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REGULAR ARTICLE

Soil pH exerts stronger impacts than vegetation type and plant diversity on soil bacterial community composition in subtropical broad-leaved forests

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Abstract
Aims Soil bacterial communities play vital roles in subtropical broad-leaved forests (SBFs), however, the mechanisms regulating their formation remain poorly understood. The present work aimed to address this question.
Methods We used dIVI (Important Value Index of deciduous canopy trees) to quantitively classify three SBFs. Soil bacterial traits such as community composition, diversity and potential interactions (via network analyses) were studied. The relationship between bacterial community composition and environmental factors was analyzed.
Results SBFs were determined as a deciduous forest (DBF, dIVI = 0.99), a mixed forest (MBF, dIVI = 0.52) and an evergreen forest (EBF, dIVI = 0.19). Soil bacterial communities were different considerably among vegetation types, which was largely attributed to soil

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pH, dIVI and plant diversity, in which soil pH exerted stronger impacts than the others (coefficients of partial Mantel tests: 0.87 for soil pH versus 0.35 for dIVI, 0.26 for plant diversity). Compared to the MBF and the EBF, the DBF exhibited significantly higher bacterial diversity and more intensive potential interactions.
Conclusions This study implies that soil pH, vegetation type and plant diversity are key driving forces of soil bacterial community composition in SBFs, which improves our understanding of mechanisms regulating soil bacterial community composition.

Keywords Environmental factors · Network analyses · Soil bacterial communities · Subtropical broad-leaved forests · Vegetation types · 16S rRNA gene

Introduction

Soil bacterial communities play vital roles in forest ecosystems and influence a large number of ecosystem processes including nutrient cycling (Fang et al. 2015), soil respiration (Monson et al. 2006), plant diversity (van der Heijden et al. 2006) and plant production (van der Heijden 2008). Moreover, they represent a large part of unseen biodiversity on Earth (Horner-Devine et al. 2003). Due to the influence of environmental factors on bacterial enzyme activity, nutrient supply, *etc*, unveiling the relationship between environmental factors and soil bacterial communities has been a long-term interest of ecologists to understand the underlying mechanisms of bacterial community composition (Bardgett and Wardle 1998; Hooper et al. 2000; Li et al. 2014; Wu et al. 2018). Although studies have shown that soil bacterial communities are dynamic integrations of multiple driving forces (e.g., vegetation type, plant diversity, soil carbon (C) content, soil pH, soil nutrient availability, climate) (Delgado-Baquerizo et al. 2016; Fierer 2006; Shen et al. 2013; Wu et al. 2018), the mechanisms regulating the formation of soil bacterial communities in subtropical broad-leaved forests (SBFs) remain poorly understood.

SBFs are typical forests of the East Asian monsoon region (20°N - 40°N, 100°E - 145°E) and they play an important role in regulating the global C cycle (Yu et al. 2014). Due to the co-existence of deciduous plant species and evergreen ones (Yu et al. 2014), SBFs are further composed of deciduous broad-leaved forests (DBFs), evergreen broad-leaved forests (EBFs), and mixed evergreen-deciduous broad-leaved forests (MBFs). Previous studies have found distinctly different plant traits (e.g., photosynthetic capacity, specific leaf area, leaf mass per area and life-span) (Ge et al. 2017; Pearse and Cobb 2014; Takashima and Hikosaka 2004) and litter traits (e.g., litter quality and quantity) (Walters and Reich 1999) between DBFs and EBFs. In addition, DBFs and EBFs also exhibit distinct soil traits such as soil nitrogen (N) availability and net N mineralization rate (Grayston 2005; Mueller and Eissenstat 2012) and soil bacterial traits such as biomass and overall community composition (Ding et al. 2015). Such heterogeneity of plant, soil and bacterial traits in SBFs provides an ideal way to study the mechanisms regulating soil bacterial community formation.

A previous study has reported that soil organic matter was the strongest driving force of soil bacterial community composition in SBFs (Ding et al. 2015). Nevertheless, limited attention has been paid to MBFs, despite they are often the zonal vegetation type of SBFs (Ge et al. 2013). Comparative studies containing all the three typical vegetation types are quite necessary to understand more comprehensively the mechanisms of soil bacterial community formation in SBFs. In addition, elucidating potential interactions among myriad bacterial members via network analyses is also an essential way to understand soil bacterial community composition and structure (Wu et al. 2016). For instance, some network topological characteristics, such as modularity, node degree and positive (or negative) links, can reflect the relationship of bacterial communities with

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environments and reveal the niche spaces of community members (de Vries et al. 2018). However, studies exploring potential bacterial interactions in SBFs remain very scarce.

In the present work, we examined soil bacterial traits of a DBF, a MBF and an EBF in south-central China, including community composition, diversity, taxa abundances and network topology. Also, we explored the relationship between soil bacterial communities and environmental factors. We aimed to address two main questions: 1) Whether the community composition, diversity, taxa abundances and network topology of soil bacterial communities differ among the three typical vegetation types of SBFs? 2) What are the main driving forces of soil bacterial community formation in SBFs?

Methods & Materials

Site description

Three SBFs (Saiwudang, Houhe and Badagongshan) in south-central China within the East Asian monsoon region were surveyed. All of them are natural restorations of destroyed forests since 1980s, and have the same soil type, i.e., mountain yellowish brown soil developing from granite, sandy shale and slate.

Saiwudang is located at the Saiwudang National Nature Reserve in Hubei Province (32°25′51.29″N, 110°45′4.29″E), with the elevation of 1108 m, annual mean temperature of 10.67 °C and annual mean precipitation of 1009.5 mm. Dominant plant species include *Quercus glandulifera* (Fagaceae), *Platycarya strobilacea* (Juglandaceae) and *Castanea henryi* (Fagaceae).

Badagongshan is located at the Badagongshan National Nature Reserve in Hunan Province (29°46′24.23″N, 110°4′26.95″E), with the elevation of 1453 m, annual mean temperature of 11.56 °C and annual mean precipitation of 1527.1 mm. Dominant plant species include *Carpinus chuniana* (Betulaceae), *Sorbus folgneri* (Rosaceae) and *Cyclobalanopsis multinervis* (Fagaceae).

