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Variations of soil bacterial diversity and metabolic function with tidal flat elevation gradient in an artificial mangrove wetland

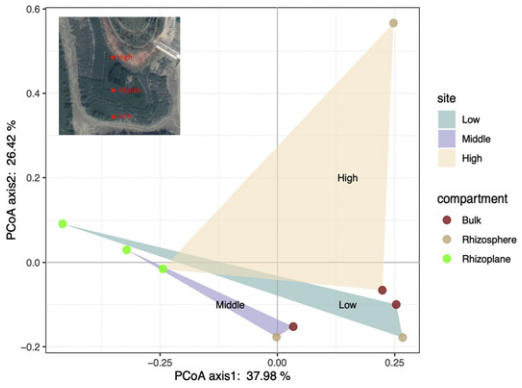
Yichen Yin, Zhongzheng Yan *

State Key Laboratory of Estuarine and Coastal Research, East China Normal University, Shanghai, China

HIGHLIGHTS

- The soil bacterial composition varied with the tidal elevation gradient.
- The bacterial diversity was highest in low tidal flat bulk and rhizosphere soil.
- Rhizosphere soil had higher bacterial diversity than the bulk soil nearby.
- Nitrospira enriched remarkably in the low tidal flat rhizosphere soil.
- Bacteria in low tidal bulk soil had the highest ability in using carbon sources.

GRAPHICAL ABSTRACT



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ABSTRACT

Understanding the sensitivity of soil bacteria to environmental fluctuations can enhance the management of microbial ecosystem services in artificial mangrove wetlands. In this study, the variation in bacterial diversity and metabolic functions in different compartments (bulk soil, rhizosphere soil, and rhizoplane) of the soil and mangrove plant along the tidal elevation gradient was studied in Xiatanwei (Xiamen China) mangrove wetland park, a *Kandelia obovata*-dominated artificial mangrove stand. With the increase of the tidal flat elevation, the soil pH, total organic matter, and soil moisture contents decreased significantly, while the soil electric conductivity and redox potential increased significantly. The bacterial diversity in the bulk soil and the rhizosphere soil both decreased with the elevation of tidal levels. The relative abundance of the dominant phyla in the bulk and rhizosphere soils decreased with the rise of the tidal flat level. A significant rhizosphere effect was observed in the roots of *K. obovata* that the rhizosphere soil had higher bacterial diversity and richness than that in the bulk soil nearby. The rhizosphere soil of *K. obovata* at the low-tidal flat was enriched with the genera Nitrospira and Planctomycetes, which are valuable for the mangrove ecosystem. The Chao1 estimator and Shannon index of the bacterial community in the rhizoplane of *K. obovata* were much lower than that in the rhizosphere and bulk soils. Results of Biolog-Eco assay show that the bacterial groups in low tidal flat bulk soil had the highest ability in utilizing the carbon sources, which was indicated by the high values of average well color development and the high McIntosh index, and the utilization ability of carbon source decreased with the increase of tidal flat levels. The variation of the soil humidity and Eh jointly shaped the diversity and metabolic function of soil bacterial communities along the tidal flat elevation gradient.

* Corresponding author at: State Key Laboratory of Estuarine and Coastal Research, East China Normal University, 500 Dongchuan Rd., Shanghai 200241, China.
E-mail address: zzyan@sklec.ecnu.edu.cn (Z. Yan).

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1. Introduction

Mangroves are evergreen woody plants occupying the intertidal zone of tropical and subtropical estuaries and coasts (Tomlinson, 1986). Mangrove ecosystem is known for the characteristics of high productivity and high decomposition rate and plays a crucial role in the energy flow and material cycling of coastal ecosystems (Lin, 1999; Ghizelini et al., 2012). Due to the high productivity, mangrove ecosystem inputs a large amount of litter into tidal flat environment every year, and the rapid decomposition of litter by microorganisms is of great significance for the circulation of carbon and nitrogen and other macroelements in mangrove ecosystem (Alongi et al., 1993; Taketani et al., 2010; Gomes et al., 2011; Ghizelini et al., 2012; Zeng et al., 2014; Priya et al., 2018). Various bacteria functional groups, such as the nitrogen-fixing bacteria, the phosphate solubilizing bacteria, the sulfate-reducing bacteria, and the metallic bacteria, all have high abundance in the mangrove habitat. These bacterial functional groups play essential roles in promoting the utilization of nutrient elements by mangrove plants (Jiang et al., 2013).

Due to the mutual influences of seawater and freshwater inputs, the physicochemical characteristics of the mangrove wetland soil (such as redox potential, salinity, organic matter content, etc.) show a high degree of spatial heterogeneity (Dias et al., 2010). Fluctuation in the hydrology of mangrove ecosystems influences the recharge of oxygen and nutrient pools, which may be intense abiotic pressure that influences the composition of bacterial communities in the tidal flat sediment (Peralta et al., 2014). The activities and composition of soil microorganisms in mangrove wetland are affected by various tidal flat soil characteristics, such as salinity (Ghizelini et al., 2012; Li et al., 2018; Ceccon et al., 2019; Tong et al., 2019; Fu et al., 2019), redox potential (Truu et al., 2009), soil organic matter content and pH (Luo et al., 2016; Li et al., 2018). Many previous studies suggested that salinity is the most important factor shaping the microbial community structure in the mangrove wetland (Ceccon et al., 2019; Tong et al., 2019; Fu et al., 2019). Salinity has a significant negative correlation with the activity and diversity of soil microorganisms, with the increase of salinity and soil osmotic pressure, some microbial groups sensitive to salt stress cannot survive, resulting in the decline of microbial community diversity (Wang et al., 2010; Tong et al., 2019). The redox status of the tidal flat soil also shapes the bacterial community. Generally, the anaerobic condition of the tidal flat soil coupled with the abundance of organic matter creates an optimal environment for the anaerobic microorganisms, such as sulfate-reducing bacteria (SRB) and methanogens (Dar et al., 2008). While under aerobic conditions, the soil respiration is mainly dominated by aerobic microorganisms (Sherman et al., 1998; Ghizelini et al., 2012). The distribution and activity of soil microorganisms in mangrove wetland are also affected by mangrove plants. Many studies have shown that mangrove plants affect the microbial species and abundance in rhizosphere soil through the so-called rhizosphere effect (Rocha et al., 2016; Yin et al., 2018). Mangrove roots release nutrients, root exudates, and oxygen into rhizosphere soil, which create an excellent habitat for microorganisms in rhizosphere soil and facilitate microbial activities (Gomes et al., 2011; Edwards et al., 2015; Sasse et al., 2018; Luo et al., 2018). The intricate root system of mangrove is also conducive to the formation of various functional bacterial guilds in the tidal flat sediment (Gomes et al., 2014). Due to the rhizosphere effect, the microbial and enzymatic activities of the rhizosphere soils are usually higher than those of the bulk soils (Luo et al., 2018).

Compared to the natural mangrove wetland, the artificial mangrove wetlands generally represent less fertile soil conditions due to the relatively shorter time of development (Hartman et al., 2008). The soil acidity and redox status of the artificial mangrove wetland is also different from that of the natural wetland and may thus shape different soil bacteria communities (Hartman et al., 2008). Understanding the extent to which soil bacteria are sensitive to environmental fluctuations can enhance the management of microbial ecosystem services in artificial wetlands (Peralta et al., 2014). Xiatanwei mangrove wetland park is an artificial wetland located in Xiamen, China. The park has 400 hm^2 of *Kandelia obovata*-dominated mangrove forests, which has been constructed since 2011 to improve the region's biodiversity and offer refreshing views (Chen et al., 2017). The tidal flat of this mangrove wetland is characterized by the distinctly differentiated tidal elevation, which will inevitably lead to the difference of tidal inundation time and the variation in soil physicochemical characteristics, such as redox potential, moisture, electric conductivity, and organic matter content. The variated tidal flat elevation makes the park an ideal experimental site for studying the spatial difference of soil microbial community composition on the gradient of physicochemical soil factors. To date, many studies have been conducted to investigate the response of soil microbial community composition of mangrove wetland under the influence of biological and abiotic factors (Ghizelini et al., 2012; Luo et al., 2016; Li et al., 2018; Ceccon et al., 2019; Tong et al., 2019; Fu et al., 2019). However, little attention has been paid to the changes of microbial community structure and function in the rhizosphere and non-rhizosphere soil on different tidal flat elevation gradients. Moreover, to the best of our knowledge, no study has been conducted yet to investigate the epiphytic bacteria presented in the rhizoplane of mangrove plants under the influences of periodic tidal flushing in field conditions. Identifying the epiphytic bacteria present in mangrove roots is crucial for understanding plant-microbe interactions under the environmental gradients. The present study, therefore, aims to investigate the variation in the diversity and metabolic function of bacteria in different compartments (bulk soil, rhizosphere soil, and rhizoplane) of Xiatanwei mangrove wetland park along the tidal elevation gradient. The next-generation sequencing and Biolog-ECO microplate methods were applied in the present study, as both of these two technologies allow a better representation of the bacterial species and functional diversity in soil (Liang et al., 2003; De Mandal et al., 2015).

2. Materials and methods

2.1. Study sites and field experiment

The field experimental sites are located in Xiatanwei mangrove wetland park, Xiamen, China (118°11′54″~118°11′58″E, 24°39′11″-24°39′14″N) (Fig. 1). This wetland park has a total planning area of 400 hm^2, which has been constructed since 2011. *Kandelia obovata* is the dominant mangrove species that distributes in patches at different tide levels. *Avicennia marina* and *Aegiceras corniculatum* are the secondary dominant species which mainly occupied the low levels of the tidal flat. Other mangrove species, such as *Bruguiera gymnorrhiza* and *Sonneratia caseolaris*, have sporadic distribution in the high levels of tidal flat. The wetland park is located in the transition zone between warm temperate zone and north subtropical zone. It is mainly affected by a marine and continental climate. The annual average temperature is 13.7–14.6 °C, and the annual average precipitation is 1000 mm.

