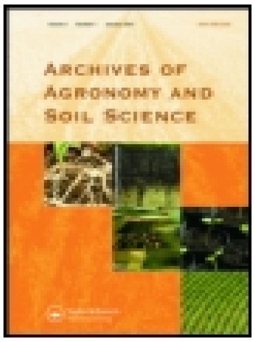

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The drivers of soil bacterial communities in rubber plantation at local and geographic scales

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Abstract

According to traditional biogeographic theory, historical contingency can influence soil microbial communities. Thus, we ask: are historical contingencies (soil profiles and geographic sampling locations), or other factors (seasonal changes and soil nutrients), important drivers of soil bacterial communities? This study used high throughput sequencing technology to investigate the soil bacterial compositions of rubber plantations at the local and geographic scales. Significant differences were detected in bacterial compositions between two study locations, Xishuangbanna and Hainan Island. Redundancy analysis showed that the most important factor driving bacterial composition was site location and total nitrogen, which explained 38.2% and 38.4% the total variance, respectively; this indicates that historical contingencies drive distinct bacterial communities in rubber plantation soils. At the local scale, there were also distinct differences in soil bacterial compositions between the dry and rainy season in both the Xishuangbanna and Hainan sites. Seasonal changes explained 13.6% and 41.4% of the total variation of soil bacterial composition in Xishuangbanna and on Hainan Island, respectively, whereas other factors had little effect on soil bacterial communities ($p < 0.001$). In conclusion, our results demonstrate that historical contingencies drive variation in bacterial composition at the geographic scale, whereas seasonal changes influence variation at the local scale.

Keywords: Xishuangbanna, Hainan Island, Rubber plantations, Soil bacteria, Historical contingency

Introduction

Rubber plantations have expanded rapidly in tropical Asia over the past two decades, and concern over their impact on the tropical environment has attracted the attention of scientists around the world (Li et al. 2015). In South China, rubber plantations are mainly distributed in Xishuangbanna and on Hainan Island, accounting for about 91.3% of the total rubber plantation area of China (Xu et al. 2014). In addition, rubber plantations account for one-third of the total flora of Xishuangbanna and about 25% of the total flora of Hainan Island (Zhai et al. 2012). Hainan Island is the largest tropical island in China (Lopez et al. 2009), and is an important biodiversity hotspot in the Indo-Burma region (Francisco-Ortega et al., 2010). The Xishuangbanna region of China is also a biodiversity hotspot within the Indo-Burma region (Myers et al. 2000). Both Hainan Island and Xishuangbanna are threatened with deforestation and environmental degradation (Li et al. 2007; Zhai et al. 2012). In addition, extensive planting of rubber plantations likely has ecological impacts on the microorganisms of soils. Soil bacteria play an important role in decomposing plant litter, by transforming it into vital nutrients which in turn can be adsorbed by plant roots (Lan et al. 2017c). In addition, bacteria which have been isolated from an agricultural area can be were used to measure microbial degradation of organic pollutants" (Erguven et al. 2016). Thus, further research on the factors controlling the distribution of soil bacteria in rubber plantations is important for forest conservation and management.

A large number of papers have been published on soil microbes in rubber plantations. Studies conducted in Indonesia (Schneider et al. 2015), Malaysia (Kerfahi et al. 2016) and South China (Lan et al. 2017a; Lan et al. 2017b; Lan et al. 2017c), have found significant differences between rubber plantations and tropical forests—in particular, the diversity of soil bacteria was higher in rubber plantations than in rainforest. Previous studies have also revealed that the microbial diversity of rubber plantations is influenced by both biotic and abiotic factors, such as soil pH (Lan et al. 2017c), seasonal changes (Lan et al. 2018), stand age (Zhou et al. 2017), and soil nutrition (Lan et al. 2017a; Lan et al. 2017b; Lan et al. 2017c). However, almost all studies on the composition and diversity of rubber plantations simply document the effects of forest conversion and other abiotic factors on soil microbial compositions; as such, they cannot reveal the mechanisms for how geographical distance influences patterns of microbe communities.

In recent years, one of the challenges of soil ecology research is to understand the mechanisms driving patterns of microbial distribution across large spatial scales (Gao et al. 2016). Previous studies have shown that geographical distance plays an important role in structuring microbial assemblages (Ge et al. 2008; Fierer and Jackson 2006). For example, the similarity of soil bacterial communities in China significantly declines with increasing geographic distance (Wang et al. 2017). Due to their different geographical locations, Xishuangbanna and Hainan Island have dissimilar climates. Hainan has a tropical marine monsoon climate; its latitude and elevation is low, and, because of its proximity to the sea, it has higher average temperature and precipitation than Xishuangbanna. Xishuangbanna has a tropical monsoon climate, with low wind speeds and rich and fertile soils (Huang et al. 1980). Long-term regional climate history is an important factor in shaping soil microbial communities, which could explain significant proportions of the variation in soil bacterial composition and richness (Martiny 2016). A recent study demonstrated that a wide range of soil bacterial taxa show predictable and consistent preferences for particular temperature conditions (Oliverio et al. 2017), and there is evidence that both current climate and paleoclimates explain a unique proportion of the variation in soil bacterial communities (Delgado-Baquerizo et al. 2017). However, due to the complex exploitation history and diverse physicochemical properties of rubber plantations soils, there is limited knowledge about how microbial communities in rubber plantations are influenced by spatial distance and environmental variables.