Houhe is located at the Houhe National Nature Reserve in Hubei Province (30°4′43.00″N, 110°32′58.89″E), with the elevation of 1568 m, annual mean temperature of 11.18 °C and annual mean precipitation of 1465.6 mm. Dominant plant species include *Sycopsis sinensis* (Hamamelidaceae), *Cyclobalanopsis glauca* (Fagaceae) and *Cyclobalanopsis oxyodon* (Fagaceae).

Plant survey

Nine plots (20 × 20 m) were randomly selected in each forest to conduct plant survey. Plants were identified to the species level. For each canopy tree species (those trees with diameter at breast height (DBH) > 5 cm) in a plot, we measured its richness, height, and DBH, then we calculated its relative frequency (the proportion of its richness relative to overall canopy tree species' richness), relative density (the proportion of its height relative to overall canopy tree species' height), and relative basal area (the proportion of its DBH relative to overall canopy tree species' DBH). Because quantitative classification of vegetation types can provide reliable and valuable ecological information of terrestrial flora (Zhang and Wang 2009), an indicator named dIVI (the Importance Value Index (IVI) of deciduous canopy trees) was used to quantitatively classify vegetation types in this study. This indicator derives from the IVI, a function of relative density, relative basal area and relative frequency of a certain plant species in a community (Curtis and Mcintosh 1951), thus it gives an overall estimation of the importance of deciduous canopy trees in a community. The IVI of each canopy tree species was determined based on the following formula: IVI = (relative frequency + relative density + relative basal area)/3. According to the Flora of China (http://foc.iplant.cn/), each canopy tree species was determined to be either deciduous or evergreen. The dIVI of a plot was the sum of IVIs of all deciduous canopy tree species, and the dIVI of a forest was the average of nine plots. Vegetation types were determined as follows: dIVI ≥ 0.75 for DBFs, 0.25 ≤ dIVI < 0.75 for MBFs, dIVI < 0.25 for EBFs. Plant diversity indexes including richness, Shannon-Wiener index and Pielou's evenness were calculated.

Soil factor measurement

Soil sampling was carried out in September 2012 before deciduous species dropped leaves. In each plot, 10–15 random soil cores (at the depth of 0–10 cm) were collected and thoroughly mixed. After sieved through a 2 mm mesh to exclude coarse gravels and plant roots, soil samples were put on ice for about 12 h before transported to laboratory. In the laboratory, each soil

sample was divided into two portions, one for soil DNA extraction (stored at −80 °C) and another for soil factor measurement (stored at 4 °C). Soil factors, including soil pH, soil organic C, total N, total potassium (K), total sulfur (S), total phosphorus (P), alkali-hydrolysable N, NH_4^+-N, NO_3^--N, plant available P, exchangeable Ca^{2+} and Fe^{3+}, were analyzed based on previous protocols (Bao 2000).

Soil DNA extraction

Soil DNA was extracted following the instruction of MoBio PowerSoil DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA), and purified by the Genomic DNA Clean & Concentrator™ Kit (Zymo Research, Irvine, CA, USA). DNA quality was detected by a NanoDrop ND-1000 Spectrophotometer (NanoDrop Technologies Inc., Wilmington, DE, USA), with the UV spectrometry absorbance ratios of 260 nm/280 nm and 260 nm/230 nm. DNA concentration was measured by PicoGreen using a FLUOstar OPTIMA fluorescence plate reader (BMG LABTECH, Jena, Germany).

16S rRNA gene amplicon sequencing

The V4 region of 16S rRNA gene was sequenced to indicate soil bacterial communities. To ameliorate amplification biases introduced by the use of long barcoded PCR primers, a two-step PCR approach with the primer pair 515F (5′-GTGCCAGCMGCCGCGGTAA-3′)/806R (5′-GGACTACHVGGGTWTCTAAT-3′) was performed (Wu et al. 2015). Primers in the first step were non-barcoded, whereas primers in the second step were barcoded. Each sample in each step of PCR had three replicates. Reaction in the first step was a 25 μl system containing 2.5 μl of 10 × AccuPrime PCR buffer II (Invitrogen, Grand Island, NY, USA), 1 μl of each primer (10 μM), 5 μl of DNA template (2 ng/μl) and 0.1 μl of AccuPrime High Fidelity *Taq* Polymerase. PCR conditions of the first step were as follows: initial denaturation, 1 min at 94 °C; annealing, 20 s at 94 °C, 25 s at 53 °C and 45 s at 68 °C; extension, 10 min at 68 °C; 10 cycles. PCR products of the first step were mixed and purified by the QIAquick Gel Extraction Kit (Qiagen, Valencia, CA, USA). The second step of PCR (20 cycles) had the same reaction system with the first one, but the DNA template was 15 μl of PCR products of the first step. PCR products of the second step were quantified by PicoGreen using a FLUOstar OPTIMA fluorescence plate reader. A total of 10 μl of PCR products and 10 μl of 0.2 N NaOH were mixed to denature DNA samples. Denatured DNA, chilled Illumina HT1 buffer and a PhiX DNA library were mixed to make a 15 pM library, and 600 μl of the mixture was loaded into an Illumina MiSeq platform (Illumina Inc., San Diego, CA, USA).

Raw sequences were separated based on sample barcodes via the function *Split libraries* of the IEG Galaxy pipeline (http://zhoulab5.rccc.ou.edu:8080). Ambiguous bases ('N') were removed via the function *Trim N* of this pipeline and only those sequences with no more than one ambiguous base were left. Forward and reverse reads were merged by *FLASH* and randomly resampled to the depth of 23,854 reads per sample. Sequences were clustered into operational taxonomic units (OTUs) using *UCLUST* at the 97% identity. After removing singletons, OTUs annotation was performed by the RDP Classifier with the 50% confidence. Bacterial diversity indexes including richness, Shannon-Wiener index and Pielou's evenness were calculated.

