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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

Table 1 – Site information in this study.

Study site	Vegetation type	Dominant community of tree and shrubs	Elevation
Liangfengya	Sub-alpine shrub (SAS)	*Rhododendron oreodoxa*	2736–2777 m
Jinhouling	Coniferous forest (CF)	*Abies fargesii* Franch	2530–2590 m
Jiuhuping	Deciduous broadleaved forest (DBF)	*Carpinus viminea*, *Quercus aliena* var. *acuteserrata*, *Fagus engleriana*	1725–1844 m
Wanjiagou	Evergreen broadleaved forest (EBF)	*Cyclobalanopsis oxyodon* (Miq.) Oerst, *Cyclobalanopsis myrsinaefolia* (Blume) Oerst, *Styrax suberifolius*	1009–1057 m

and environmental factors. All analyses were performed in the Vegan package (v.1.15-1) in R (v.2.9.1) (http://www.r-project.org/).

2. Results

2.1. Soil Acidobacteria community composition and structure

To determine the soil Acidobacteria community composition and structure in the Shennongjia Mountain soil, the soil microbial communities were analyzed by 16S rRNA gene meta-sequencing. A total of 4480 Acidobacteria OTUs were detected (Table 2). Phylogenetic analysis showed that 19 known subdivisions as well as an unclassified phylotype existed in these forest sites. At the subdivision level, 1268 (28.30%) OTUs were derived from Subdivision 6, a subdivision with the highest number of detectable OTUs, followed by Subdivision 1 (934, 20.84%), Subdivision 2 (898, 20.04%), Subdivision 3 (393, 8.77%) and Subdivision 4 (324, 7.23%) (Table 2). These five dominant subdivisions accounted for over 85% of all the Acidobacteria OTUs detected. Among the 19 known Acidobacteria subdivisions, 14 were detected in all sample plots. Subdivisions 9 and 20 only existed in the EBF, Subdivision 18 was only found in EBF and DBF, and Subdivisions 22 and 25 were not detected in SAS (Table 2).

To further analyze the differences in Acidobacteria composition and structure, DCA was performed with the relative abundance values of sequencing data. Four distinct clusters were formed and were well separated among samples (Fig. 1). The results of nonparametric multivariate statistical tests, MRPP, anosim and adonis, showed significant differences ($P < 0.01$) based on the abundance of all OTUs detected at 4 sampling sites (Table S2). These results showed the soil Acidobacteria community composition and structure was significantly different among these 4 study sites.

2.2. Acidobacteria diversity patterns along an elevation gradient

The soil Acidobacteria diversity patterns along an elevational gradient were analyzed by the number of sequences, number of OTU and Shannon index (Table 3). In these four sites, the sequence number ranged from 2325.25 ± 223.77 to 3621.00 ± 250.75, the OTU number ranged from 1018.88 ± 72.75 to 757.50 ± 37.81, and the Shannon index ranged from 6.78 ± 0.06

Table 2 – Numbers of Acidobacteria OTUs at subdivision level detected in four forest sites.