Understanding the relative influences of contemporary disturbance and historical contingency is at the core of biogeography (Martiny et al. 2006). Contemporary disturbances include application of fertilizers, such as N, P, K, or organic manure, as well as cultivation management. However, historical contingencies can result in different soil profiles at different geographic sampling locations (Ge et al. 2008). In this case, the contemporary disturbances of rubber plantations in Xishuangbanna and Hainan Island should be similar, because rubber plantations at the two locations were managed in a similar fashion. Therefore, we wondered whether historical contingency was the main factor affecting soil bacterial communities in rubber plantations, i. e., whether geographical distance is related to distinct variation in soil bacterial composition. On the other hand, at local scales, the heterogeneity of soil is low due to the reduced distance among soil sampling locations—in this case we wondered whether seasonal change would be the main driving factor for soil bacterial compositions. In all, we focused on the effects of distance (geographical and local) on soil bacterial compositions and diversity based on an analyses of high throughput sequencing technology. Here, we aim to understand what factors control the soil bacterial compositions and diversity of rubber plantations in tropical regions of China at both local and geographical scales. We tested the following hypotheses: (1) historical contingency is the main driving factor of soil bacterial community, which would result in distinct bacterial compositions at the geographical scale (2) at the local scale, seasonal changes would be the main factors influencing the soil bacterial community. Our results provide important knowledge that can be used to maintain the health and stability of soil ecosystems, as well as guide decisions for managers of rubber plantations.

Materials and Methods

Study site

We measured soil bacteria community composition at two sites. The first site is located in Menlun town, Xishuangbanna Dai national minority autonomous prefecture, south of Yunnan province. This site borders Myanmar to the southwest and Laos to the southeast. The second site is located in Danzhou, on the northwestern quarter of Hainan Island. Xishuangbanna has a tropical monsoon climate with two seasons: dry (November to April) and rainy (May to October). Mean annual temperature is 21.0 °C and mean annual precipitation is 1532 mm; about 80% of this precipitation occurs during the rainy season (Zhang and Cao 1995; Cao and Zhang 1997; Zhu 2006; Zhu et al. 2006). Hainan Island is the largest tropical island in China, with an area of 33,920 km^2 (Lopez et al. 2009). The island is an important biodiversity hotspot of the Indo-Burma region (Francisco-Ortega et al. 2010). Hainan Island has a tropical marine monsoon climate. Similar to Xishuangbanna it has a dry season from November to April and rainy season from May to October (Luo 1985). The annual average temperature is 23.5 °C and the mean annual precipitation is 1815 mm; approximately 84% of this precipitation accumulates in the rainy season.

Sample collection

In order to test the first hypothesis, i.e. historical contingency is the main driving factor of the soil bacterial community at the geographical scale, we established a total of 22 plots (20 × 20 m each) at the two sites; 12 of these plots were in Danzhou, Midwest of Hainan Island and the remaining 10 were in Menglun town, Xishuangbanna, southwest of China. In order to test the second hypothesis that seasonal change is the main driving factor at the local scale, we had to minimize the contribution of other factors affecting the soil bacterial communities; therefore we selected these soil samples within 1 square kilometer. All rubber plantation soils in Xishuangbanna and on Hainan Island are ulitisols (FAO, 1998). Soil samples at 0 to 20 cm depths were collected in the dry season (from March to April) and rainy season (from May to September). We randomly selected five soil samples at each plot, then mixed these five soil samples into one composite sample. This resulted in a total of 44 composite soil samples; 20 samples from Xishuangbanna and 24 samples from Hainan Island. Previous research showed that soil nutrition is important for soil bacterial compositions and diversity (Lan et al. 2017a). Therefore, relationships between soil nutrition and bacterial compositions were analyzed to confirm whether soil nutrition is important for soil bacterial communities at the geographical and local scale. Soil properties, such as total nitrogen (TN), total phosphorus (TP), total potassium (TK), water content (WC), soil pH (pH), available potassium (AK), available phosphorus (AP), were determined by following soil analysis methods described in Lu (1999). Alkaline hydrolyzation diffusion method was used to analyze the hydrolytic nitrogen (Hy_N) (Lu 1999). Soil properties are shown in Table 1.