Statistical analyses

Dissimilarity of bacterial community composition among vegetation types was examined by the principal coordinates analysis (PCoA) and three non-parametric multivariate analyses, including the multi-response permutation procedure (MRPP), the multivariate analysis of variance (Adonis), and the analysis of similarity (ANOSIM). Above analyses were performed via the functions *pco, mrpp, adonis*, and *anosim* in the R package *vegan*. One-way ANOVA with post-hoc (Tukey HSD) was performed via the IBM SPSS statistics (version 23.0) to compare environmental factors and bacterial diversity indexes among vegetation types. Bacterial indicator genera were identified using the function *multipatt* in the R package *indicspecies*, based on following thresholds: specificity (the probability of a detected genus belonging to the surveyed site) > 0.8, fidelity (the probability of finding a certain genus in the surveyed site) = 1.0 (De Caceres 2009). To reveal the linkages of environmental factors and bacterial community composition, we performed partial Mantel tests via the function *mantel.partial* and the canonical correspondence analysis (CCA) via the function *cca* in the R package *vegan.* To ensure the reliability of our results, the multiple regression on distance matrices (MRM)

based on the Euclidean distance, via the function *MRM* in the R package *ecodist*, was also performed to verify the results of partial Mantel tests and the CCA. Only those environmental factors that simultaneously meet $P < 0.05$ in partial Mantel tests, the CCA and the MRM were selected as environmental factors that significantly influence soil bacterial community composition. Moreover, Pearson's correlations between those selected environmental factors and the first component of PCoA (PCo1) of bacterial OTUs, bacterial diversity, and relative abundances of bacterial taxa were performed via SPSS.

Network construction

Network analyses have been widely used to reveal potential interactions among bacterial taxa (de Vries et al. 2018). In this study, to reveal how vegetation type influence potential bacterial interactions, we constructed three vegetation type-specific networks with the same threshold of 0.97. To reveal environmental factors that influence network topological properties, we constructed a meta-network containing both bacterial OTUs and environmental factors, with the threshold of 0.81. To ensure reliability, only the OTUs or environmental factors with >75% occurrence across overall samples were selected to construct networks (Deng et al. 2012). For vegetation type-specific networks, those OTUs with 7 or more detections out of 9 replicates were selected. For the meta-network, those OTUs and environmental factors with 20 or more detections out of 27 replicates were selected. Network construction was based on the Random Matrix Theory (RMT) algorithm, via an open-access pipeline named Molecular Ecological Network Analyses (MENA) (http://ieg4.rccc.ou.edu/mena/) (Deng et al. 2012; Zhou et al. 2011).

Fast-greedy modularity optimization was applied to separate network modules, i.e., groups that have tighter connections within the group than outside the group. For each vegetation type-specific network and the meta-network, a total of 100 random networks with the same amounts of nodes and links were constructed via MENA. Overall network topological properties included total nodes, total links, total modules, percentage of positive links, average degree, average clustering coefficient, average path distance, modularity and maximal node degree. To test whether vegetation type-specific networks and the meta-network have typical properties of biological networks (e.g., scale free, small-world, hierarchy, modularity), their topological properties were compared with those of their corresponding random networks. Cytoscape (version 3.5.1) (Shannon et al. 2003) was used to visualize network topological structure.

Some network scores (e.g., connectivity) have the potential to identify putative keystone taxa that have large impacts in maintaining bacterial network topological structure and ecosystem functioning (Banerjee 2018). In this study, according to the values of within-module connectivity (Zi) and among-module connectivity (Pi) (Olesen et al. 2006), keystone taxa including network hubs ($Zi > 2.5$, $Pi > 0.62$), module hubs ($Zi > 2.5$, $Pi \leq 0.62$) and connectors ($Zi \leq 2.5$, $Pi > 0.62$) were selected (Guimera 2005).

Results

Plant and soil factors

A total of 84 canopy tree species were recorded in the three SBFs, composing of 55 deciduous species and 31 evergreen species (Table S1). Based on the dIVI (Table 1), Saiwudang (dIVI = 0.99) was classified as a DBF, Badagongshan (dIVI = 0.52) was classified as a MBF, and Houhe (dIVI = 0.19) was classified as an EBF. The EBF exhibited significantly lower plant Shannon-Wiener index (2.61 ± 0.13) and plant richness (21 ± 3) ($P < 0.001$) than the DBF (3.11 ± 0.40, 49 ± 12) and the MBF (3.23 ± 0.32, 56 ± 5) ($P = 0.001$, Table 1).

The DBF exhibited significantly less soil nutrients than the MBF and the EBF ($P < 0.05$, Table 1). For example, soil organic C in the DBF was 65.20% of that in the MBF, total N was 62.91% of that in the MBF and 67.58% of that in the EBF, total P was 42.37% of that in the MBF and 38.46% of that in the EBF, total S was 38.68% of that in the MBF and 46.07% of that in the EBF. However, soils of the DBF contained significantly more plant available P (8.95 ± 3.47 mg kg^{-1}) than the EBF (5.34 ± 2.12 mg kg^{-1}) ($P = 0.019$). The MBF exhibited significantly higher soil NH_4^+-N (1.02 times higher than the DBF, 3.90 times higher than the EBF) ($P < 0.001$). Whereas, soil pH of the EBF (6.72 ± 0.72) was significanlly higher than the DBF (4.48 ± 0.48) and the MBF (4.12 ± 0.18) ($P < 0.001$), so were the total K (1.66 times higher than the DBF, 0.65 times higher than the MBF) ($P < 0.001$) and Ca^{2+} (3.59 times higher than the DBF, 4.01 times higher than the MBF) ($P = 0.015$).

