



Linkage of soil organic matter composition and soil bacterial community structure as influenced by dominant plants and hydrological fluctuation in Poyang Lake

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Abstract

Purpose We evaluated the role of water levels and plant-associated effects on the composition of bacterial communities and the soil organic matter (SOM) composition in wetland ecosystem.

Materials and methods Soil (0–15 cm) associated with *Phragmites communis*, *Triarrhena lutarioriparia*, *Carex cinerascens*, and *Zizania latifolia* was sampled in different water levels (as proxied by sampling time) to analyze soil SOM composition via diffuse reflectance infrared Fourier transform spectroscopy in the mid-infrared range analysis and to analyze soil bacterial communities by high-throughput 16S rRNA gene sequencing.

Results and discussion Soil dominant SOM composition (1623–1635 cm^{-1} and 3444–2697 cm^{-1}) were obviously influenced by water levels not plant species ($p < 0.05$). Proteobacteria, Chloroflexi, Acidobacteria, and Firmicutes were the most abundant phyla and exhibited significantly different distributions across the soils with *Z. latifolia*, *P. communis*, *T. lutarioriparia*, and *C. cinerascens* communities and the non-plant flat mud soil ($p < 0.05$). Redundancy analysis and variation partitioning analysis indicated that the Wc, active organic carbon, TC_{stem} , Tem_{soil} , and water level significantly influenced the dominant soil bacterial taxonomic composition, while the soil bacteria may influence the SOM composition.

Conclusions These findings suggested that soil SOM composition and bacterial communities were strongly affected by plant species and water levels. This study provides an in-depth insight into how specific SOM components related to the different distributions of the specific bacterial taxonomic groups that are responsible for key ecological functions in wetland ecosystem soils.

Keywords Poyang Lake · Soil organic matter · MidDRIFTS · Soil microbial communities · Water level

1 Introduction

Soil organic matter (SOM) plays an important role in a wide range of soil processes and is a key element that determines the edaphic properties. For example, the SOM influences the

maintenance of soil structure, its water retention capacity, its nutrient cycling activities, and the stimulation of biological activity (Sharma et al. 2017). In particular, the distribution of the SOM in an environment can dictate the rate at which the SOM accumulates or is degraded (Błońska et al. 2021). More broadly, the rate at which the SOM accumulates depends on the ratio of the SOM inputs (organic matter produced in situ and ex situ) to the SOM outputs (e.g., decomposition and erosional processes). These processes are strongly related to numerous edaphic physical and chemical properties, the plant species that are present in a system, and the microbial activities (Wang et al. 2016b; Li et al. 2020).

In particular, microorganisms are the crucial soil component that may account for up to 30% of the biomass of the Earth (Whitman et al. 1998; Bar-On et al. 2018). Microbial population is critical to the decomposition and transformation of organic matter, as well as to the remineralization

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of nutrients, which highlight their crucial roles in global biogeochemical cycling (Sheng et al. 2016; Xiao et al. 2018, 2020). Numerous studies have determined that SOM content or component influence the microbial community structures of ecosystems and that these characteristics are considered one of the major factors influencing the underlying variations in microbial communities (Stepanuskas et al. 2003; Sheng et al. 2016). Recent advances in high throughput DNA sequencing have provided significantly greater resolution data on the composition of microbial communities, particularly with respect to environmental parameters (temperature, pH, etc.) (Jiang et al. 2016; Singer et al. 2016; Xiao et al. 2017a, b; Xiao et al. 2019) and the SOM. Indeed, recent investigations have shown that microbial communities play a key role in the formation of stable SOM in soils (Kallenbach et al. 2016), can be functionally redundant in SOM degradation processes (Banerjee et al. 2016), and that SOM cycling processes are related to the diversity of soil microbial communities (Banerjee et al. 2016).

Wetlands represent one of the largest biological carbon pools on Earth and play a critical role in the global carbon cycle, despite the fact that they only cover a small fraction of the Earth's land surface (Wang et al. 2016b). Poyang Lake is the largest freshwater lake in China, and it harbors a wetland system with ecologically critical functions (Han et al. 2015; Liu et al. 2020) such as the maintenance of carbon storage, sustaining biodiversity, and providing a water resource (Zhang et al. 2012; Wang et al. 2016c). The unique hydrological characteristics of the lake result in heterogeneous environments, which affect the vegetation growth and soil/sediment microbial community characteristics via variations in the wetland's physicochemical and environmental properties (Chen et al. 2010; Wang et al. 2016b; Shen et al. 2021). In addition, the spatiotemporal variation in the soil microbial community compositions of Poyang Lake is related to water level fluctuations and the distribution of vegetation; however, the exact mechanisms underlying these relationships and the high diversity within the microbial communities of the wetlands have not been sufficiently addressed.

SOM exhibits complex chemical compositions, which originate from vegetation-dependent growth, species-specific patterns (Negassa et al. 2019), and microbial processes (Kallenbach et al. 2016). Although it is recognized as a critical factor controlling microbial community variation, little is known about how SOM composition and their origins related to the compositions of microbial community. Providing a better understanding of such relationships will help us to better understand the process of SOM mineralization and persistence among different types of soils (Xiao et al. 2017a, b), especially in wetlands that are critical for global C cycling. In this study, the effects of locally dominant aquatic plants on the physicochemical traits of edaphic, SOM composition, and the soil bacterial

community structures were analyzed for Poyang Lake at different water levels. Specifically, we investigated the following: (1) edaphic characters, the SOM composition, and soil microbial community structure under different water levels and under different dominant plants and (2) whether changes in SOM composition related to the shifts of soil microbial community structure and diversity. The results of this study provide important insights into the relationship among dominant plants, SOM chemical composition, and soil microbial communities in wetland ecosystems.

2 Materials and methods

2.1 Site characteristics

Poyang Lake is located on the southern bank of the lower Yangtze reach (28° 22'–29° 45' N and 115° 47'–116° 45' E). The climate of the area is characterized as subtropical, humid, and monsoonal, with a mean annual precipitation of 1620 mm and an annual average temperature of ~17 °C (Zhang et al. 2015b). The water levels in Poyang Lake vary based on the season. The flood season extends from April to September, the dry season from January to March, and the normal season from October to December, during which the water levels are intermediate between the flood and dry seasons. Periodic variation in lake water levels (WL) also leads to characteristic environmental fluctuations in the areas between the lake's beaches and grasslands (Du et al. 2017; Zeng et al. 2019).

The aquatic vegetation in Poyang Lake is species-rich and distributed over ~2262 km², which accounts for 80.8% of the wetland area (Guan et al. 1987). Peng et al. (2003) reported that *Carex cinerascens* and *Zizania latifolia* account for the highest coverage and the highest biomass among the Poyang Lake vegetation, respectively; however, *Phragmites communis* and *Triarrhena lutarioriparia* can also constitute up to 80% of the aboveground biomass of the lake (Du et al. 2017).

To evaluate plant species composition on the soil organic carbon (SOC) composition and soil bacterial community structure under the periodic variation in lake water level, 0–15 cm of bulk soil associated with four plant species (*P. communis*, *T. lutarioriparia*, *C. cinerascens*, and *Z. latifolia*) were sampled using a 7.5-cm auger at the Nanjishan location (NJS) in November of 2014 (normal: water level of about 14 m) and in January (dry: water level of about 12 m) and April (flood: water level of about 16 m) of 2015. In addition, 0–15 cm of bulk soil associated with two plant species (*T. lutarioriparia* and *C. cinerascens*) were also sampled in January (dry: water level of about 19 m), April (flood: water level of about 21 m), and November of 2015 (normal: water level of about 20 m) at Dahuchi in Wucheng town (WC) on

Poyang Lake (Fig. S1). In addition, mud flats without plants were sampled at the NJS and WC sites as a control. At each site, triplicate plots were selected for each plant species. At each plot, five samples were collected and homogenized to create a composite sample. After collection, the samples were divided into three components, and one of which was used for immediate chemical analysis, the other portions were stored at $-80\text{ }^{\circ}\text{C}$ for subsequent DNA extraction, and the left was air dried for Fourier-transform infrared spectroscopy (FT-IR) analysis. In addition, a portable electronic thermometer was used to measure the in situ temperature (Tem_{soil}) at each sampling site.

At each sampling location, each plant in the quadrat ($50\times 50\text{ cm}$) was carefully excavated to a depth of 30 cm using a stainless-steel spade to analyze the biomass of *T. lutarioriparia* and *C. cinerascens* communities and to a depth of 40 cm to analyze the biomass of *P. communis* and *Z. latifolia* communities. The excavation depths were chosen in order to ensure the collection of all plant roots. Both the aboveground and belowground plant components were washed using distilled water, and then, they were oven-dried at $70\text{ }^{\circ}\text{C}$ for 48 h, after which they were weighed. Then, the belowground biomass was calculated from the roots ($\text{Biom}_{\text{root}}$) and the aboveground biomass from the stems and leaves ($\text{Biom}_{\text{stem}}$).

2.2 Soil properties analyses

The soil pH, electrical conductivity (EC), and total dissolved solids (TDS) of the supernatant of a distilled water and soil suspension prepared at a 1:2.5 soil:water ratios were measured potentiometrically. The soil water content (Wc) was determined after drying fresh subsamples of each soil at $105\text{ }^{\circ}\text{C}$ for 24 h and calculating the difference in the weights of the fresh and oven-dried samples. The soil microbial biomass carbon (MBC) was determined using the chloroform-fumigation extraction method (Vance et al. 1987; Jiang et al. 2012), wherein fumigated and non-fumigated soils (10 g dry weight equivalent) were extracted with 40 mL of 0.5 M K_2SO_4 (soil/extractant ratio 1:4). The samples were shaken for 30 min, and then, they were filtered through 0.45- μm Whatman filter paper into separate vials for MBC analysis using the method described by Wu et al. (1990).

