



Soil Bacterial Community Structure in Different Micro-Habitats on the Tidal Creek Section in the Yellow River Estuary

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Tidal creeks have attracted considerable attention in estuary wetland conservation and restoration with diverse micro-habitats and high hydrological connectivity. Bacterial communities act effectively as invisible engines to regulate nutrient element biogeochemical processes. However, few studies have unveiled the bacterial community structures and diversities of micro-habitats soils on the tidal creek section. Our study selected three sections cross a tidal creek with obviously belt-like habitats “pluff mudflat – bare mudflat – *Tamarix chinensis* community – *T. chinensis*-*Suaeda salsa* community – *S. salsa* community” in the Yellow River estuarine wetland. Based on soil samples, we dissected and untangled the bacterial community structures and special bacterial taxa of different habitats on the tidal creek section. The results showed that bacterial community structures and dominant bacterial taxa were significantly different in the five habitats. The bacterial community diversities significantly decreased with distance away from tidal creeks, as well as the dominant bacteria Flavobacteriia and δ -Proteobacteria, but in reverse to Bacteroidetes and Gemmatimonadetes. Moreover, the important biomarkers sulfate-reducing bacteria and photosynthetic bacteria were different distributions within the five habitats, which were closely associated with the sulfur and carbon cycles. We found that the bacterial communities were heterogeneous in different micro-habitats on the tidal creek section, which was related to soil salinity, moisture, and nutrients as well as tidal action. The study would provide fundamental insights into understanding the ecological functions of bacterial diversities and biogeochemical processes influenced by tidal creeks.

Keywords: tidal creek, micro-habitats, bacterial community, sulfate-reducing bacteria, ecological functions

INTRODUCTION

Estuary wetlands, between ocean and terrestrial ecosystems, play important ecological functions in climate change regulation, biodiversity preservation, and environmental remediation (Fennessy, 2014; Murray et al., 2019; Xiao et al., 2019). In the front estuary wetlands by field investigation and aerial photography, there are a variety of small and different micro-habitats around tidal creeks,

which compose the tidal creek salt marshes. Tidal creek salt marshes are active and critical to biogeochemical processes and biological diversities with high hydrological connectivity (Mallin and Lewitus, 2004; Vandenbruwaene et al., 2012; Cui et al., 2016). Along with the frequent and long-time tidal alternation, the tidal creek salt marshes comprise many different micro-habitats and have orderly occurred in habitat successions with unvegetated mudflat initiation, vegetation colonization, organic and inorganic sediment deposition, and upper marsh elevation (Wilson et al., 2014; Chiról et al., 2018; Wu et al., 2020). For example, the micro-habitats are bare lands and/or the *Spartina alterniflora* community near tidal creeks due to long-time flooding and in the upper lands away from tidal creeks colonized by more plant communities like *Suaeda glauca*, *Salicornia europaea*, and *Phragmites communis* (Kim, 2018; Liu et al., 2020). It should be notable that the diverse micro-habitats on the tidal creek section are to advantage to maintain the eco-functions, including biogeochemical processes, matter exchanges, environmental resilience, and so on (Arriola and Cable, 2017; Tan et al., 2020; Trifunovic et al., 2020; Wu et al., 2020).

It is extensively focused on that bacterial communities that are indispensable to understanding and untangling the estuary wetland eco-functions, because engines act as a driver for soil carbon and nitrogen turnover processes, environment resistance, resilience, and so on (Huang et al., 2020; Zou et al., 2020; Coban et al., 2022). Previous studies have demonstrated that bacterial communities are greatly affected by many environmental factors, such as pH, organic matter, nutrient availability, soil salinity, and moisture (Fierer, 2017). In coastal wetland, soil salinity and nutrients were regarded as the important environmental filters (An et al., 2019). As well, soil bacterial community structures and functions, like sulfate-reducing and nitrifying bacteria, were significantly different, ranging from oligohaline to hypersaline habitats (Li et al., 2019; Zhang et al., 2020). Thus, it is important to unveil the relationships between bacterial communities and habitats in tidal creek salt marshes to better understand eco-functions of estuary wetlands.

The Yellow River estuary wetland is focused by previous studies on micro-habitat types, biogeochemical processes, and eco-functions of wetlands (Zhao et al., 2010; Yu et al., 2018; Gong et al., 2021). Several recent studies have found that bacteria communities have existed in great variations, which were relevant to geographic patterns, season variations, plant types, and soil salinities (Lv et al., 2016; Zhang et al., 2017; Zhang et al., 2020; Li et al., 2021). However, it is poorly to announce bacterial community structures in the micro-habitat soils on the tidal creek section, which would limit our understanding of the biogeochemical processes and eco-functions in estuary wetland ecosystem. Herein, the present study has selected a tidal creek to investigate the bacterial community structures and unveil the keystone bacteria in response to the soil biogeochemical processes of different micro-habitats. Our hypotheses are that (1) dominant bacteria and bacterial biomarkers should be different across the five micro-habitats on the section of the tidal creek, (2) the differences may be related to the effects of tidal action and soil properties together.