DNA extraction and PCR amplification using Illumina MiSeq sequencing

Soil bacterial DNA was extracted from 0.5 g of fresh soil with the E.Z.N.A.®Soil DNA Kit (Omega Bio-tek, Norcross, GA, USA). We selected the universal primers 338F (5’-ACTCCTACGGGAGGCAGCAG-3’) and 806R (5’-GGACTACHVGGGTWTCTAAT-3’) to amplify the V3-V4 hypervariable regions of the bacteria 16S rRNA gene (Xu et al. 2016). The PCR reactions were performed in triplicate, and samples were analysed in a 20 μL mixture containing 4 μL of 5 × FastPfu Buffer, 2 μL of 2.5 m MdNTPs, 0.80 μL of each primer (5 μM), 0.4 μL of FastPfu Polymerase, and 10 ng of template DNA (Lan et al. 2017c). Amplicons were extracted from 2% agarose gels and purified using the AxyPrep DNA GelExtraction Kit (Axygen Biosciences, Union City, CA, USA) according to the manufacturer’s instructions. Amplicons were quantified using QuantiFluor™ -ST (Promega, USA) (Lan et al. 2017c). Purified amplicons were pooled in equimolar and paired-end sequenced (2 × 250) on an Illumina MiSeq platform at Shanghai Majorbio Bio-pharm Technology Co., Ltd. We deposited the raw reads data into the NCBI Sequence Read Archive (SRA) database (Accession Number: SRP108394, SRP117120).

Statistical and bioinformatics analysis

Raw fastq files were de-multiplexed and quality-filtered (removing sequences with a mismatch to the barcode or primer sequence) using QIIME (version 1.17). Singleton sequences and sequences within an expected error greater than 0.5 were removed. Operational Taxonomic Units (OTUs) were defined as units with 97% similarity (Stackebrandt et al. 1994), based on a cutoff using UPARSE (Edgar 2013). Chimeric sequences were identified and removed using UCHIME (Edgar 2013). In order to identify the taxonomic composition of the bacterial community, the phylogenetic affiliation of each 16S rRNA gene sequence was analysed by RDP Classifier against the SILVA database using a confidence threshold of 70% (Amato et al. 2013). To estimate the diversity of the bacterial community, the coverage percentage, Shannon’s diversity, Simpson index as wells as ACE were calculated for each sample using MOTHUR (Schloss et al. 2009). The coverage percentage was defined using Good’s method (Good 1953).

Based on the UniFrac dissimilarity values, Principal Coordinate Analysis (PCoA), was performed to reveal the spatial variation between the microbial communities from the two study sites and seasons. By using the ‘Vegan’ package within R, redundancy analysis (RDA) was used to reveal correlations between the microbial communities and environmental factors. To further confirm that there is a significant difference between taxonomic compositions of bacterial communities from the two sites and seasons, we used analysis of similarities (ANOSIM).

Results

Taxonomic composition

DNA was extracted from rubber plantation soil samples from sites located in Xishuangbanna and on Hainan Island. The MiSeq platform was used for 16S rRNA gene sequencing. There was a total of 6,34,472 quality-filtered and chimera-checked 16S rRNA gene sequences obtained from 44 soil samples. The number of sequences for each sample was highly variable, from 9,898 to 23,673. Among all DNA samples, there were a total of 1,692 OTUs belonging to 628 species, 340 genus, 219 families, 110 orders, 57 classes, and 25 Phyla. At the geographical scale, the proportion of the dominant phylum differed between the two sites (Figure 1A). The most abundant phylum in Hainan was Proteobacteria (34.1%), followed by Acidobacteria (25.8%), and then by Chloroflexi (12.1%). The most abundant phylum in Xishuangbanna was also Proteobacteria (22.9%), however the next most abundant was Firmicutes (22.1%), followed by Actinobacteria (21.2%), and then by Acidobacteria (10.8%). The percentage of Acidobacteria in Hainan was more than twice that of Xishuanbanan ($p < 0.001$). However, the percentage of Firmicutes in Hainan (2.7%) was much lower than in Xishuangbanna ($p < 0.001$) (Figure 1a). At the local scale, the proportion of the dominant phylum differed between dry and rainy seasons in both Hainan Island (Figure 1b) and Xishuangbanna(Figure 1c).

At the geographical scale, principal coordinates analysis (PCoA) of the soil bacterial communities also showed considerable spatial variation in bacterial taxonomic compositions, at the phylum level between the two sites (Figure 2a). The PCoA results show that the soil samples from the two sites occupied different portions of coordinate space, indicating that the two sites have dissimilar bacterial compositions. On Hainan Island, PCoA results showed soil samples distributed in different regions of the panel (Figure 2b). In Xishangbanna, soil samples appear mixed throughout the panel. (Figure 2c). However, the ANOSIM results confirmed that there are significant difference between dry and rainy seasons at $p < 0.01$ (Table 2).