Fresh soil samples (equivalent to a 10-g oven-dried weight) were extracted after being shaken with 30 mL of distilled water for 30 min on an end-over-end shaker set at approximately 240 g, followed by centrifugation for 20 min at $8000\times g$. The sample supernatants were filtered through a 0.45- μm Whatman nylon filter into separate vials for dissolved organic carbon (DOC) analysis using the method described by Luo et al. (2007) and Jiang et al. (2017). The active organic carbon (AOC) and SOC were measured using the methods described by Jiang et al. (2017). The total C and N contents of

the soils (TC_{soil} and TN_{soil}), plant roots (TC_{root} and TN_{root}), and plant stems (TC_{stem} and TN_{stem}) were measured using a Euro Vector CHNS-O EA3000 (Ovette, Italy) elemental analyzer. FT-IR spectral investigation of SOM composition via diffuse reflectance infrared Fourier transform spectroscopy in the mid-infrared range (MidDRIFTS) analysis is a cost-effective and rapid method of quantifying the carbon compound abundances and distributions of diverse soil compositions (Sharma et al. 2017). In particular, MidDRIFTS can be used to identify SOM functional groups and predict the SOM quality/stability associated with soil organic carbon turnover rates in environmental matrices (Fultz et al. 2014; Parikh et al. 2014; Mirzaeitalarposhti et al. 2016). In this study, MidDRIFTS spectra were recorded using a Nicolet FTIR6700 spectrophotometer (USA). Briefly, pellets were prepared by pressing 1–4 mg of air-dried soil and 400 mg of KBr (Fluka Analytical) under vacuum. The soils were dried at $105\text{ }^{\circ}\text{C}$ and homogenized with a mortar and pestle prior to pressing. Immediately after pellet preparation, the spectra were acquired in the range of $4000\text{--}400\text{ cm}^{-1}$ using a 4 cm^{-1} resolution and 64 scans to generate each acquisition. Then, the spectral data processing was conducted using the OPUS 6.5 software package as described by Bernier et al. (2013). The spectral processing included (i) corrections for atmospheric CO_2 and water concentrations, (ii) baseline corrections, and (iii) the use of a second derivative to smooth the spectra and reduce noise. After baseline correction (Fig. S2), the relative absorbance intensity of each spectra band was divided by 796 cm^{-1} (Bernier et al. 2013). The FT-IR bands were interpreted based on protocols described by Seddaiu et al. (2013) and Sharma et al. (2017). In addition, the SOM functional groups were classified using the method described by Fultz et al. (2014) and Wang et al. (2016a). The MidDRIFT spectra of the soils exhibited signals at 3696, 3621, 3450, 3444, 2923, 2852, 1635, 1623, 1384, 1108, 1031, 1008, 914, 796, 779, 694, 536, and 470 cm^{-1} . The signals ranging from 3696 to 3444 cm^{-1} can be attributed to O–H stretching from the carboxylic acids, phenols, and alcohols or to N–H stretching from amines and amides. The signals at 2852 and 2923 cm^{-1} are aliphatic C–H stretching signals. In addition, the signals at 1623 and 1635 cm^{-1} are from O–H bending and C=O stretching from the carboxylic acids, amides, and ketones. The signal at 1384 cm^{-1} corresponds to symmetric COO– stretching, while the signals below 1100 cm^{-1} are due to C–O stretching, O–H bending of the –COOH groups, C–O stretching of the polysaccharides, and Si–O–Si stretching.

2.3 Soil biological activity

The soil enzyme activities (urease, catalase, and sucrase) were measured using the methods described by Lu (2000) and Jiang et al. (2017): (i) catalase, using the permanganometric method; (ii) urease, using the phenol sodium hypochlorite

colorimetric method to determine the level of ammonium produced; and (iii) sucrose, using the 3,5-dinitro salicylic acid colorimetric method. Finally, soil rubisco activity was measured using the methods described by Wu et al. (2014) and Cao et al. (2017). In the lab, the CO₂ representing the basic soil respiration (BR) was trapped in the Ba(OH)₂, and the remaining Ba(OH)₂ was neutralized by titration in order to determine the soil CO₂ concentrations.

2.4 Soil DNA extraction, PCR amplification, and high-throughput sequencing of the bacterial 16S rRNA genes

Soil bacterial community DNA was extracted from the soil samples using an E.Z.N.A. Soil DNA Kit (Omega Bio-tek, Norcross, GA, USA) according to the manufacturer's protocol. Triplicate DNA extractions were performed for each soil sample, and then the extractions were pooled. The 16S rRNA gene V3-V4 hypervariable regions were amplified using the universal bacterial primers 338F 5'-barcode-*ACTCCTACGGGAGGCAGCA*-3' and 806R 5'-*GGACTA CHVGGGTWCTAAT*-3' (Zhang et al. 2015a). The above "barcode" represents a unique barcode nucleotide sequence specific to each sample, which allows for multiplex sequencing. The PCR (polymerase chain reaction) mixtures contained 10 ng of template DNA, 4 µL of FastPfu Buffer, 2 µL of dNTPs (2.5 mM stock concentration), 0.8 µL of each primer (5 µM stock concentration), 0.4 µL of FastPfu Polymerase, and ddH₂O up to 20 µL. The PCR conditions were as follows: 95 °C for 3 min, followed by 25 cycles of 30 s at 95 °C, 30 s at 55 °C and 45 s at 72 °C, and a final extension at 72 °C for 10 min. The amplicons were gel-purified using 2% agarose gels and an AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA). The PCR product concentrations were determined using a QuantiFluor™-ST quantification kit (Promega, USA). Then, the purified amplicons were pooled and used as template for paired-end sequencing (2 × 300 bp) on the Illumina Miseq platform (Illumina, San Diego, CA, USA) at the sequencing center of Majorbio BioPharm Technology Co. Ltd. (Shanghai, China).

The raw fastq files were demultiplexed, and the reads were quality-filtered using the QIIME 1.17 pipeline with the following criteria: (i) The 300-bp reads were truncated at any site receiving an average quality score of < 20 over a 50-bp sliding window, and the reads were subsequently discarded when they were shorter than 50 bp in length. (ii) An exact match to the barcode sequence was required, while those with ≥ 2 nucleotide mismatches to the primer were discarded, as were any sequences containing ambiguous nucleotide positions. (iii) The paired-end sequences that did not overlap by at least 10 bp were discarded, while the rest were assembled based on the overlapping sequence. Then,

the operational taxonomic units (OTUs) were generated from the raw reads using a 97% nucleotide similarity cut-off level with the UPARSE 7.1 (<http://drive5.com/uparse/>) package. Further, chimeric sequences were identified and removed using the UCHIME software package (http://www.drive5.com/uchime/uchime_download.html). The taxonomic association corresponding to each 16S rRNA gene sequence was generated using the RDP Classifier (<http://rdp.cme.msu.edu/>) and the Silva (sival128/16 s) 16S rRNA gene database and a confidence threshold of 70%. The 16S rRNA gene OTU table was used to calculate the alpha diversity metrics including the OTU abundances and several diversity metrics, including the Ace, Chao1, Shannon, and Simpson indices, as well as the diversity coverage analysis. The diversity metrics were used to evaluate the community's richness and diversity, while the principal coordinate analyses were used to evaluate the between-sample community compositional differences. The above analyses were conducted in QIIME 1.17. The raw sequence data was deposited in the NCBI Short Read Archive (SRA) BioProject PRJNA549560 under accession numbers SRR9325875 to SRR9325913.

2.5 Real-time PCR quantification of *Cbbl* and 16S rRNA gene abundances

The abundances of the rubisco large subunit (*Cbbl*) and the 16S rRNA genes were determined using real-time quantitative PCR (qPCR) as described by Yuan et al. (2012), with the *Cbbl*-specific (K2f primer: 5'-ACC AYCAAGCCSAAGCTSGG-3', V2r primer: 5'-GCCTTC SAGCTTGCCSACCRC-3') and the 16S rRNA gene-specific primers (16S_F primer: 5'-AGAGTTTGATC-MTGGCTCAG-3', 16S_R primer: 5'-GCTGCCTCCCGT AGGAGT-3'). The qPCRs were conducted in triplicate in total reaction volumes of 10 µL, where each reaction mixture contained Power qPCR PreMix (GENEray), 0.15 µM of each primer (0.2 µL), 1 µL of DNA template (~ 5 ng), and 8.8 µL deionized H₂O. The qPCR amplification was conducted using the following parameters: 30 s at 95 °C followed by 40 cycles of 95 °C for 10 s, 62 °C for 40 s, and 72 °C for 30 s. After each run, the melting curve of each reaction was used to discriminate between the specific and non-specific qPCR signals. The qPCR reactions were conducted and analyzed using an ABI7900 Real-Time PCR System (PerkinElmer, Applied Biosystems, USA). The standard curves were generated using tenfold serial dilutions of plasmids containing partial gene fragments of *Cbbl* and 16S rRNA genes over a range of 10³–10⁹ copies µL⁻¹. The *Cbbl* and 16S rRNA gene copy numbers were automatically calculated using the SDS 2.3 software package as part of the Real-Time PCR System.

2.6 Statistical analysis

One-way analysis of variance (ANOVA) and multivariate (general linear model) tests were used to identify significant differences in the edaphic biochemical characters, soil organic matter composition, and microbial community data among plant species and water levels followed by HSD Tukey's test ($p=0.05$) using the SPSS 21 software package. Statistically significant differences were defined as follows: *: $p < 0.05$; **: $p < 0.01$; and ***: $p < 0.001$. Spearman's correlation coefficient was used to evaluate the correlations between the soil edaphic physicochemical and biochemical properties, the soil SOM spectral data, and the soil microbial community compositional data using the SPSS 21 software package. The effects of plant species and water levels on soil bacterium community dissimilarity were performed using “adonis” and “anosim” function within “vegan” package in the R 3.5.3. The linear discriminant analysis was also done with R Project for statistical computing (<https://www.r-project.org/>) to identify specific microbial taxa associated with the plant species and water levels, and the LDA value > 4 was selected. Redundancy analysis (RDA) and variation partitioning analysis (VPA) were performed to determine the extent to which the environment factors and soil organic chemical components could explain the bacterial community composition using the Canoco 5.0 software (www.canoco5.com). Graphical visualizations of the results were generated using the Origin 2018 software suite.

3 Results

3.1 Soil edaphic and plant biomass traits under different host plant species and water levels

Plant types and water levels had significant influence on most of the soil traits (Table 1). Soil content of TC, TN, and AOC was the highest in *Z. latifolia*, with mean value of 21.43, 0.21, and 7.70 mg g⁻¹ respectively ($p < 0.001$), and the lowest in *P. communis* with mean value of 5.48, 0.08, and 3.54 mg g⁻¹, respectively (Table 1). Soil DOC concentration and SOC and MBC contents were the highest in the *T. lutarioriparia* (DOC 2.54 mg L⁻¹, SOC 673 mg g⁻¹, MBC 1274 mg kg⁻¹) and were the lowest in the mud flat soils (DOC 1.99 mg L⁻¹) and *Z. latifolia* (SOC 347 mg g⁻¹; MBC 903 mg kg⁻¹), respectively. At each plant soil (not including the mud flat soils), the soil traits were significant influenced by the water levels (Table 1). The soil traits in Table 1 always were the highest at normal water level in the *Z. latifolia* soil. Most soil traits in Table 1 were the highest in the dry water level for the *T. lutarioriparia* soil.

The total carbon of roots and the total nitrogen from roots and stems/leaves differed strongly among four plants

($p < 0.05$), while the total carbon from the stems/leaves exhibited no significant difference ($p > 0.05$) (Table S1). Plant biomass from the roots and stems/leaves showed no obvious difference between the four plant species ($p > 0.05$) (Table S1). Water levels influenced the biomass and TC and TN contents of plant stem and leaves ($p < 0.05$) (Table S1).

