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The differentiation of soil bacterial communities along a precipitation and temperature gradient in the eastern Inner Mongolia steppe

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ABSTRACT

Understanding the differentiation of soil bacterial communities under precipitation and temperature gradients is crucial for assessing the impacts of environmental filters on ecosystem structure and function. Here we investigated spatial variations of bacterial communities along a precipitation and temperature transect in the eastern Inner Mongolia steppe, China. The aims are to understand the biogeographic pattern and key drivers shaping soil bacterial communities along the transect. Our results showed that the soil bacterial community along the 451-km transect exhibited the distance-decay relationship, decreasing in community similarity with geographic distance. Obvious changes in the bacterial community structure occurred at an annual precipitation from 215 to 261 mm, which was close to the boundary between arid and semi-arid systems. The relative abundances of Proteobacteria, Bacteroidetes, and Acidobacteria increased with precipitation, while those of Actinobacteria, Chloroflexi, and Gemmatimonadetes decreased. Environmental filtering was observed to be the key in shaping bacterial biogeographic patterns, and climate conditions exert indirect effects on soil bacterial communities mainly through direct effects on soil properties. Soil pH and plant coverage were important to soil bacterial communities in both arid and semi-arid steppes. Our findings provided insights for understanding the linkages among geographic distance, environmental filters, and soil bacterial communities in Eurasian steppe ecosystems.

1. Introduction

Climate has a large impact on plant community, soil properties, biodiversity, and functions of terrestrial ecosystems (Kardol et al., 2010; Kelly and Goulden, 2008). It is well documented that aboveground net primary production increases with mean annual precipitation across various ecosystem types (Huxman et al., 2004). Similarly, changes in precipitation regimes may alter the soil microbial community structure and function, ultimately inducing the shifts of belowground ecosystem processes such as decomposition and nutrient cycling (Schimel et al., 2007; Schimel and Schaeffer, 2012). Some studies have investigated biogeographic patterns of the soil microbial community along the precipitation and temperature gradients, and most studies show that microbial biogeography is primarily controlled by soil variables (Angel et al., 2010; Bachar et al., 2010; Fierer and Jackson, 2006). However, previous studies using microbial biomass measurements (Serna-Chavez et al., 2013) or low-resolution microbial profiling methods (Chen et al., 2015; Hu et al., 2014) were not able to discern whether the microbial community structure or particular taxonomic groups were more or less sensitive to precipitation and temperature gradients.

A greater amount of evidence indicates that microbial assembly displays non-random environmental distributions (Angel et al., 2010; Fierer, 2008; Hanson et al., 2012; Lee et al., 2012; Prober et al., 2015). It is expected that an assortment of microbial communities (biogeographic patterns) will be shown along an environmental gradient based on certain mechanisms if environmental factors play key roles. Spatial scale is important in determining the variation patterns of microbial community structures, because environmental conditions are often scale-dependent (Bardgett and van der Putten, 2014). Under

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such conditions, a distance-decay relationship often emerges in which taxonomy dissimilarity increases with geographic distance. The distance–decay relationship, as one example of biogeographical patterns for microbes, has a strong context-dependency (Martiny et al., 2006; Wang et al., 2013). It may vary depending on microbial groups, sampling seasons, and ecosystem types (Pasternak et al., 2013) or the interactive effects of multiple factors.

Environmental factors influencing the microbial community and diversity mainly include climate, soil physical and chemical properties, and plant properties (Angel et al., 2010; Fierer and Jackson, 2006; Prober et al., 2015). Abiotic factors, such as soil moisture, pH, and soil available carbon, may result in predictable shifts in the soil bacterial compositions (Fierer et al., 2007; Fierer and Jackson, 2006; Goldfarb et al., 2011). Several studies show that abiotic factors could potentially be the primary driving forces changing microbial diversity and community in desert soil (Cary et al., 2010; Fierer et al., 2012; Lee et al., 2012). These abiotic factors include extreme moisture and temperature conditions, high soil pH and salinity, or negligible plant-carbon inputs. However, the responses of the microbial biomass, diversity, and community structure to environmental factors may be different. It shows that the bacterial biomass increases with precipitation; however, bacterial diversity is often independent of precipitation depending on survey scales. Moreover, the compositions of bacterial communities are distinct to each site along the transect from the Mediterranean to semi-arid areas and arid sites in Israel (Bachar et al., 2010). It supports the notion that the microbial community is unique to each ecosystem (Bachar et al., 2010; Pasternak et al., 2013). Significant differences in soil microbial communities and functional attributes are also observed between desert and non-desert systems based on metagenomic analysis (Fierer et al., 2012). This implicates the occurrences of different mechanisms shaping bacterial communities along a specific transect.