MATERIALS AND METHODS

Soil Sampling and Soil Physicochemical Properties Analysis

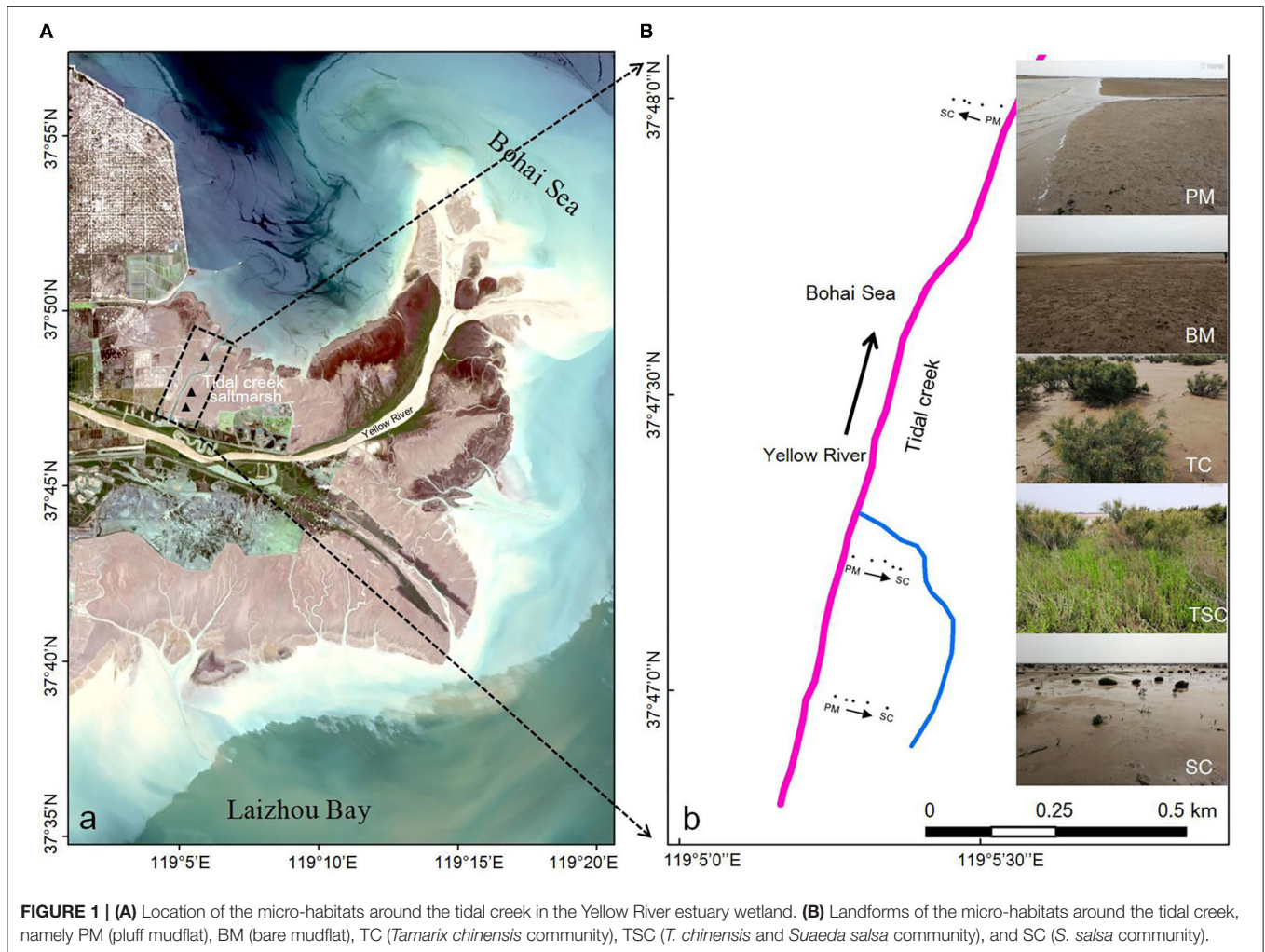
We selected a tidal creek (37°46′–37°49′N, 119°5′–119°6′E), approximately 6,430-m length and 110–190-m width in the Yellow River estuarine wetland, located at Dongying City, Shandong Province, Eastern China (Figure 1A). Along the tidal creek, three sections, 200 m away from each other, were set, and each section was divided into five micro-habitats according to hydrologic conditions and the vegetation community, including pluff mudflat (PM), bare mudflat (BM), *Tamarix chinensis* community (TC), *T. chinensis-Suaeda salsa* community (TSC), *S. salsa* community (SC) (Figure 1B). In detail, PM was closest to the tidal creek with long-time flooding and no plant coverage. BM suffered medium-time flooding and uncovered vegetation, but more fiddler crab bioturbation. Compared with the lower micro-habitats of PM and BM, the upper micro-habitats of TC, TSC, and SC were short-time flooding by spring tidal current and colonized with two dominant halophytes of *T. chinensis* and *S. salsa*.

The soil samples (2–10 cm) in every habitat were collected with three repetitions in July 2018. All of the soil subsamples were quickly sealed in sterile Eppendorf tubes and stored in liquid nitrogen for 16S rRNA analysis, and the others were air dried for soil physicochemical analyses in the laboratory.

Soil physicochemical properties consisting of soil moisture content (SMC), pH value, electrical conductivity (EC), soil organic carbon (SOC), total nitrogen (TN), and total phosphorus (TP) were measured using standard soil test methods as described by the agriculture protocols for China (Lu, 2000). In brief, SMC was determined by weight loss after drying 20 g of wet soil at 105°C for 24 h. Soil pH and EC were determined by a pH meter and an electronic probe (the soil-to-water ratio was 1:5). The SOC, TN, and TP were determined by the potassium dichromate heating oxidation-volumetric method, Kjeldahl nitrogen method, Mo-Sb anti spectrophotometric method, respectively.

Soil Bacterial DNA Extraction and PCR Amplification

Our study used the E.Z.N.A.® soil DNA Kit (Omega Bio-Tek, Norcross, GA, U.S.) to extract microbial DNA from soil samples. The final DNA concentration and purification were determined by a NanoDrop 2000 UV-vis spectrophotometer, and DNA quality was checked by 1% agarose gel electrophoresis. The V3-V4 hypervariable regions of 16S rRNA were selected to identify bacteria species (Yang et al., 2018), and amplified using the barcoded primers 338F/806R (5′-ACTCCTACGGGAGGCAGCAG-3′/5′-GGACTACHVGGGTWTCTAAT-3′) from the qualified DNA templates. Briefly, the PCR reactions were amplified using the following program: 3 min of initial denaturation at 95°C, followed by 27 cycles of denaturation at 95°C for 30 s, primer annealing at 55°C for 30 s, elongation at 72°C for 45 s, and a final extension of 10 min at 72°C. The resulted PCR products were extracted from a 2% agarose gel and purified using the AxyPrep DNA Gel Extraction Kit. All of the purified PCR products were quantified using QuantiFluor™-ST (Promega, USA).