Soil bacterial community composition

After resampling, 644,058 high-quality 16S rRNA gene reads were obtained from 27 soil DNA samples, and were clustered into 10,456 OTUs at the 97% similarity level. Different vegetation types exhibited significantly different soil bacterial community composition, as revealed by the PCoA plot (Fig. 1a) and three non-parametric dissimilarity tests ($P = 0.001$, Table S2). In composition, the DBF exhibited significantly higher bacterial diversity ($P < 0.001$), including the Shannon-Wiener index (6.63 ± 0.38 for the DBF versus 6.14 ± 0.29 for the MBF, 5.83 ± 0.35 for the EBF) and richness (3377 ± 540 for the DBF versus 2445 ± 229 for the MBF, 2737 ± 258 for the EBF) (Table 1).

Different vegetation types also exhibited significantly different relative abundances of bacterial phyla (Fig. 1b, $P < 0.05$). For example, the relative abundance of Verrucomicrobia in the DBF ($8.72\% \pm 1.68\%$) was significantly higher than in the MBF ($5.55\% \pm 1.27\%$) and in the EBF ($3.89\% \pm 1.71\%$) ($P < 0.001$). The relative abundance of Chloroflexi in the MBF ($1.55\% \pm 0.73\%$) was significantly higher than in the DBF ($0.61\% \pm 1.19\%$) and in the EBF ($0.77\% \pm 0.26\%$) ($P < 0.001$). Relative abundances of Actinobacteria and Firmicutes were significantly higher in the EBF ($12.56\% \pm 4.00\%$, $5.79\% \pm 4.83\%$) than in the DBF ($7.15\% \pm 1.69\%$, $0.68\% \pm 0.11\%$) and in the MBF ($7.85\% \pm 1.28\%$, $1.84\% \pm 1.11\%$) ($P < 0.001$).

In addition, relative abundances of bacterial genera were also clearly different among vegetation types (Fig. 1c & Table S3, $P < 0.05$). In comparison, the DBF exhibited higher relative abundances of *Bradyrhizobium*, *Rhizomicrobium*, *Steroidobacter* and *Gemmatimonas* than other vegetation types; the MBF exhibited higher relative abundances of *Rhodoplanes*, *Kitasatospora* and *Actinoallomurus*; and the EBF exhibited higher relative abundances of *Arthrobacter* and *Sporosarcina.* Bacterial indicator genera of each vegetation type, i.e., those genera that occur only in a specific forest site (De Caceres 2009), were also different: 5 genera were characteristic for the DBF, 4 for the MBF and 23 for the EBF (Table S4). Relative abundances of those indicator genera ranged from $< 0.01\%$ (e.g., *Desulfomonile*, *Longilinea* and *Pseudomonas*, which were indicator genera of the EBF) to 1.08% (e.g., *Sporosarcina*, which was another indicator genus of the EBF).

Linkages between environmental factors and bacterial communities

Soil pH, dIVI and plant diversity (i.e., plant Shannon-Wiener index) were environmental factors that significantly influenced soil bacterial community composition, as revealed by both partial Mantel tests ($P < 0.01$, Table 2) and the CCA (CCA model: $P = 0.001$) (Fig. 2a & Table 2). According to the correlation coefficients in partial Mantel tests, soil pH ($r_M = 0.87$) exerted stronger impacts than the other two factors ($r_M = 0.35$ for dIVI, $r_M = 0.26$ for plant diversity). In accordance, the MRM also verified the importance of soil pH ($P = 0.001$), dIVI ($P = 0.008$) and plant diversity ($P = 0.029$) (MRM model: $P = 0.001$). The correlation coefficients in MRM also verified the stronger impacts of soil pH ($R = 1365.38$ for soil pH versus $R = 506.45$ for dIVI, $R = 311.17$ for plant diversity). Besides, soil pH had higher explanation to the PCo1 of bacterial OTUs ($R^2 = 0.92$ for soil pH versus $R^2 = 0.48$ for dIVI, $R^2 = 0.38$ for plant diversity) (Fig. 2b).

Soil pH, dIVI and plant diversity also significantly correlated with bacterial diversity ($r = -0.41 \sim 0.67$, $P < 0.05$) (Fig. 2c) and relative abundances of bacterial phyla ($r = -0.83 \sim 0.77$, $P < 0.05$) (Table 3). For example, soil pH positively influenced relative abundances of Actinobacteria, Bacteroidetes and Firmicutes ($r = 0.62 \sim 0.68$, $P < 0.01$), while negatively influenced relative abundances of Acidobacteria, Verrucomicrobia and Gemmatimonadetes ($r = -0.48 \sim -0.83$, $P < 0.05$) (Table 3). dIVI and plant diversity positively influenced relative abundances of Acidobacteria, Verrucomicrobia and Gemmatimonadetes ($r = 0.45 \sim 0.77$, $P < 0.05$), while negatively influenced relative abundances of Actinobacteria and Firmicutes ($r = -0.41 \sim -0.59$, $P < 0.05$). In addition, many bacterial genera shared significant correlations with soil pH, dIVI and plant diversity simultaneously, such as *Arthrobacter*, *Bradyrhizobium*, *Sporosarcina*, *Rhizomicrobium*, *Granulicella*, *Phenylobacterium*, *Gemmatimonas* etc. ($r = -0.84 \sim 0.92$, $P < 0.05$).

Network topological properties

The meta-network and three vegetation type-specific networks were scale-free (R^2 of power-law $= 0.81 \sim 0.95$), small-world and modular, with the values of

Table 1 Comparison of environmental factors (including plant and soil factors) and bacterial diversity indexes among vegetation types

