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Soil bacterial community composition and diversity in relation to edaphic properties and plant traits in grasslands of southern China

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ABSTRACT

To identify the key roles and underlying mechanism for assembling soil microbial community structures at regional scales, we examined soil bacterial community compositions from 20 locations in a transect of grasslands of southern China. The bacterial community was sequenced for microbial 16S ribosomal RNA gene amplicons using Illumina MiSeq technology. The soil microbial community diversity was analyzed for plant, soil, geographic properties, and pure spatial distance based on a distance-based approach and with variation partitioning based on canonical redundancy analysis. The soil bacteria richness and alpha diversity index showed marginal positive relationship with plant richness and Shannon index. The bacterial community compositions of both the taxonomic and phylogenetic structures were best explained by the soil pH and plant diversity and soil nutrient availability, with the peak richness at pH 6.8. While the plant, soil and geographic factors were correlated with bacteria community dissimilarity, soil pH and plant diversity, nitrogen availability were relatively independent dominant community assemblage by quantifying taxonomic and phylogenetic turnover. Mantel tests indicated the assembly of soil bacterial community was predominated by the determinant processes. Overall, our findings suggest plant functional traits and abiotic soil properties (e.g., soil pH and inorganic nitrogen) collectively drive soil bacterial diversity patterns but are not limited by pure spatial distance in grasslands of southern China.

1. Introduction

Soil microorganisms are very abundant and diverse, and play an important role in ecosystem function and maintenance (Fierer and Jackson, 2006; Dini-Andreote et al., 2016). Bacteria account for a large proportion of the soil microbial community composition and diversity and are closely related to ecosystem function and services, including the biochemistry cycle, energy flow and degradation of pollutant substances (Bodelier, 2011; Bardgett and van der Putten, 2014; Jing et al., 2015). It has been suggested that the patterns of microbial diversity are mainly regulated by multiple environmental factors, such as climate, topography, soil properties and vegetation type (Griffiths et al., 2011; Xiong et al., 2012; Yun et al., 2014), but the conclusions remain controversial probably due to environmental heterogeneity (Lauber et al., 2009; Lindstrom and Langenheder, 2012). Thus, understanding the drivers of the patterns of microbial diversity in terrestrial ecosystems remains a challenge (Martiny et al., 2006; Bodelier, 2011; Nemergut et al., 2011).

Soil pH has been considered to be the most important factor for determining soil microbial community composition and diversity at continental (Fierer and Jackson, 2006; Griffiths et al., 2011), regional (Wang et al., 2015) and plot scales (Yao et al., 2014). But the composition and diversity of the soil microbial composition in response to environmental factors at different spatial scales remains a widely debated topic (Lozupone and Knight, 2007; Jing et al., 2015). For example, at the ecosystem scale, soil microbial community composition and diversity are mainly controlled by the vegetation, primarily due to changes in plant litter and root exudates affecting the growth and activity of soil microbes (Bainard et al., 2016; Deng et al., 2016). At the regional scale, some abiotic factors (soil pH, soil temperature and moisture, inorganic nitrogen and phosphorus, etc.) are more important for regulating the microbial community assembly than vegetation (Fierer and Jackson, 2006; Martiny et al., 2011; French et al., 2017). However, some studies have demonstrated that different inputs of plant-derived organic carbon exert more significant effect on microbial communities and composition than soil properties (Snajdr et al., 2013; Urbanova et al., 2015). Generally, litter (with low C: N ratio) input significantly facilitates the relative abundance of bacteria with a high-growth rate, while litter (with high C: N ratio) input advances those bacteria with a low-growth rate (Fanin and Bertrand, 2016; Zhang

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et al., 2016). Accordingly, plant traits and diversity that affect soil microbial community composition and diversity can differently interact with soil properties in various terrestrial ecosystems (Fanin and Bertrand, 2016; Supramaniam et al., 2016).

Soil microbial community structure is influenced primarily by niche-related and neutral processes in marine and terrestrial ecosystems (e.g. Stegen et al., 2012; Wang et al., 2013a; Tripathi et al., 2015). The classical perspective hypothesizes that microbes lack dispersal limitation because their unique characteristics, such as their small size and high local abundance, may lead to high dispersal and low extinction rates (Martiny et al., 2006; Lindstrom and Langenheder, 2012). However, numerous recent studies have revealed that stochastic processes and dispersal limitations are important factors in structuring the assembly of microbial communities. Dispersal limitation plays an important role in shaping the biogeographic patterns of micro-organism dynamics, including fungi (Peay et al., 2010; Adams et al., 2013), nematodes (Nielsen et al., 2014), and bacteria (Bell, 2010). Thus, large dispersal and environmental factors collectively may have significant effects on bacterial community structure (e.g., Bell, 2010; Chase and Myers, 2011; Hao et al., 2016).

A community phylogenetic structure test is used to test or disentangle the relative importance of underlying niche-related and neutral processes in shaping community structure (Stegen et al., 2012; Wang et al., 2013a). The variation in the relative influences of deterministic and stochastic processes across environmental gradients can be inferred by comparing them with randomization procedures (null models) (Chase and Myers, 2011; Stegen et al., 2012). If a community structure deviates from a randomization process, a nonrandom community phylogenetic structure is expected to indicate the occurrence of a niche-based process, such as competitive interaction or environmental filtering; otherwise, a stochastic process governs the microbial community structure (Chase and Myers, 2011; Lindstrom and Langenheder, 2012; Nemergut et al., 2013).