Illumina MiSeq16S rRNA High-Throughput Sequencing and Data Processing

Purified amplicons were pooled in equimolar and paired-end sequenced (2×300) on an Illumina MiSeq platform (Illumina, San Diego, USA) according to the standard protocols by Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China). Raw fastq files were quality-filtered by Trimmomatic and merged by FLASH with the following criteria: (1) The reads were truncated at any site receiving an average quality score < 20 over a 50-bp sliding window. (2) Sequences of overlap being longer than 10 bp were merged according to their overlap with mismatch no more than 2 bp. (3) Sequences of each sample were separated according to barcodes (exactly matching) and Primers (allowing 2 nucleotide mismatching), and reads containing ambiguous bases were removed.

Operational taxonomic units (OTUs) were clustered with a 97% identity cutoff using UPARSE (version 7.0.1090, <http://drive5.com/uparse/>), with a novel “greedy” algorithm that performs chimera filtering and OTU clustering simultaneously. The taxonomy of each 16S rRNA gene sequence was analyzed by RDP Classifier algorithm ([\[rdp-classifier/\]\(https://sourceforge.net/projects/rdp-classifier/\)\) against the Silva project’s version 138 release \(<https://www.arb-silva.de/>\) using a confidence threshold of 70%. Mothur 1.30.2 and Qiime 1.9.1 have calculated the bacterial \$\alpha\$ -diversity and \$\beta\$ -diversity, respectively.](https://sourceforge.net/projects/</p>
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Statistical Analysis

The differences in soil physicochemical properties, bacterial α -diversity, and species were estimated by one-way ANOVA analysis in SPSS 22. Bacterial β -diversity analysis was displayed with principal coordinate analysis (PCoA) based on the weighted normalized unifracs (WNU) metric. Heatmap analysis and redundancy analysis (RDA) were used to find the differential OTUs, and the relationships between bacteria and soil physicochemical properties in the five habitats, respectively. All biomarkers of the five bacterial communities have been identified by linear discriminant analysis (LDA) effect size (LDA > 3 , $p < 0.05$) on the Galaxy (<https://huttenhower.sph.harvard.edu/galaxy/root>) to mine special biomarkers and explain the differences in different bacterial communities (Segata et al., 2011).

RESULTS

Soil Physicochemical Properties

As shown in **Table 1**, the values of SOC, TN, EC, and SMC were significantly different among micro-habitats ($p < 0.05$). In detail, the SOC content was highest in SC and followed in TSC, TC, BM, and PM, with means of $7,368.23 \pm 10$, $6,508.12 \pm 83$, $5,960.18 \pm 76$, $5,844.81 \pm 56$, $4,659.71 \pm 49$ mg·kg⁻¹, respectively. The TN contents in upper micro-habitats (TC, TSC, and SC) were higher than in lower micro-habitats (PM and BM), with the range from 298.77 to 328.42 mg·kg⁻¹ vs. 164.84 to 240.07 mg·kg⁻¹. As well, the soil EC in vegetation micro-habitats was higher than in the two bare mudflats, with a range from 3.11 to 5.85 ms·cm⁻¹ vs. 66 to 1.47 ms·cm⁻¹. The SMC was $34 \pm 0.02\%$ in PM, which was highest among all the micro-habitats. However, there were no significant differences in pH values ($p = 0.208$) and TP contents ($p = 0.38$) among the five micro-habitats.

Overview of 16S rRNA High-Throughput Sequencing and Bacterial OTU Diversity

The study has got 702,472 high-quality amplicons with an average length of 440 bp in 15 soil samples, and 99.81% of them were even distributed into the ranges from 401 to 460 bp in length (**Figure 2A**). After picking out the chimeras and single sequences, it generalized 534,284 valid reads and clustered into a total of 4,657 valid OTUs in the five micro-habitats (**Table 2**). With Good's coverage scores ranging from 98.42 to 99.41% as a result, there were most OTUs in BM (2,155), and followed by TC (1,947), PM (1,915), SC (1,384), and TSC (1,048). The bacterial α -diversity analysis showed that community richness estimators ACE, Chao1, and diversity index Shannon were significantly different in the five micro-habitat soils (all $p < 0.01$), except for Simpson index ($p = 0.107$). ACE, Chao1, and Shannon index of PM, BM, and TC were significantly higher than that of the TSC and SC. With the increase of sample sequences, the rarefaction curves of bacterial OTUs and Shannon-Wiener index have approached the plateaus (**Figures 2B,C**), which indicated that our subsampling analysis can reflected the bacteria diversity in each sample. Furthermore, the bacterial β -diversity explained the OTUs separation with PCoA ($R^2 = 0.558$, $p = 0.001$), which showed a significant variance among the five micro-habitats. The first axis PC1 and second axis PC2 explained 55.16% of the total variance with PCoA (**Figure 2D**). Together, the bacterial α - and β -diversity implied that bacterial community structures were

different between the lower micro-habitats vs. the upper micro-habitats.

Bacterial Community Structures in Different Micro-Habitats

At the bacterial OTU level, there were 573 shared bacterial OTUs in five micro-habitats, accounting for 22.31% (PM), 18.56% (BM), 19.29% (TC), 31.04% (TSC), and 23.86% (SC), respectively (**Figure 3A**). On the contrary, 170 OTUs were individual in PM (6.62%), BM (5.05%), TC (4.91%), TSC (11.38%), and SC (8.03%), respectively. Moreover, 67 bacterial classes were shared and accounted for 59.82% (PM), 56.78% (BM), 55.83% (TC), 79.76% (TSC), and 66.34% (SC) (**Figure 3B**). However, only a few bacteria were uniquely or commonly observed in the other combinations with 1 to 16 overlapped classes, even no shared, which implied that bacterial taxa were relatively stable at the class level vs. at the OTU level across the five micro-habitats.

The dominant bacterial classes of the five habitats were γ -Proteobacteria (15.76%), α -Proteobacteria (10.89%), Bacteroidetes IncertaeSedis (9.04%), Gemmatimonadetes (8.3%), Flavobacteriia (8.94%), Actinobacteria (7.31%), δ -Proteobacteria (7.22%), Anaerolineae (4.2%), Acidobacteria (3.8%), Sphingobacteriia (3.41%), and so on (**Figure 3C**). Of them, Bacteroidetes IncertaeSedis and Gemmatimonadetes in upper micro-habitats (SC, TSC, and TC) were obviously higher than them in lower micro-habitats (PM and BM), with 16.04–0.8% ($p = 0.02$) and 11.74–2.09% ($p = 0.02$), while Flavobacteriia and δ -Proteobacteria were decreased from PM to SC with 14.16–3.25% ($p = 0.04$) and 12.58–4.96% ($p = 0.02$). In addition, Acidobacteria ($p = 0.03$) and Sphingobacteriia ($p = 0.04$) were significantly different in the five micro-habitats.