Bacterial diversity

Our results showed that there were no obvious differences in the ACE index between soil bacterial communities from Xishuangbanna and Hainan Island (Figure 3a, b). However, the Shannon index of Hainan was higher than that of Xishuangbanna ($p < 0.001$). On Hainan Island, both ACE ($p < 0.001$) and Shannon diversity ($p < 0.05$) in the dry season was higher than in the rainy season (Figure 3c, d). However, in Xishangbanna, ACE ($p < 0.05$) and Shannon diversity ($p < 0.001$) in the dry season was lower than in the rainy season (Figure 3e, f).

At the geographical scale, the first and second axes of RDA ordination explained 52.5% and 8.5% of the total variance, respectively ($p = 0.001$) (See Figure 4a). This combination of variables explained 62.7% of the total variance of phylum abundances. Site explained 38.2%, and seasonal changes explained 7.4% of the total variance (Table 3); TN, TP and TK explained 38.4%, 13.9%, 19.1% respectively. Soil pH, SOM and WC explained 8.9%, 29.5%, and 24.1% respectively. Hy_N also was one of the most importing factors affecting soil bacterial compositions. The RDA results also revealed correlations between phylum composition and soil properties. For instance, Proteobacteria and Acidobacteria are positively correlated with TP and TK, and Firmicutes are positively correlated with WC and TN. In addition, Proteobacteria and Acidobacteria are positively correlated with soil samples in Hainan, whereas Firmicutes and Actinobacteria are positively correlated with soil samples in Xishuangbanna. At the local scale, only seasonal change is the most important factor ($p < 0.01$) affecting soil bacterial compositions (Table 3), which explained 41.4% in Hainan Island

(Figure 4b) and 13.6% in Xishuangbanna (Figure 4c).

Discussion

Effects of soil properties on bacterial community

In this study, using Illumina high-throughput sequencing of 16S rRNA genes, we analyzed the effects of geographic distance and environmental variables on the soil bacterial composition of rubber plantations in Xishuangbanna and on Hainan Island. Our results showed there is a significant difference in soil bacterial compositions and diversity of rubber plantations between the two sites. Distinct geographic sampling locations and soil profiles represent historical contingencies (Ge et al. 2008). Soils in both the Xishuangbanna and Hainan sites are the same type. However, there are significant differences in soil properties between the sites. The soil pH of Hainan is higher than in Xishuangbanna, which results in higher abundance of Acidobacteria. Soil pH explained 8.9% of the total variance of the phylum composition of the soils in rubber plantations. Our results support the general belief that soil pH is one of the most important factors affecting soil microbial diversity at a regional scale (Fierer and Jackson 2006; Tripathi et al. 2012; Cao et al. 2016). Thus, soil pH is likely the best predictor of soil diversity in acid soils (Fierer and Jackson 2006). Our results also confirmed research showing that soil pH is important in structuring soil bacterial communities in Southeast Asia (Tripathi et al 2012).

Another important factor influencing soil bacteria is water content. Water content in Hainan was lower than in Xishuangbanna—mostly due to the higher content of soil organic matter, which can improve soil's water holding capacity (Nath et al. 2014). The higher water content in Xishuangbanna resulted in a higher abundance of Planctomycetes—Aquatic bacteria—in Xishuangbanna compared to Hainan (Figure 1a). Water content explained 29.5% of the total variance of phylum composition, indicating that water content was an important factor driving differences in soil bacterial communities (Rasche et al. 2011).

Our results showed that Proteobacteria and Acidobacteria were the most abundant bacterial groups in rubber plantation soils from both sites; these results are consistent with a previous study conducted in tropical Asia (Kerfahi et al. 2016). However, the proportion of Acidobacteria in Hainan was significantly higher than in Xishuanbanna, whereas the proportion of Firmicutes in Xishuangbanna was higher than in Hainan. The Acidobacteria are believed to be oligotrophs; they are small cells and can use a wide variety of complex carbon substrates (Fierer et al. 2007). The relative abundance of Firmicutes in Xishuangbanna was significantly higher than in Hainan (which has lower soil nutrition). The Firmicutes are generally believed to be copiotrophs because they are capable of rapid growth (Mueller et al. 2015). Thus, we conclude that groups of oligotrophs dominate the bacterial community in Hainan, whereas groups of copiotrophs dominate the bacterial community in Xishuangbanna. Total nitrogen (N) was lower in Hainan than in Xishuangbanna, and our analyses showed that total nitrogen was one of the most important factors influencing soil bacterial composition, explaining 38.35% of the variance. Previous studies also found that the relative abundance of Chloroflexi had a negative correlation with soil N (Mueller et al. 2015). This may be the reason the proportion of Chloroflexi in Xishuangbanna is lower than in Hainan. Our results are consistent with previous studies that find relative abundances of Acidobacteria, Chloroflexi, and Proteobacteria decrease in soils with increasing soil N. Thus, soil N is one of the most important factors influencing soil bacterial compositions.