In order to study the bacterial composition in different compartments (bulk soil, rhizosphere soil, and rhizoplane) of the soil and plant at different levels of tide flat, a rhizo-bag field planting experiment was conducted in Xiatanwei mangrove wetland in April 2019. Three sites with different soil redox potential (Eh) was set in the tidal flat for the rhizo-bag planting experiment (Fig. 1), i.e., high (Eh, 329.96 ± 0.17 mV), middle (Eh, 265.56 ± 0.35 mV), and low (Eh, 188.35 ± 0.31 mV). Rhizo-bags (30-μm nylon mesh, 9 cm diameter, 15 cm height) was used to plant the mangrove seedling in order to differentiate the bulk soil from rhizosphere soil (Nie et al., 2015). Five rhizosphere bags were planted at each site, and three matured and uniform propagules of *K. obovata* were planted in each rhizosphere bag. Plant and soil samples were collected 70 days after the plantation. The seedlings were carefully removed from rhizo-bag, and the adhering soil (rhizosphere soil) and soil outside the rhizo-bags (bulk soil) were collected and stored in aseptic zip-lock plastic bags, respectively. The soil samples

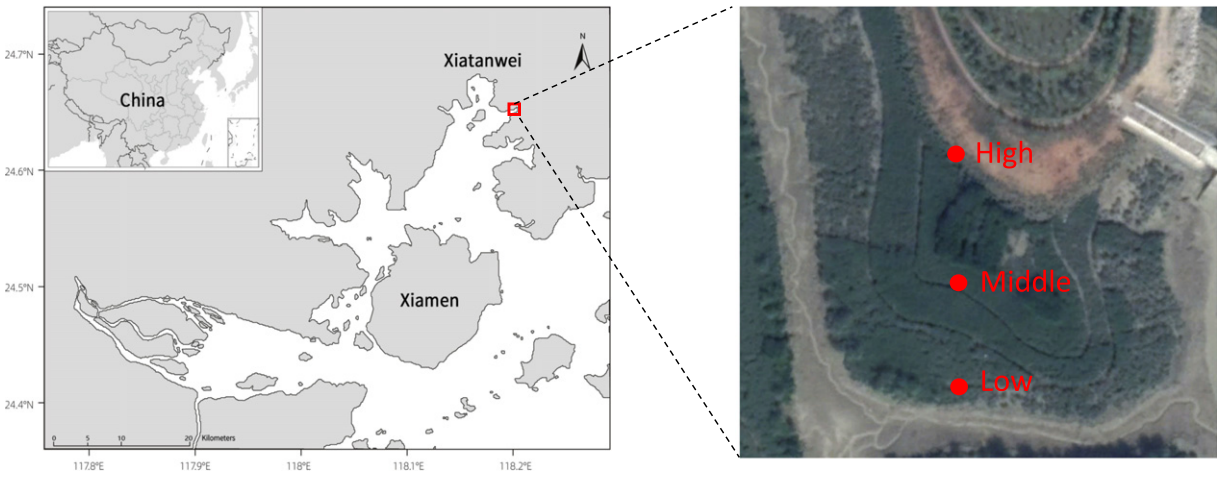

Fig. 1. Location of the experimental site.

were placed in iceboxes containing dry ice and brought back to the laboratory for 16S rDNA sequencing and Biolog-ECO microplate-based metabolism analysis. The roots of *K. obovata* were also brought back to the laboratory with dry ice for the extraction of bacterial DNA in rhizoplane.

2.2. Determination

2.2.1. Soil physicochemical parameters

Soil pH, moisture, and electrical conductivity (EC) were measured in situ by a portable soil moisture/temperature/salinity meter (WE-2, Delta-T, England). Eh was measured in situ by a portable redox potentiometer (FJA-6, Nanjing Chuandi Instrument Equipment Co., Ltd.). The soil total organic matter (TOM) was estimated by the classic Loss-On-Ignition method (Heiri et al., 2001). In brief, the sediment samples were oven-dried at 105 °C overnight, cooled in a desiccator, and weighed before combusting at 550 °C for 6 h in a muffle furnace. After combustion, the samples were cooled in a desiccator and reweighed. The TOM contents of the sediments were calculated using the following equation:

$$TOM = \frac{W_{bc} - W_{ac}}{W_{bc}} \times 100\%$$

where W_{bc} and W_{ac} are the sediment weights before and after combustion, respectively.

2.2.2. Extraction of the bacterial DNA and 16 s rDNA sequencing

DNA in the bulk soil, rhizosphere soil, and the rhizoplane were extracted using the PowerSoil® DNA Extraction kit (MoBio, USA) for the corresponding sample. The concentration and purity were measured using the NanoDrop One (Thermo Fisher Scientific, MA, USA). The bacterial DNA in the rhizoplane of the root was extracted according to the method by Hu et al. (2015). The lateral root of *K. obovata* was washed triple times with sterile water to remove the soil adhering to the root surface. About 1 g of fresh lateral root of *K. obovata* was agitated in 10 mL of pre-cold dithionite–citrate–bicarbonate (DCB) solution containing 0.3 mol L^{-1} sodium citrate ($Na_3C_6H_5O_7 \cdot 2H_2O$), 1 mol L^{-1} sodium bicarbonate ($NaHCO_3$), and 60 g L^{-1} of sodium dithionite ($Na_2S_2O_4$) at 25 °C for 3 h. The DCB extract was combined and centrifuged at 16,000 ×*g* for 10 min, the supernatant was discarded, and the precipitates were used for DNA extraction for the bacteria present in the rhizoplane (Hu et al., 2015).

16S rRNA genes of distinct regions (V3-V4) were amplified used specific primer, 338F (5'-ACTCCTACGGGAGGCAGCA-3′) and 806R (5'-GGACTACHVGGGTWTCTAAT-3′), with 12 bp barcode. PCR reactions, containing 25 μl 2× Premix Taq (Takara Biotechnology, Dalian Co. Ltd., China), 1 μL each primer (10 μM) and 3 μl DNA (20 ng μL^{-1}) template in a volume of 50 μL, were amplified by thermocycling: 5 min at 94 °C for initialization; 30 cycles of 30 s denaturation at 94 °C, 30 s annealing at 52 °C, and 30 s extension at 72 °C; followed by 10 min final elongation at 72 °C. The PCR instrument was BioRad S1000 (Bio-Rad Laboratory, CA, USA). PCR products were mixed in equidensity ratios according to the GeneTools Analysis Software (Version 4.03.05.0, SynGene). Then, the mixed PCR products were purified with EZNA Gel Extraction Kit (Omega, USA). Sequencing libraries were generated using NEBNext® UltraTM DNA Library Prep Kit for Illumina® (New England Biolabs, MA, USA) following the manufacturer's instructions and index codes were added. The library quality was assessed on the Qubit@ 2.0 Fluorometer (Thermo Fisher Scientific, MA, USA) and Agilent Bioanalyzer 2100 system (Agilent Technologies, Waldronn, Germany). At last, the library was sequenced on an Illumina Hiseq2500 platform, and 250 bp paired-end reads were generated.

2.2.3. Biolog-ECO microplate-based metabolism assay

The overall ability of soil microbial community to utilize carbon sources was determined by the Biolog-ECO microplate (Biolog Inc., California, USA). For the analysis, 3 g fresh soil sample was diluted in 27 mL sterile saline (0.85%) in a baffled flask and the flask was shaken on a shaker at 200 r min^{-1} for 30 min. Then, the flask was kept still for 15 min to allow the precipitation. The supernatant of 5 mL was serially diluted with 45 mL sterile water in baffled flasks until a suspension of 1:100 was achieved. The suspension was inoculated into the Biolog-ECO microplate with a volume of 150 μL in each well. The microplate was incubated in an incubator at 25 °C, and the absorbance of the reaction mixture in the microplate at 590 and 750 nm was read by a microplate reader (Tecan infinite M200 Pro, Switzerland) at 24 h intervals for a total time of 168 h.

For the analysis of the Biolog-ECO data, the average well color development (AWCD) (an index for the bacterial activity) and the McIntosh index of the bacterial community were calculated according to the following equations:

$$AWCD = \sum (C_i - R)/n,$$

$$\text{McIntosh index} = \sqrt{\left(\sum n_i^2\right)},$$

where C_i is the value of absorbance at 590 and 750 nm from the wells containing different carbon sources, R is the value of absorbance of the blank well, and n is the number of the carbon sources in the microplate (The Biolog-ECO microplate has 31 kinds of carbon sources). n_i is the relative absorbance of each well at 590 and 750 nm.

2.3. Data analyses

The mean and standard deviations of the soil physicochemical characteristics and the indices of functional diversity of different samples were calculated. Parametric one-way ANOVA and posthoc multiple comparisons (Turkey's test) were conducted to determine the significant differences in different samples with R software (v.3.6.1). For the 16 s rDNA sequencing data, five indices of the alpha diversity, including PD whole tree, chao1, dominance, Shannon index, Simpson index, were calculated at the OTU level with QIIME (V1.9.1). The shifts in the relative abundance of the bacteria at the phylum and genus levels were displayed as a barplot with the Vegan package in R software. Principal Coordinate Analysis (PCoA) was performed to explore the similarity of bacterial communities in different samples at the genus level. PCoA analysis was displayed by the ggplot2 package in R software. In order to identify the effects of soil physiochemical variables on soil bacterial community composition, a canonical correspondence analysis (CCA) was performed at the genus levels using the Vegan package for R software.

3. Results

3.1. Variations in soil physicochemical properties at different levels of tidal flat

The physicochemical properties of soil in different levels of the tidal flat are shown in Table 1. With the increase of the tidal flat elevation, the soil pH, TOM and WET decreased significantly ($p < .05$), while the soil EC and Eh increased significantly ($p < .05$) (Table 1).

3.2. Changes in bacterial diversity at different levels of tidal flat

The α-diversity indices, including Chao1, Shannon index, PD whole tree, Simpson index, and dominance, are shown in Table 2. The abundance and dominance of the bacterial community in the bulk and rhizosphere soil increased with the elevation of tidal flat, while the diversity decreased. On the contrary, the diversity of the bacterial community within the rhizoplane of *K. obovata* increased with the elevation of tidal flat.