3.2 Soil enzymatic activities and soil bacterial abundance under different host plant species and water levels

Plant types and water levels had significant influence to the enzymatic activities (urease, catalase, sucrose, and rubisco) ($p < 0.05$) (Table 2). Compared the soil enzymatic activity of different plant species at each water level: at normal water level, the catalase, sucrose, and rubisco activities were significantly different for different plant types, and the order is as follows: mud flat soil $>$ *Z. latifolia* $>$ *C. cinerascens* $>$ *T. lutarioriparia* $>$ *P. communis*, mud flat soil $>$ *C. cinerascens* $>$ *T. lutarioriparia* $>$ *Z. latifolia* $>$ *P. communis*, and *P. communis* $>$ *Z. latifolia* $>$ *C. cinerascens* $>$ *T. lutarioriparia* $>$ mud flat soil, respectively; at dry water level, the rubisco and *Cbbl* were influenced by the different plant types, with the order *C. cinerascens* $>$ *T. lutarioriparia* $>$ *P. communis* $>$ *Z. latifolia* $>$ mud flat soil and *Z. latifolia* $>$ *T. lutarioriparia* $>$ *P. communis* $>$ *C. cinerascens* $>$ mud flat soil; at the flood water level, the BR, catalase, and urease were also influenced with the sequence of *Z. latifolia* $>$ mud flat soil $>$ *C. cinerascens* $>$ *P. communis* $>$ *T. lutarioriparia*, *Z. latifolia* $>$ mud flat soil $>$ *C. cinerascens* $>$ *P. communis* $>$ *T. lutarioriparia* and *T. lutarioriparia* $>$ *C. cinerascens* $>$ *Z. latifolia* $>$ *P. communis* $>$ mud flat soil. The soil rubisco enzymatic activity and soil bacterial 16S rRNA gene abundance were significantly different under five soils with different plant species and were the lowest for the mud flat soils ($p < 0.05$) (Table 2). The carbon fixed functional gene *Cbbl* was not significantly different under different plant species ($p > 0.05$) (Table 2).

Comparing the soil enzymatic activity across three water levels at each soil, the water level had important influence on the soil enzymatic activities, such as at the mud flat soil, the urease, catalase and sucrose activities were the highest in the normal water level, and the lowest in the dry water level, or flood level ($p < 0.05$) (Table 2). The 16S rRNA and *Cbbl* richness were significantly different ($p < 0.05$) (Table 2), while the soil rubisco enzymatic activity was not significantly different for different water levels ($p > 0.05$) (Table 2).

3.3 SOM compositions determined by MidDRIFT spectroscopy under different host plant species and water levels

Significant differences in relative peak intensity (470–1108 cm⁻¹) (Table 3) were clearly observed

Table 1 Mean \pm standard error of the soil traits based on plant types or water levels

Soil traits	Water level	Mud flat soil	<i>Z. latifolia</i>	<i>C. cinerascens</i>	<i>T. lutarioriparia</i>	<i>P. communis</i>
Wc	Normal	55.81 \pm 8.67bA	130.89 \pm 13.03aA	57.80 \pm 12.06bA	45.50 \pm 4.38bA	34.30 \pm 0.95bB
	Dry	65.31 \pm 10.90aA	58.79 \pm 9.08aB	44.08 \pm 4.58aA	42.03 \pm 7.14aA	37.94 \pm 3.19aB
	Flood	53.26 \pm 3.04bA	86.87 \pm 22.15aAB	51.29 \pm 4.95bA	37.20 \pm 3.44bA	49.42 \pm 2.48bA
pH	Normal	5.48 \pm 0.11aA	4.72 \pm 0.01bB	5.27 \pm 0.04aA	5.43 \pm 0.14aA	5.66 \pm 0.13aA
	Dry	6.10 \pm 0.22aA	5.56 \pm 0.25abA	5.57 \pm 0.21abA	4.91 \pm 0.03bB	5.52 \pm 0.24abA
	Flood	6.07 \pm 0.21aA	5.74 \pm 0.05abA	5.45 \pm 0.06bA	5.38 \pm 0.07bA	5.45 \pm 0.07bA
Tem _{soil}	Normal	16.00 \pm 0.00aA	11.67 \pm 0.33aB	14.07 \pm 1.26aA	16.22 \pm 0.87aA	14.00 \pm 0.58aAB
	Dry	9.33 \pm 0.33aB	8.67 \pm 0.33aC	10.00 \pm 0.63aB	11.00 \pm 0.52aB	11.00 \pm 1.00aB
	Flood	16.17 \pm 0.17aA	16.33 \pm 0.33aA	16.33 \pm 0.21aA	17.17 \pm 0.31aA	16.33 \pm 0.33aA
EC	Normal	0.26 \pm 0.16abA	0.42 \pm 0.11aA	0.08 \pm 0.00bB	0.09 \pm 0.01bB	0.07 \pm 0.01bA
	Dry	0.13 \pm 0.02aA	0.12 \pm 0.02aB	0.12 \pm 0.01aA	0.14 \pm 0.01aA	0.10 \pm 0.02aA
	Flood	0.16 \pm 0.08aA	0.10 \pm 0.01aB	0.08 \pm 0.01aB	0.08 \pm 0.00aB	0.07 \pm 0.00aA
TDS	Normal	0.13 \pm 0.08abA	0.21 \pm 0.05aA	0.04 \pm 0.00bB	0.05 \pm 0.01bB	0.04 \pm 0.01bA
	Dry	0.06 \pm 0.01aA	0.06 \pm 0.01aB	0.06 \pm 0.00aA	0.07 \pm 0.01aA	0.05 \pm 0.02aA
	Flood	0.08 \pm 0.04aA	0.05 \pm 0.01aB	0.04 \pm 0.00aB	0.04 \pm 0.00aB	0.04 \pm 0.00aA
AOC	Normal	4.07 \pm 1.76bA	11.66 \pm 2.31aA	2.40 \pm 0.68bB	6.58 \pm 0.31bA	2.01 \pm 0.27bB
	Dry	8.61 \pm 2.07aA	6.49 \pm 1.37aA	6.43 \pm 1.24aA	6.28 \pm 0.99aA	4.13 \pm 0.65aA
	Flood	5.15 \pm 0.84aA	4.96 \pm 0.10aA	4.84 \pm 0.83aAB	3.82 \pm 0.22aB	4.47 \pm 0.36aA
DOC	Normal	2.04 \pm 0.45aA	2.86 \pm 0.12aA	2.11 \pm 0.40aAB	2.06 \pm 0.25aB	1.31 \pm 0.17aB
	Dry	1.77 \pm 0.21bA	1.65 \pm 0.35bA	1.66 \pm 0.15bB	2.97 \pm 0.16aA	2.65 \pm 0.49abA
	Flood	2.19 \pm 0.24aA	2.18 \pm 0.47aA	2.97 \pm 0.08aA	2.59 \pm 0.14aAB	2.49 \pm 0.07aAB
SOC	Normal	440.0 \pm 54.4abA	529.6 \pm 63.3abA	219.2 \pm 84.4bA	578.4 \pm 92.4abA	836.2 \pm 33.8aA
	Dry	696.2 \pm 242.9aA	167.3 \pm 21.9aB	429.6 \pm 99.8aA	801.8 \pm 98.1aA	320.7 \pm 109.3aB
	Flood	631.2 \pm 113.1aA	342.9 \pm 115.8aAB	554.6 \pm 175.5aA	637.3 \pm 175.0aA	387.3 \pm 90.0aB
MBC	Normal	1138.8 \pm 210.2abA	2183.3 \pm 698.9aA	574.8 \pm 128.2bA	786.6 \pm 269.8abB	924.9 \pm 397.0abA
	Dry	323.6 \pm 73.0bA	170.7 \pm 98.4bB	1055.9 \pm 278.1abA	2156.2 \pm 483.8aA	373.2 \pm 262.2bA
	Flood	1042.4 \pm 407.7aA	356.2 \pm 131.0aB	406.8 \pm 85.0aA	878.1 \pm 214.0aAB	429.5 \pm 179.3aA
BR	Normal	82.0 \pm 13.8bA	255.8 \pm 10.2aA	128.7 \pm 31.1abA	113.4 \pm 29.4bAB	83.8 \pm 26.8bA
	Dry	107.8 \pm 31.9aA	148.9 \pm 29.0aA	122.6 \pm 29.3aA	132.0 \pm 34.3aA	87.9 \pm 59.7aA
	Flood	69.8 \pm 11.7abA	141.7 \pm 74.7aA	41.4 \pm 10.5bA	25.8 \pm 7.8bB	34.1 \pm 8.1bA
TN _{soil}	Normal	1.68 \pm 0.62bA	4.27 \pm 0.57aA	1.36 \pm 0.21bA	1.05 \pm 0.14bB	0.42 \pm 0.03bB
	Dry	1.25 \pm 0.26abA	1.18 \pm 0.24abB	1.46 \pm 0.19abA	1.91 \pm 0.13aA	0.76 \pm 0.14bB
	Flood	0.97 \pm 0.17aA	0.77 \pm 0.10aB	1.02 \pm 0.20aA	0.88 \pm 0.08aB	0.93 \pm 0.04aA
TC _{soil}	Normal	14.73 \pm 5.35bA	48.77 \pm 7.44aA	12.14 \pm 2.04bA	9.16 \pm 1.35bB	4.50 \pm 0.59bA
	Dry	8.83 \pm 1.99abA	9.64 \pm 2.42abB	12.41 \pm 1.96abA	17.11 \pm 1.65aA	5.48 \pm 0.75bA
	Flood	6.60 \pm 1.16aA	5.89 \pm 0.33aB	7.57 \pm 1.37aA	6.18 \pm 0.67aB	6.46 \pm 0.73aA
TC _{Nratio}	Normal	8.84 \pm 0.10bA	11.38 \pm 0.21aA	8.72 \pm 0.33bA	8.59 \pm 0.28bA	10.72 \pm 0.71aA
	Dry	7.22 \pm 0.45aB	7.97 \pm 0.55aB	8.44 \pm 0.38aA	8.91 \pm 0.38aA	7.36 \pm 0.31aB
	Flood	6.84 \pm 0.12aB	7.79 \pm 0.70aB	8.78 \pm 1.55aA	6.99 \pm 0.41aB	6.90 \pm 0.60aB

Different capital letters within the same volume indicate significant differences ($p < 0.05$) among three water levels with the same plant type soil, and different low case letters within the same volume indicate significant differences ($p < 0.05$) among different plant type soils at the same water level

