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Community structure and elevational diversity patterns of soil Acidobacteria

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ABSTRACT

Acidobacteria is one of the most dominant and abundant phyla in soil, and was believed to have a wide range of metabolic and genetic functions. Relatively little is known about its community structure and elevational diversity patterns. We selected four elevation gradients from 1000 to 2800 m with typical vegetation types of the northern slope of Shennongjia Mountain in central China. The vegetation types were evergreen broadleaved forest, deciduous broadleaved forest, coniferous forest and sub-alpine shrubs. We analyzed the soil acidobacterial community composition, elevational patterns and the relationship between Acidobacteria subdivisions and soil enzyme activities by using the 16S rRNA meta-sequencing technique and multivariate statistical analysis. The result found that 19 known subdivisions as well as an unclassified phylotype were presented in these forest sites, and Subdivision 6 has the highest number of detectable operational taxonomic units (OTUs). A significant single peak distribution pattern ($P < 0.05$) between the OTU number and the elevation was observed. The Jaccard and Bray–Curtis index analysis showed that the soil Acidobacteria compositional similarity significantly decreased ($P < 0.01$) with the increase in elevation distance. Mantel test analysis showed the most of the soil Acidobacteria subdivisions had the significant relationship ($P < 0.01$) with different soil enzymes. Therefore, soil Acidobacteria may be involved in different ecosystem functions in global elemental cycles. Partial Mantel tests and CCA analysis showed that soil pH, soil temperature and plant diversity may be the key factors in shaping the soil Acidobacterial community structure.

Introduction

Acidobacteria is one of the most dominant and abundant phyla in soil, with more than 30% or even 50% of 16S rRNA gene sequences belonging to the Acidobacteria phylum (Quaiser et al., 2003; Janssen, 2006; Stott et al., 2008; Challacombe and Kuske, 2012). Members of the Acidobacteria have also been found in aquatic (Pham et al., 2008), extreme (Hobel et al., 2005; Kishimoto et al., 1991) and polluted environments (Barns et al., 2007), as well as wastewater systems (Lapara et al., 2000). Because of their wide distribution, the

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soil Acidobacteria may be important constituents of a variety of ecosystems and drivers of different ecosystem processes (Kielak et al., 2010). Some phylogenetic analyses of 16S rRNA gene sequences have defined 26 major subdivisions of the Acidobacteria phylum (Barns et al., 2007), but the majority of subdivisions still lack cultured representatives (Kielak et al., 2010). In spite of their dominant presence, relatively little is known about their metabolic activity, elevational diversity patterns, and the responses to environment variables in soil or other environments (Kielak et al., 2009).

Elevational gradients are characterized by dramatic changes in climate and biotic turnover over short geographic distances (Bryant et al., 2008). They have played a foundation role in the development of ecological and biogeographical studies (Briggs and Humnbries, 2004), and in predicting the potential consequences of climate change (Bryant et al., 2008). At present, most of the studies of elevational diversity patterns have focused on plant and animal species (Lomolino, 2001; McCain, 2009, 2010). In recent years the development of molecular biology techniques and the extraction of DNA from bulk environmental samples have promoted the understanding of microbial elevational diversity in soil and other environments (Bryant et al., 2008; Fierer et al., 2011; Wang et al., 2012; Shen et al., 2013). Previous research has yielded two different results for acidobacterial elevational patterns, including no significant influence (Fierer et al., 2011; Shen et al., 2013) and a monotonous decrease (Bryant et al., 2008; Singh et al., 2012) with increasing elevation. These studies have focused on Acidobacteria at the phylum level and have not analyzed the trends along elevational gradients at subdivision level. Furthermore, the environmental drivers influencing Acidobacteria elevational diversity patterns remain unclear.