3.3. Changes in microbial community composition in different tidal flats

Differentially abundant OTUs were obtained in different compartments (bulk soil, rhizosphere soil, and rhizoplane) of the soil and the plant root (Fig. 2A). The OTUs of different compartments were the most abundant in the samples collected from the middle tidal flat. The overlap in the OTUs of different compartments also varied with the tidal flat levels with the most prominent overlap found in the middle tidal flat, 2925 out of the 3820 OTUs enriched in the rhizosphere are also enriched in either the bulk soil or rhizoplane. The exclusive OTUs in rhizosphere soil and bulk soil showed the opposite trend with the rise of the tidal levels, which increased in bulk soil while decreased in rhizosphere soil (Fig. 2A).

The composition of the bacterial communities (phylum and genus levels) in the bulk soil, rhizosphere soils, and rhizoplane from all the samples are presented in Fig. 2B&C. At phylum level, the top 10 phyla were Proteobacteria (32.7–90.8%), Fusobacteria (0.5–44.2%), Epsilonbacteraeota (0.4–32.2%), Chlorofloxi(0.4–17.9%), Bacteroides (1.3–16.4%), Firmicutes(1.1–13.1%), Acidobacteria(0.3–3.2%), Gemmatimonadetes (0.2–3.4%), Actinobacteria(0.1–4.7%) and Nitrospira(0.1–6.0%). The majority of the sequences belong to the phylum Proteobacteria, which had the highest relative abundance in rhizoplane (90.8%) and the lowest relative abundance in rhizosphere soil (32.7%) of *K. obovata* at the low tidal level. The relative abundances of the dominant phyla in different samples varied with the tidal flat levels. The relative abundances of Proteobacteria, Actinobacteria, Chlorofloxi, Planctomycetes, and Acidobacteria in bulk soils decreased with the increasing of tidal elevation, while the relative abundances of Epsilonbacteraeota increased (Fig. 2A). In rhizosphere soil, the relative abundances of Acidobacteria, Actinobacteria, Chlorofloxi, Nitrospira, and Planctomycetes also decreased with the elevation of tidal flat, while the relative abundances of Proteobacteria and Bacteroidetes increased (Fig. 2A). The relative abundance of Nitrospira in the low level of tidal flat soil was about 41-fold of that in the high level of tidal flat. The relative abundance of Proteobacteria in the rhizoplane of *K. obovata* was much higher than that in bulk and rhizosphere. With the elevation of the tidal flat, the relative abundance of Proteobacteria in the rhizoplane decreased while the relative abundance of Epsilonbacteraeota increased. The relative abundances of Acidobacteria, Actinobacteria, Epsilonbacteraeota, Bacteroidetes, Fusobacterium, and Nitrospira in the rhizoplane of *K. obovata* were the least compared with those of bulk soil and rhizosphere soil at the same tide level.

At the genus level, the relative abundances of different dominant genera in each soil component (bulk soil and rhizosphere soil) gradually increased with the increasing of tidal flat levels (Fig. 2C). In rhizoplane, however, the relative abundances of major genera decreased with the increasing of tidal flat elevation, which is consistent with the change of dominance index at different tidal flats (Table 2). The genus *Sulfurimonas* dominated the bulk soil at the high tidal flat, and the relative abundance of this genus in the high tidal flat samples was significantly higher than that in the low tidal flat samples (Figs. 2C & 3C). In rhizosphere soil, the genera *Psychrobacter* and *Photobacterium* showed high abundances in the high tidal flat samples (Figs. 2C & 3C, Fig. S1). In the rhizoplane of *K. obovata*, *Vibrio* was the most dominant genus, which contributed about 34.6–59.6% of the total community DNA, and the relative abundance of *Vibrio* in rhizoplane decreased with the increasing of tidal flat level (Figs. 2C & 3C, Fig. S1). The distributions of different genera in the different components (bulk soil, rhizosphere soil,

Table 2
Diversity indices of the bacterial community in different samples (For different samples, Ko represents *K. obovata*; H, M, and L represent the high, middle and low tidal levels, respectively; S, P, and IP represent the bulk soil, rhizosphere soil, and rhizoplane, respectively).

Samples	PD whole tree	Chao1	Dominance	Shannon	Simpson
Ko-S-H	204	3251.6	0.045	7.602	0.9553
Ko-S-M	215	3441.5	0.060	7.490	0.9400
Ko-S-L	212	3113.4	0.020	8.715	0.9800
Ko-P-H	129	2009.7	0.049	6.056	0.9514
Ko-P-M	240	3776.3	0.007	9.286	0.9932
Ko-P-L	265	3179.2	0.004	9.796	0.9964
Ko-IP-H	148	2320.9	0.036	7.111	0.9644
Ko-IP-M	154	2457.5	0.059	6.844	0.9414
Ko-IP-L	106	1773.2	0.108	5.394	0.8923

Table 1
Soil physiochemical properties at different levels of tidal flat of the experimental site (Different superscript lowercase letters indicate the data are significant difference at $P < .05$).

Tidal level	pH	Humidity	EC	TOM	Eh
Low	7.32 ± 0.01^{c}	72.31 ± 0.08^{c}	1534.2 ± 0.20^{c}	9.80 ± 0.02^{b}	188.35 ± 0.31^{c}
Middle	6.85 ± 0.07^{b}	67.66 ± 0.07^{b}	1600.33 ± 0.08^{b}	9.67 ± 0.22^{ab}	265.56 ± 0.35^{b}
High	6.35 ± 0.06^{a}	56.59 ± 0.21^{a}	1660.44 ± 0.29^{a}	9.44 ± 0.07^{a}	329.96 ± 0.17^{a}

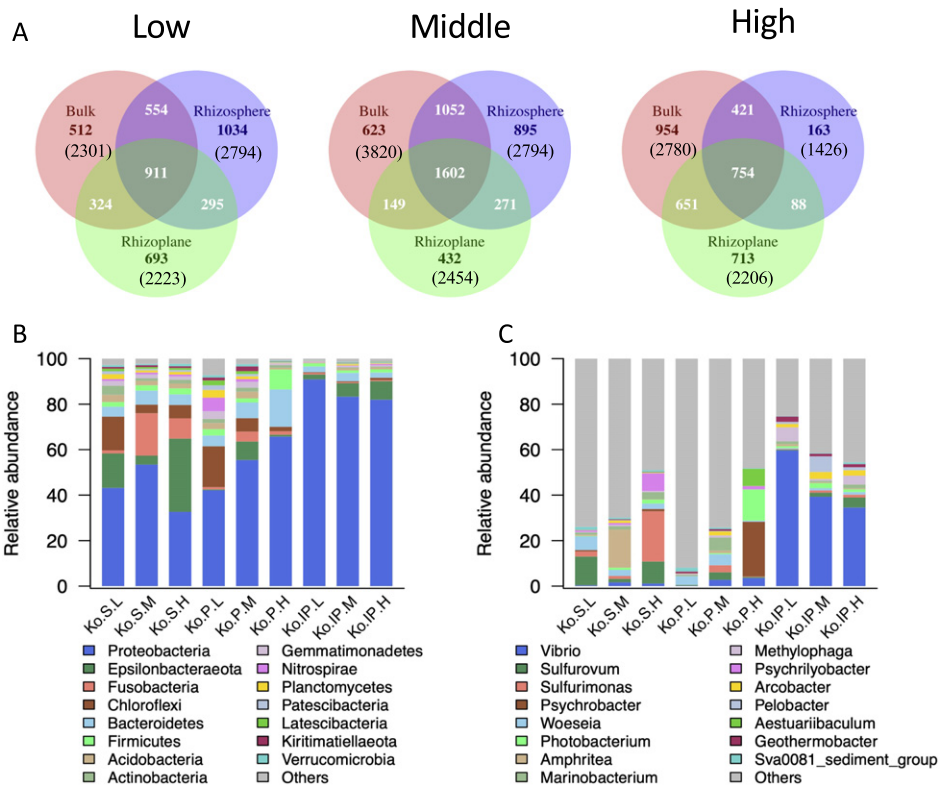

Fig. 2. (A)Venn diagrams showing the number of operational taxonomic units excluded and shared in different rhizospheric soil samples (B) Classification of columnar diagram of different samples at the phylum level. (C) Classification of columnar diagram of different samples at the genus level (For different samples, Ko represents *K. obovata*; H, M, and L represent the high, middle and low tidal levels, respectively; S, P, and IP represent the bulk soil, rhizosphere soil, and rhizoplane, respectively).

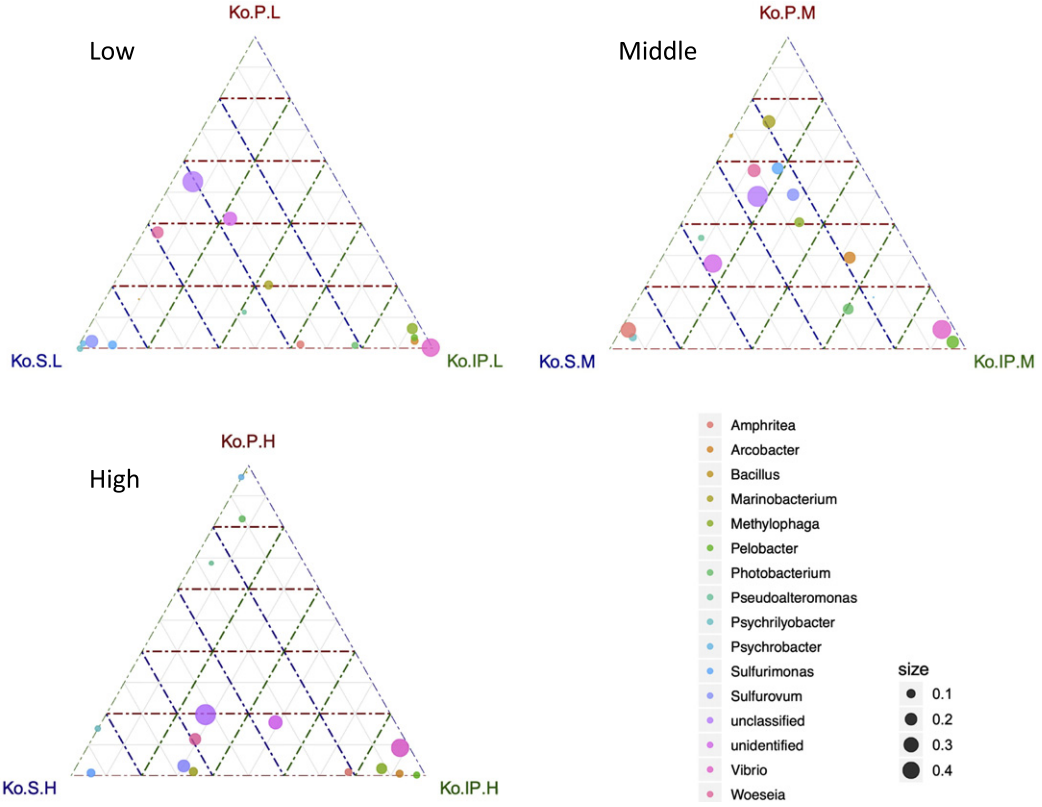

Fig. 3. Ternary plot shows the relative occurrence of the top 15 abundant genus (circles) in different compartments (bulk soil, rhizosphere soil, and rhizoplane) at different levels of tidal flat (For different samples, Ko represents *K. obovata*; H, M, and L represent the high, middle and low tidal levels, respectively; S, P, and IP represent the bulk soil, rhizosphere soil, and rhizoplane, respectively).