The top 50 bacterial OTUs were selected to compare the OTU abundances and taxa to characterize the variations of bacterial community structures (**Figure 4**). Fourteen OTUs were significantly enriched in PM, BM, and TC ($p < 0.05$), which belonged to eight bacterial families of *JTB255*, *Flavobacteriaceae*, *Unknown γ -Proteobacteria*, *Sva1033*, *Rhodobacteraceae*, *Rhodobiaceae*, *Rhodospirillaceae*, and *OM1 clade*. Meanwhile, about 20 OTUs were abundant in TC, TSC, and SC, widely mapped into *Flavobacteriaceae*, *Rhodobacteraceae*, *Trueperaceae*, unclassified *Chloroflexi*, *OM1 clade*, etc.

TABLE 1 | The heterogeneous soil properties in the tidal creek salt marsh.

Site	SMC (%) [*]	pH	EC (ms/cm) [*]	SOC (mg/kg) [*]	TN (mg/kg) [*]	TP (mg/kg)
PM	0.24 ± 0.02	8.07 ± 0.42	0.66 ± 0.07	4,659.71 ± 49	273.4 ± 22.44	43.91 ± 8.38
BM	0.25 ± 0.05	7.97 ± 0.30	1.47 ± 0.52	5,844.81 ± 56	154.84 ± 14.18	38.96 ± 1.44
TC	0.24 ± 0.04	7.62 ± 0.62	3.11 ± 1.06	5,960.18 ± 76	288.4 ± 20.69	40.02 ± 21.49
TSC	0.22 ± 0.01	7.79 ± 0.27	5.85 ± 0.79	6,508.12 ± 83	298.77 ± 23.55	42.29 ± 11.55
SC	0.24 ± 0.01	7.24 ± 0.39	5.29 ± 1.1	7,368.23 ± 10	305.09 ± 9.22	30.63 ± 7.28

The asterisks (*) indicate the soil properties are significantly different, and the $p < 0.05$.