Subdivision	Total [a] (%)	Average [b]			
		EBF	DBF	CF	SAS
Acidobacteria	4480 (100.00)	1018.88 ± 72.75 b	757.50 ± 37.81 a	800.13 ± 36.02 a	892.25 ± 28.03 ab
Subdivision 1	934 (20.84)	70.50 ± 12.24 a	140.88 ± 14.74 b	169.50 ± 10.88 b	362.13 ± 24.59 c
Subdivision 2	898 (20.04)	56.25 ± 12.84 a	212.00 ± 29.71 b	245.00 ± 19.06 b	296.25 ± 19.06 b
Subdivision 3	393 (8.77)	59.13 ± 8.01 a	77.88 ± 5.46 a	85.75 ± 6.09 a	126.00 ± 8.14 b
Subdivision 4	324 (7.23)	126.25 ± 13.40 c	47.75 ± 9.06 b	28.50 ± 3.19 b	2.25 ± 0.37 a
Subdivision 5	69 (1.54)	22.38 ± 1.95 b	12.00 ± 1.35 a	9.75 ± 1.47 a	5.63 ± 0.92 a
Subdivision 6	1268 (28.30)	500.00 ± 73.25 c	171.25 ± 22.66 b	151.38 ± 8.10 b	42.00 ± 5.57 a
Subdivision 7	122 (2.72)	28.50 ± 1.56 a	28.63 ± 1.27 a	38.63 ± 1.41 b	23.88 ± 2.56 a
Subdivision 9	5 (0.11)	2.00 ± 0.63	0	0	0
Subdivision 10	5 (0.11)	2.00 ± 0.63	0	0	0
Subdivision 11	13 (0.29)	5.13 ± 0.91 c	2.63 ± 0.63 b	0.88 ± 0.23 a	0.50 ± 0.19 a
Subdivision 12	5 (0.11)	0	0.88 ± 0.40 b	0.50 ± 0.19 b	1.13 ± 0.30 b
Subdivision 13	22 (0.49)	0.75 ± 0.25 a	1.25 ± 0.16 a	6.38 ± 0.94 b	9.00 ± 0.53 c
Subdivision 15	30 (0.67)	5.00 ± 0.65 ab	3.38 ± 0.38 a	5.13 ± 0.64 b	4.50 ± 0.63 ab
Subdivision 16	113 (2.52)	46.75 ± 3.93 d	25.50 ± 2.21 c	17.13 ± 1.34 b	7.50 ± 1.05 a
Subdivision 17	114 (2.54)	44.13 ± 6.69 c	13.75 ± 2.84 b	15.50 ± 2.41 b	2.38 ± 0.46 a
Subdivision 18	1 (0.02)	0.75 ± 0.16 c	0.38 ± 0.18 b	0	0
Subdivision 20	1 (0.02)	0.25 ± 0.16	0	0	0
Subdivision 22	30 (0.67)	11.75 ± 1.63 c	2.75 ± 0.59 b	4.13 ± 0.61 b	0
Subdivision 25	18 (0.40)	7.25 ± 0.84 c	2.38 ± 0.75 b	1.00 ± 0.27 ab	0
Unclassified	26 (0.58)	5.25 ± 0.82 b	2.00 ± 0.63 a	1.88 ± 0.44 a	1.50 ± 0.19 a

The same lowercase letters within the same row mean the difference of subdivision was not significant, whereas the difference was significant ($P < 0.05$).

[a] Data represent total numbers of Acidobacteria OTUs detected by meta-sequencing across all 32 samples.

[b] Data represent the mean value and standard error of OTUs detected using 8 samples in different forest sites.

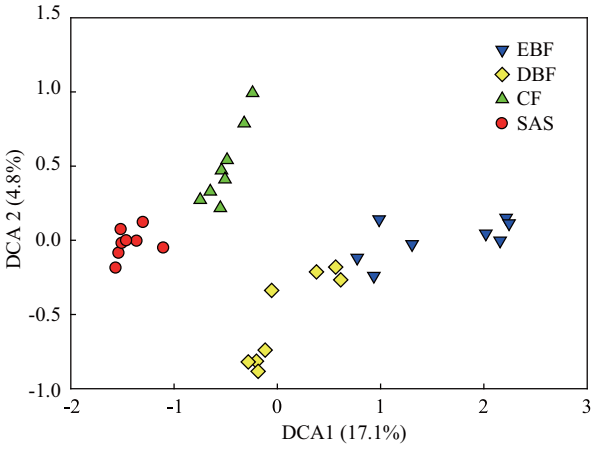

Fig. 1 – DCA analysis of soil Acidobacteria community structure based on the relative abundances of OTUs detected by meta-sequencing.