and rhizoplane) varied with the tidal flat levels according to the ternary plot (Fig. 3). With the increase of tidal levels, the dominant bacteria in bulk soils has changed from *Sulfurovum* at low tide flat to *Sulfurimonas* + *Sulfurovum* at the high tidal flat (Fig. 3C, Fig. S1). The dominant bacteria in the rhizosphere changed from *Nitrospiraceae* at low tidal level flat to *Photobacterium* and *Psychrobacter* at the high tidal flat (Fig. 3C). The dominant bacteria in the rhizoplane of *K. obovata* were almost consistent along with different tidal levels, which were mainly the genera *Vibrio* and *Pelobacter*.

3.4. The similarity of bacterial composition among different samples

The bacterial community composition in the bulk and rhizosphere soil showed high similarity at low and middle tidal flat according to the and hierarchical clustering and PCoA analyses (Fig. 4A&B). The bacterial composition in the rhizoplane of *K. obovata* was clearly separated from that in bulk and rhizosphere soil at different tidal flat along the PCoA axis 1, which explained up to 37.98% of dissimilarity (Fig. 4B). The distance between the rhizosphere soil and the bulk soil at the low and middle tidal flat was relatively close, which indicates the high similarity in bacterial composition (Fig. 4 A&B). The clustering distance of rhizosphere soil and bulk soil is far at the high tidal flat, which coincided with the results of PCoA.

3.5. Relationship between bacterial community and soil physicochemical properties

CCA was used to analyze the relationship between the soil physicochemical properties and the composition of bacterial communities of different samples (Fig. 5). According to CCA results, it can be seen that the soil humidity and Eh had great influences on the composition of dominant bacteria in the samples. Due to the collinearity problem, other soil factors, such as pH, temperature, EC, and TOM, were not included in the CCA analysis. Soil humidity had a high positive impact on the bacterial community composition in the rhizoplane of *K. obovata* at the different tidal flat, while soil Eh showed a high impact on the bacterial community composition in bulk soil and rhizosphere soil at the different tidal flat. The soil humidity was positively correlated

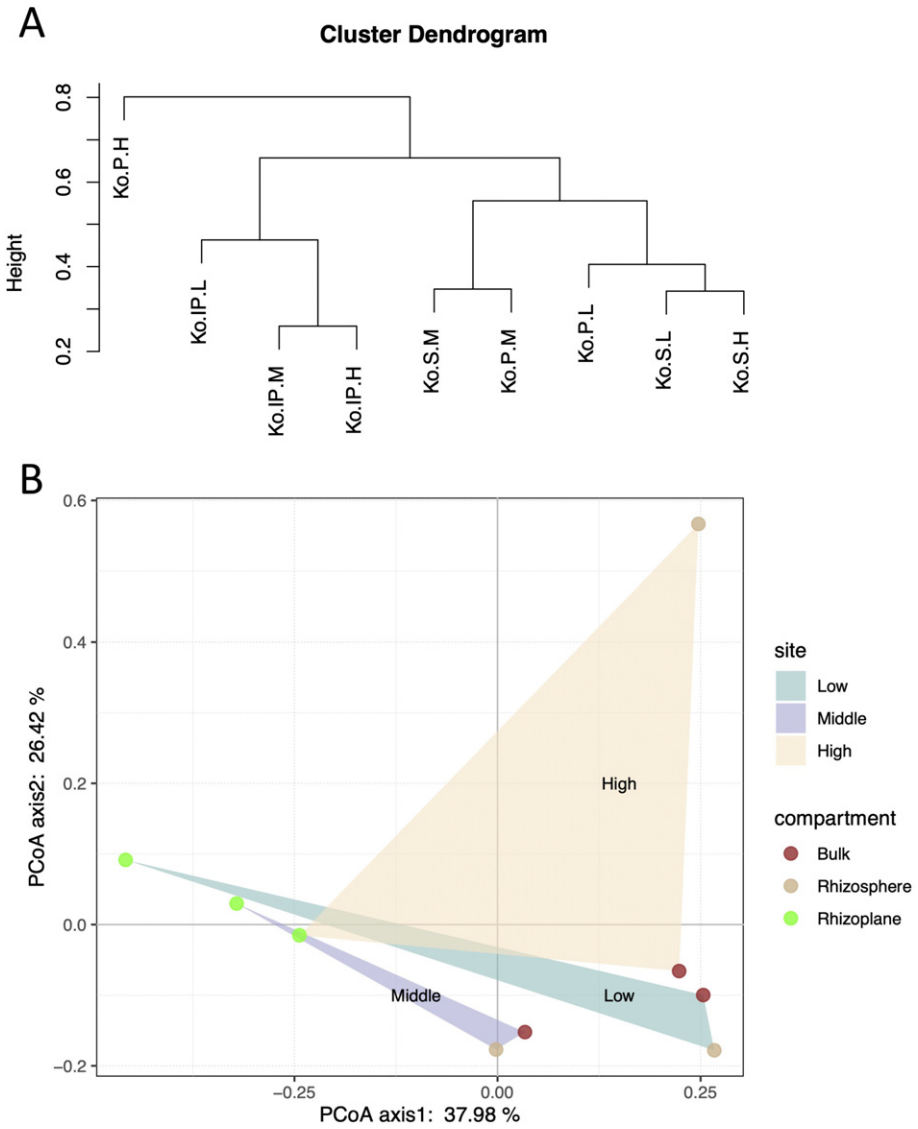

Fig. 4. (A) Principal Coordinate Analyses (PCoA) analysis of the bacterial community presented in bulk soil, rhizosphere soil and rhizoplane at different levels of tidal flat; (B) hierarchical clustering analysis of the samples (For different samples, Ko represents *K. obovata*; H, M, and L represent the high, middle and low tidal levels, respectively; S, P, and IP represent the bulk soil, rhizosphere soil, and rhizoplane, respectively).

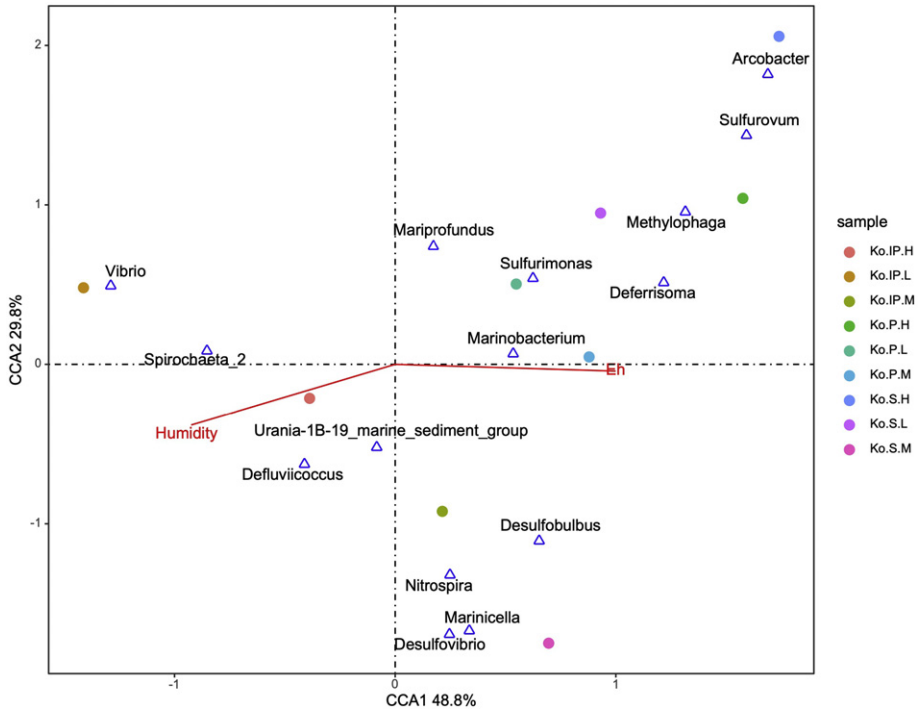

Fig. 5. Canonical correspondence analysis (CCA) showing the relationships among the major microbial genera and the soil physiochemical characteristics (For different samples, Ko represents *K. obovata*; H, M, and L represent the high, middle and low tidal levels, respectively; S, P, and IP represent the bulk soil, rhizosphere soil, and rhizoplane, respectively).

with the abundance of the genera *Vibrio*, *Spirochaeta*, and *Defluviicoccus*, while Eh was positively correlated with the genera *Marinobacterium*, *Desulfobulbus*, *Sulfurimonas, Sulfurovum*, and *Arcobacter*.