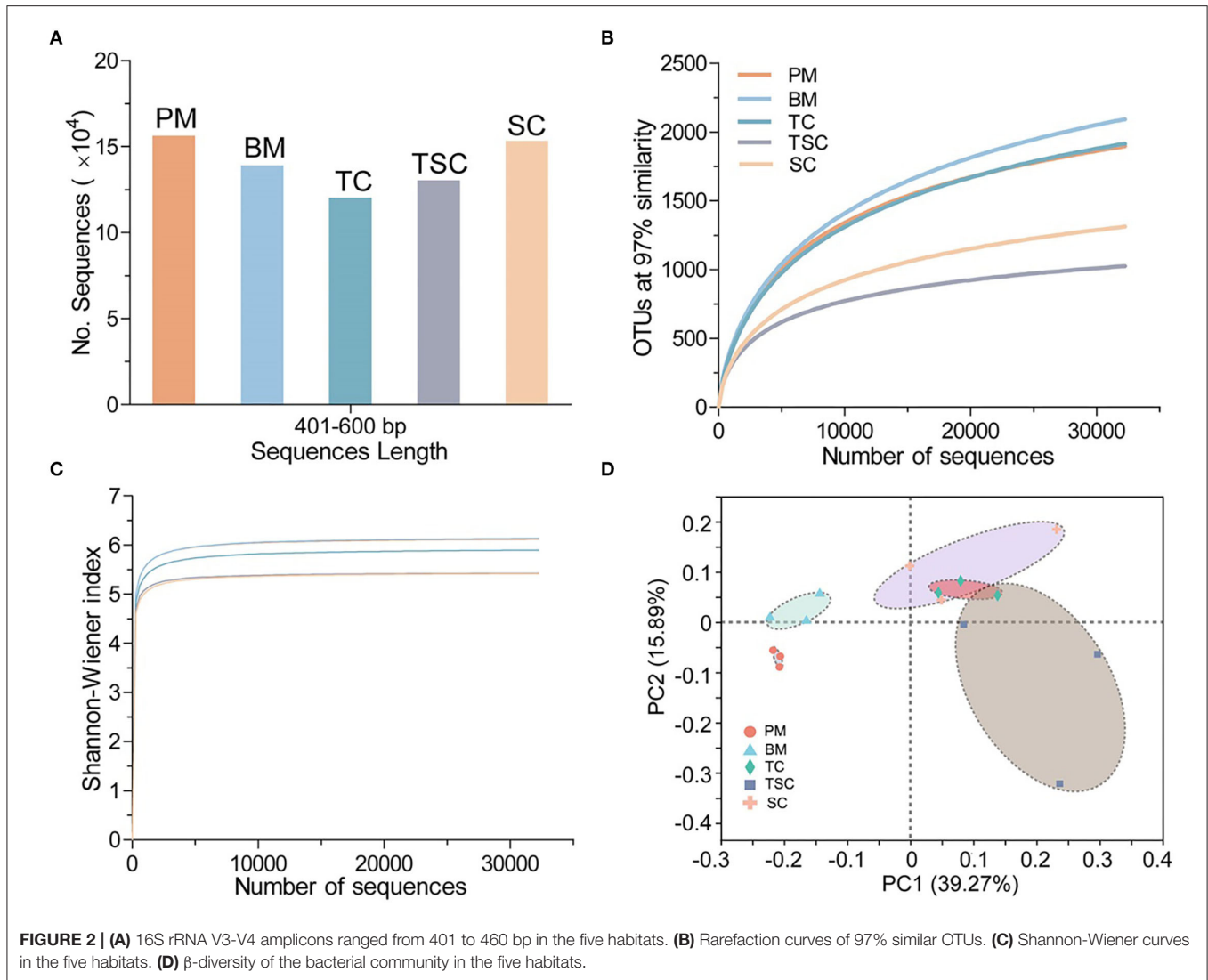


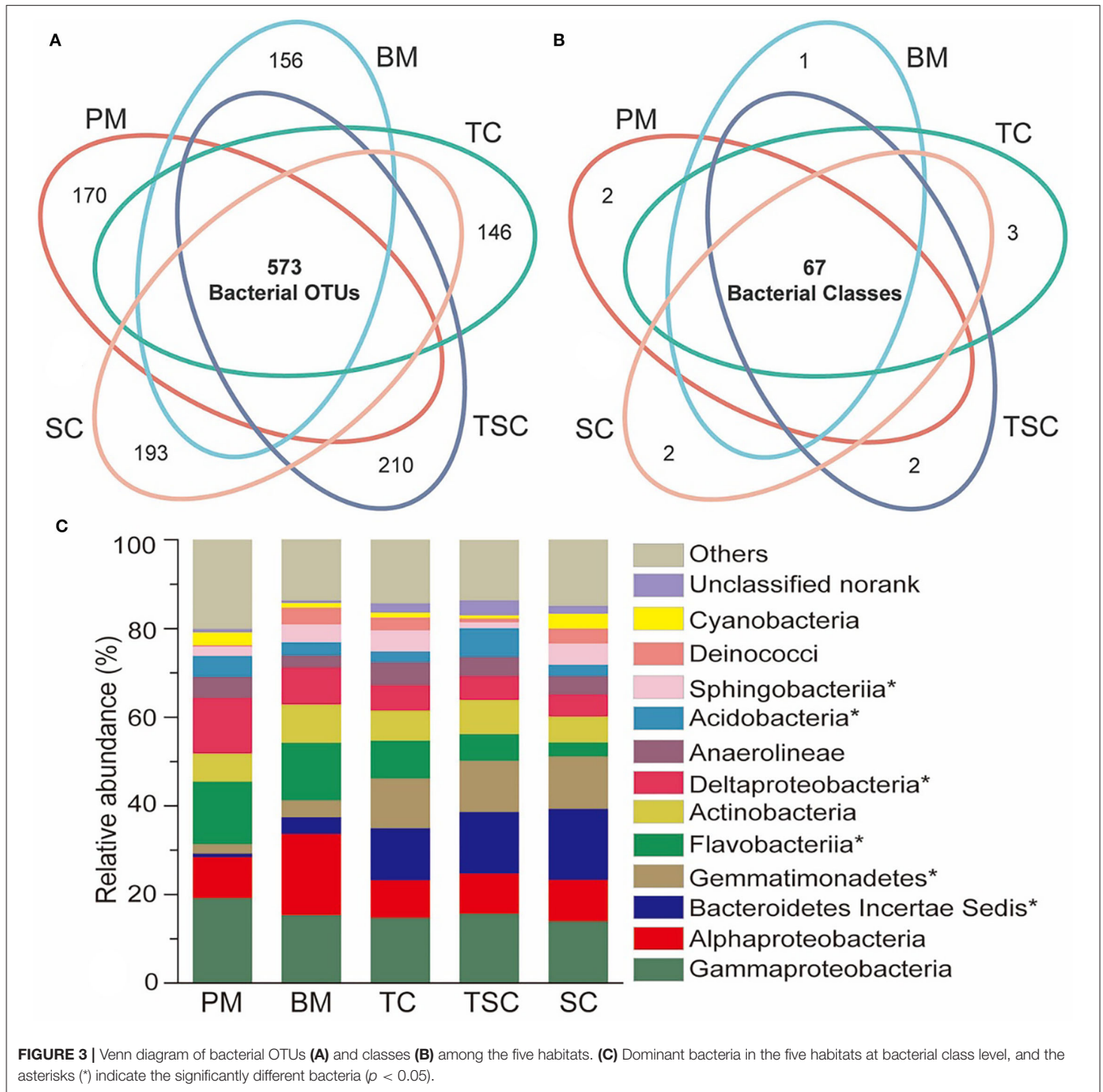
TABLE 2 | The bacterial communities in valid sequence reads, 97% OTUs, Good's Coverage, and bacterial α -diversity indices.

Site	Reads	OTUs	Good's coverage	ACE	Chao1	Shannon index	Simpson index
PM	33,680	2,568	98.57%	2,268	2,310	6.12	0.0062
BM	35,768	3,088	98.22%	2,598	2,581	6.14	0.0063
TC	34,356	2,971	98.42%	2,354	2,375	5.89	0.0106
TSC	3,5607	1,846	99.35%	1,198	1,217	5.43	0.0107
SC	38,684	2,402	98.96%	1,611	1,635	5.42	0.0157

Bacterial Biomarkers in Different Micro-Habitats

A total of 129 bacterial biomarkers were identified in the five micro-habitats, with 63 biomarkers (12 bacterial classes) in PM, 16 (5 classes) in BM, 9 (4 classes) in TC, 33 (2 phyla and 8 classes) in TSC, and 8 (2 classes) in SC, respectively (**Supplementary Table S1**). The bacterial communities of PM and TSC had more biomarkers, which mainly clustered into the