	DBF* (Saiwudang)	MBF* (Badagongshan)	EBF* (Houhe)
Plant factors			
dIVI	0.99 ± 0.03 a†	0.52 ± 0.10 b	0.19 ± 0.07 c
Shannon-Wiener index	3.11 ± 0.40 a	3.23 ± 0.32 a	2.61 ± 0.13 b
Richness	49 ± 12 a	56 ± 5 a	21 ± 3 b
Pielou's evenness	0.80 ± 0.06 a	0.81 ± 0.08 a	0.86 ± 0.06 a
Soil factors			
Soil pH	4.48 ± 0.48 b	4.12 ± 0.18 b	6.72 ± 0.72 a
Organic carbon (C) (g kg^{-1})	42.32 ± 10.94 b	64.91 ± 20.71 a	53.58 ± 19.44 ab
Total nitrogen (N) (g kg^{-1})	3.19 ± 0.87 b	5.07 ± 1.38 a	4.72 ± 1.36 a
Total potassium (K) (g kg^{-1})	0.70 ± 0.36 b	1.13 ± 0.16 b	1.86 ± 0.57 a
Total phosphorus (P) (g kg^{-1})	0.25 ± 0.08 b	0.59 ± 0.07 a	0.65 ± 0.26 a
Total sulfur (S) (g kg^{-1})	0.41 ± 0.12 b	1.06 ± 0.12 a	0.89 ± 0.30 a
NH_4^+-N (mg kg^{-1})	41.59 ± 7.16 b	83.83 ± 27.71 a	17.11 ± 10.16 c
NO_3^--N (mg kg^{-1})	5.14 ± 5.97 b	43.48 ± 20.05 a	36.40 ± 10.15 a
Alkali-hydrolysable N (mg kg^{-1})	291.33 ± 70.55 b	510.19 ± 106.37 a	417.03 ± 89.99 a
Plant available P (mg kg^{-1})	8.95 ± 3.47 a	6.74 ± 1.62 ab	5.34 ± 2.12 b
Ca^{2+} (g kg^{-1})	4.71 ± 3.09 b	4.32 ± 1.96 b	21.64 ± 22.54 a
Fe^{3+} (g kg^{-1})	13.78 ± 1.94 b	34.24 ± 2.45 a	34.05 ± 9.10 a
Bacterial diversity			
Shannon-Wiener index	6.63 ± 0.38 a	6.14 ± 0.29 b	5.83 ± 0.35 b
Richness	3377 ± 540 a	2445 ± 229 b	2737 ± 258 b
Pielou's evenness	0.82 ± 0.03 a	0.79 ± 0.03 a	0.74 ± 0.04 b

* DBF: the deciduous broad-leaved forest. MBF: the mixed deciduous-evergreen broad-leaved forest. EBF: the evergreen broad-leaved forest

† Different letters next to values (mean ± standard deviation, $n = 9$) indicate significant difference ($P < 0.05$, one-way ANOVA with Tukey HSD) among vegetation types

average clustering coefficient, average path distance and modularity being clearly larger than those of their corresponding random networks (Table S5). Soil pH and dIVI were revealed as important nodes for the meta-network with degree ≥ 10 (Fig. 3a). Keystone taxa of the meta-network included OTU_151 (a module hub, belonging to the genus *Dokdonella*), OTU_26591 (a module hub, belonging to the phylum γ-Proteobacteria) and OTU_27879 (a module hub, belonging to the genus *Rhodoplanes*) (Fig. 3a).

With the same threshold of 0.97, the three vegetation type-specific networks had different topological properties (Fig. 3b-3d). In comparison, the network of DBF contained the highest total nodes (868) and links (1942) but the lowest total modules (52) (Fig. 3b & Table S5). Whereas, the network of MBF contained the lowest total nodes (511) and links (674) but the highest total modules (62) (Fig. 3c & Table S5). Similarly, the network of DBF had the highest average degree (4.475), whereas the network of MBF had the lowest (2.638) (Table S5). Node degree was limited to 20 for the network of MBF, whereas more than 20 nodes were with degree over 20 for the network of DBF (left panel of Fig. S1). In addition, the DBF had the highest number of keystone taxa (25 module hubs and 27 connectors) (Fig. 3b, right panel of Fig. S1 & Table S6), whereas the MBF had the lowest (11 module hubs and 2 connectors) (Fig. 3c, right panel of Fig. S1 & Table S7). For the DBF and the MBF, no common genera were shared between those indicator genera and keystone taxa (Table S4, S6 & S7). Whereas, for the EBF, *Desulfomonile*, *Lysobacter*, *Microvirga*, and *Brevundimonas* were both indicator genera and keystone taxa (Table S4 & S8).

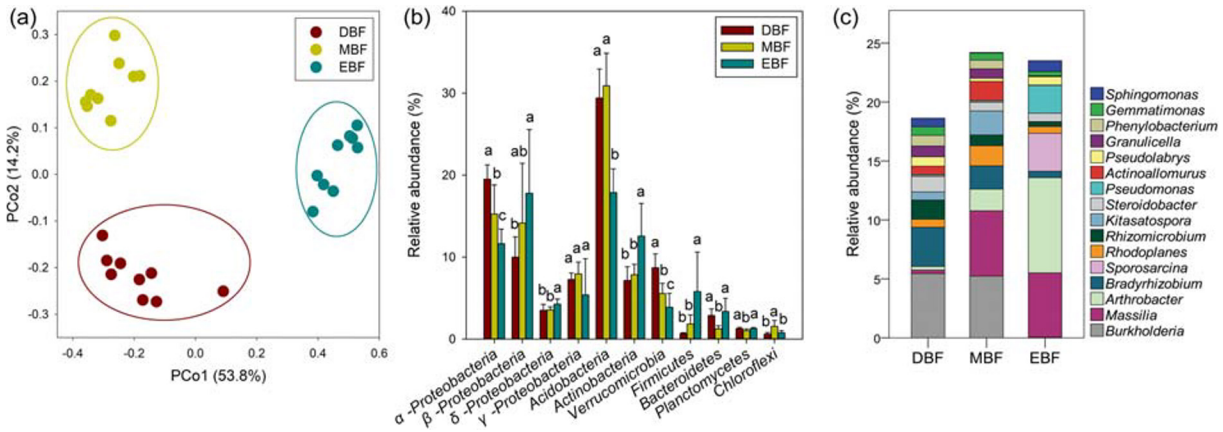

Fig. 1 Different vegetation types exhibit significantly distinct **(a)** soil bacterial community composition, indicated by the principal coordinates analysis (PCoA) based on the 16S rRNA gene data, **(b)** relative abundances of the most abundant bacterial phyla (> 1.00%), and **(c)** relative abundances of the most abundant bacterial genera (> 0.50%). DBF: the deciduous broad-leaved forest. MBF: the mixed deciduous-evergreen broad-leaved forest. EBF: the evergreen broad-leaved forest. Different letters above error bars indicate significant differences ($P < 0.05$, one-way ANOVA with Tukey HSD) among vegetation types