3.6. Functional diversity of soil microorganisms

For the Biolog-ECO assay, the value of AWCD is usually proportional to the intensity of the metabolic activity of microorganisms, and the McIntosh index reflects the ability of microbial communities to utilize carbon sources. The AWCD value of different samples increased with the increase of incubation time, and the values reached stable at 168 h (Fig. 6). The ability of soil microorganism to utilize carbon sources varied with the tidal flat level. The AWCD value and the McIntosh index of the low tidal flat bulk soil sample were the highest, indicated the microbial groups in the low tidal flat bulk soil had the highest ability in utilizing the carbon sources (Table 3). In rhizosphere soil, however, the value of the AWCD and McIntosh index showed no significant difference among different tidal flat (Table 3).

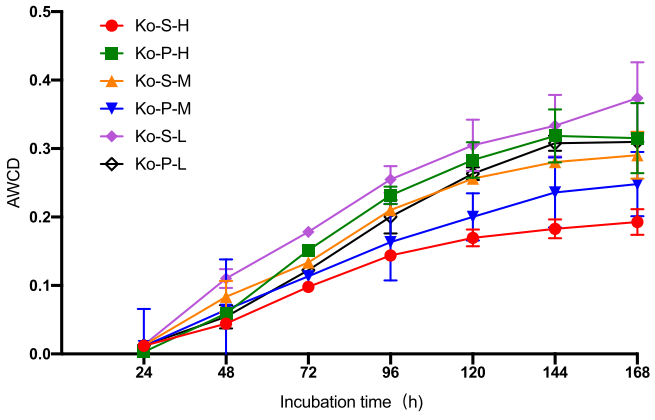

Fig. 6. Changes in AWCD of the bulk and rhizosphere soil samples with incubation time (For different samples, Ko represents *K. obovata*; H, M, and L represent the high, middle and low tidal levels, respectively; S and P represent the bulk soil and rhizosphere soil, respectively).

3.7. Utilization of carbon sources by soil microorganisms

In order to investigate the utilization of soil microbial community to different carbon sources, a principal component analysis (PCA) was performed based on the AWCD data (after standardization) at 168 h of incubation (Fig. 7). There were obvious spatial differences in the utilization of carbon sources by soil microorganisms in the coordinate system. The cumulative contribution of PC1 and PC2 was 82.2%, among which the contribution of PC1 was 59.4%, and the contribution of PC2 was 16.0%. Table S1 shows the scores of six major carbon sources on the principal component. A higher score indicates a greater influence of the carbon source on the two principal components. The easy-to-use carbon sources, such as carbohydrates, carboxylic acid, amino acid, polymers, and amino amides, all scored higher in the positive direction of PC1, while the difficult-to-use carbon sources, lipids, scored higher in the positive direction of PC2 (Table S1). The bulk soils of *K. obovata* at the low and high tidal flat were located in different quadrants, which indicated that PC1 and PC2 could clearly distinguish the microbial community of the bulk soil of *K. obovata* at different levels of tidal flat. The low tidal flat bulk and rhizosphere soil had the highest score on the

Table 3
Functional diversity index of soil microbial community in bulk soil, rhizosphere soil and rhizoplane of *K. obovata* in different levels of tidal flat (For different samples, Ko represents *K. obovata*; H, M, and L represent the high, middle and low tidal levels, respectively; S and P represent the bulk soil and rhizosphere soil, respectively; Different superscript lowercase letters indicate the data are significant difference at $P < .05$).

Sample name	McIntosh index	AWCD
Ko-S-H	2.59 ± 0.31^{c}	0.19 ± 0.01^{c}
Ko-S-M	3.74 ± 0.12^{b}	0.29 ± 0.03^{ab}
Ko-S-L	4.81 ± 0.51^{a}	0.37 ± 0.05^{a}
Ko-P-H	2.83 ± 0.11^{c}	0.31 ± 0.05^{ab}
Ko-P-M	2.64 ± 0.05^{c}	0.25 ± 0.05^{bc}
Ko-P-L	2.82 ± 0.03^{c}	0.31 ± 0.01^{ab}

positive direction of PC1 and showed closely positive correlations with the easy-to-use carbon sources, which indicated the high carbon sources utilization ability.

Clustering analysis has been performed based on the AWCD data to look into the differences in the utilization of different carbon sources of the bacteria in different samples (Fig. 8). The main carbon sources in bulk soil of *K. obovata* at the low tidal flat were polymers (glycogen) and carbohydrates (*N*-acetyl-D-glucosamine, d-cellobiose and D-Mannitol), and the utilization of these carbon sources decreased with the increase of tidal flat level. The central carbon sources for the bacterial communities in the rhizosphere soil of *K. obovata* were polymers (glycogen, Tween 40), carboxylic acid (γ - hydroxylic acid and D-malic acid) and carbohydrates (d-cellobiose), and the utilization capacity of these carbon sources also decreases with the increase of tidal flat level.

4. Discussion

In the study, the composition and the relative proportions of the dominant phyla found in Xiatanwei mangrove wetland park was quite similar with other mangrove wetlands around the world (Dias et al., 2010; Jiang et al., 2013; Xu et al., 2014; Alzubaidy et al., 2016; Basak et al., 2016; Tian et al., 2017; Ceccon et al., 2019). For example, a comparable study showed that the bacteria in a 10 years old constructed mangrove wetland in China was phylogenetically related to Proteobacteria (most dominant), Acidobacteria, Firmicutes, Nitrospirae, Gemmatimonadetes, Chloroflexi and Cyanobacteria (Tian et al., 2017). Proteobacteria is a ubiquitous and abundant phylum that distributes widely in marine environments and plays important roles in the nitrogen fixation and nutrient cycling (Kersters et al., 2006; An et al., 2019; Sun et al., 2019). In this study, the sequences affiliated with Proteobacteria contributed to the highest percentage of the community DNA (32.7–90.8%), which indicated that the bacteria of this phylum are the dominant player in the nitrogen fixation and nutrient cycling in this artificial mangrove wetland. Unlike previous studies, Fusobacteria and Epsilonbacteraeota (Previously was known as Epsilonproteobacteria, the fifth validly described class of the phylum Proteobacteria, Waite et al., 2017) were found to be prevalent in the bulk soil and rhizosphere soil of *K. obovata* (Fig. 2B). The phyla Fusobacteria and Epsilonbacteraeota are mainly composed of anaerobic bacteria commonly found in marine sediments (Waite et al., 2017). Fusobacteria (2.4%) was also found to be an endophytic dominant phylum in the root roots of *Phragmites australis* in a constructed wetland (Li et al., 2010). The reduced conditions and the availability of organic matters may

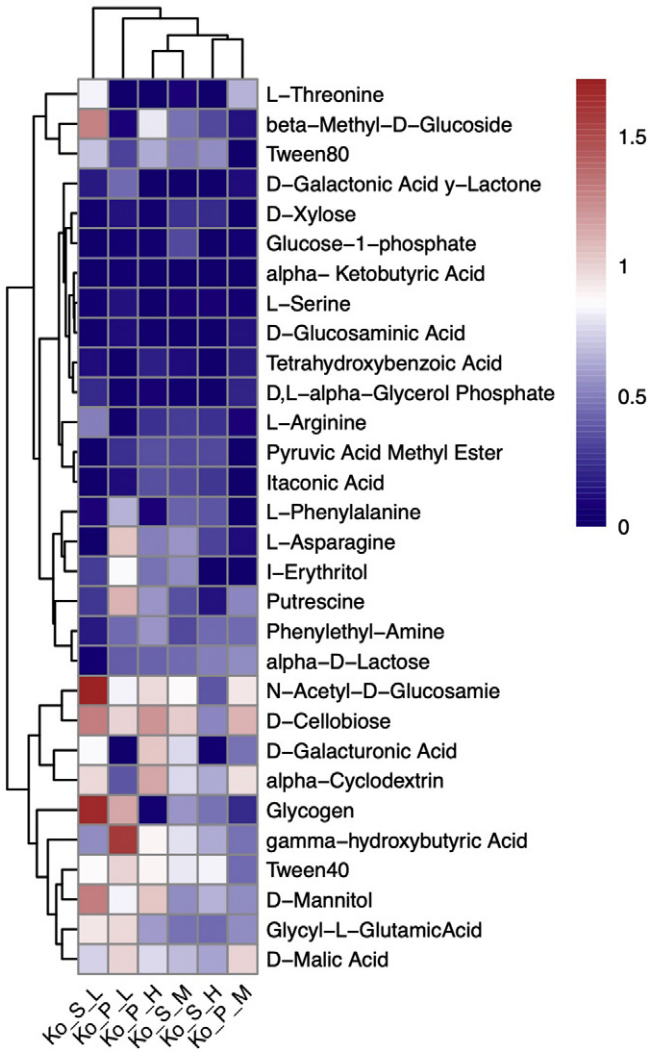

Fig. 8. Spearman correlation heatmap showing the preference of the carbon source utilization of the microbial community in different samples (For different samples, Ko represents *K. obovata*; H, M, and L represent the high, middle and low tidal levels, respectively; S and P represent the bulk soil, and rhizosphere soil, respectively).

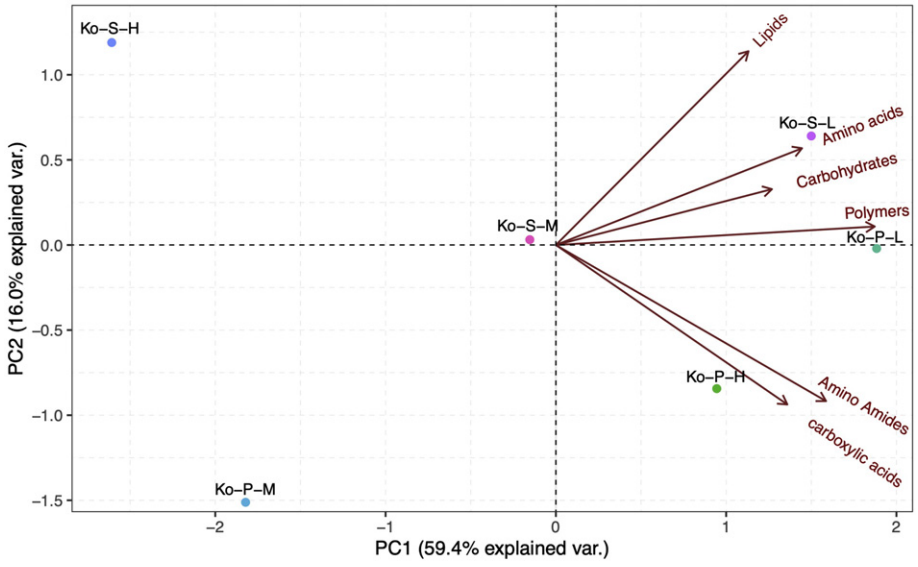

Fig. 7. Principal component analysis showing the utilization of carbon substrates by the soil microbial in different samples (For different samples, Ko represents *K. obovata*; H, M, and L represent the high, middle and low tidal levels, respectively; S and P represent the bulk soil and rhizosphere soil, respectively).

favor the maintenance of these phyla in the tidal flat sediment (Maintinguer et al., 2015).