Wc water content of soil (%), Tem_{soil} soil temperature ($^{\circ}$ C), EC electrical conductivity, TDS total dissolved solids, TC_{soil} total carbon content of soil (mg/g), TN_{soil} total nitrogen content of soil (mg/g), C_{N ratio} ratio of total carbon content to total nitrogen content in soil, soil active organic carbon (mg/g), soil dissolved organic carbon (mg/L), soil organic carbon (mg/kg), and soil microbial biomass carbon (mg/kg)

Table 2 Mean \pm standard error of the soil enzyme activity, soil bacterial and C-fixing gene richness and alpha diversity based on plant types or water levels

Soil enzyme and genes	Water level	Mud flat soil	<i>Z. latifolia</i>	<i>C. cinerascens</i>	<i>T. lutarioriparia</i>	<i>P. communis</i>
BR	Normal	82.0 \pm 13.8bA	255.8 \pm 10.2aA	128.7 \pm 31.1abA	113.4 \pm 29.4bAB	83.8 \pm 26.8bA
	Dry	107.8 \pm 31.9aA	148.9 \pm 29.0aA	122.6 \pm 29.3aA	132.0 \pm 34.3aA	87.9 \pm 59.7aA
	Flood	69.8 \pm 11.7abA	141.7 \pm 74.7aA	41.4 \pm 10.5bA	25.8 \pm 7.8bB	34.1 \pm 8.1bA
Catalase	Normal	0.65 \pm 0.06aA	0.55 \pm 0.17abA	0.53 \pm 0.08abA	0.25 \pm 0.02bA	0.22 \pm 0.04bB
	Dry	0.36 \pm 0.05aB	0.36 \pm 0.06aA	0.23 \pm 0.04aB	0.29 \pm 0.03aA	0.17 \pm 0.03aB
	Flood	0.61 \pm 0.03abA	0.75 \pm 0.12aA	0.40 \pm 0.05bcAB	0.35 \pm 0.05cA	0.38 \pm 0.02bcA
Urease	Normal	7.38 \pm 1.74aA	8.29 \pm 5.66aA	5.48 \pm 1.03aA	7.91 \pm 3.06aA	1.33 \pm 0.23aA
	Dry	3.04 \pm 1.04aB	9.36 \pm 2.63aA	10.75 \pm 4.20aA	13.52 \pm 3.18aA	8.50 \pm 3.03aA
	Flood	2.46 \pm 0.81bB	3.79 \pm 0.51abA	6.37 \pm 0.83abA	7.70 \pm 1.27aA	3.72 \pm 0.75abA
Sucrase	Normal	0.70 \pm 0.10aA	0.10 \pm 0.02bA	0.36 \pm 0.08abA	0.31 \pm 0.14abB	0.07 \pm 0.02bA
	Dry	0.26 \pm 0.07aB	0.44 \pm 0.15aA	0.56 \pm 0.09aA	0.90 \pm 0.19aA	0.44 \pm 0.20aA
	Flood	0.22 \pm 0.04aB	0.33 \pm 0.07aA	0.53 \pm 0.14aA	0.36 \pm 0.07aB	0.51 \pm 0.11aA
Rubisco	Normal	17.87 \pm 3.88bA	73.04 \pm 4.33abA	63.33 \pm 21.00abA	54.40 \pm 13.41abA	120.45 \pm 23.71aAB
	Dry	27.20 \pm 4.45bA	62.17 \pm 39.22abA	132.49 \pm 19.43aA	100.24 \pm 27.32abA	62.94 \pm 6.17abB
	Flood	43.51 \pm 8.67bcA	33.41 \pm 8.65cA	127.05 \pm 28.60abA	62.55 \pm 18.03bcA	139.87 \pm 13.46aA
16srRNA	Normal	1.97 \pm 0.73aA	2.40 \pm 0.34aB	6.30 \pm 0.18aA	5.17 \pm 1.13aA	3.70 \pm 0.04aA
	Dry	2.77 \pm 0.53aA	3.45 \pm 0.12aA	3.12 \pm 0.17aA	2.97 \pm 0.13aA	3.45 \pm 0.17aA
	Flood	3.43 \pm 0.13aA	3.59 \pm 0.10aA	3.29 \pm 0.11aA	3.11 \pm 0.11aA	3.24 \pm 0.26aA
<i>Cbbl</i>	Normal	1309.8 \pm 199.1aA	80.7 \pm 42.1aB	1132.5 \pm 531.6aA	585.5 \pm 192.3aA	475.7 \pm 130.3aA
	Dry	141.2 \pm 33.9cB	786.0 \pm 148.2aA	239.5 \pm 92.1bcA	494.3 \pm 65.3abA	348.3 \pm 24.1bcA
	Flood	240.2 \pm 62.3aB	563.3 \pm 79.8aA	533.0 \pm 163.8aA	436.8 \pm 130.8aA	728.7 \pm 86.2aA

Soil basic respiration (mL/kg 24 h); soil catalase activity (mL 0.1 mg KMnO₄/g min); soil urease activity (mg NH₃-N/g 24 h); soil sucrase activity (mg/g 24 h); soil rubisco activity (nmol CO₂/kg min); soil 16S rRNA gene (10⁵ copies/mg); soil *Cbbl* gene (copies/mg); different capital letters within the same volume indicate significant differences ($p < 0.05$) among three water levels with the same plant type soil, and different lowercase letters within the same volume indicate significant differences ($p < 0.05$) among different plant type soils at the same water level

among different plant types and also were found in 914–1108 cm⁻¹, 1623 and 1635 cm⁻¹, and 3444–3697 cm⁻¹ (Table 3) across three water levels ($p < 0.05$). The lowest peak intensity in the overall soil spectra was observed in the *T. lutarioriparia* community soils, while the highest was observed in the *P. communis* and *Z. latifolia* community soils (914–1108 cm⁻¹) (Table 3), and the trend was mostly found at the dry water level. The relative peak intensity from 1623, 1635, 3444 to 3621 cm⁻¹ showed no significant difference among different plant types. The relative peak intensities of 1623, 1635, 3444, 3450, and 3621 cm⁻¹ were the highest in flooded water level and the lowest in the normal water level period for the *C. cinerascens* and *Z. latifolia*, while the 2852- and 2923 cm⁻¹ peak intensities were the highest in dry water level and the lowest in the normal water level period (Table 3).

3.4 Soil bacteria alpha diversity and community composition under different host plant species and water levels

A total of 2,106,617 high-quality 16S rRNA gene sequences were obtained comprising a total of 6035 OTUs. The bacterial diversity was particularly high in the soils sampled in this study, e.g., detection of 58 phyla, 134 classes, 260 orders, 464 families, 798 genera, and 1638 species in total. The sobs (1587–2166), Chao1 (2158–2918), and Shannon (5.65–6.35) indices showed significantly different among the soils associated with different plant species ($p < 0.05$) (Fig. 1) at each water level. In contrast, significant differences in the diversity patterns were not observed across the three water levels (normal, dry, and flood periods) for each plant species and mud flat soils except the *T. lutarioriparia* ($p > 0.05$) (Fig. 1). The

Table 3 Mean \pm standard error of the seventeen spectra absorbance intensity of soil organic matter composition based on plant types or water levels