Shennongjia Mountain is located in the northwestern region of Hubei Province, Central China, and is in the transition belt from the sub-tropical zone to the warm temperate zone (Ma et al., 2008). The vertical vegetation distribution on Shennongjia Mountain is very distinct, from the evergreen broadleaved forest to sub-alpine shrub (Zhao et al., 2005). Therefore, Shennongjia Mountain presents an ideal location to test the soil microbial elevational patterns. In this study, we selected four elevation gradients from 1000 to 2800 m, including evergreen broadleaved forest, deciduous broadleaved forest, coniferous forest and sub-alpine shrubs. Along these gradients, we analyzed the microbial diversity distributions using the 16S rRNA meta-sequencing technique. The aims of this study were to address the following questions: (1) What are the soil Acidobacteria community composition and structure? (2) How does the diversity of soil Acidobacteria vary along elevational gradients and distance? (3) What environmental factors drive Acidobacteria elevational patterns?

1. Materials and methods

1.1. Site and sampling

The study site is located in Shennongjia Mountain (31°15′N–31°57′N, 109°59′E–110°58′E). The annual mean air temperature is 7.2°C and the annual precipitation is about 1500 mm in Shennongjia Mountain area (Ma et al., 2008). The vertical vegetation distribution is very distinct, including evergreen broadleaved forest, deciduous broadleaved forest, conifer forest and sub-alpine shrubs from altitudes 200 to 2800 m, and the plant species habitats are natural and mature (Zhao et al., 2005).

In this study, four elevation gradients were selected combined with the typical plant types on the northern slope of Shennongjia Mountain, including evergreen broadleaved forest (EBF), deciduous broadleaved forest (DBF), coniferous forest (CF) and sub-alpine shrubs (SAS). The soil type is mountain yellow brown soil (Zhao et al., 2005), and the detailed information on these sites is listed in Table 1. At each site, eight plots (20 × 20 m) were established and the distance between adjacent plots was about 20 m. In each plot, ten to fifteen soil cores at a depth of 0–10 cm were taken, mixed thoroughly and remove roots and stones. Soil samples were preserved at −80°C until DNA extraction.

1.2. Plant diversity and soil geochemical analyses

Plant diversity was surveyed at each plot, including the plant species, number, height and canopy of each tree or shrub, and diameter at breast height of trees (DBH > 5 cm) and shrubs (DBH > 1 cm). Average soil temperature at each plot was measured by placing a Long-Thermometer probe at 10 cm depth in relatively open patches. The soil moisture, soil pH, total soil organic carbon, total nitrogen, available nitrogen and soil enzyme activities of cellulase, glucanase, polyphenol oxidase and amylase were measured as previously described by Bao (1999), and the data were presented in Table S1.

1.3. DNA extraction, purification and quantification

Soil microbial genomic DNA was extracted by freeze-grinding mechanical lysis as described previously (Zhou et al., 1996). The crude DNA was purified using a minicolumn purification method (Zhou et al., 1996).

1.4. The DNA sequencing and data analysis

Based on the V4 hypervariable region of bacterial 16S rRNA, the PCR primers, F515: GTGCCAGCMGCCGCGG, and R806: GGACTACHVGGGTWTCTAAT were selected and tagged (Caporaso et al., 2011, 2012). The amplification mix contained 10 units of AccuPrime High Fidelity Taq polymerase (Invitrogen, Grand Island, USA) and 10 ng Genomic DNA. The PCR products were purified and run using a Miseq Benchtop for 2 × 150 bp paired-end sequencing (Illumina, San Diego, USA). All sequences were aligned using the RDP Infernal Aligner, and complete linkage clustering was used to define Acidobacteria OTUs with 97% identity as a cutoff (Deng et al., 2012). The number of detected OTUs and sequences of Acidobacteria at different levels of classification were counted. Details of amplicon preparation, sequencing and data analysis were described in He et al. (2010) and Deng et al. (2012).

1.5. Statistical analysis

Soil Acidobacteria community structure was calculated using the Shannon–Weaver index (H′) with online software (http://ieg.ou.edu/). Detrended Correspondence Analysis (DCA) was used to determine the changes in Acidobacteria community structure along different elevational gradients. We used the Bray–Curtis similarity index to calculate distance matrices from OTU data for the Multi-Response Permutation Procedure (MRPP) (McCune and Grae, 2002) and ANOSIM and adonis (Anderson, 2001) to examine whether significant effects on soil microbial community existed in these sites. Partial Mantel tests and canonical correspondence analysis (CCA) were used to evaluate the linkages between soil Acidobacteria community structure