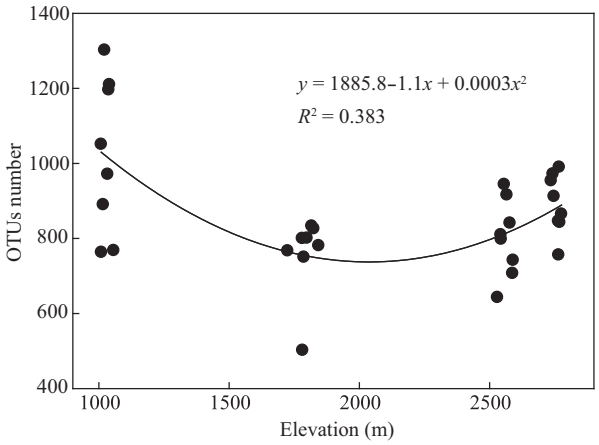

Fig. 2 – Acidobacterial diversity pattern of OTU numbers along the elevational gradients on Shennongjia Mountain.

to 6.51 ± 0.05. A significant single peak distribution pattern ($P < 0.05$) between the OTU number and the elevation at different sample sites was observed (Fig. 2, Table 3).

The Acidobacteria diversity patterns at subdivision levels along an elevational gradient in four sites were varied. We observed three different results for soil Acidobacteria elevation patterns at the subdivision level, for example, the dominant Subdivisions 1, 2 and 3 showed a monotonous increase with increasing elevation, the dominant Subdivisions 4, 5, 6, 16, and 17 showed a monotonous decrease with increasing elevation, and the dominant Subdivisions 7 and 10 showed no significant trend with elevation change (Table 2).

2.3. β-Diversity patterns of Acidobacteria along an elevational distance gradient

To detect the β-diversity among different sites along an elevational gradient, we analyzed the soil Acidobacteria β-diversity using the Jaccard and Bray–Curtis index. The Jaccard and Bray–Curtis index ranged from 0.526 to 0.624 and 0.377 to 0.490 within these sites, and from 0.748 to 0.914 and from 0.599 to 0.848 between different sites (Table S3), respectively. The pairwise Acidobacteria compositional dissimilarities across the whole elevational gradient significantly ($P < 0.001$) increased with the corresponding changes in elevational distance (Fig. 3). Thus, the soil Acidobacteria phylum showed a significant elevational distance–decay relationship.

Table 3 – Summary of Acidobacteria numbers of sequences, OTUs and Shannon index at 4 different forest soil sites.

Sample site	No. of sequences	No. of OTUs (0.03)	Shannon index
EBF	3196.63 ± 403.83	1018.88 ± 72.75	6.78 ± 0.06
DBF	2325.25 ± 223.77	757.50 ± 37.81	6.51 ± 0.05
CF	2384.50 ± 211.02	800.13 ± 36.02	6.56 ± 0.04
SAS	3621.00 ± 250.75	892.25 ± 28.03	6.62 ± 0.03

2.4. Linking between the Acidobacteria community structure and environmental factors

The relationships between OTUs of dominant Acidobacteria subdivisions and soil key enzyme activities were analyzed using the Mantel test (Table 4). We analyzed the enzyme activities of polyphenol oxidase, sucrase, amylase and glucanase, and the results showed that the OTUs of dominant soil Acidobacteria subdivisions have various relationships with the enzyme activities. For example, OTU number of Subdivision 1 was significantly correlated ($P < 0.01$) with polyphenol oxidase activity, OTU number of Subdivision 2 was significantly correlated ($P < 0.05$) with sucrose and glucanase enzyme activities, OTU number of Subdivision 6 is significantly correlated ($P < 0.01$) with amylase activity, and amylase activity was significantly correlated ($P < 0.05$) with most of the subdivisions. Therefore, soil Acidobacteria may be related to different ecosystem functions in global elemental cycles.