Discussion

Predominant impacts of soil pH on soil bacterial communities

In line with another study in Chinese subtropical broad-leaved forests (Pei et al. 2016), soil pH governed soil bacterial community composition more than any other measured environmental factors (Table 2). The considerably high explanation of soil pH (53.8%) to soil bacterial community composition (Fig. 2b) concurred with several previous studies (Baath 2003; Fierer 2006; Rousk et al. 2010; Shen et al. 2013) regardless of the technique used and sampling scale, indicating that soil pH is a universal driving force of soil bacterial communities. For example, with the application of Phospholipid Fatty Acid (PLFA) technique, soil pH explained 50% of soil bacterial variance in European broad-leaved forests (Baath 2003). Moreover, with the application of Terminal-Restriction Fragment Length Polymorphism (T-RFLP) technique, soil pH explained approximately 70% of diversity variance of soil bacterial communities at the global scale (Fierer 2006).

Predominant impacts of soil pH were probably owing to the narrow pH ranges for optimal growth of soil bacteria and the role of soil pH in controlling accessibility of organic C and other nutrients (Rousk et al. 2010). For instance, the strong, negative correlation between soil pH and relative abundance of Acidobacteria ($r = -0.83$, Table 3) emphasized the soil

Table 2 Linkages between bacterial community composition and environmental factors, revealed by partial Mantel tests and the canonical correspondence analysis (CCA)

Environmental factors	Partial Mantel tests		CCA	
	r_M	*P*	F	*P*
Soil pH*	0.87	**0.001**†	4.18	**0.001**
dIVI*	0.35	**0.001**	9.43	**0.001**
Plant Shannon-Wiener index*	0.26	**0.004**	3.48	**0.001**
Plant richness	0.62	**0.001**	NA‡	NA
Plant Pielous's evenness	0.08	0.117	NA	NA
Organic carbon (C)	−0.23	1.000	2.44	**0.014**
Total nitrogen (N)	−0.35	1.000	NA	NA
Total potassium (K)	0.36	**0.001**	NA	NA
Total phosphorus (P)	−0.03	0.626	2.20	**0.034**
Total sulfur (S)	−0.16	0.998	3.07	**0.002**
NH_4^+-N	0.38	**0.001**	NA	NA
NO_3^--N	−0.23	1.000	NA	NA
Alkali-hydrolysable N	−0.41	1.000	NA	NA
Plant available P	0.12	0.056	NA	NA
Fe^{3+}	−0.03	0.645	NA	NA

* Soil pH, dIVI and plant diversity (i.e., plant Shannon-Wiener index) were revealed as environmental factors that significantly influence soil bacterial community composition by both partial Mantel tests and the CCA

† Bold values indicate significance at the $P < 0.05$ level

‡ NA indicates no available results for those environmental factors in the CCA model

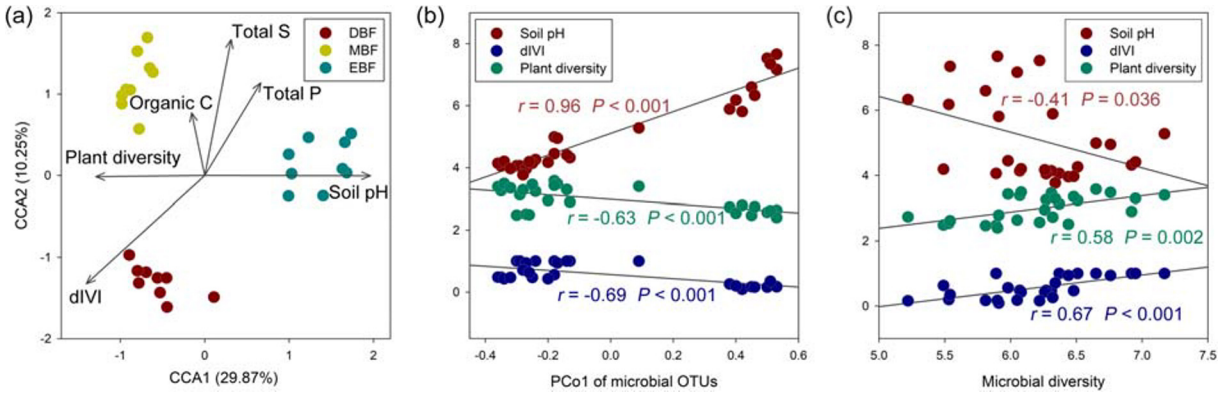

Fig. 2 Linkages between environmental factors and soil bacterial communities. **(a)** The canonical correspondence analysis (CCA) revealed that bacterial community composition was significantly ($P = 0.001$) related to soil pH, dIVI, plant diversity, organic carbon (C), total sulfur (S) and total phosphorus (P). **(b)** Significant Pearson's correlations of soil pH, dIVI, and plant diversity with the first component of PCoA (PCo1) of bacterial OTUs. **(c)** Significant Pearson's correlations of soil pH, dIVI, and plant diversity with bacterial diversity

pH-dependency for optimal growth of this phylum, which was also detected in the Changbai Mountain soils of China (Shen et al. 2013), the American Continent soils (Jones et al. 2009) and in Arctic soils (Männistö and Tiirola 2007). Soil pH-dependency was not unique to Acidobacteria: relative abundances of Actinobacteria, Bacteroidetes and Gemmatimonadetes also significantly correlated with soil pH in our study (Table 3) and previous work (Rousk et al. 2010; Shen et al. 2013). In addition, the importance of soil pH for maintaining the bacterial network in SBFs (Fig. 3a) suggested that soil pH may control the development of bacterial interactions and foster those bacteria-involved ecosystem processes in SBFs. However, future research is required to clarify whether soil pH itself influences bacterial communities directly, or indirectly through regulating many other environmental factors that co-vary with soil pH (Jones et al. 2009).