Effects of distance (geographical and local) on bacterial community

A key maxim of biogeography is that the present distribution pattern of species is a result of the combined effects of contemporary environmental factors and historical contingencies (Martiny et al. 2006). Therefore, the two most important factors driving distinct microbial compositions and structures are contemporary environmental disturbances and historical contingencies (Ge et al. 2008). Contemporary disturbances mainly include management activities such as fertilization, weeding, irrigation, etc., whearas historical contingency mainly includes geographical location and soil characteristics (Ge et al. 2008). In this study, contemporary disturbances at sites in Xishuangbanna and on Hainan Island were similar, because rubber plantations at these sites had similar management systems.

There is growing evidence that microbial composition, spatial distribution, and diversity are related to spatial scale (Martiny et al. 2006; Fierer and Jackson 2006). At the local scale (less than one kilometer), the main factor influencing bacterial composition was seasonal change, which explained 41.4% and 13.6% of the total variation in soil bacterial compositions in soils in Hainan and Xishuangbanna, respectively. Our results are consistent with a previous study that found that seasonal variation influences microbial community structure (Lan et al. 2018; Rasche et al. 2011; Habekost et al. 2008).

Bacterial community composition becomes more dissimilar with different environments, as species are selected from the local taxa pool based on their niche preferences (Wang et al. 2017). At the geographic scale, soil properties in Xishuangbanna and Hainan were somewhat different because differences in the environments of the two sites increases with increasing geographic distance. For example, TN, WC and soil pH of soils from Xishuangbanna were significantly higher than soils from Hainan Island, whereas TP and TK were lower. Our results revealed that geographic distance (sampling site), explained 38.2% of the total variation of bacterial compositions at the phylum level, indicating that spatial location is an important factor driving soil bacteria communities. This variation is likely because the climate and soil properties of Hainan and Xishuangbanna are different. However, our results are not consistent with a previous study conducted by Fierer and Jackson (2006), who found that environmental variables, but not geographical distance, are the main factors affecting soil microbial composition, concluding that higher similarity of environmental variables would result in higher similarity of soil bacterial communities regardless of the distance between them. However, our results are consistent with many other studies reporting that microbial community patterns are related to geographic position (Green et al. 2004; Horner-Devine et al. 2004), because distinct geographic sampling locations can be representative of historical contingencies (Ge et al. 2008). Thus, we conclude that historical contingencies drive soil bacteria community composition in rubber plantations at the geographical scale.

Conclusion

Rubber plantations located in Xishuangbanna and on Hainan Island have different climate regimes and significant differences in soil properties, which results in significant variation in soil bacterial communities. Our results clearly confirm that historical contingency is one of the main driving factors for the assembly of soil bacterial communities at the geographical scale, whereas seasonal changes are one of the most important factors influencing soil bacteria community assembly at the local scale. These results are theoretically and practically important to improve production activities of rubber plantations. In particular, managers should consider the seasonal and regional variations of soil bacterial communities when assessing microbial fertilization.

Author Contributions

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Conflict of Interest Statement

The authors declared that they have no conflicts of interest to this study.

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Table 1. General characteristics and soil properties of sampling plots in Xishuangbanna and on Hainan Island. WC: Water content; pH: Soil pH. SOM: Soil organic matter; TN: Total nitrogen; TP: Total phosphorus; TK: Total potassium; AK: Available potassium; AP: Available phosphorus; Hy_N: Hydrolytic nitrogen

Sampling sites	Precipitation (mm)	Altitude (m)	Soil pH	WC (%)	Organic matter (g/kg)	TK (g/kg)	TP (g/kg)	TN (g/kg)	AK (mg/kg)	AP (mg/kg)	Hy_N (mg/kg)
Hainan	1823	130	3.9±0.6	16.1±3.6	18.7±3.2	24.8±1.5	0.8±0.4	0.9±0.3	64.4±29.3	17.7±10.9	31.5±4.0
Xishuangbanna	1500	580	4.8±0.2	34.3±4.3	23.2±1.4	10.7±1.4	0.5±0.1	2.4±0.1	68.3±10.8	1.5±0.4	156.8±24.3

Table 2. ANOSIM results for different groups of bacterial compositions (OTU, Operational Taxonomic Units) of rubber plantation soils in Xishuangbanna and on Hainan Island (Permutation number = 999).