Absorbance intensity	Water level	Mud flat soil	<i>Z. latifolia</i>	<i>C. cinerascens</i>	<i>T. lutarioriparia</i>	<i>P. communis</i>
R470	Normal	3.85 \pm 0.43aA	5.71 \pm 0.00aA	4.31 \pm 0.62aA	4.72 \pm 0.57aA	3.72 \pm 0.27aC
	Dry	4.97 \pm 0.24bA	5.17 \pm 0.03bB	4.90 \pm 0.19bA	4.50 \pm 0.25bA	7.22 \pm 0.38aA
	Flood	4.51 \pm 0.34aA	5.56 \pm 0.18aAB	4.54 \pm 0.65aA	3.96 \pm 0.45aA	5.90 \pm 0.22aB
R536	Normal	3.37 \pm 0.35aA	5.17 \pm 0.00aA	3.72 \pm 0.67aA	4.06 \pm 0.60aA	3.34 \pm 0.43aB
	Dry	4.57 \pm 0.37bA	5.14 \pm 0.12abA	4.47 \pm 0.32bA	4.21 \pm 0.29bA	6.51 \pm 0.27aA
	Flood	4.40 \pm 0.38aA	5.51 \pm 0.21aA	4.28 \pm 0.65aA	3.59 \pm 0.41aA	5.58 \pm 0.24aA
R694	Normal	0.60 \pm 0.05bA	0.78 \pm 0.00abA	0.73 \pm 0.03abA	0.71 \pm 0.04abA	0.88 \pm 0.11aA
	Dry	0.73 \pm 0.05abA	0.84 \pm 0.03abA	0.74 \pm 0.04abA	0.66 \pm 0.03bA	0.98 \pm 0.14aA
	Flood	0.71 \pm 0.04aA	0.84 \pm 0.02aA	0.74 \pm 0.06aA	0.74 \pm 0.06aA	0.84 \pm 0.04aA
R779	Normal	0.91 \pm 0.02aA	0.81 \pm 0.00aB	0.89 \pm 0.05aA	0.86 \pm 0.08aA	1.05 \pm 0.02aA
	Dry	0.88 \pm 0.01aA	0.86 \pm 0.01aA	0.86 \pm 0.01aA	0.89 \pm 0.01aA	0.85 \pm 0.04aB
	Flood	0.88 \pm 0.01aA	0.89 \pm 0.01aA	0.90 \pm 0.02aA	0.95 \pm 0.03aA	0.88 \pm 0.02aB
R914	Normal	2.52 \pm 0.12aA	3.56 \pm 0.00aB	2.56 \pm 0.37aA	2.81 \pm 0.39aA	2.73 \pm 0.37aB
	Dry	3.22 \pm 0.26aA	3.81 \pm 0.07aA	3.13 \pm 0.30aA	3.07 \pm 0.28aA	4.12 \pm 0.03aA
	Flood	3.21 \pm 0.28aA	3.95 \pm 0.07aA	3.07 \pm 0.41aA	2.62 \pm 0.28aA	3.89 \pm 0.19aA
R1008	Normal	8.00 \pm 0.62aA	12.11 \pm 0.00aA	8.40 \pm 1.36aA	9.44 \pm 1.62aA	7.58 \pm 0.93aB
	Dry	10.40 \pm 0.71bA	11.24 \pm 0.26bA	10.20 \pm 0.59bA	9.17 \pm 0.51bA	15.16 \pm 1.26aA
	Flood	10.54 \pm 0.57abA	12.19 \pm 0.33aA	9.98 \pm 0.99abA	8.26 \pm 0.67bA	11.71 \pm 0.52abA
R1031	Normal	8.82 \pm 0.75aA	13.65 \pm 0.00aA	9.35 \pm 1.56aA	10.44 \pm 1.89aA	8.35 \pm 1.09aB
	Dry	11.50 \pm 0.80bA	12.34 \pm 0.30bB	11.33 \pm 0.60bA	10.05 \pm 0.53bA	17.12 \pm 1.69aA
	Flood	11.68 \pm 0.61abA	13.45 \pm 0.38aAB	11.04 \pm 1.06abA	9.11 \pm 0.73bA	12.75 \pm 0.58abAB
R1108	Normal	4.68 \pm 0.32aA	6.90 \pm 0.00aA	4.73 \pm 0.65aA	5.18 \pm 0.66aA	4.34 \pm 0.50aB
	Dry	5.56 \pm 0.28bA	5.80 \pm 0.10bB	5.51 \pm 0.23bA	5.16 \pm 0.15bA	7.42 \pm 0.32aA
	Flood	5.59 \pm 0.20aA	6.07 \pm 0.17aB	5.39 \pm 0.42aA	4.72 \pm 0.33aA	5.88 \pm 0.38aAB
R1384	Normal	0.24 \pm 0.07aA	0.41 \pm 0.00aA	0.22 \pm 0.06aA	0.28 \pm 0.12aA	0.52 \pm 0.14aA
	Dry	0.27 \pm 0.08aA	0.28 \pm 0.03aB	0.25 \pm 0.06aA	0.22 \pm 0.05aA	0.47 \pm 0.04aA
	Flood	0.40 \pm 0.08aA	0.34 \pm 0.02aB	0.43 \pm 0.07aA	0.38 \pm 0.07aA	0.27 \pm 0.03aA
R1623	Normal	0.71 \pm 0.14aA	0.86 \pm 0.00aA	0.79 \pm 0.16aB	0.96 \pm 0.26aA	0.92 \pm 0.41aA
	Dry	1.09 \pm 0.28aA	1.03 \pm 0.11aA	1.02 \pm 0.13aAB	0.90 \pm 0.16aA	0.98 \pm 0.30aA
	Flood	1.42 \pm 0.18aA	1.09 \pm 0.06aA	1.44 \pm 0.22aA	1.07 \pm 0.30aA	0.84 \pm 0.06aA
R1635	Normal	0.78 \pm 0.15aA	0.95 \pm 0.00aA	0.86 \pm 0.18aB	1.06 \pm 0.29aA	1.02 \pm 0.47aA
	Dry	1.16 \pm 0.29aA	1.13 \pm 0.11aA	1.11 \pm 0.15aAB	0.99 \pm 0.17aA	1.08 \pm 0.33aA
	Flood	1.55 \pm 0.20aA	1.19 \pm 0.06aA	1.58 \pm 0.24aA	1.19 \pm 0.34aA	0.91 \pm 0.06aA
R2852	Normal	0.08 \pm 0.02aA	0.13 \pm 0.00aA	0.17 \pm 0.07aA	0.25 \pm 0.14aA	0.13 \pm 0.05aA
	Dry	0.15 \pm 0.03bA	0.13 \pm 0.01bA	0.12 \pm 0.03bA	0.12 \pm 0.03bA	0.36 \pm 0.10aA
	Flood	0.17 \pm 0.03aA	0.16 \pm 0.02aA	0.17 \pm 0.02aA	0.18 \pm 0.05aA	0.16 \pm 0.02aA
R2923	Normal	0.13 \pm 0.02aA	0.25 \pm 0.00aA	0.27 \pm 0.11aA	0.40 \pm 0.23aA	0.25 \pm 0.09aA
	Dry	0.24 \pm 0.05abA	0.21 \pm 0.03abA	0.21 \pm 0.04abA	0.18 \pm 0.04bA	0.48 \pm 0.17aA
	Flood	0.27 \pm 0.05aA	0.24 \pm 0.03aA	0.26 \pm 0.03aA	0.29 \pm 0.08aA	0.21 \pm 0.02aA
R3444	Normal	2.46 \pm 0.31aA	2.55 \pm 0.00aB	2.66 \pm 0.55aB	3.17 \pm 0.79aA	3.40 \pm 1.53aA
	Dry	3.56 \pm 0.89aA	3.62 \pm 0.35aAB	3.66 \pm 0.55aAB	3.16 \pm 0.57aA	4.23 \pm 1.68aA
	Flood	5.09 \pm 0.64aA	3.86 \pm 0.28aA	5.43 \pm 0.96aA	4.22 \pm 1.33aA	3.06 \pm 0.10aA
R3450	Normal	2.46 \pm 0.31aA	2.55 \pm 0.00aB	2.66 \pm 0.55aB	3.17 \pm 0.79aA	3.40 \pm 1.52aA
	Dry	3.56 \pm 0.89aA	3.62 \pm 0.35aAB	3.66 \pm 0.55aAB	3.16 \pm 0.57aA	4.24 \pm 1.69aA
	Flood	5.08 \pm 0.64aA	3.86 \pm 0.28aA	5.43 \pm 0.96aA	4.22 \pm 1.33aA	3.06 \pm 0.10aA
R3621	Normal	1.80 \pm 0.21aB	2.64 \pm 0.00aA	2.04 \pm 0.39aA	2.24 \pm 0.43aA	2.18 \pm 0.69aA
	Dry	2.49 \pm 0.26aAB	2.84 \pm 0.08aA	2.55 \pm 0.19aA	2.26 \pm 0.17aA	3.32 \pm 0.70aA
	Flood	2.92 \pm 0.14aA	2.94 \pm 0.13aA	3.02 \pm 0.27aA	2.44 \pm 0.31aA	2.76 \pm 0.13aA
R3697	Normal	1.02 \pm 0.17aA	1.93 \pm 0.00aA	1.29 \pm 0.29aA	1.34 \pm 0.26aA	1.32 \pm 0.35aA
	Dry	1.58 \pm 0.18bA	1.98 \pm 0.10abA	1.58 \pm 0.17abA	1.40 \pm 0.14bA	2.47 \pm 0.43aA
	Flood	1.57 \pm 0.13aA	1.95 \pm 0.04aA	1.57 \pm 0.25aA	1.28 \pm 0.13aA	1.97 \pm 0.15aA

Different capital letters within the same volume indicate significant differences ($p < 0.05$) among three water levels with the same plant type soil, and different lowercase letters within the same volume indicate significant differences ($p < 0.05$) among different plant type soils at the same water level

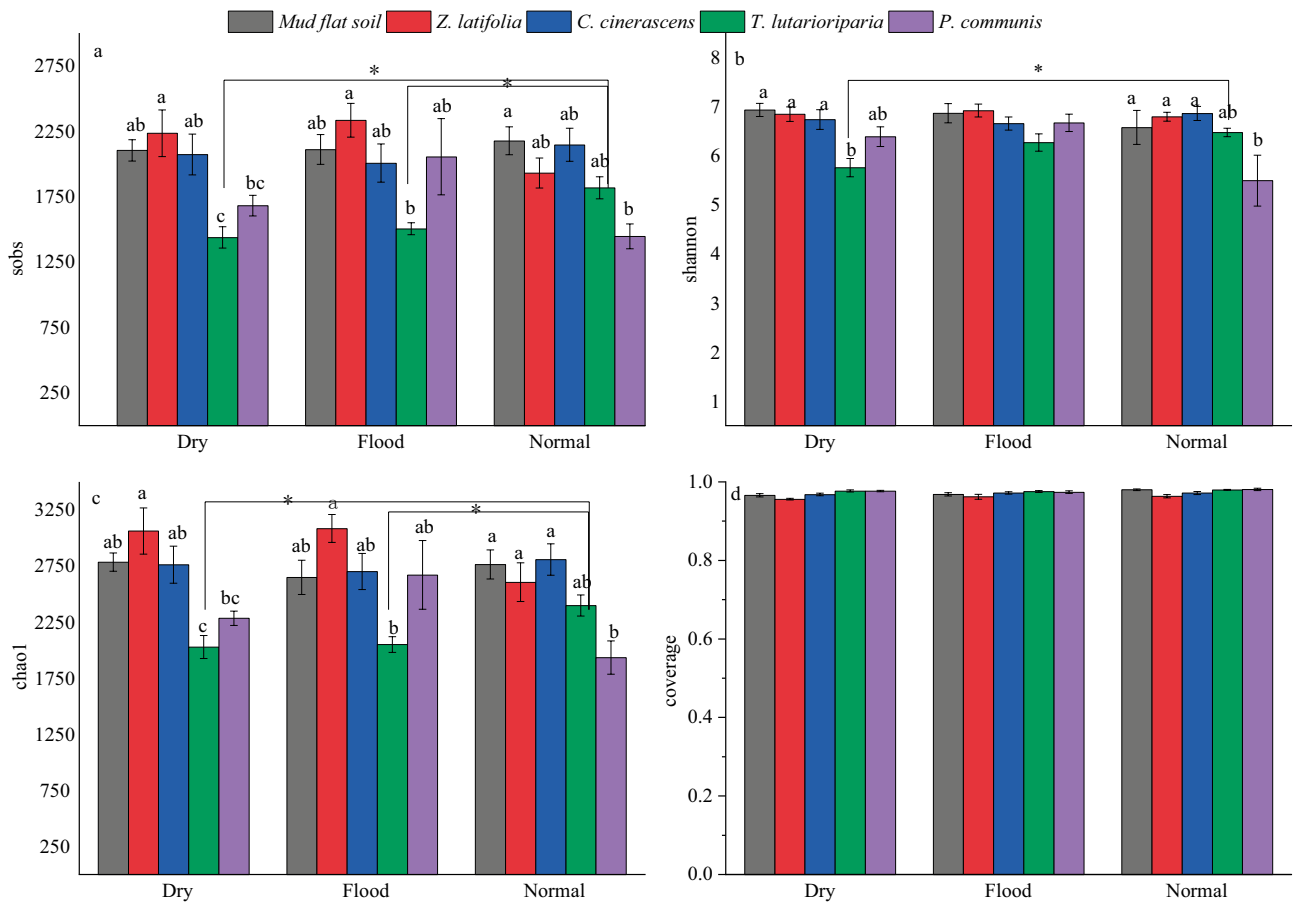


Fig. 1 Bacterial α diversity in different plant species and mud flat soils (a: sobs, b: Shannon, c: chao1, and d: coverage)

bacterial communities could be clearly separated across three water levels and among four plant species and mud flat soils, based on the NMDS of the OTUs (Fig. 2).