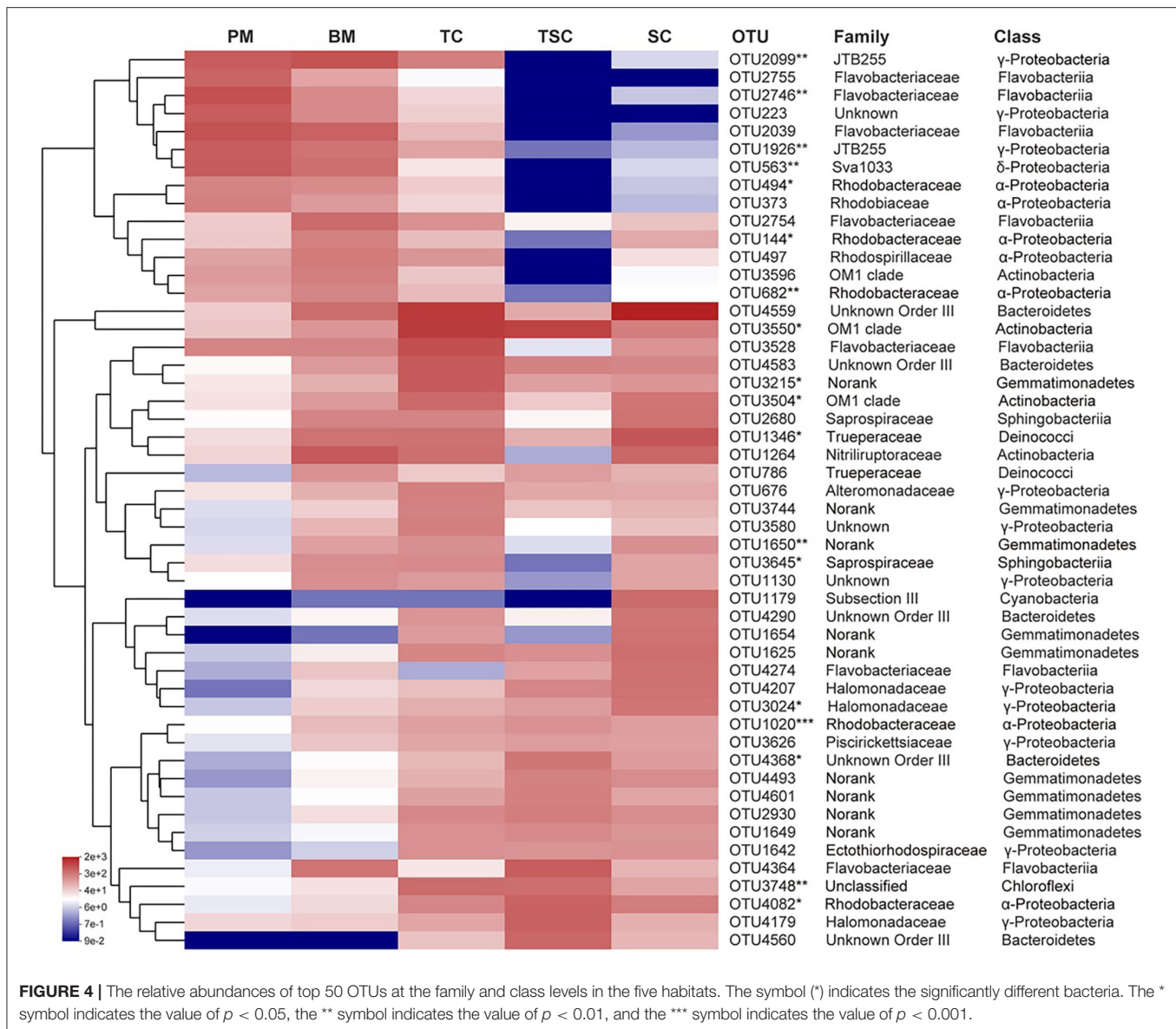
classes of α -, δ -, γ -Proteobacteria, Flavobacteriia, Acidobacteria, Actinobacteria, etc. At the bacterial genus level, these biomarkers belonged to 60 genera, and most enriched in PM with 29 bacterial genera, followed by in BM (12), TSC (10), TC (5), and SC (4) (**Figure 5**). For example, the result found that 10 genera (*Desulfococcus*, *Desulfosarcina*, the *Sva0081* sediment group, no-rank *Desulfobulbaceae*, unclassified *Desulfobulbaceae*, *Desulfobulbus*, *Syntrophobacteraceae*, *Desulfuromonadales*,



unclassified *Desulfuromonadales*, and *Geothermobacter*) of sulfate-reducing bacteria (SRB) were the biomarkers in PM and BM. In addition, aerobic anoxygenic phototrophic bacteria (AAPB) were also significantly different and diverse in the five micro-habitats with 14 bacterial genera, such as *Rhodobacteraceae*, *Rhodospirillaceae*, and *Roseovarius*. It would be noted that several AAPBs were abundant in *Rhodobacteraceae* (5.42%), *Rhodospirillaceae* (1.68%), *Ectothiorhodospiraceae* (1.05%), *Subsection III* (0.56%), *Rhodobiaceae* (0.48%).

The Relationship Between Bacterial Community Structures and Soil Physicochemical Properties

At the bacterial class level, the first axis RDA1 and second axis RDA2 have explained 47.56% variances between bacterial community structures and soil physicochemical properties (Figure 6A). The RDA result showed that bacterial community structures of TC, TSC, and SC were positively related to SOC, TN, and EC but negatively related to SMC, pH,



and TP, that of PM and BM in reverse. Furthermore, our study selected the top 20 bacterial classes and 50 bacterial families to unveil the relationship with soil properties. In detail, heatmap analysis showed that the classes Bacteroidetes, Phycisphaerae, Gemmatimonadetes, and unclassified Chloroflexi were positively related to SOC, TN, and EC, in contrast to α -, δ -Proteobacteria, and Flavobacteriia (Figure 6B). Moreover, the bacterial classes (e.g., Flavobacteriia, Verrucomicrobiae, Phycisphaerae) were significantly affected by SMC and pH. At the family level, the result showed that 26 bacteria were closely related to SOC, TN, EC, and SMC (Figure 6C). The majority of them were the dominant class α -, δ -, γ -Proteobacteria, Gemmatimonadetes, Bacteroidetes, and Flavobacteriia, suggesting that the soil properties of SOC, TN, EC, and SMC were the important environmental factors to alter the bacterial community structures in the five micro-habitats.