Partial Mantel test was performed to analyze the major environmental factors responsible in shaping soil Acidobacteria community structure along an elevational gradient. The results of the Partial Mantel test showed that soil Acidobacteria was significantly correlated with soil ($P < 0.01$) and plant ($P < 0.05$) factors (Table S4). However, the relationship between different subdivisions and soil or plant factors is variable (Table S4). For example, Subdivisions 1, 2 and 3 are significantly influenced ($P < 0.05$) by soil and plant factor and Subdivisions 4, 5, 6, 16 and 17 are significantly influenced ($P < 0.01$) by soil factor.

CCA was used to identify the major environmental variables controlling the soil Acidobacteria microbial community structure. The plant Shannon index, soil temperature, soil pH and soil moisture appeared to be the important environment factors controlling the microbial community structure since they had a long projection on Axes 1 and 2, which represented the major variation among microbial communities (Fig. 4).

3. Discussion

Acidobacteria is one of the most dominant and abundant phyla in soils and 26 major subdivisions have been defined

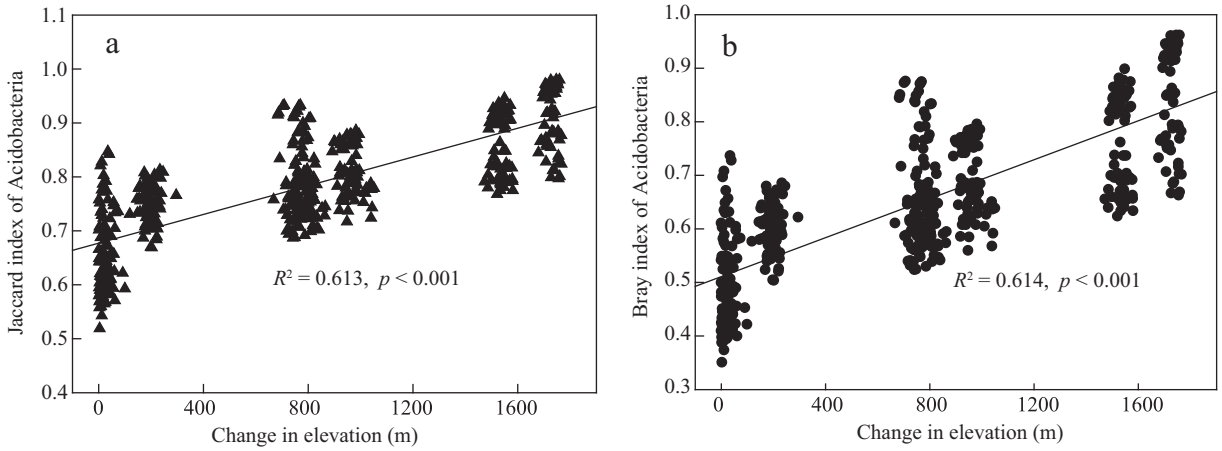

Fig. 3 – Relationships between the ß-diversity of Jaccard (a) and Bray–Curtis (b) and change in elevation distance.

based on 16S rRNA gene sequences (Barns et al., 2007). A large number of reports showed that the most dominant subdivisions in different soil environments are different. Barns et al. (2007) surveyed two soil samples in New Mexico and Utah and showed that Subdivisions 4 and 6 comprised 42.8% and 45.6% of sequences in Acidobacteria 16S rRNA gene libraries. Eichorst et al. (2011) found that the proportion of subdivision 4 sequences was the highest in agricultural soil that contained less carbon than grassland soils. Our results showed that Subdivision 6 is the most dominant in Shennongjia Mountain soils, and the prevalence of Subdivision 6 is consistent with the previous studies (Eichorst et al., 2007; Hansel et al., 2008). Sang-Hoon and Cho (2009) revealed that Acidobacterial Subdivision 1 could be globally distributed and has been frequently observed at high abundance in soil environments, indicating that this subdivision might be well adapted to various soil environments. Therefore, the Acidobacterial Subdivisions of 1, 4, and 6 may be the most dominant groups in the soil environment.