The top 15 phyla and top 15 genera based on the abundance > 1% was analyzed in this study. Proteobacteria was the most abundant phylum in the Poyang Lake soils (26.60% of the

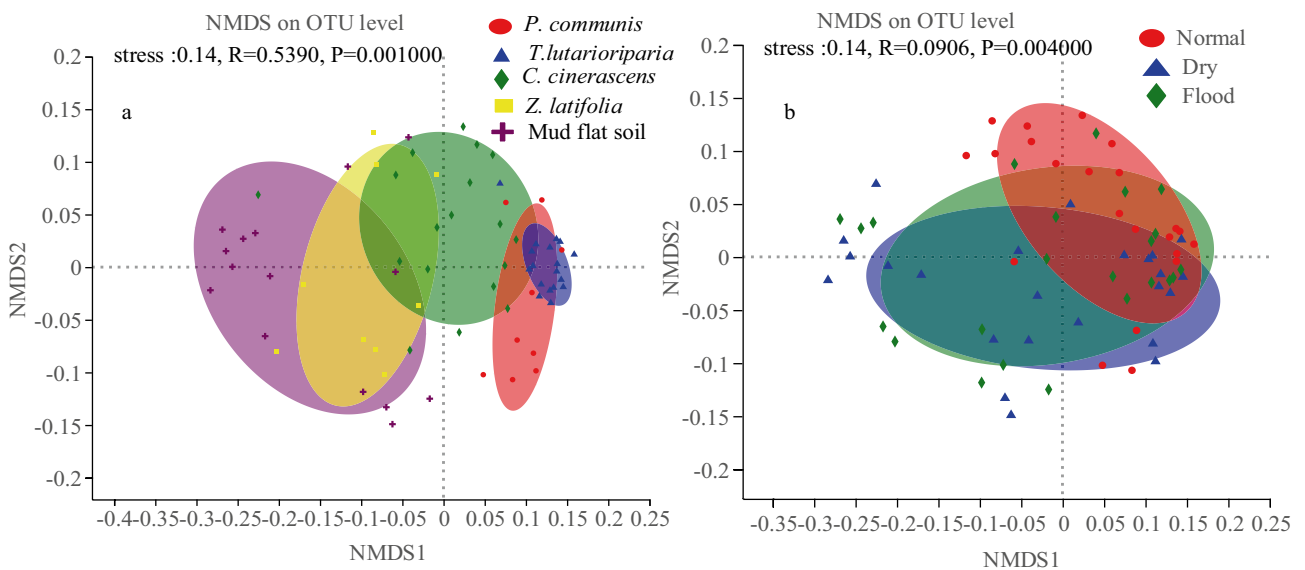


Fig. 2 Non-metric multidimensional scaling (NMDS) plot base on the Bray–Curtis dissimilarities of the relative abundance of the OTU for different plant type soils (a) and different water levels (b)

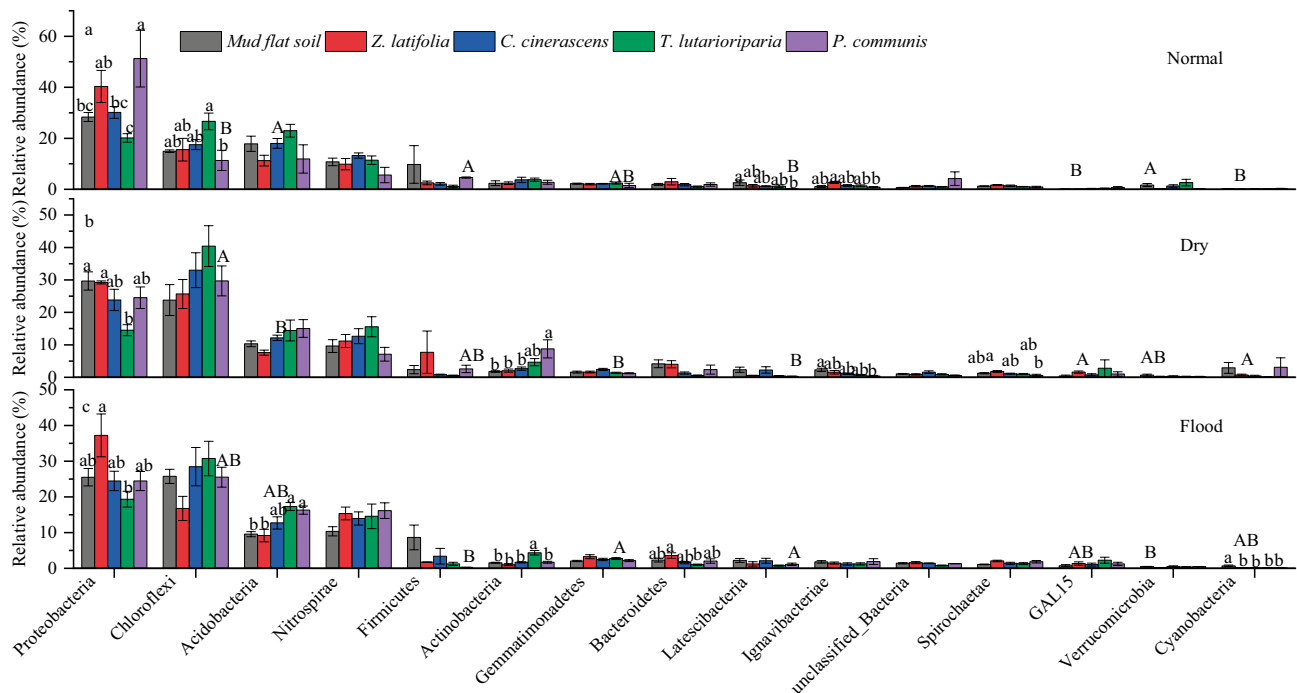


Fig. 3 One-way analysis of variance (ANOVA) tests for statistically significant 15 phylum-level taxonomic differences associated with different plant types at normal, dry, and flood water levels. Different capital letters in Fig. 3 indicate significant differences ($p < 0.05$)

among three water levels with the same plant type soil, and different lowercase letters within Fig. 3 indicate significant differences ($p < 0.05$) among different plant type soils at the same water level

total 16S rRNA gene data). In addition, several other phyla were present in the soil communities including Chloroflexi (mean 25.69%), Acidobacteria (mean 14.11%), Nitrospirae (mean 12.09%), Firmicutes (mean 3.05%), Actinobacteria (mean 2.99%), Gemmatimonadetes (mean 2.10%), and Bacteroidetes (mean 2.03%). Nine phyla had significantly different relative abundances in the four plant species and mud flat soils (Fig. 3). Proteobacteria constituted the most abundant phylum in the *Z. latifolia* (mean: 35.48%) and *P. communis* (mean 33.44%) community soils, and to a lesser extent in the mud flat soils (mean 27.75%) and *T. lutarioriparia* soils (mean 18.03%) ($p < 0.001$). Chloroflexi and Acidobacteria were most abundant in *T. lutarioriparia* soils but had the lowest abundance in the *Z. latifolia* soil communities ($p < 0.05$ and $p < 0.01$). Firmicutes were the most abundant in the mud flat soils ($p < 0.05$), while Actinobacteria were the most abundant in the *T. lutarioriparia* soils ($p < 0.01$). The soils from the different plant species also harbored significantly different relative abundances of four of the lesser abundant phyla: Bacteroidetes, Latescibacteria, Ignavibacteriae, and Spirochaetae ($p < 0.01$) (Fig. 3a). In addition, five of 15 genera were significantly different among the four plant species and mud flat soils ($p < 0.05$ or $p < 0.01$) (Fig. 4).

Water levels were also significantly correlated with the relative abundances of Chloroflexi ($p < 0.001$),

Acidobacteria ($p < 0.01$), Gemmatimonadetes ($p < 0.01$), GAL15, and Cyanobacteria ($p < 0.01$) (Fig. 3). At the genus level, four genera (*g_SBR2076*, *g_Subgroup1*, *g_Gemmatimonadaceae*, and *Lactococcus*) were significantly different for the three water levels (Fig. 4). The *g_SBR2076* was the lowest in the normal water level ($p < 0.001$) and the *g_Subgroup1* was the highest in the normal water level period ($p < 0.05$). The *g_Gemmatimonadaceae* and *Lactococcus* were the lowest in the dry water level period ($p < 0.01$).

The LDA results showed that the LDA scores of Proteobacter and Actinobacter were significantly high in the soils of *P. communis* at the dry and normal water levels (Fig. S3). The Chloroflexi and Acidobacteria were significantly high in the soils of *T. lutarioriparia* at the dry and normal water levels. The Firmicutes was significantly high in the mud flat soils of at the normal water level. The LDA revealed that the specific genera were found from different plant species soils and three water levels (Fig. S4). The *P. communis* soils with *g_unclassified_Bacteria* were specific at the normal water level, and the *P. communis* soils with *c_Actinobacter* were significantly higher at the dry water level. The *g_Subgroup1* (Acidobacteria), *g_HSB_OF53_F07*, and *g_Ktedonobacteria*