The variation of bacterial diversity in the bulk soil and the rhizosphere soil along different tidal levels showed a similar trend, which decreased with the elevation of tidal levels. The dominant phyla in the bulk and rhizosphere soil of the low-level tidal flat were Acidobacteria, Actinobacteria, Chloroflexi, Nitrospira, and Planctomycetes. The relative abundance of these phyla decreased with the rise of tidal flat level, with the significant increase of soil EC and Eh and the significant decrease of soil pH. Soil salinization is usually associated with the increase of EC. The variation of soil salinity may change the abundances of soil bacterial communities and affected their function in saline coastal ecosystems (Wang et al., 2019). Previous studies suggested that the wetland trophic status, soil salinity, and soil moisture content play essential roles in governing the biogeographic distribution of sediment bacterial community in mangroves across China (Zhang et al., 2014; Tong et al., 2019). Most of the dominant phyla in mangrove sediment, such as Proteobacteria and Acidobacteria, are facultative organisms that can survive in water-saturated anaerobic habitats (Zhang et al., 2014). In the study, the water-saturated low tidal flat soil had lower salinity and higher organic matter content which was conducive for the survival of most bacteria and may thus increase the bacterial diversity. As the two main factors in tidal flat wetland, soil moisture content and Eh are usually closely related, and the moisture content of the soil is often used as the indicator of soil Eh. Based on the CCA analysis, it was not surprising to see that the soil humidity and Eh jointly shaped the composition of the bacteria communities across the samples collected at the different tidal flat. Other soil factors, such as pH, EC, and TOM, covaried with the soil humidity and Eh and might also shape the bacterial communities in the samples (Table 1). Results showed that the relative abundance of Acidobacteria increased with the soil pH, whereas the abundance of Proteobacteria decreased in the rhizosphere soil as the soil pH increased. Similar results were also reported by Zhang et al. (2014). However, Hartman et al. (2008) found the relative abundance of the acidophilic Acidobacteria in peat soil is promoted by low pH (pH = 4) and is inhibited in the soil of near neutral (pH on neutral or slight alkalinity). Yang et al. (2019) found that the bacterial abundance in coastal wetland soil was not affected by soil pH, and they suggested soil pH is a vital factor in the determination of bacterial community composition rather than abundance. In the present study, the soil pH of different levels of tidal flat fluctuated around the neutral, but the pH of low tidal flat soil (7.32) was significantly higher than that of high tidal flat soil (6.35), and Acidobacteria had the highest relative abundance in low tidal flat soil with higher pH. This may be related to the soil characteristics of mangroves wetland, as the soil type in mangrove wetland is a typical acid sulfate soil, prolonged tidal flooding in the low tidal flat will lead to a significant increase in the pH of acid soil (Zhang et al., 1991).

Compared to bulk soil, one notable difference in rhizosphere soil was the relative abundance of the phyla Proteobacteria and Bacteroidetes, which showed a clearly increasing trend with the rise of the tidal elevation. The phyla Proteobacteria and Bacteroidetes are known to be the most prominent heterotrophic organisms in marine surface waters (Stevens et al., 2005). The increase in the relative abundance of these two phyla was mainly represented by the genera *Psychrobacter* (Proteobacteria), *Photobacterium* (Proteobacteria), *Aestuariibaculum* (Bacteroidetes), *Marinobacterium* (Proteobacteria) and *Marinomonas* (Proteobacteria) (Fig. 3, Fig. S1). Most of these genera are salt-tolerant (such as *Psychrobacter*, *Photobacterium*, *Aestuariibaculum*, *Marinobacterium, Marinomonas*) and strictly aerobic bacteria (such as *Psychrobacter*, *Photobacterium*, *Aestuariibaculum*) (Bowman, 2006; Mathew et al., 2015; Jeong et al., 2013). With the rise of tidal flat elevation, the most significant change in soil physicochemical factors is the increase in soil redox potential and salinity. Moreover, the aeration of the rhizosphere soil likely being better than that of the bulk soil due to the widespread radial oxygen loss of mangrove root. In this case, it is reasonable to see the increase in the abundance of these salt-tolerant and obligated aerobic bacteria in rhizosphere soil.

The rhizosphere soil receives continuously nutrient input from the exudation of plant roots, which make the rhizosphere a carbon-rich niche for the establishment of microbial communities (Gomes et al., 2014; Chen et al., 2016; Sasse et al., 2018). In this study, rhizosphere soil has higher bacterial diversity than bulk soil (Table 2), which indicates that the mangrove plants have a significant rhizosphere effect on the composition of soil microbial community in mangrove wetland. Similar results were also reported by Tong et al. (2019), who compared the biogeographic distribution of sediment bacterial community in six mangroves across China, and found that plantation showed a positive influence on sediment bacterial abundance, richness, and diversity. Jiang et al. (2013) also found that bulk sediment inside the mature mangrove forest Mai Po Ramsar Wetland in Hong Kong had a higher bacterial α-diversity than mudflat sediment without vegetation. Gomes et al. (2014) found that root systems of *Avicennia schaueriana* and *Laguncularia racemosa* are associated with increased bacterial dominance, lower richness and compositional shifts of sediment bacterial communities.

In the present study, it was worth to note that the rhizosphere soil of *K. obovata* at the low-tidal flat was enriched with a very high abundance of Nitrospira and Planctomycetes, especially the phylum Nitrospira. The relative abundance of Nitrospira was about 7 and 41-fold of that in low-tidal flat bulk soil and high-tidal flat rhizosphere soil of *K. obovata*, respectively. Similar results were also reported by Jiang et al. (2013) that the rhizosphere soil of mangrove had a higher abundance of Nitrospirae than the bulk sediment nearby. Nitrospirae, as an aerobic chemolithoautotrophic nitrite-oxidizing bacterium, mainly participate in the transformation of ammonia or ammonium salt into nitrate in the soil and increase the utilization of nitrogen nutrition by plants (Aguilar et al., 2019). Many anammox bacteria affiliated with the phylum Planctomycetes are also suggested to drive the anaerobic ammonium oxidation (anammox) and play essential roles in the nitrogen transformation process in mangrove ecosystems (Li et al., 2018). The enrichment of bacteria of these two phyla in rhizosphere soil of *K. obovata* is valuable for the plants and the mangrove ecosystem, which might play important biological roles by removing nitrogen from the eutrophic water bodies in mangrove wetland. In the present study, the relative abundance of the genera *Sulfurovum* and *Sulfurimonas* (both belong to Epsilonproteobacteria) in the bulk soil were much higher than that in the rhizosphere soil of *K. obovata* (Fig. 2C). *Sulfurovum* and *Sulfurimonas* are sulfur-oxidizing bacteria that have been found to be abundant in sulfur-rich environments and grow anaerobically by oxidizing sulfur-containing compounds as energy resources, and these genera are known to be essential players in the process of sulfide-oxidation and denitrification in marine environments (Behera et al., 2014; Zhang et al., 2018). also found that the genera *Sulfurimonas*, *Sulfuricurum*, and *Sulfurovum* dominate the low tidal subsurface sediment of the mangrove-inhabited mudflat. The redox potential of the rhizosphere soil is probably higher than that of the bulk soil due to the root radial oxygen loss of mangrove plants, which can partly explain why the relative abundance of these two anaerobic genera is lower in rhizosphere soil.

Rhizoplane is a critical interface between plants and soil, which serves as a separate microhabitat from the rhizosphere and is colonized by the microorganisms firmly attached to the root surface (Edwards et al., 2015; Chen et al., 2016). The colonization of bacteria in rhizoplane has been described to be linked to root exudation and root mucilage (hydrated polysaccharides sloughed off from the root tip) through host-bacteria specific interactions and recognition processes (Compant et al., 2010). In the present study, the Chao1 and Shannon indexes of the bacterial community in the rhizoplane of *K. obovata* were much lower than those in the rhizosphere and bulk soils. These results are in accordance to previous studies that only a subset of the microbes that are enriched in the rhizosphere can bind the rhizoplane, and the

richness and diversity of bacteria in rhizoplane are usually lower than that in the rhizosphere and bulk soil (Edwards et al., 2015; Chen et al., 2016). Compare to bulk and rhizosphere soils, the rhizoplane of *K. obovata* possessed a much higher abundance of Proteobacteria; as high as 91% of the total community DNA in rhizoplane was affiliated with Proteobacteria in the low tidal flat. The relative abundance of dominant phyla in the bulk or rhizosphere soils, such as Firmicutes and Chloroflexi, were also substantially decreased in rhizoplane. Similar results were also reported by Chen et al. (2016), that the rhizoplane of ryegrass harbored decreased relative abundances of Firmicutes and Chloroflexi and increased relative abundances of Bacteroidetes and Proteobacteria. The root exudate may account for the highly enriched Proteobacteria in rhizoplane, as Proteobacteria are generally copiotrophic microorganisms, which thrive under conditions of high nutrient availability (Chen et al., 2016). The bacterial in rhizoplane of *K. obovata* had high similarity in composition at different tidal levels, which are mainly dominated by the genera *Vibrio* and *Methylophaga*. Moreover, the relative abundance of the genera *Vibrio* and *Methylophaga* in rhizoplane of *K. obovata* were much higher than that in bulk or rhizosphere soil, and the relative abundance of this genera decreased with the increasing of the tidal flat level. The genus Vibrio are widespread in aquatic environments and are known for their symbiotic and pathogenic interactions with saltmarsh and mangrove rhizospheres (Gomes et al., 2014). Gomes et al. (2014) found that the antagonistic strain *Vibrio* sp. PP05 had a strong association with mangrove roots and might have antagonistic activities against other pathogenic bacteria. The genus *Methylophaga* are strict aerobic methylotrophic bacteria that usually isolated from the marine environment; bacteria in this genus have been shown to be involved in methanol assimilation and the denitrification process in marine environments (Auclair et al., 2010).