Microbial diversity patterns along elevational gradients are an extremely interesting and widely debated topic for ecologists, as they are among the fundamental rules underlying microbial biogeography (Martiny et al., 2011). At present, several studies on acidobacterial elevation patterns at phylum level have been reported and the trends were variable (Fierer et al., 2011; Wang et al., 2012). In this study, we found different trends at the subdivision level and this is the first time, to our knowledge, that the elevation patterns have been analyzed at the subdivision level. Three trends for Acidobacteria elevational patterns at the subdivision level can be summarized: no significant influence (Subdivisions 7 and 10), a monotonous decrease (Subdivisions 1, 2 and 3) and increase (Subdivisions 4, 5, 6, 16 and 17) with an increase in elevation. The acidobacterial elevation patterns are determined by different trends in the subdivision elevational patterns. In diverse soil environments, the most dominant subdivision is variable, which leads to different elevational patterns for Acidobacteria. Further study is needed to analyze the subdivision elevational pattern in different soil environments.

Based on the phylogenetic diversity and ecological distribution, Acidobacteria is expected to have a wide range of metabolic and genetic functions (Hugenholtz et al., 1998; Barns et al., 1999). Genomic evidence from cultured bacteria suggested that the role of Acidobacteria Subdivisions 1 and 3 in nitrogen cycling in soil and sediment is to facilitate the reduction of nitrate, nitrite, and possibly nitric oxide based on three complete genome sequences of isolates of "*Solibacter usitatus*" (Subdivision 3), "*Korebacter versatilis*" (Subdivision 1), and "*Acidobacterium capsulatum*" (Subdivision 1) (Ward et al., 2009). Eichorst et al. (2011) revealed that Subdivisions 1 and 3 have the potential to play an active role in the degradation of plant polymers in bulk soil and in utilization of sugars from

Table 4 – Relationships of soil Acidobacteria subdivisions and soil enzyme activities by Mantel test.

Subdivision	Polyphenol oxidase activity		Sucrase activity		Amylase activity		Glucanase activity	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Subdivision 1	0.364	0.007						
Subdivision 2	0.108	0.082	0.108	0.039	0.112	0.080	0.190	0.004
Subdivision 3	0.153	0.042	0.083	0.099				
Subdivision 4					0.521	0.004		
Subdivision 5					0.253	0.062		
Subdivision 6					0.573	0.002		
Subdivision 7			0.145	0.051	0.217	0.043	0.157	0.039
Subdivision 10					0.663	0.001		
Subdivision 16			0.113	0.093	0.516	0.001		
Subdivision 17					0.594	0.001		

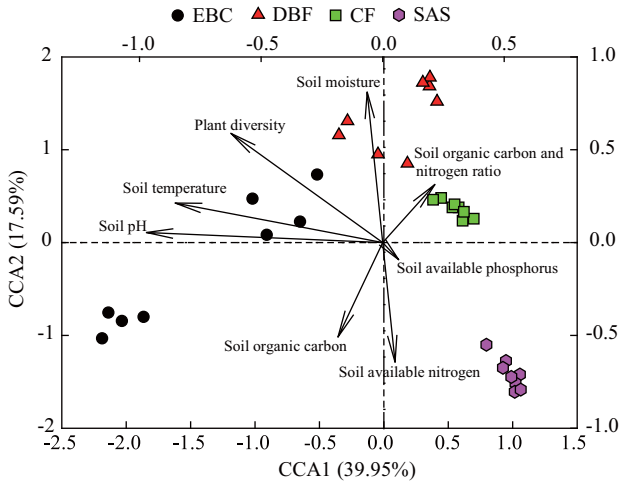

Fig. 4 – Canonical correspondence analysis (CCA) of acidobacterial microbial diversity and soil environmental variables.

