking's paradigm that 'Everything is everywhere'.

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1. Introduction

While extreme cold desert environments may be characterized by paucity of soil nutrients, and challenging climates, they still produce abundant microbial populations (Treonis et al., 2002; Ziolkowski et al., 2013; Yadav et al., 2015), even though they may appear hostile to the most larger living organisms. Perhaps because of their faster evolutionary rates and higher genetic diversity (Whitman et al., 1998; Blackwell, 2011; Li et al., 2014), microorganisms are more capable of adapting to harsh environments than macroorganisms, playing pivotal roles in biogeochemical cycling and ecosystem functioning (Yergeau et al., 2007; Chan et al., 2013). Recently, the diversity patterns and community assemblage processes of uncultured microorganisms in extreme environments have gained increasing attention. For example, Frossard et al. (2015) found that the intensity of wetting events and history of soil water regime had an interactive effect on soil microbial community composition in hot Namib Desert, while Shi et al. (2015) reported that soil microbial community composition was shaped by vegetation type on Arctic tundra. Recently, Cox et al. (2016) proposed that Antarctic soil fungal communities shared significantly more species with those in the distant Arctic, suggesting that a few fungal species with great dispersal ability are also able to colonize and dominate in cold and arid environments.

The Ngari region, which we focus on in this study, is located in the western Tibetan Plateau. It is characterized by severe cold, hyperaridity, strong wind and high ultraviolet radiation, and has been called the "arid core" of the Asiatic Plateau (Troll, 1972).

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Because of its remote location and harsh environments, few people enter this region, and correspondingly studies on its regional biodiversity are limited. The 1976 Interdisciplinary Scientific Expedition of the Chinese Academy of Sciences recorded 241 vascular plant species, and revealed the significant effects of climate, soil and space on plant community composition within the Ngari (Chang and Gauch, 1986). Recently, we reported the soil bacterial distribution in the Ngari, and also found that both environmental selection and dispersal limitation significantly influenced bacterial assemblages in the surface and subsurface soil layers (Chu et al., 2016).

Similarly to soil bacteria, fungi are also essential components of belowground biodiversity (Uroz et al., 2016; Peay et al., 2016), and their various functional guilds maintain a wide range of ecosystem processes, such as belowground carbon transportation (Klein et al., 2016), plant litter decomposition (Voriskova and Baldrian, 2013), controls on the coexistence and relative abundance of plant species (Lewis, 2010; Rudgers et al., 2010), and effects on plant growth (Parniske, 2008). Nevertheless, niche types, diversity patterns and community assemblage processes tend to differ between soil fungi and bacteria (Rousk et al., 2010; Geremia et al., 2016; Peay et al., 2016). Compared with bacteria, fungi are more capable of decomposing recalcitrant organic materials (Clipson et al., 2006), adapting to soil conditions of low nitrogen and high C:N ratio (Strickland and Rousk, 2010), and tolerating acidic soils (Rousk et al., 2009). As a follow-on from our recent study of soil bacterial distribution in the Ngari (Chu et al., 2016), a broad overview of the range of fungal communities is now appropriate.

High-throughput sequencing (HTS) provides fungal ecologists an efficient approach to studying soil fungal communities and their relationship to the surrounding environment (Lindahl et al., 2013; Balint et al., 2016). In recent and analogous broad scale studies, Shi et al. (2014) found that space, temperature and vegetation significantly affected soil fungal communities of forests in western China, while Pellissier et al. (2014) proposed that soil fungal communities of grasslands were mainly structured by soil properties, temperature and plant communities in the Western Swiss Alps. In an agricultural ecosystem in the black soil zone of northeast China, it was also reported that geographic distance and soil properties structured soil fungal communities (Liu et al., 2015). However, to our knowledge, regional scale studies on fungal community assemblages have rarely been carried out in both cold and hyperarid environments, such as Ngari (Pointing and Belnap, 2012). In this kind of special environment, soil depth may produce a stronger contrast of soil physicochemical and niche properties between the different layers: the surface soil may have higher nutrient availability and arrival of immigrant microbes, whereas the deeper soil may provide a more amenable environment for microbial activity, blocking the harmful UV radiation as well as extreme fluctuations in temperature and water potential. Therefore, based on the above suppositions, it is worth exploring how the fungal diversity, community composition and assembly process vary with soil depth. Moreover, taking into account soil depth can also help us to develop a more comprehensive understanding of soil fungal ecology in such an extreme environment, even though more than 50% of microbial biomass and biological activity occur in the surface soil for the most soil types (Tedersoo et al., 2014).