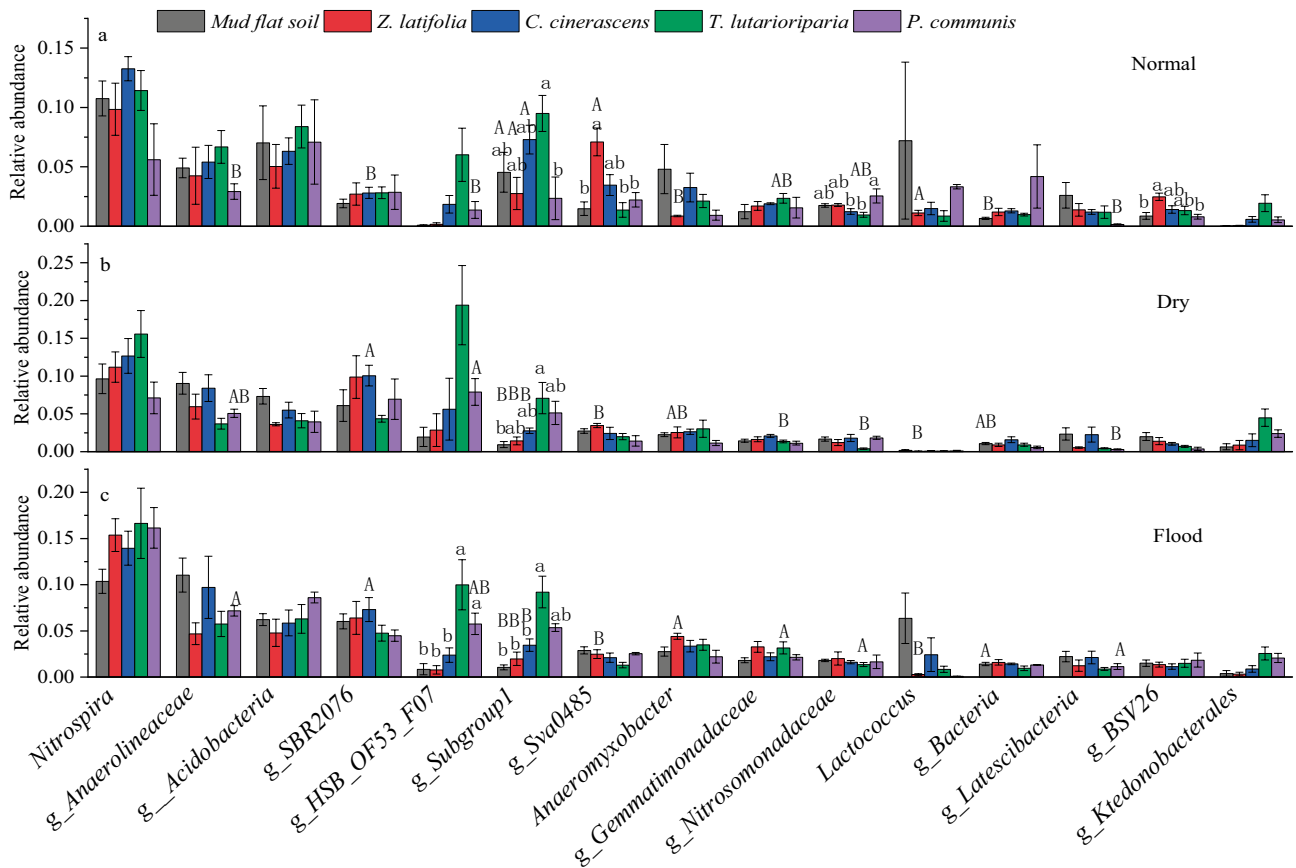


Fig. 4 One-way analysis of variance (ANOVA) tests for statistically significant 15 genus-level taxonomic differences associated with different plant types at normal, dry, and flood water levels. Different capital letters in Fig. 4 indicate significant differences ($p < 0.05$)

among three water levels with the same plant type soil, and different low case letters within Fig. 4 indicate significant differences ($p < 0.05$) among different plant type soils at the same water level

were significantly increased at normal and dry water level for the *T. lutarioriparia* soils, respectively. The *g_SBR2076* was significantly high in the soils of *C. cinerascens* at the dry water level. The *g_Sva048* and *g_Gemmatimonadetes* were strong high in the *Z. latifolia* soils at the normal and flood water levels. The *g_Lactobacillales*, *Lactococcus*, *Latescibacteria*, and *Anaeromyxobacter* were significantly high for the mud flat soils at the normal water level, and the *g_Anaerolineaceae* was high for the mud flat soils at the flood water level.

3.5 Influence of plant, soil, and its organic matter on soil bacterial community

The correlation analyses were done between the soil traits, the soil organic matter composition, and the soil bacterial community, both at phylum and genus levels (Figs. 5, 6, S5 and S6).

Soil pH were positively correlated with Firmicutes ($p < 0.01$) and GAL15 ($p < 0.01$) and negatively relative

to Actinobacteria phylum ($p < 0.01$); AOC had negative influences on the soil GAL15 ($p < 0.01$) (Fig. S5a). The Wc and catalase negatively influenced the Actinobacteria and Chloroflexi phyla and also positively influenced the Ignavibacteriae and Bacteroidetes phyla, while TC_{stem} had the positive role as the Wc and catalase did (Fig. S5a). At the genus level, water level positively correlated with the genera of *Lactococcus*, *Latescibacteria*, and *Anaeromyxobacter* and negatively relative to the genera of *g_Sva0485* and *g_SBR2076* ($p < 0.001^{***}$, 0.01^{**}) (Fig. S5b).

The relative peak intensity of the 3444–3696-cm⁻¹ signal functional groups (corresponding to the carboxylic acid, phenol, alcohol, amines, and amide functional groups) is significantly and negatively correlated with the relative abundances of Actinobacteria and Spirochaetae ($p < 0.05$). The 3621–3697-cm⁻¹-signal functional groups are positively correlated with the phylum of GA15 ($p < 0.05$). In addition, the abundances of the 2852–2953-cm⁻¹-signal functional groups (aliphatic

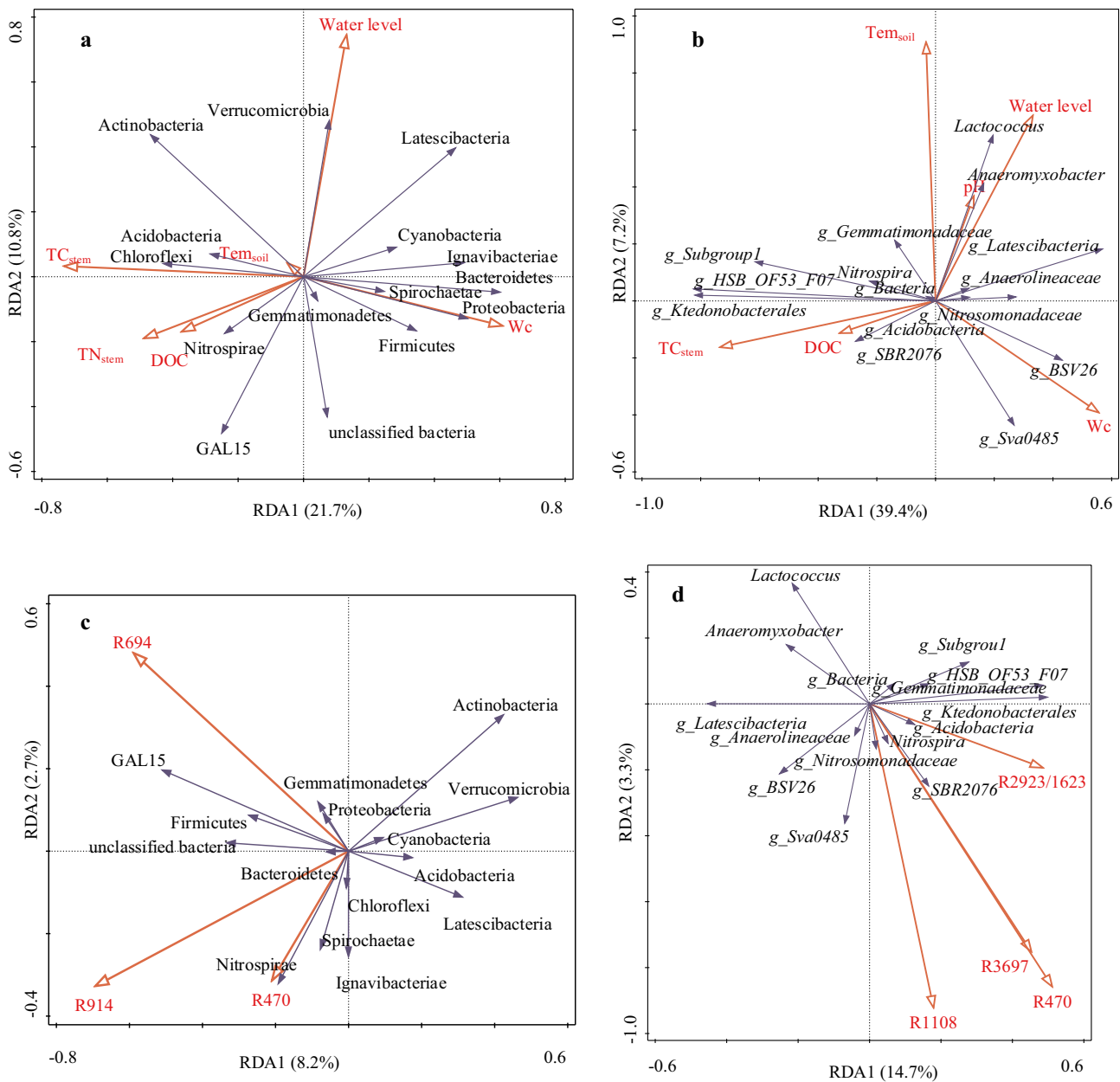


Fig. 5 Results of redundancy analysis (RDA) between soil physicochemical properties and microbial community structures in phylum (a) and genus (b) levels, and between soil organic chemical components and microbial community structures in phylum (c) and genus (d) levels

C–H stretching signals) are negatively correlated with the Verrucomicrobia ($p < 0.05$). The functional groups corresponding to the 1623–1635- cm^{-1} signals (O–H bending and C=O stretching from carboxylic acids, amides, and ketones) have negative correlation with the Actinobacteria ($p < 0.01$ and $p < 0.05$). The 1384- cm^{-1} -signal functional group (symmetric COO⁻ stretching) is negatively correlated with the relative abundances of the Verrucomicrobia

and Spirochaetae ($p < 0.01$). The functional groups with signals $< 1100 \text{ cm}^{-1}$ are negatively correlated with the relative abundances of the Actinobacteria and Verrucomicrobia (Fig. S6a). The functional groups associated with 3444–3450 cm^{-1} , 1623–1635 cm^{-1} , and 2852–2953 cm^{-1} signals are positively correlated with the g_SBR2076 (Chloroflexi) ($p < 0.01$). In addition, 1384- cm^{-1} signals are negatively correlated with the Anaeromyxobacter

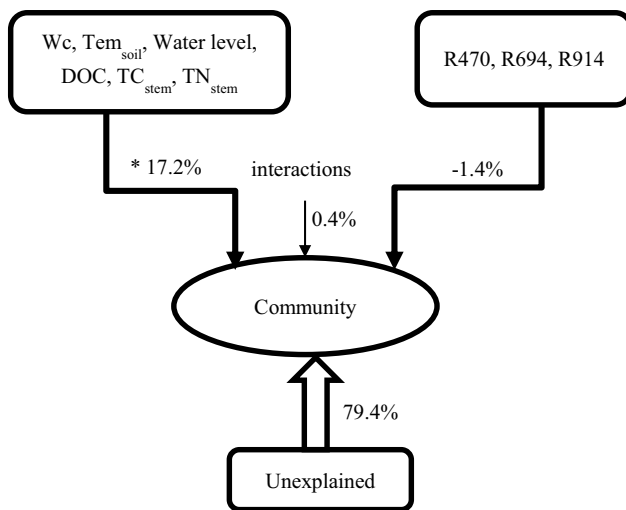


Fig. 6 Variation partition analysis (VPA) based on the relative abundance of 15 phyla with soil traits and soil organic matter composition across the three water level with four plant species and mud flat soils

($p < 0.01$). The $\leq 1100\text{-cm}^{-1}$ signals are negatively correlated with the *Lactococcus* (Chloroflexi) ($p < 0.01$) and positively correlated with the *g_Sva0485* (Proteobacteria) ($p < 0.05$) (Fig. S6b).