plant root exudates at various concentrations in the rhizosphere. However, the ecological roles and metabolic activities of uncultured bacteria in the natural environment are still unknown, especially in soil (Lee et al., 2008). Soil enzymes, mainly from soil microorganisms, play a crucial role in maintaining nutrient cycling and can reflect the circumstances of biological metabolism and substance transformation in soil environments. Our results showed that different soil Acidobacteria subdivisions have various correlations with several key soil enzyme activities. Subdivisions 4, 5 and 6 are only correlated ($P < 0.1$) with amylase activity, which are hydrolytic enzymes that promote the decomposition of starch. Subdivisions 2, 3, 7 and 16 are correlated ($P < 0.1$) with the sucrase activity, which is an extracellular enzyme that catalyzes the hydrolysis of sucrose and fructose, and the increased activity of sucrase may be ascribed to the increased total organic carbon and soil fertility in soil (Ge et al., 2009). Therefore, soil Acidobacteria at the subdivision level may be involved in different ecosystem functions in global elemental cycles.

Elevational patterns on mountainsides could be influenced by other environmental driving factors (Singh et al., 2012), and climatic and biotic factors may be the major drivers (Bryant et al., 2008; Rahbek, 2005). Soil pH is one of the key factors to influence Acidobacteria community composition and structure. Our studies showed that the responses of subdivisions to soil pH are different. Subdivisions 1, 2 and 3 are significantly positively correlated ($P < 0.01$) with soil pH, and the other subdivisions are significantly negatively correlated ($P < 0.01$) with soil pH, except for Subdivision 7. The previous studies also showed that soil pH is a strong indicator of Acidobacteria community composition (Yin et al., 2010). Sait et al. (2006) found that Subdivision 1 was strongly related to soil pH, and these bacteria appear to be numerically abundant in soils with pH below 6. Bryant et al. (2007) observed that Subdivision 4 was more abundant in arid soils, and was not detected in soils with pH of less than 4.0 (Barn et al., 1999). The abundance of Subdivisions 1, 2, 3, 12, and 13 was negatively correlated with pH, while Subdivisions 4, 6, 7, 10, 11, 16, 17, 18, 22 and 25 had positive correlations with pH (Jones et al., 2009; Lauber et al., 2009). In addition, multiple members of the Acidobacteria have been found to be abundant in alkaline soils (Dunbar et al., 1999, 2002).

Plant communities can influence associated soil microbial communities through the types and amounts of carbon and nutrient inputs, and by changing temperature and water content of the soil (Myers et al., 2001; Waldrop and Firestone, 2004). Different plant species can be associated with different communities as evidenced by fatty acid (Myers et al., 2001), and physiological (Waldrop and Firestone, 2004) and DNA techniques (Kuske et al., 2002). Therefore, the different plant types along elevation gradient are an important factor in shaping the microbial elevation patterns. Recent studies showed that the Acidobacteria is in general oligotrophic. For example, the proportions of Acidobacteria were reported to be significantly lower in nutrient-rich rhizosphere soils than in bulk soils (Kielak et al., 2009), and were less abundant in more nutrient-rich agricultural soils (Lopez-Lozano et al., 2013). Eichorst et al. (2011) examined correlations between the percentages of Subdivision 4 with various edaphic properties and found that carbon availability appeared to be one of the factors influencing the Acidobacteria community composition. Our studies showed that Acidobacteria is significantly correlated with plant diversity.

4. Conclusions

In summary, Acidobacterial diversity patterns along elevational gradients were analyzed by the 16S rRNA high-throughput sequencing technique. We found that the dominant subdivision in different soil environments is variable and they may be involved in different ecological metabolic processes. The Acidobacterial shannon index indicated a significant single peak in soil Acidobacteria diversity ($P < 0.05$) with an increase in elevation, and the Jaccard and Bray–Curtis index showed that the Acidobacteria compositional similarity significantly decreased ($P < 0.01$) with an increase in elevational distance. Soil pH, soil temperature and plant diversity may be the key factors in shaping soil Acidobacteria community composition and structure.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jes.2014.06.012.

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