In the present study, there was a vast difference in the ability of soil bacteria to utilize carbon source at different levels of tidal flat, the microbial groups in low tidal flat bulk soil had the highest capacity in using the carbon sources as indicated by the highest values of AWCD and the McIntosh index (Table 3). The central carbon sources that utilized at low tidal flat bulk soil were easy-to-use carbon sources, such as polymers (glycogen, α-Cyclodextrin), carbohydrates (*N*-acetyl-D-glucosamine, D-cellobiose, and D-Mannitol, β-methyl-D-Glucoside) and amino acids (Glycyl-L-Glutamic Acid). The utilization of these carbon sources decreased with the increase of tidal flat level. These results suggest that the high abundance and diversity of microbial communities in the low tidal flat soil correspond to the high utilization capacity of carbon sources. The bacteria presented in the mangrove wetland soil prefer to the utilization of the more readily available substrates, such as carbohydrates, amino acids, and amino amides. Compared to that of the high tidal flat soil, the moisture content and the redox condition of the low tidal flat soil were more anoxic and reducing, which was conducive to the survival of heterotrophic microorganisms, and the increase of heterotrophic microorganisms will contribute to the improvement of their carbon utilization ability. The variation of physicochemical properties of tidal flat soils along the elevation gradient may also affect the carbon sources utilization capacity of microbial communities. Thottathil et al. (2008) found that when the soil salinity was close to 0, the microorganisms in the soil tended to use carbohydrates as carbon source, and the increase of soil salinity would change the utilization type of carbon source into a carboxylic acid and amino acid. The higher salinity condition is more conducive for the proliferation of the autochthonous (halo-tolerant) bacterial community with an increase in the utilization of carboxylic/amino acids.

Mangrove forests are essential "blue carbon" sinks, which store large amounts of organic carbon (Simone et al., 2019). The results of this study show that the mangrove wetland in low tide flat is more conducive to the storage of soil organic carbon, and the soil organic carbon content in Xiatanwei mangrove wetland is also higher in low tide flat (Table 1). The characteristics of long-term flooding and anaerobic environment of low tide flat make the soil respiration governed mainly by sulfur and Fe reduction, and the mineralization rate of the soil is significantly inhibited, which is helpful to the accumulation of the soil organic carbon. Soil microbial diversity is the primary maintainer of C flux balance in mangrove wetland (Otero et al., 2017; Simone et al., 2019). In this study, the bacterial diversity of mangrove soil decreased with the elevation of the tidal flat. Gram-negative bacteria, such as Proteobacteria, Actinobacteria, Chloroflexi, Planctomycetes, and Acidobacteria, all have high abundance in low tidal flat soil. Most of the Gram-negative bacteria are fast-growing bacteria, and their carbon sources are mainly simple and easy to use carbon sources (Yin et al., 2018). The analysis of carbon source utilization of Biolog-ECO also shows the same results. Overall, this study shows that the soil and rhizosphere microbial community structure and carbon metabolism of Xiatanwei mangrove wetland have high spatial variability, which also causes the spatial difference of carbon accumulation in mangrove.

5. Conclusions

The present study provides a comprehensive comparison of the bacterial community in different compartments (bulk soil, rhizosphere soil, and rhizoplane) of the soil and the mangrove plants along the tidal flat elevation gradients in an artificial mangrove wetland. Results show that bacterial diversity in the bulk soil and the rhizosphere soil decreased with the increasing of tidal elevation, while the epiphytic bacterial diversity in roots of *K. obovata* increased with the increasing of tidal elevation. The dominant phyla mainly enriched in the low tidal flat bulk and rhizosphere soil, which make the bacterial groups in low tidal soil had the highest ability in utilizing the carbon sources. A significant rhizosphere effect was observed in the roots of *K. obovata* that the rhizosphere soil had higher bacterial diversity and richness than that in the bulk soil nearby, especially in the low tidal flat. The variation of the soil humidity and Eh jointly shaped the diversity and metabolic function of soil bacterial communities along the tidal flat elevation gradient. The present study also revealed that Nitrospira and Planctomycetes had a remarkable enrichment in the low tidal flat rhizosphere soil of *K. obovata*, which is valuable for the plants and the artificially constructed mangrove wetland by removing nitrogen from the eutrophic water bodies. The rhizoplane of *K. obovata* was predominantly colonized by the genera *Vibrio* and *Methylophaga* at different tidal levels, the functional role of these bacteria in plantemicrobe interactions and their influences on the plant fitness in the in artificial mangrove wetland await further investigations.

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CRediT authorship contribution statement

Yichen Yin: Investigation, Resources, Visualization, Formal analysis. **Zhongzheng Yan:** Conceptualization, Writing - original draft, Supervision, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Aguilar, L., Gallegos, Á., Arias, C.A., Ferrera, I., Sánchez, O., Rubio, R., Pérez, C., 2019. Microbial nitrate removal efficiency in groundwater polluted from agricultural activities with hybrid cork treatment wetlands. Sci. Total Environ. 653, 723–734.

Alongi, D.M., Christoffersen, P., Tirendi, F., 1993. The influence of forest type on microbial-nutrient relationships in tropical mangrove sediments. J. Exp. Mar. Biol. Ecol. 171, 201–223.

Alzubaidy, H., Essack, M., Malas, T.B., Bokhari, A., Motwalli, O., Kamanu, F.K., Alam, I., 2016. Rhizosphere microbiome metagenomics of gray mangroves (Avicennia marina) in the Red Sea. Gene 576, 626–636.

An, J., Liu, C., Wang, Q., Yao, M., Rui, J., Zhang, S., Li, X., 2019. Soil bacterial community structure in Chinese wetlands. Geoderma 337, 290–299.

Auclair, J., Lépine, F., Parent, S., Villemur, R., 2010. Dissimilatory reduction of nitrate in seawater by a Methylophaga strain containing two highly divergent narG sequences. ISME J 4, 1302.

Basak, P., Pramanik, A., Sengupta, S., Nag, S., Bhattacharyya, A., Roy, D., Bhattacharyya, M., 2016. Bacterial diversity assessment of pristine mangrove microbial community from Dhulibhashani, Sundarbans using 16S rRNA gene tag sequencing. Genomics Data 76–78.

Behera, B.C., Mishra, R.R., Dutta, S.K., Thatoi, H., 2014. Sulphur oxidising bacteria in mangrove ecosystem: A review. Afr J Biotechnol 13 (29), 2897–2907.

Bowman, J.P., 2006. The genus psychrobacter. The Prokaryotes: Volume 6: Proteobacteria: Gamma Subclass, pp. 920–930.

Ceccon, D.M., Faoro, H., da Cunha Lana, P., de Souza, E.M., de Oliveira Pedrosa, F., 2019. Metataxonomic and metagenomic analysis of mangrove microbiomes reveals community patterns driven by salinity and pH gradients in Paranaguá Bay, Brazil. Sci. Total Environ. 694, 133609.

Chen, L., Brookes, P.C., Xu, J., Zhang, J., Zhang, C., Zhou, X., Luo, Y., 2016. Structural and functional differentiation of the root-associated bacterial microbiomes of perennial ryegrass. Soil Biol. Biochem. 98, 1–10.

Chen, X.W., Li, X., Zeng, J.L., Tan, W.J., Zhou, X.P., Hong, W.S., Cai, L.Z., 2017. Meiofauna communities in artificial mangrove wetland in Xiatanwei of Tong'an bay, Xiamen. J Xiamen Univ Nat Sci 56, 351–358.

Compant, S., Clément, C., Sessitsch, A., 2010. Plant growth-promoting bacteria in the rhizo-and endosphere of plants: their role, colonization, mechanisms involved and prospects for utilization. Soil Biol. Biochem. 42, 669–678.

Dar, S.A., Kleerebezem, R., Stams, A.J., Kuenen, J.G., Muyzer, G., 2008. Competition and coexistence of sulfate-reducing bacteria, acetogens and methanogens in a lab-scale anaerobic bioreactor as affected by changing substrate to sulfate ratio. Appl. Microbiol. Biotechnol. 78 (6), 1045–1055.

De Mandal, S., Panda, A.K., Bisht, S.S., Kumar, N.S., 2015. First report of bacterial community from a bat guano using Illumina next-generation sequencing. Genomics Data 4, 99–101.

Dias, A.C., Andreote, F.D., Rigonato, J., Fiore, M.F., Melo, I.S., Araújo, W.L., 2010. The bacterial diversity in a Brazilian non-disturbed mangrove sediment. Anton Leeuw. Int. J. G. 98, 541–551.

Edwards, J., Johnson, C., Santos-Medellín, C., Lurie, E., Podishetty, N.K., Bhatnagar, S., Sundaresan, V., 2015. Structure, variation, and assembly of the root-associated microbiomes of rice. Proc. Natl. Acad. Sci. U. S. A. 112, E911–E920.

Fu, G., Han, J., Yu, T., Huangs, S.L., Zhao, L., 2019. The structure of denitrifying microbial communities in constructed mangrove wetlands in response to fluctuating salinities. J. Environ. Manag. 238, 1–9.

Ghizelini, A.M., Mendonça-Hagler, L.C.S., Macrae, A., 2012. Microbial diversity in Brazilian mangrove sediments: a mini review. Braz. J. Microbiol. 43, 1242–1254.

Gomes, N.C., Cleary, D.F., Calado, R., Costa, R., 2011. Mangrove bacterial richness. Comm Integ Biol 4, 419–423.