DISCUSSION

Tidal creek salt marshes have characterized as frequently tidal flooding and strongly hydrological connectivity, and shape active and uneven ecosystems with several small and diverse micro-habitats (Mooraki et al., 2009; Cabezas et al., 2017; Wang et al., 2021). Some studies have shown that these micro-habitats were important to maintain health estuary wetland eco-functions, such as carbon capture and storage, wetland restoration and buffering disturbances (Wu et al., 2020; Glaser et al., 2021). In field investigation, there were five micro-habitats of pluff mudflat, bare mudflat, *T. chinensis*, *T. chinensis*-*S. salsa*, and *S. salsa* around the tidal creek. This may be due to that tidal creek greatly altered microtopography, soil seed colonization, and vegetation succession *via* tidal fluctuation in the estuary wetland (Chang et al., 2010; Zhu et al., 2021). These micro-habitats around tidal creeks generated significantly different soil properties of soil

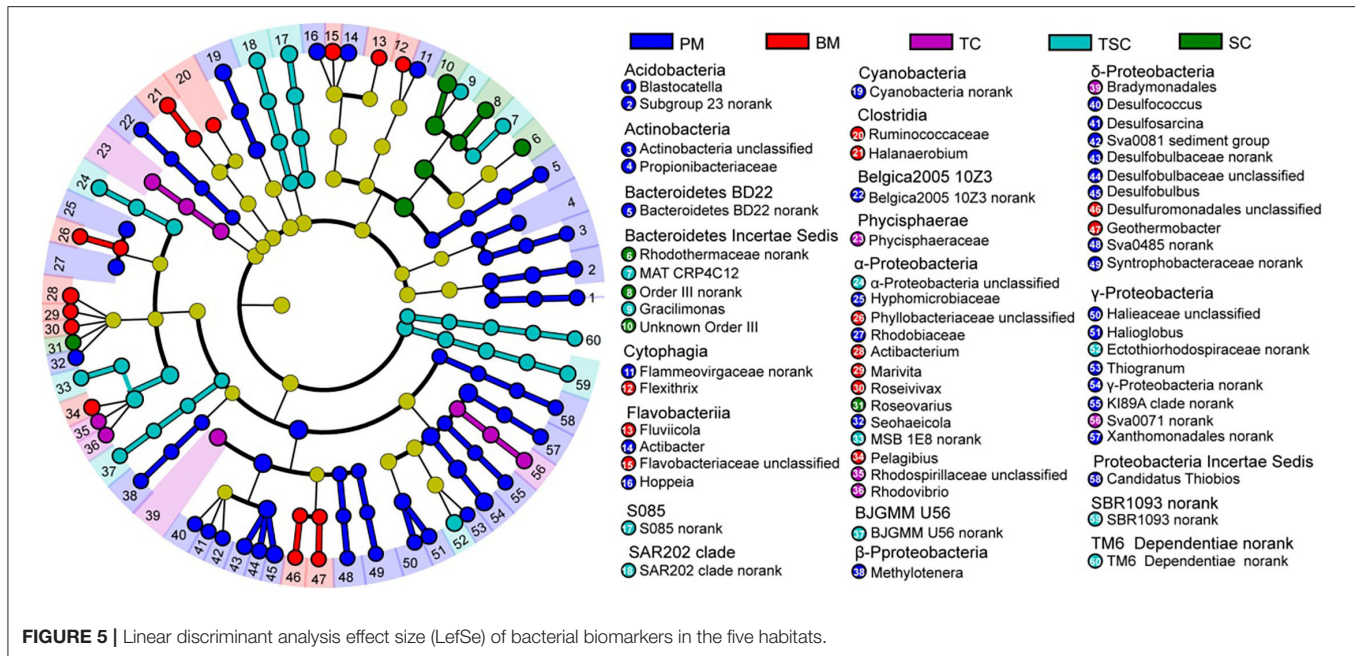


FIGURE 5 | Linear discriminant analysis effect size (LefSe) of bacterial biomarkers in the five habitats.

moisture, salinity, and nutrients (Table 1). Because of near tidal creeks and frequent tidal flooding, SMC of the lower micro-habitats (pluff and bare mudflats) was higher. However, the upper micro-habitats (*T. chinensis*, *T. chinensis*-*S. salsa*, and *S. salsa* communities) were suffered by short-time flooding and strong evaporation, which should be the major reasons and thus to aggregate the higher EC and lower SMC in these surface soils (Kearney and Fagherazzi, 2016; Zhou et al., 2020). Moreover, soil nutrients of the lower micro-habitats were taken away by tidal fluctuation, meanwhile accumulated in the upper micro-habitats due to litter decompositions (Chomel et al., 2016; Koceja et al., 2021; Yang et al., 2021).

The present study found the bacterial community structures were significantly different in the five micro-habitats on the tidal creek sections, and these differences may be greatly affected by the tidal action and soil properties together. On one hand, the bacterial community structures of lower micro-habitats (PM and BM) had more diversities than these of upper micro-habitats (TC, TSC, and SC). This may be due to that more frequent tidal action contributed to the passive dispersal of bacterial taxa *via* the marine bacteria. It has been confirmed that several marine bacteria were enrichment in PM and BM, including the dominant bacterial families *JTB 255* (γ -Proteobacteria) (Dykma et al., 2015), *Flavobacteriaceae* (Flavobacteriia) (Cho and Giovannoni, 2004), and *OM1 clade* (Actinobacteria) (Morris et al., 2012). In addition, the soil properties may contribute main influence to the differences in bacterial community structures (Figure 6A). Although pH was regarded as the most important environmental factor to affect soil bacterial communities (Fierer, 2017; Xun et al., 2019), the soil nutrient, salinity, and moisture were more important to the bacterial community structures in

our study. Many pieces of evidence have supported our result that the soil nutrient availability and salinity were the predominant reasons for bacterial communities in estuary wetland (An et al., 2019; Li et al., 2019; Rath et al., 2019; Zhang et al., 2020). On the other hand, the differences in bacterial community structures were also exhibited in dominant bacterial taxa, in particular with a high variable in the α -, δ -, γ -Proteobacteria, Bacteroidetes, Gemmatimonadetes, Flavobacteriia, Acidobacteria, and Sphingobacteriia, accounting for about 70% (Figure 3C). Indeed, the study found EC, SMC, SOC, and TN may be greatly responsible for them between the lower and upper micro-habitats (Figures 6B,C).