Regardless of the narrow range (4.1–6.8), soil pH varied significantly among vegetation types in this study (Table 1). Given that the three SBFs shared similar soil parent material (granite, sandy shale and slate), soil type (mountain yellowish brown soil), soil horizon (0–10 cm, surface soil layer) and climate (the East Asian monsoon region), much higher soil pH of the EBF than the DBF and the MBF (Table 1) was likely attributed to different modification effects of plants on soil pH. As reported in previous studies, modification effects of plants on soil pH vary between species (e.g. Fabaceae vs. Poaceae) and growth forms (e.g., forbs vs. shrubs, deciduous trees vs. evergreen trees) (Bardgett et al. 1999; Falkengren-Grerup et al. 2006; Yan 2000), probably as a result of different quality and quantity of root exudates and different ability in the release, uptake and allocation of organic acids (Finzi and Canham 1998).

Importance of vegetation type and plant diversity in influencing soil bacterial communities

The application of quantitative indicator of vegetation types into microbial ecology is rare. From this perspective, for the first time, the use of dIVI in our study provided a bridge to statistically correlate aboveground plant communities with belowground bacterial communities in SBFs. Inconsistent with the results of the previous study (Ding et al. 2015), the close relationships among dIVI, plant diversity and soil bacterial community composition (Fig. 2a & Table 2) suggested that aboveground plant community was a major regulator of belowground bacterial community in SBFs. This inconsistence is probably because that the number of plant parameters was insufficient in the previous study (only the cover-abundance value of each plant species) (Ding et al. 2015) comparing with our study (four plant parameters, i.e., dIVI, Shannon-Wiener index, Richness and Pielou's evenness), which may underestimate the importance of plantation in shaping soil bacterial communities.

Significant linkage of vegetation type and soil bacterial community composition, diversity and network topological properties (Fig. 2a, 3a & Table 2) implied that the deciduousness and evergreenness of plant species had substantial effects on soil bacterial communities in SBFs. Soil bacterial diversity of the DBF was much

Table 3 Pearson's correlations of soil pH, dIVI and plant diversity with relative abundances of the most abundant bacterial phyla (> 1.00%) and genera (> 0.50%)

	Soil pH		dIVI		Plant diversity	
	r	*P*	r	*P*	r	*P*
Phyla						
Proteobacteria	−0.03	0.874	−0.08	0.707	−0.24	0.239
Acidobacteria	−0.83	**< 0.001***	0.62	**0.001**	0.59	**0.001**
Verrucomicrobia	−0.60	**0.001**	0.77	**< 0.001**	0.45	**0.020**
Actinobacteria	0.62	**0.001**	−0.59	**0.001**	−0.41	**0.032**
Bacteroidetes	0.63	**< 0.001**	−0.08	0.699	−0.29	0.143
Planctomycetes	0.34	0.084	0.06	0.756	−0.25	0.212
Firmicutes	0.68	**< 0.001**	−0.51	**0.006**	−0.41	**0.033**
Gemmatimonadetes	−0.48	**0.012**	0.57	**0.002**	0.50	**0.008**
Chloroflexi	−0.20	0.311	−0.19	0.341	0.24	0.223
Genera						
Burkholderia	−0.78	**< 0.001**	0.64	**< 0.001**	0.33	0.089
Massilia	0.17	0.387	−0.43	**0.025**	−0.34	0.079
Arthrobacter	0.77	**< 0.001**	−0.75	**< 0.001**	−0.49	**0.009**
Bradyrhizobium	−0.68	**< 0.001**	0.80	**< 0.001**	0.42	**0.028**
Sporosarcina	0.68	**< 0.001**	−0.40	**0.037**	−0.43	**0.025**
Rhodoplanes	−0.62	**0.001**	−0.05	0.808	0.51	**0.006**
Rhizomicrobium	−0.65	**< 0.001**	0.92	**< 0.001**	0.43	**0.027**
Kitasatospora	−0.68	**< 0.001**	0.19	0.344	0.47	**0.013**
Steroidobacter	−0.18	0.357	0.59	**0.001**	0.18	0.374
Pseudomonas	0.38	0.050	−0.34	0.082	−0.35	0.073
Actinoallomurus	−0.79	**< 0.001**	0.27	0.180	0.49	**0.009**
Pseudolabrys	−0.02	0.916	0.08	0.686	< 0.01	0.993
Granulicella	−0.77	**< 0.001**	0.66	**< 0.001**	0.39	**0.042**
Phenylobacterium	−0.84	**< 0.001**	0.80	**< 0.001**	0.56	**0.002**
Gemmatimonas	−0.48	**0.012**	0.57	**0.002**	0.50	**0.008**
Sphingomonas	0.69	**< 0.001**	−0.07	0.733	−0.36	0.067

* Bold values indicate significance at the $P < 0.05$ level

higher than that of the EBF and of the MBF (Table 1), indicating that the deciduous forest soil is a more diverse habitat. A possible reason is that deciduous plants and evergreen plants are likely to produce litter and organic matter with different chemical composition, thus control the nutrient supply of soil bacteria (Eisenhauer et al. 2010) and influence the modification of soil physical or chemical environmental factors (Urbanová and Šnajdr 2015). Litter produced by evergreen plants generally decompose slower than litter of deciduous plants (Dorrepaal et al. 2005), which may explain why significantly lower soil organic C was detected in the DBF (Table 1). In accordance with the poorer soil organic C in the DBF, positive correlations were found between dIVI and oligotrophs including Acidobacteria, Verrucomicrobia and Gemmatimonadetes (Table 3), members of which generally occur in habitats with less nutrients (Hanada and Sekiguchi 2014; Ramirez-Villanueva et al. 2015; Ward et al. 2009). In addition, positive correlations between dIVI with important N-fixers including members of *Rhizomicrobium*, *Bradyrhizobium* and *Burkholderia* (Table 3) (Coenye 2003; Itakura et al. 2009; VanInsberghe et al. 2015) indicated that soil of the DBF harbored more N-fixing bacteria to compensate the rather limited N condition (Table 1).