Gomes, N.C., Cleary, D.F., Pires, A.C., Almeida, A., Cunha, A., Mendonça-Hagler, L.C., Smalla, K., 2014. Assessing variation in bacterial composition between the rhizospheres of two mangrove tree species. Estuar Coast Shelf S 139, 40–45.

Hartman, W.H., Richardson, C.J., Vilgalys, R., Bruland, G.L., 2008. Environmental and anthropogenic controls over bacterial communities in wetland soils. Proc. Natl. Acad. Sci. U. S. A. 105, 17842–17847.

Heiri, O., Lotter, A.F., Lemcke, G., 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. J. Paleolimnol. 25, 101–110.

Hu, M., Li, F., Liu, C., Wu, W., 2015. The diversity and abundance of as (III) oxidizers on root iron plaque is critical for arsenic bioavailability to rice. Sci. Rep. 5, 13611.

Jeong, S.H., Park, M.S., Jin, H.M., Lee, K., Park, W., Jeon, C.O., 2013. Aestuariibaculum suncheonense gen. Nov., sp. nov., a marine bacterium of the family Flavobacteriaceae isolated from a tidal flat and emended descriptions of the genera Gaetbulibacter and Tamlana. Int J Syst Evol Micr 63, 332–338.

Jiang, X.T., Peng, X., Deng, G.H., Sheng, H.F., Wang, Y., Zhou, H.W., Tam, N.F.Y., 2013. Illumina sequencing of 16S rRNA tag revealed spatial variations of bacterial communities in a mangrove wetland. Microb. Ecol. 66, 96–104.

Kersters, K., De Vos, P., Gillis, M., Swings, J., Vandamme, P., Stackebrandt, E., 2006. Introduction to the Proteobacteria. The Prokaryotes: Volume 5: Proteobacteria: Alpha and Beta Subclasses, pp. 3–37.

Li, Y.H., Zhu, J.N., Zhai, Z.H., Zhang, Q., 2010. Endophytic bacterial diversity in roots of Phragmites australis in constructed Beijing Cuihu wetland (China). FEMS Microbiol. Lett. 309, 84–93.

Li, P., Li, S., Zhang, Y., Cheng, H., Zhou, H., Qiu, L., Diao, X., 2018. Seasonal variation of anaerobic ammonium oxidizing bacterial community and abundance in tropical mangrove wetland sediments with depth. Appl. Soil Ecol. 130, 149–158.

Liang, W., Wu, Z.B., Cheng, S.P., Zhou, Q.H., Hu, H.Y., 2003. Roles of substrate microorganisms and urease activities in wastewater purification in a constructed wetland system. Ecol. Eng. 21, 191–195.

Lin, P., 1999. Mangrove Ecosystem in China. Science Press, Beijing.

Luo, L., Wu, R.N., Meng, H., Li, X.Y., Gu, J.D., 2016. Seasonal and spatial variations in diversity and abundance of bacterial laccase-like genes in sediments of a subtropical mangrove ecosystem. Int. Biodeterior. Biodegradation 114, 260–267.

Luo, L., Wu, R., Gu, J.D., Zhang, J., Deng, S., Zhang, Y., He, Y., 2018. Influence of mangrove roots on microbial abundance and ecoenzyme activity in sediments of a subtropical coastal mangrove ecosystem. Int. Biodeterior. Biodegradation 132, 10–17.

Maintinguer, S.I., Sakamoto, I.K., Adorno, M.A.T., Varesche, M.B.A., 2015. Bacterial diversity from environmental sample applied to bio-hydrogen production. Int J Hydrogen Energ 40, 3180–3190.

Mathew, D.C., Ho, Y.N., Gicana, R.G., Mathew, G.M., Chien, M.C., Huang, C.C., 2015. A rhizosphere-associated symbiont, Photobacterium spp. strain MELD1, and its targeted synergistic activity for phytoprotection against mercury. PLoS One 10, e0121178.

Nie, S.A., Li, H., Yang, X.R., Zhang, Z.J., Weng, B.S., Huang, F.Y., Zhu, G.B., Zhu, Y.G., 2015. Nitrogen loss by anaerobic oxidation of ammonium in rice rhizosphere. ISME J 9, 2059–2067.

Otero, X.L., Mendez, A., Nobrega, G.N., Ferreira, T.O., Santisotaboada, M.J., Melendez, W., Macias, F., 2017. High fragility of the soil organic C pools in mangrove forests. Mar. Pollut. Bull. 119 (1), 460–464.

Peralta, A.L., Ludmer, S., Matthews, J.W., Kent, A.D., 2014. Bacterial community response to changes in soil redox potential along a moisture gradient in restored wetlands. Ecol. Eng. 73, 246–253.

Priya, G., Lau, N.S., Furusawa, G., Dinesh, B., Foong, S.Y., Amirul, A.A.A., 2018. Metagenomic insights into the phylogenetic and functional profiles of soil microbiome from a managed mangrove in Malaysia. Agri Gene 9, 5–15.

Rocha, L.L., Colares, G.B., Nogueira, V.L., Paes, F.A., Melo, V.M., 2016. Distinct habitats select particular bacterial communities in mangrove sediments. International J Microbiol 2016.

Sasse, J., Martinoia, E., Northen, T., 2018. Feed your friends: do plant exudates shape the root microbiome? Trends Plant Sci. 23, 25–41.

Sherman, R.E., Fahey, T.J., Howarth, R.W., 1998. Soil-plant interactions in a neotropical mangrove forest: iron, phosphorus and sulfur dynamics. Oecologia 115 (4), 553–563.

Simone, R., Cotta, L., Lira, et al., 2019. Exploring bacterial functionality in mangrove sediments and its capability to overcome anthropogenic activity. Mar. Pollut. Bull. 141, 586–594.

Stevens, H., Stübner, M., Simon, M., Brinkhoff, T., 2005. Phylogeny of Proteobacteria and Bacteroidetes from oxic habitats of a tidal flat ecosystem. FEMS Microbiol. Ecol. 54, 351–365.

Sun, H., Jiang, J., Cui, L., Feng, W., Wang, Y., Zhang, J., 2019. Soil organic carbon stabilization mechanisms in a subtropical mangrove and salt marsh ecosystems. Sci. Total Environ. 673, 502–510.

Taketani, R.G., Dias, A.C.F., Andreote, F.D., 2010. Microbial diversity from mangroves sediments: Insights from culture independent approaches. Mangroves Ecology Biology and Taxonomy. Nova Science Publishers Inc, Hauppauge, NY.

Thottathil, S.D., Balachandran, K.K., Jayalakshmy, K.V., Gupta, G.V.M., Nair, S., 2008. Tidal switch on metabolic activity: salinity induced responses on bacterioplankton metabolic capabilities in a tropical estuary. Estuar Coast Shelf S 78, 665–673.

Tian, T., Tam, N.F., Zan, Q., Cheung, S.G., Shin, P.K., Wong, Y.S., Chen, Z., 2017. Performance and bacterial community structure of a 10-years old constructed mangrove wetland. Mar. Pollut. Bull. 124, 1096–1105.

Tomlinson, P.B., 1986. The Botany of Mangroves. Cambridge Tropical Biology Series. Cambridge University Press, Cambridge.

Tong, T., Li, R., Wu, S., Xie, S., 2019. The distribution of sediment bacterial community in mangroves across China was governed by geographic location and eutrophication. Mar. Pollut. Bull. 140, 198–203.

Truu, M., Juhanson, J., Truu, J., 2009. Microbial biomass, activity and community composition in constructed wetlands. Sci. Total Environ. 407 (13), 3958–3971.

Waite, D.W., Vanwonterghem, I., Rinke, C., Parks, D.H., Zhang, Y., Takai, K., Woyke, T., 2017. Comparative genomic analysis of the class Epsilonproteobacteria and proposed reclassification to Epsilonbacteraeota (phyl. Nov.). Front. Microbiol. 8, 682.

Wang, Z., Xin, Y., Gao, D., Fengmin, L.I., Morgan, J., Xing, B., 2010. Microbial community characteristics in a degraded wetland of the Yellow River Delta. Pedosphere 20 (4), 466–478.

Wang, M., Chen, S., Chen, L., Wang, D., Zhao, C., 2019. The responses of a soil bacterial community under saline stress are associated with cd availability in long-term wastewater-irrigated field soil. Chemosphere 236, 124372.

Xu, Z., Hansen, M.A., Hansen, L.H., Jacquiod, S., Sørensen, S.J., 2014. Bioinformatic approaches reveal metagenomic characterization of soil microbial community. PLoS One 9, e93445.

Yang, W., Jeelani, N., Zhu, Z., Luo, Y., Cheng, X., An, S., 2019. Alterations in soil bacterial community in relation to Spartina alterniflora Loisel. Invasion chronosequence in the eastern Chinese coastal wetlands. Appl. Soil Ecol. 135, 38–43.

Yin, P., Yin, M., Cai, Z., Wu, G., Lin, G., Zhou, J., 2018. Structural inflexibility of the rhizosphere microbiome in mangrove plant Kandelia obovata under elevated CO_2. Mar. Environ. Res. 140, 422–432.

Zeng, J., Zhao, D.Y., Liu, P., Yu, Z.B., Huang, R., Wu, Q.L., 2014. Effects of benthic macrofauna bioturbation on the bacterial community composition in lake sediments. Can. J. Microbiol. 60, 517–524.

Zhang, X., Luo, X., Chen, Y., 1991. The mangrove and the acid tidal flat soil. J Nat Resour 6 (1), 55–62.

Zhang, X., Xu, S., Li, C., Zhao, L., Feng, H., Yue, G., Cheng, G., 2014. The soil carbon/nitrogen ratio and moisture affect microbial community structures in alkaline permafrost-affected soils with different vegetation types on the Tibetan plateau. Res. Microbiol. 165, 128–139.

Zhang, X., Hu, B.X., Ren, H., Zhang, J., 2018. Composition and functional diversity of microbial community across a mangrove-inhabited mudflat as revealed by 16S rDNA gene sequences. Sci. Total Environ. 633, 518–528.