The grasslands of southern China are distributed over a vast geographical area in thirteen provinces of China and cover more than 1/6 of the total grassland areas of China (Sun et al., 2015). Grasslands of southern China are characterized by fragmented habitats with a wide soil pH variation range and variable nutrients compared to northern grassland in China (Zhang et al., 1998; Sun et al., 2015; Xiong et al., 2017). These grasslands are also characterized by high productivity and make an important contribution to the global soil carbon and nitrogen stocks due to the good hydrothermal conditions (Zhang et al., 1998; Sun et al., 2015). However, little is known about the underlying mechanisms by which environmental factors impact the soil microbial community assembly in this area. To address this scientific issue, we investigated the drivers of the patterns of the bacterial community composition and diversity at this regional extent. In addition to evaluating phylogenetic signals and inferring ecological processes, we also quantified the relative roles of deterministic and stochastic processes in constructing these communities. We hypothesized that a high fragmentation of patch habitats would result in dispersal limitation, which could play an essential role in structuring the bacterial community. The objectives of this study were to examine (1) the bacterial community composition and diversity in the grasslands of southern China and related plant and soil variations related to taxonomic and phylogenic β diversity; (2) the relative roles of deterministic and stochastic processes in driving the community distribution.

2. Methods and materials

2.1. Study site and sample collection

A field study was conducted on a large scale (29.3 N to 32.6 N, 107.4 E to 112.3 E) across the Chongqing Area and Hubei province (approximately 366.5 km from east to west and 460.7 km from north to south) with 20 sites in a grassland transect of south China (Fig. 1). The climate was predominantly continental monsoon. The elevation (Alt) of this region ranged from 120 to 1655 m, with the mean annual temperature (AMT) ranging from 8.9 to 17.4 °C and mean annual precipitation (AMP) ranging from 864 to 1522 mm. The soil types involved in this work were predominantly yellow, yellow-brown, red, purple and dark brown soils and meadow soil types (Chinese soil classification system) (Zhang et al., 1998). The vegetation across transect was dominated by herbaceous shrubs with rare small shrubs, including *Triarrhena sacchariflora, Cynodon dactylon*, *Kyllinga brevifolia*, *Bidens pilosa L.*, *Trifolium repens L.*, *Poa annua L.,* and *Artemisia annua L.*

Soil samples from 20 sites were collected in August 2015. At each sampling site, a large 50 m × 50 m plot was established, and five 1 m × 1 m subplots were selected within each large plot (located at the four corners and center of each site), and in each plot six random 5 cm-diameter soil cores were collected and just aggregated for reducing sampling errors. In each plot, latitude, longitude and altitude were recorded by GPS (eTrex Venture, Garmin, USA). The climatological data were extracted from nearest meteorological stations or a global data base (http://www.worldclim.org/) using location information (latitude and longitude. In each subplot, the plant abundance, cover, and mean height were recorded for each species. Plant aboveground biomass was clipped in summer (August), which represent the annual aboveground net primary production according to primary criteria of virtually no carryover of living biomass from previous year due to a distinct dormant season and negligible decomposition of biomass produced during the growing season (Knapp et al., 2007), and then over-dried at 70 °C to constant weight. After removing surface litter and plant residuals from each subplot, six random soil samples were taken from the 0–10 cm layer using a cylindrical soil sampler (2.5 cm diameter) and were thoroughly mixed and pooled as one composite sample for subsequent chemical and microbial analyses. Soil samples were immediately preserved at −20 °C in fridge for transport to the laboratory as soon as possible. Each sample was sieved through a 2.0 mm sieve and then separated into two parts: one was stored at −20 °C for physical and chemical analysis, and the other one was stored at −80 °C for DNA extraction.

2.2. Soil and plant physical and chemical analysis

Soil pH was measured in a soil water suspension (1:2.5 w: v) with a digital pH meter. Soil moisture was gravimetrically determined as the difference from fresh soil dried at 105 °C for 24 h. Soil ammonium (NH_4^+-N) and nitrate (NO_3^--N) were measured by a continuous flow analyzer (SAN + +; Skalar, Breda, the Netherlands) after extraction from fresh soil with a 2 M KCl solution (soil: solution, 1:5). The soil organic C (SOC) and N (SON) contents were measured as previously described (Cheng et al., 2011). In brief, aliquots (approximately 10 g) of dried soil samples were treated with 1 N HCl for 24 h at room temperature to remove inorganic carbon, and the SOC and SON concentrations were determined by an element analyzer (Vario EL, Elementar Analysensysteme, Hanau, Germany). Plant C and N were chosen from the dominant species which total biomass exceeded 80 percentage of the total biomass in community. Five plants were selected as repeats of each species in every site for plant C and N measurement. Then, we calculated the community levels' C and N content by the sum of dominant species content contribution divided by relative biomass. As for biodiversity, we calculated species Richness, Shannon Diversity and Simpson Diversity in the Vegan package.

2.3. Soil DNA extraction and MiSeq sequencing of 16S rRNA gene amplicons

For each sample, soil DNA was extracted from 0.5 g of fresh soil using an MO BIO DNA extraction kit (MO BIO Laboratories, Carlsbad, CA, USA). The concentration and quality of the extracted DNA were checked using a NanoDrop Spectrophotometer (NanoDropTechnologies