The Inner Mongolia steppe lies in the eastern part of the Eurasian steppe. Some studies have assessed the effects of environmental factors on microbial communities at arid and semi-arid Inner Mongolian steppe ecosystems. It is reported that soil organic carbon is the main positive predictor of microbial biomass (Hu et al., 2014). Apart from the dominant effect of precipitation, plant and soil properties could also regulate soil microbial communities characterized with the phospholipid fatty acid method in the Inner Mongolia steppe (Chen et al., 2015; Yao and Zhu, 2015). However, biogeographic patterns and key driving factors shaping bacterial community structure remain further elusive at a fine taxon detail in this cold and dry steppe ecosystem. It is necessary to test the relative importance of climate, soil, and plant community factors simultaneously on bacterial communities at the regional scale.

In this study, we surveyed soil bacterial communities using the pyrosequencing technique in nine sites covering arid and semi-arid steppes in the east Inner Mongolia, China, which spans 451 km along a precipitation and temperature gradient. We focused on two questions in this study. First, we studied the variation patterns of soil bacterial communities associated with the climate gradient in the Inner Mongolia steppe. Second, we simultaneously tested the relative importance of climate, soil, and plant community factors on bacterial communities and analyzed the different environmental factors shaping bacterial community assemblage between arid and semi-arid systems.

2. Materials and methods

2.1. Study site descriptions

Nine sites were selected along the precipitation and temperature transect from the west to east in eastern Inner Mongolia, northern China (Fig. 1). These sites were distributed from latitude 43°37.926′ to 44°00.411′ N and from longitude 112°10.276′ to 117°45.856′ E. The ecosystem types along the precipitation and temperature transect change from arid steppe (T1 to T4) to semi-arid steppe (T5 to T9) from west to east. The topography consists of gently rolling hills and tablelands, with an elevation ranging from 933 m in the west to 1251 m in the east. Based on the long-term meteorological data (1901–2009), the mean annual temperature ranges from 0.91 to 3.48 °C, and the mean annual precipitation ranges from 167.5 to 333.3 mm, 70–80% of which occurs in the growing season (May–August). The main plant species in arid and semi-arid steppes were shown in Table 1. In this study, we employed an aridity index (AI, the ratio of average annual precipitation to potential evapotranspiration) based on United Nations Environment Programme (Middleton and Thomas, 1992) to quantify the drought occurrence at each study site. The AI can reflect the interactive effects of

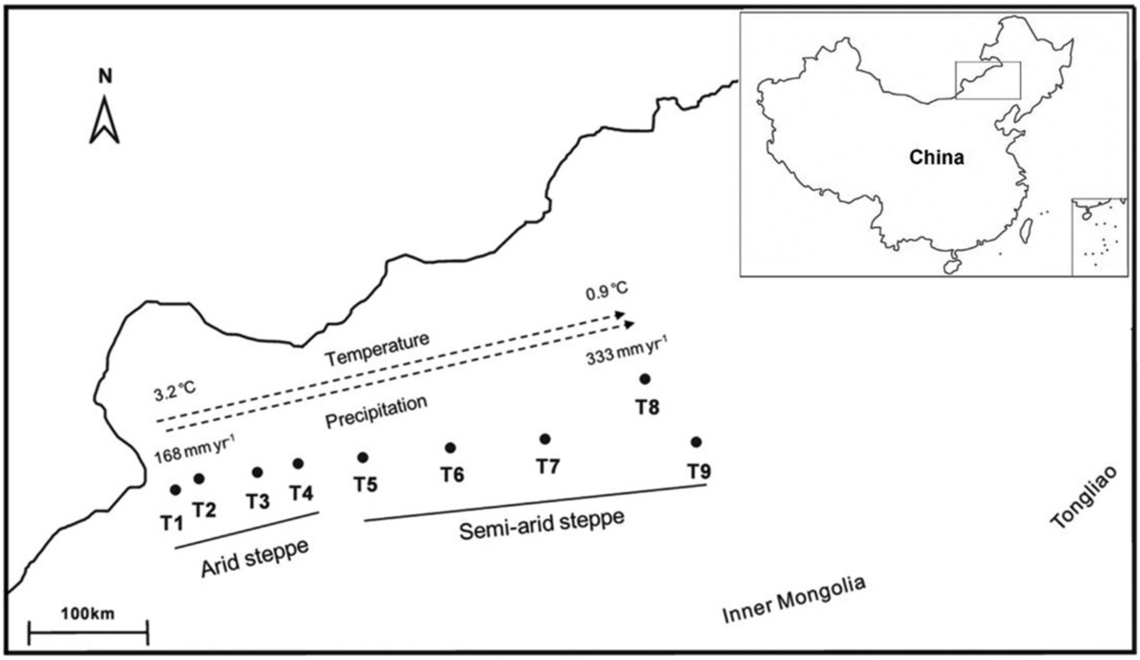

Fig. 1. Sampling sites along the precipitation and temperature transect across eastern Inner Mongolia steppe in northern China.