Geographic Scale (Hainan and Xishuangbanna)			**Local Scale (Seasonal effect on Hainan)**			**Local Scale (Seasonal effect in Xishuangbanna)**		
Levels	**R Value**	***p* Value**	**Levels**	**R Value**	***p* Value**	**Levels**	**R Value**	***p* Value**
Phylum	0.7	< 0.001	**Phylum**	0.5	0.001	**Phylum**	0.3	0.001
Family	0.9	< 0.001	**Family**	0.6	0.001	**Family**	0.3	0.003
OTU	0.9	< 0.001	**OTU**	0.5	0.001	**OTU**	0.3	0.002

Table 3. Percentage of variation in microbial communities explained by soil parameters, based on RDA results. SOM: Soil organic matter; TN: Total nitrogen; TP: Total phosphorus; TK: Total potassium; WC: Water content; pH: Soil pH. AK: Available potassium; AP: Available phosphorus; Hy_N: Hydrolytic nitrogen

Geographic Scale			**Local Scale (Hainan)**			**Local Scale (Xishuangbanna)**		
Groups	**%**	***p Value***	***Groups***	***%***	***p Value***	***Groups***	***%***	***p Value***
Site	38.2	0.001						
Season	7.4	0.001	Season	41.4	0.001	Season	13.6	0.001
TN	38.4	0.001	TN	7.7	0.082	TN	4.9	0.329
TP	13.9	0.011	TP	5.4	0.139	TP	4.9	0.384
TK	19.1	0.002	TK	8.4	0.115	TK	22.0	0.002
pH	8.9	0.001	pH	27.3	0.003	pH	9.0	0.152
WC	29.5	0.001	WC	5.2	0.209	WC	11.5	0.004
SOM	24.1	0.001	SOM	17.7	0.008	SOM	1.1	0.867
AK	6.0	0.005	AK	15.0	0.053	AK	20.1	0.017
AP	16.9	0.001	AP	3.7	0.446	AP	30.6	0.002
Hy_N	37.5	0.001	Hy_N	15.1	0.012	Hy_N	1.9	0.518