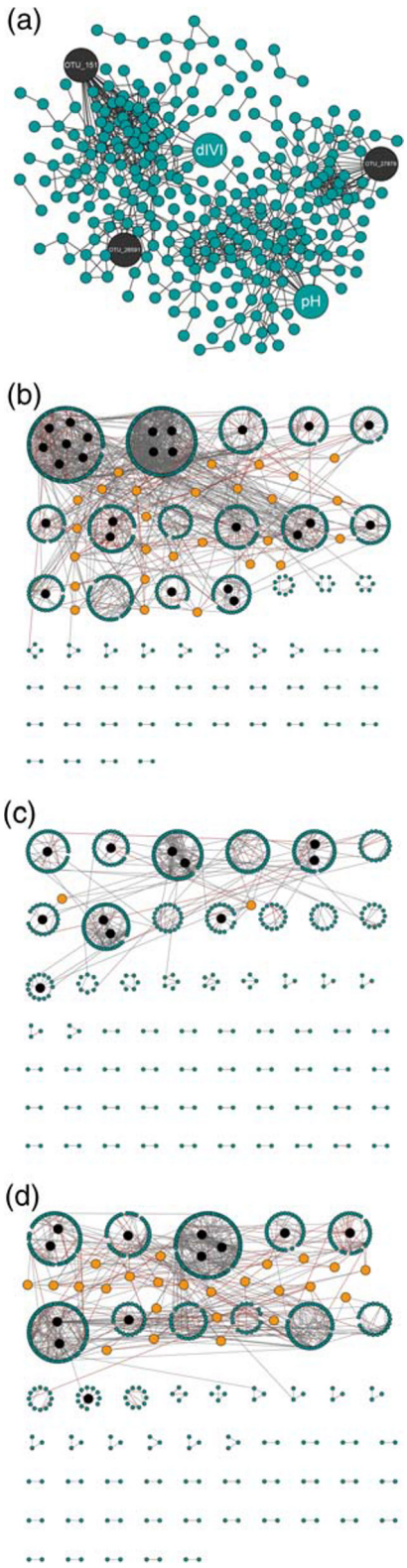

Fig. 3 Topological structure of **(a)** the meta-network containing overall bacterial OTUs and environmental factors, **(b)** the network of the deciduous broad-leaved forest (DBF), **(c)** the network of the mixed deciduous-evergreen broad-leaved forest (MBF), and **(d)** the network of the evergreen broad-leaved forest (EBF). Each dot indicates a node and each line indicates a link. Larger black and green dots of **(a)** indicate bacterial keystone taxa of the meta-network and important environmental factors that influence the meta-network (i.e., soil pH with node degree of 16 and dIVI with node degree of 10), respectively. Nodes of **(b-d)** are separated into modules based on the fast-greedy modularity optimization method. Larger black and orange dots of **(b-d)** indicate module hubs and connectors, respectively. Grey lines of **(b-d)** indicate positive links and red lines indicate negative links

Plant diversity was another explanation of bacterial sensitivity to changes of plant communities. Consistent with previous findings (Habekost et al. 2008; Thoms et al. 2010; Zak et al. 2003), the positive correlation between plant diversity and soil bacterial diversity (Fig. 2c) suggested that terrestrial ecosystems with higher plant diversity usually exhibited higher soil bacterial diversity. One explanation is niche complementarity: higher plant diversity can provide more diversified litter composition as a result of more diversified plant biochemical components, thus more diversified nutrient pools are available to microorganisms, which facilitates higher bacterial diversity (Guenay et al. 2013; Tilman et al. 2001).

The highest network complexity and number of keystone taxa in the DBF (Fig. 3b, S1 & Table S5) indicated that soil bacterial members of DBFs were the most connected with each other, which confirmed previous findings (Ding et al. 2015). On the contrary, soil bacterial members of MBFs appeared to be the least connected (Fig. 3c, S1 & Table S5). Since complex bacterial networks potentially suggest higher resistance to environmental disturbance (Montoya et al. 2006), soil bacterial communities beneath DBFs may be the most resistant to environmental disturbance, whereas those beneath MBFs may be the most vulnerable. Meanwhile, larger number of correlations in the DBF was probably caused by higher spatial heterogeneity of this vegetation type, but the potential impact of spatial heterogeneity on correlation network topology is still poorly understood. In a recent study in agricultural ecosystems, keystone taxa of microbial ecological networks were reported to have no common with indicator taxa (Banerjee et al. 2019). However, in our study, regardless of low relative

abundances (< 0.14%), *Desulfomonile*, *Lysobacter*, *Microvirga*, and *Brevundimonas* played roles as both keystone taxa and indicator genera in the EBF (Table S4 & S8). These findings supported that importance of microbial taxa was not necessarily determined by their abundances in the community (Banerjee 2018).

Conclusions

In conclusion, the three typical vegetation types of SBFs (i.e., DBFs, MBFs and EBFs) exhibit significantly different soil bacterial communities with varying composition, diversity and network topological properties. Environmental factors that strongly influence bacterial community composition include soil pH, vegetation type and plant diversity, among which soil pH exerts stronger impacts than the others. For the first time, this study shows that the quantitative indicator of vegetation type 'dIVI' is a good predicator of soil bacterial communities of SBFs, hence should be taken into consideration when predicting soil bacterial community composition and diversity. Our study provides a more comprehensive understanding of bacterial biodiversity in SBFs and insights on mechanisms underlying the composition pattern of such belowground 'dark matters' in subtropical ecosystems.

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Data accession High-throughput sequencing data can be found in GenBank databases by the accession number SRP062748 (http://trace.ncbi.nlm.nih.gov/Traces/sra/?study=SRP062748).

Compliance with ethical standards

Declarations of interest None.

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