Based on the RDA and VPA, the soil trait group (WC, Tem_{soil} , wl, DOC, TC_{stem} , and TN_{stem} , contribution = 17.4%, $p < 0.01$, $p(\text{adjust}) < 0.01$; Figs. 5a, b and 6) significantly contributed to the bacterial community composition, while soil organic matter group (R470, R694, and R914, contribution = -1.4% , $p < 0.05$, $p(\text{adjust}) > 0.05$; Figs. 5c, d and 6) had negative contribution to the bacterial community composition.

4 Discussion

4.1 Effect of plant types and water level shift on the SOM chemical composition of Poyang Lake

SOM stabilization and decomposition are multifaceted, dynamic processes (Dohnalkova et al. 2017). In this study, we found that the plant species composition significantly influences the total C and N of soils, and plant roots and stems/leaves ($p < 0.05$) (Tables 1 and S1), but is not significantly correlated with the SOM chemical composition at the normal and flood water level ($p > 0.05$) (Table 3). While, at the dry water level, the relative peak intensity of 470, 536, 694, 1008, 1031, 1108, 2852, 2923, and 3697 cm^{-1} were significantly different among the four plant species associated soils and mud flat soils (Table 3). Eskelinen et al. (2009) reported that the SOM quality is not certainly explained by

differences in the samples associated with the same plant functional group (i.e., either forbs or shrubs), also being linked to the forb-shrub vegetation gradients. By comparison, this study found that the water level variation had an important role to the SOM composition as reviewed by Luo et al. (2019). Most of the mean relative peak intensity was lowest during the normal water level season in November (Table 3) ($p < 0.05$). The dry water level had the highest relative peak intensity for those groups with signal below 1100 cm^{-1} (e.g., 914, 1031, and 1008 cm^{-1}) ($p < 0.05$), which correspond to functional groups in the polysaccharides and minerals or organic silicates (Table 3), while the flood water level had the highest relative peak intensity for groups with signals of 1623–1635 and 3445–3621 cm^{-1} (Table 3). Colombani et al. (2019) reported that the oxidation reduction potential (ORP) is always positive, suggesting oxic and sub-oxic redox conditions, due to a general lack of SOM and readily available substrates like low molecular weight organic acids. In the study, the water content of the normal water level is still high, but the soil dissolved oxygen is slowly increased at this time. This condition may increase the soil microbial activity (16S rRNA abundance) and also influenced the soil organic matter composition (the lowest DOC and SOC, the lowest of most relative peak intensity) (Tables 1 and 3). In the *Z. latifolia* community, the BR and AOC were significantly higher than those in another plant species, especially in *P. communis* (Tables 1 and 2), which was due to the higher water content of its soils with reducing environment. This condition was not beneficial for the accumulation of SOM (Table 2) and also not for the absorbance of the spectra (Table 3). That is to say, the BR and AOC are related with the soil organic matter compositions, and the relationship was reported by Matamala et al. (2019) that readily bioavailable organic compounds are often the initial and major contributors to soil respiration.

4.2 Effect of plant types and water level shift on the soil bacterial community in the Poyang Lake

Plant species can influence soil microbial communities in natural wetlands (Luo et al. 2018; Chen et al. 2019). There have been a wide variety of published results assessing different microbial communities in *C. cinerascens* and *T. lutari-oriparia*, and/or *P. communis* in Poyang Lake (Liu et al. 2015; Wang et al. 2017a, b). Most studies have reported that soil microbial community composition is strongly influenced by the dominant plant species. In this study, nine of the 15 phyla were significantly influenced by the plant species (Fig. 3a, b, and c). The α diversity had significantly different among the four plant species and mud flat soils, with trends as follows: *Z. latifolia* > *C. cinerascens* > mud flat soil > *P. communis* > *T. lutari-oriparia* and *Z. latifolia* > mud flat soil > *C.*

cinerascens > *P. communis* > *T. lutarioriparia*, respectively ($p < 0.05$) (Fig. 1). We also found that Nitrospirae (12.09%), Gemmatimonadetes (2.10%), and GAL15 (1.01%) groups did not exhibit significant abundance differences among the soils from the different plant species ($p > 0.05$) (Fig. 3), but there are significantly different across three water levels. The result was accordance with the report of Wang et al. (2017a), who suggests that the soil microbial community composition is influenced by plant species, including water levels and soil biochemical characteristics. Consistent with their results, in this study, the water levels significantly influenced the relative abundances of numerous phyla, including Gemmatimonadetes, Chloroflexi, Acidobacteria, and Actinobacteria (Fig. 3).

4.3 Effects of soil edaphic and plant traits on soil bacterial community

It is important to note that the different samples were characterized by different soil temperatures, pH values, and water levels, etc. (Tables 1 and 2). Previous studies have indicated that soil moisture, temperature, and pH influence soil bacterial community composition and diversity (Eskelinen et al. 2009; Cheng et al. 2017; Tian et al. 2017). Microorganisms also play key roles in the decomposition and transformation of organic matter and in the remineralization of other nutrients in ecosystems (Jin et al. 2017). In this study, the soil microbial communities (the phylum and the genus level) were significantly influenced by the soil edaphic physicochemical and biochemical properties (Fig. 5a, b and S5). The higher content of edaphic and plant traits (TC_{stem} and TN_{stem}) may contribute to the soil organic matter accumulation, while the other higher edaphic traits such as BR, AOC, Wc, and catalase are either always easily used by soil microbes or are adverse to other soil microbes. Coolen et al. (2011) reported that the relative high abundance of Acidobacteria was found in soils with low carbon availability and soils with low pH, and this also supported the negative relationship between Acidobacteria with AOC and pH (Fig. 5a).

4.4 Effects of soil SOM compositions on bacterial community

Plant species composition is closely associated with the soil nutrient composition, and especially with the SOM quantities and qualities, which subsequently influence the soil microbial community characteristics (Eskelinen et al. 2009; Banerjee et al. 2016). Although SOM variation was not significantly correlated with the host plant species, these compounds are still directly used as metabolic substrates for microbial populations in soils. As has been shown elsewhere, the lability or recalcitrance of SOM pools influences soil microbial diversity and composition (Eskelinen et al. 2009; Banerjee

et al. 2016; Tian et al. 2017; Xiao et al. 2017a, b). Nevertheless, the relationships between the soil chemical composition and soil microbial populations are indeed very complex (Fig. 5c, d and S6). Among the functional groups indicated in Figs. S6a and S6b, those associated with the 3444–3696- cm^{-1} signal bands are particularly important because the OH and NH stretching features typically indicate the presence of relatively labile SOM (Calderón et al. 2011b). Thus, it is somewhat surprising that some of these bacterial taxonomic groups were negatively correlated with the abundance of labile SOM (Fig. S6a). For example, Proteobacteria are generally considered to be fast-growing, “weed-like” species that consume labile nutrients, which helps to explain their global dominance in soils (Fierer et al. 2007); however, it is possible that other compounds producing the above FT-IR signals may not be significantly labile (e.g., phenolics or aliphatics), which explains the negative correlation between their abundances in certain microbial taxonomic groups.

Signals in the range of 2852–2923 cm^{-1} indicate the presence of aliphatic CH stretching of the methyl and methylene groups, corresponding to the C in the light soil fraction (Calderón et al. 2011a), which is also characteristic of high-quality prairie soils (Calderón et al. 2011a). *Lactococcus* is negatively correlated with the presence of 2852–2923 cm^{-1} spectra. Consequently, the *Lactococcus* taxa may play an important role in the maintenance of soil quality and stability (Fig. S6b). In addition, the functional group associated with the 1384- cm^{-1} signal (carboxylate group) is negatively correlated with the relative abundances of Verrucomicrobia, but it is negatively correlated with *Anaeromyxobacter*. In addition, the functional group indicated by the 1623–1635- cm^{-1} signals was negatively correlated with Actinobacteria and Spirochaetae (Fig. S6a). These results suggested that the Actinobacteria and Verrucomicrobia play an important role in decomposing SOM. Thus, their relationship to these specific SOM spectral profiles may indicate similar metabolic associations to such compounds in the Poyang Lake sediments. Nevertheless, most of the phyla are not significantly correlated with the SOM functional compositions (Fig. S5c and S6a). Davinic et al. (2012) suggested that the effect of the SOM chemistry on the bacterial community composition may be defined by aggregate-specific patterns. In addition, these analyses indicate that the most prevalent taxa in the soils are not those that are strongly correlated with the chemical variation within each aggregate-size class or that the dominant taxa respond less dynamically to shifts in the SOM composition than they do to the low abundance bacterial taxa. This interpretation is consistent with the concept of a “rare microbial biosphere” composed of low-abundance populations in natural environments, which may respond to environmental fluctuations more rapidly than the dominant

organisms, consequently acting as a “microbial seed bank” (Aanderud et al. 2015).

Soil bacteria have different preference for substrates. The functional groups associated with signals below 1100 cm^{-1} were negatively correlated with the relative abundances of Actinobacteria, and Verrucomicrobia (Fig. S6a). Specifically, the 470-, 694-, 914-, 1008-, and 1031-cm^{-1} spectra are positively correlated with the GAL15. The 1050-cm^{-1} spectral signal is attributed to C=O stretching from polysaccharides and/or Si–O vibrations due to possible mineral impurities, which have not been completely removed from the dried soils, although the band in this region may also arise from phosphate groups (Rulmont et al. 1991). In addition, the peaks in the $900\text{--}700\text{-cm}^{-1}$ spectral region are attributed to the presence of phosphate groups (Rulmont et al. 1991). Finally, strong signals in the $1100\text{--}1000\text{-cm}^{-1}$ and $900\text{--}700\text{-cm}^{-1}$ regions indicate an abundance of Si–O functional groups (Rulmont et al. 1991) due to a high abundance of mineral formation in the samples (Seddaiu et al. 2013; Mirzaei-talarposhti et al. 2016; Dhillon et al. 2017; Parolo et al. 2017; Sharma et al. 2017).

5 Conclusions

The SOM composition and soil bacterial communities varied under the different plant species in Poyang Lake with hydrological fluctuations. The soil traits and activity were mostly influenced by the plant species and water levels. The soil organic matter composition was mainly influenced by the water levels. The soil microbial diversity indices were affected by the plant species, not the water level. The relationship between SOM composition and soil bacterial communities was complex, which may be determined by the metabolism process, i.e., SOM stabilization and decomposition are multifaceted dynamic processes.

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Author contribution Yumei Jiang and Du Zhu conceived and designed the investigation; Jinfeng Wang performed field and laboratory work; Yumei Jiang and Zhibin Zhang analyzed the data; Juan Chen and Qinggui Zeng contributed materials, reagents, and/or analysis tools; and Yumei Jiang wrote the manuscript. We thank Manyun Zhang and Leilei Xiao for their revised suggestion.

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Data Availability All data generated or analyzed during this study are included in this manuscript.

Declarations

Competing interests The authors declare no competing interests.

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