Figure legend

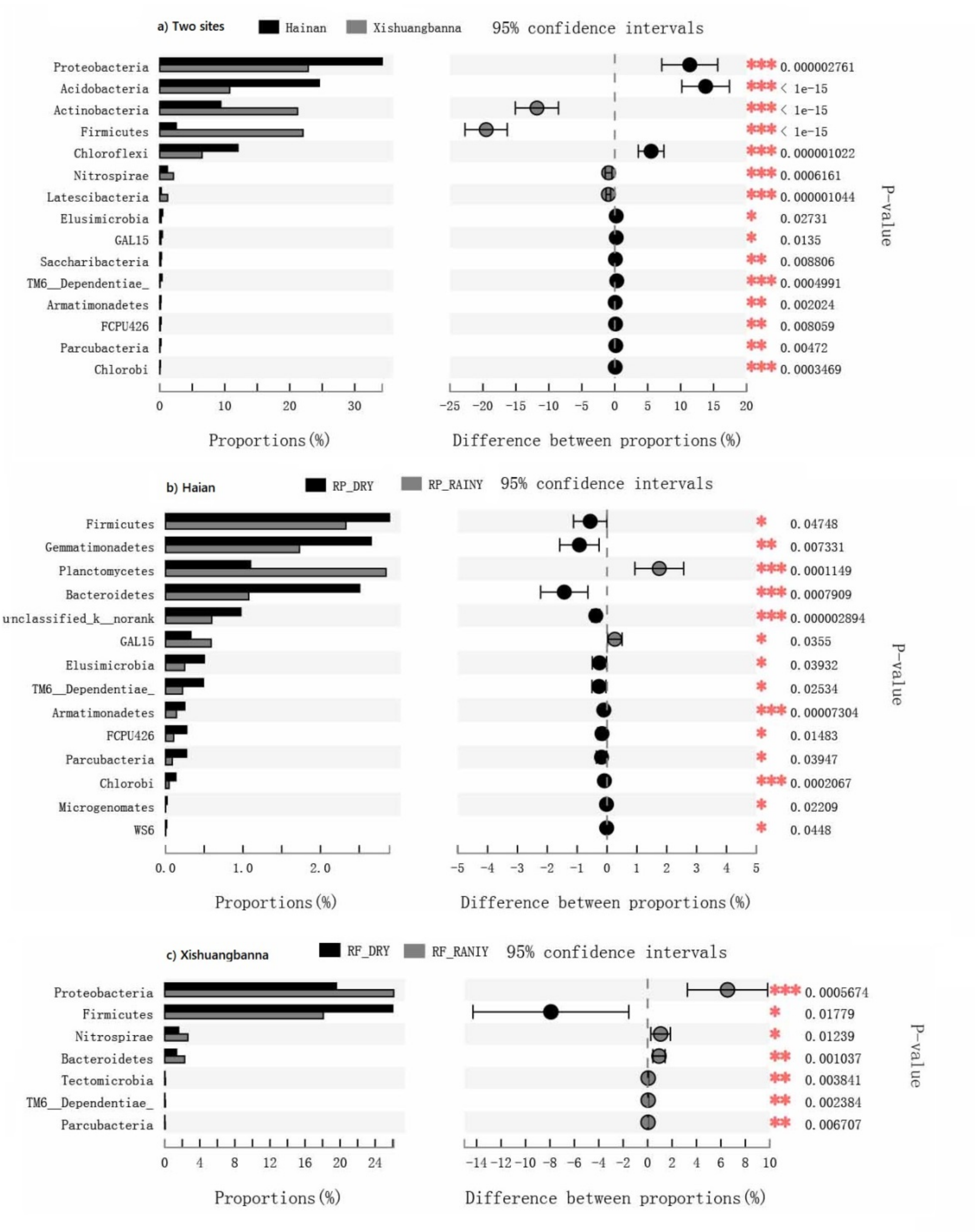

Figure 1. Soil bacterial compositions (phylum level) of rubber plantations of South China. (a: Hainan and Xishuangbanna; b: Dry season and rainy season in Hainan; c: Dry season and rainy season in Xishuangbanna) *: $p < 0.05$; **: $p < 0.01$; *** $p < 0.001$

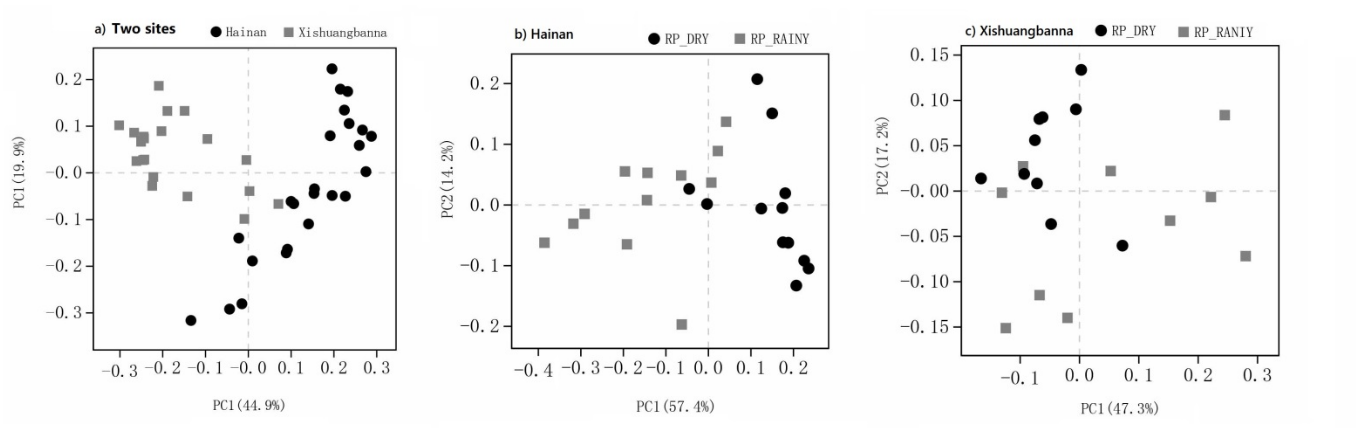

Figure 2. Principal coordinates analysis (PCoA) of the soil bacterial compositions (phylum level) in rubber plantations of South China. (a: Hainan and Xishuangbanna; b: Dry season and rainy season in Hainan; c: Dry season and rainy season in Xishuangbanna)