Recent years, SRB and AAPB have got many attentions on sulfur cycling, carbon mineralization, and sequestration in the coastal wetland (Stegman et al., 2014; Jørgensen et al., 2019; Rolando et al., 2022). The present study found SRB and AAPB were characterized as the bacterial biomarkers in tidal creek salt marsh, and may partly result in the differences of structures and functions. SRB were widely distributed in anoxic environments, and the lower micro-habitats (PM and BM) were suffered by long-time seawater flooding and abundance SO_4^{2-} , which were suitable for the SRB groups (Zelege et al., 2013). Our study found that SRB of 10 genera were great enrichment, which suggests that they may be the potential indicators of the sulfur cycle in lower micro-habitats. Moreover, AAPB were genetically diverse in Proteobacteria (Bryant and Frigaard, 2006; Ritchie and Johnson, 2012), in agreement with our results across α -, β -, and γ -Proteobacteria (Figure 5). Some studies reported that *Rhodobacteraceae* were high in abundance up to 25% of the total bacterial community in seawater (Buchan et al., 2005; Lenk et al., 2012). In the present study, the *Rhodobacteraceae* (*Actibacterium*, *Marivita*, *Roseivivax*, *Roseovarius*, and *Seohaicicola*) were greatly

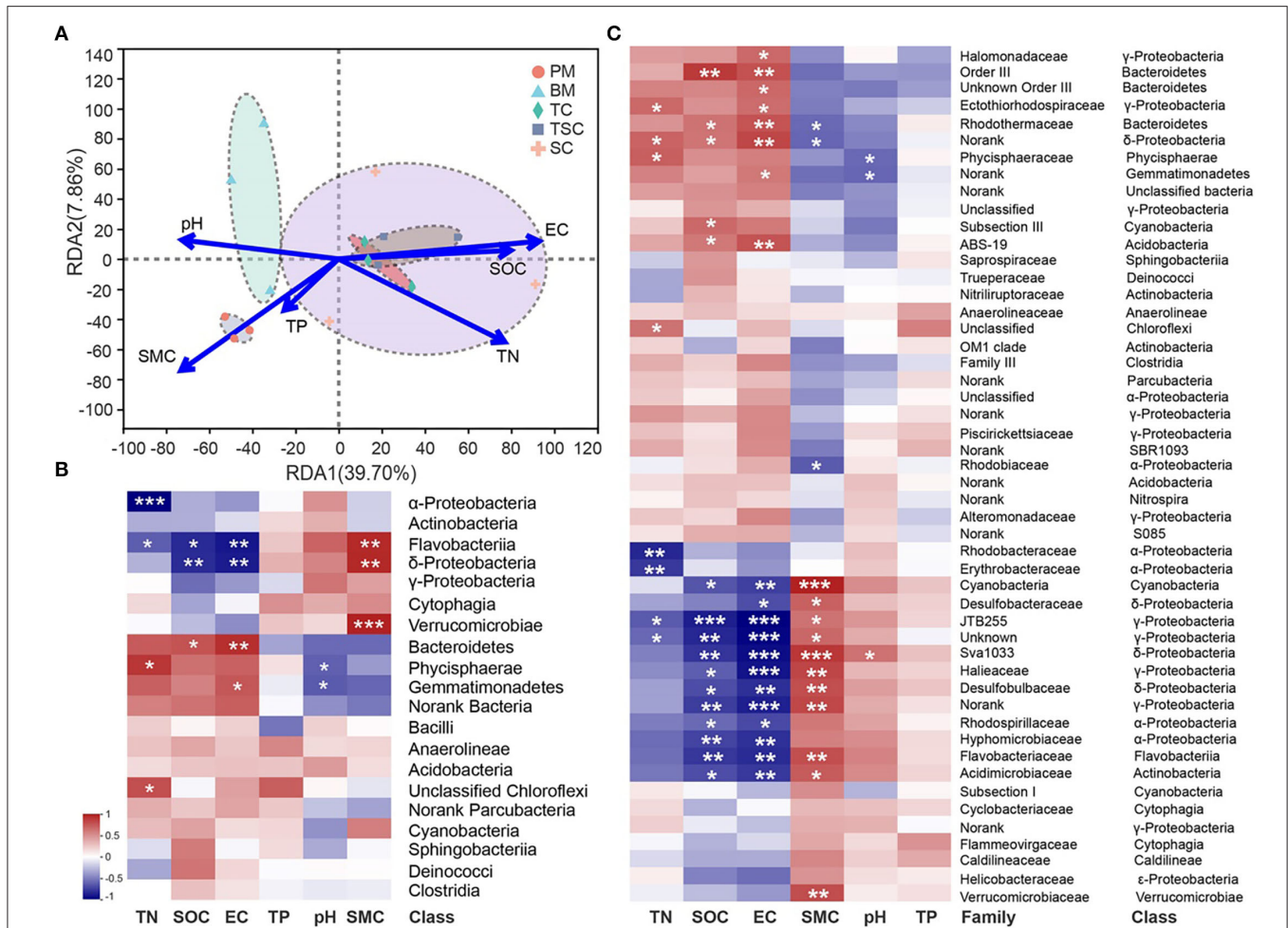


FIGURE 6 | (A) Redundancy analysis (RDA) between soil properties and bacterial community structures at class level. The correlation heatmaps of soil properties and dominant bacteria at class **(B)** and family **(C)** level. The symbol (*) indicates the significantly different bacteria. The * symbol indicates the value of $p < 0.05$, the ** symbol indicates the value of $p < 0.01$, and the *** symbol indicates the value of $p < 0.001$.

enriched in the lower micro-habitats (PM and BM), which may be associated with dispersal between the lower micro-habitats and seawater. In addition, the *Rhodospirillaceae* was abundant in upper micro-habitats (TC, TSC, and SC). Several studies have reported that *Rhodospirillaceae* was ability to N_2 fixation and positive relation of soil nutrient contents and plant successions (Madigan et al., 1984; Ding et al., 2017).

CONCLUSION

Our study found that the bacterial communities were greatly diverse and heterogeneous in the tidal creek salt marsh, and the diversities were greatly altered by the effects of tidal action, soil salinity, moisture, and nutrients. In particular, the important biomarker taxa of SRB and AAPB groups were close correspondence in different micro-habitats. These results provide fundamental insights into unveiling bacterial community diversities and important bacterial biomarkers of different micro-habitats.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are publicly available. This data can be found at NCBI: <http://www.ncbi.nlm.nih.gov/bioproject/851955>, or with the accession number: PRJNA851955.

AUTHOR CONTRIBUTIONS

ZW: conceptualization, writing—original draft, and editing. KY: resources and formal analysis. DZ, YL, BG, YY, XW, ZR, WW, and XC: investigation and data curation. JYa: visualization. JYu: supervision and review. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.950605/full#supplementary-material>

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