In this study, we used Illumina MiSeq platform to sequence fungal communities from samples taken at two soil depths (0–15 cm as the surface soil and 15–30 cm as the subsurface soil) at 13 sites in Ngari, Tibet. The horizontal distance between sites varied from 14 km to 925 km. We addressed the difference in fungal diversity and community composition between different soil layers, as well as the relative roles of stochastic and deterministic processes in community assemblages between layers. Different community assemblage processes should prevail in the surface and subsurface soil. We hypothesize that stochastic processes should dominate fungal assemblages in the surface soil due to high dispersal in harsh environments (Favet et al., 2013; Itani and Smith, 2016), whereas deterministic processes may be expected to dominate fungal assemblages in the subsurface soil, considering its closed microhabitat and stable environment.

In addition, we proposed two ancillary hypotheses on diversity and community composition, respectively. One hypothesis was that fungal diversity is much lower in the subsurface soil relative to the surface soil, considering the reduced immigration and low nutrient availability in deeper soils. The other was that fungal community dissimilarity across the depth profile (0–30 cm) should be comparable to that found over large spatial distances (14–925 km), because niche differentiation caused by soil depth is expected to be at least as strong as any spatial effects of regional geographic distance occurring within the same layer of the desert soil.

2. Materials and methods

2.1. Soil sampling

Soil samples were collected at 13 sites over a broad area (~300 000 km^2) in western Tibet, China during July to August 2011 (Fig. 1). At each site, the surface soil (0–15 cm of depth) was collected from five random locations within a given square plot (10 m × 10 m) and homogenized as a single soil sample, while the corresponding subsurface soil (15–30 cm of depth) was collected simultaneously and then mixed as another soil sample within each site. All the samples collected in the field were packed in sterilized polyethylene bags, and transported to the lab in portable car refrigerators as quickly as possible. The twenty-six soil samples were then divided into two subsamples: One was stored at 4 °C to determine the soil properties, and the other was stored at −80 °C prior to DNA extraction.

2.2. The collection of environmental data

The environmental data included three geographic variables (latitude, longitude and elevation), four climatic variables (mean annual temperature—MAT, mean annual precipitation—MAP, annual potential evapo-transpiration—PET and annual Aridity), and eight soil properties (pH, soil conductivity, soil moisture—SM, total soil carbon—TC, total soil nitrogen—TN, C:N ratio, dissolved organic carbon—DOC and dissolved total nitrogen—DTN). DTN is the sum of ammonium, nitrate and dissolved organic nitrogen. The measurement of soil properties was described in our recent study on soil bacterial communities (Chu et al., 2016), and soil conductivity was newly determined with a soil to water ratio of 1:5 by conductivity meter (Mettler Toledo FE30, Shanghai, China). MAT and MAP were compiled from the WorldClim database (www.worldclim.org) at 30 arc second resolution. PET and Aridity were obtained from CGIAR-CSI Global-Aridity and Global-PET database (http://www.cigar-csi.org). In addition, net primary productivity—NPP was compiled from the Atlas of the Biosphere (www.sage.wisc.edu/atlas/maps.php).

2.3. DNA extraction and MiSeq sequencing

Total DNA from each sample were extracted under sterile conditions from 0.5 g of soil by using a FastDNA® Spin kit (Bio 101, Carlsbad, CA, USA) according to the manufacturer's instruction, and stored at −40 °C. Extracted DNA was diluted to approximately 25 ng/μl with sterilized distilled water and stored at −20 °C until use. Then the diluted DNA were frozen-transported to the

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