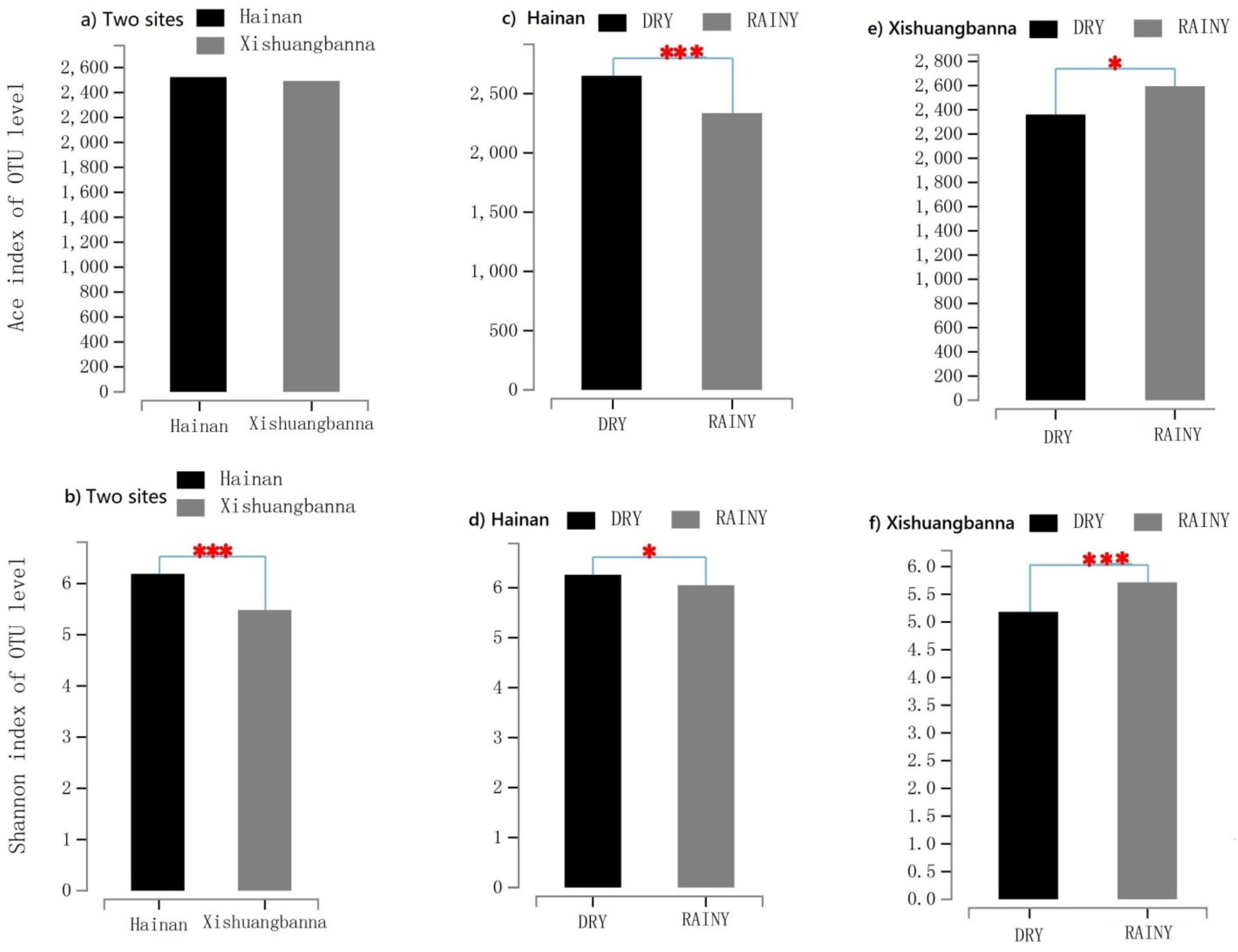

Figure 3. Diversity indices of soil bacterial communities of rubber plantation of south China. (a, b: Hainan and Xishuangbanna; c, d: Dry season and rainy season in Hainan; e, f: Dry season and rainy season in Xishuangbanna)

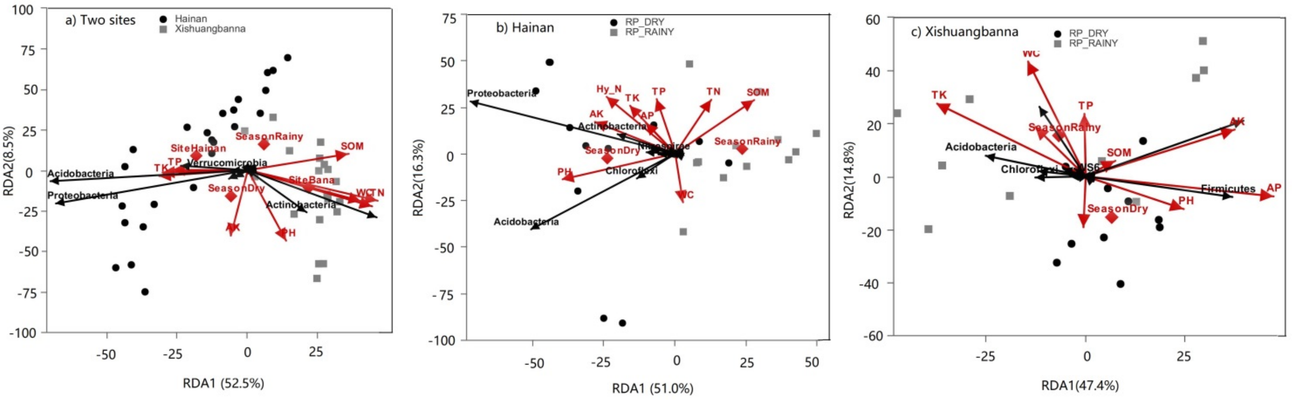

Figure 4. Redundancy analysis of the study plots and phylum compositions of soil bacteria in rubber plantations, South China. (A: Hainan and Xishuangbanna; B: Dry season and rainy season in Hainan; C: Dry season and rainy season in Xishuangbanna) SOM: Soil organic matter, TN: Total nitrogen, TP: Total phosphorus, TK: Total potassium, WC: Water content, pH: Soil Ph; AK: Available potassium; AP: Available phosphorus; Hy_N: Hydrolytic nitrogen