

Article

Sediment Bacteria and Driving Factors in Intertidal Flats and Vegetated Zones of Mangrove Ecosystems in the Northern Beibu Gulf During Summer

Jiaodi Zhou ^{1,2}, Peng He ², Zhijun Dai ³, Dongliang Lu ^{2,*}, Bin Yang ⁴, Hu Huang ^{1,2,*}, Zeyu Wang ², Solomon Felix Dan ² and Wen Song ⁴

¹ Guangxi Laboratory on the Study of Coral Reefs in the South China Sea, Guangxi University, Nanning 530004, China; zhoujodie@bbgu.edu.cn

² Guangxi Key Laboratory of Marine Environmental Disaster Processes and Ecological Protection Technology, Beibu Gulf University, Qinzhou 535011, China; hepeng@bbgu.edu.cn (P.H.); zeyu_wang24@163.com (Z.W.); solomondan@bbgu.edu.cn (S.F.D.)

³ State Key Laboratory of Estuarine and Coastal Research, East China Normal University, Shanghai 200050, China; zjdai@sklec.ecnu.edu.cn

⁴ Jiangsu Key Laboratory of Marine Biotechnology, Jiangsu Ocean University, Lianyungang 222005, China; binyang@jou.edu.cn (B.Y.); wens343126@163.com (W.S.)

* Correspondence: ldl@bbgu.edu.cn (D.L.); mrhuanghu@126.com (H.H.)

Abstract

Mangrove sediments harbor complex bacterial communities that play critical roles in ecosystem functioning. In this study, we investigated the spatial patterns and environmental drivers of sediment bacterial communities across intertidal flats and vegetated zones in five representative mangrove habitats spanning the Northern Beibu Gulf, South China. Utilizing high-throughput 16S rRNA gene amplicon sequencing, we analyzed bacterial composition and diversity from sediments collected in Qinzhou, Fangchenggang, and Beihai. Results indicated that bacterial communities were dominated by *Proteobacteria* (37–45%), followed by *Bacteroidota* and *Acidobacteriota*; however, a considerable proportion of taxa remained unclassified, particularly in intertidal flats. Bacterial richness and diversity were generally higher in vegetated zones, where sediments were more acidic and nutrient-rich, whereas intertidal sediments were more alkaline and contained higher chlorophyll-*a* (Chl-*a*) concentrations. Beta-diversity analysis revealed distinct differences in community structures between zones and regions, which were shaped by both deterministic environmental filtering and stochastic processes. Redundancy analysis (RDA) indicated that bacterial communities assembly driven by niche differentiation influences salinity (Sal), pH, biogenic silica (BSi), total phosphorus (TP), and total nitrogen (TN), as these factors vary across sites due to differing environmental filtering intensities. These findings highlight the distinct differences in mangrove sediment bacterial communities between intertidal flats and vegetated zones, which are shaped by local sediment physicochemical conditions and regional environmental gradients. They provide critical insights for the conservation and restoration of mangrove ecosystems.

Keywords: mangrove sediment; bacterial communities; environmental drivers; 16S rRNA amplicon quencing; Beibu Gulf

Academic Editor: Yizhi Sheng

Received: 28 May 2026

Revised: 13 July 2026

Accepted: 17 July 2026

Published: 21 July 2026

Copyright: © 2026 by the authors.

Licensee MDPI, Basel, Switzerland.

This article is an open access article distributed under the terms and conditions of the [Creative Commons Attribution \(CC BY\) license](https://creativecommons.org/licenses/by/4.0/).

1. Introduction

Mangroves, situated in the transitional zones between marine and terrestrial environments, exhibit remarkable biodiversity and ecological functions. They serve as habitats for numerous species and play key roles in nutrient cycling and carbon storage [1,2]. Bacterial communities within mangrove sediments are pivotal to the biogeochemical cycles, contributing to the cycling of organic matter and nutrients and to the detoxification of xenobiotics, thereby supporting the productivity and functionality of mangrove ecosystems [3]. Bacteria serve as the key drivers of ecological processes in mangrove sediments. On the one hand, heterotrophic bacteria decompose mangrove litter, regulate the mineralization and long-term burial of organic carbon, and ultimately determine the blue carbon sink capacity of mangrove ecosystems [4,5]. On the other hand, functional groups such as denitrifiers and sulfate-reducing bacteria dominate nitrogen removal and sulfur metabolism, balancing biogenic elements in the intertidal flats [6–8]. Meanwhile, sediment bacteria transform heavy metals and degrade terrestrial pollutants, performing coastal water purification functions [9,10]. The presence or absence of mangrove vegetation drastically alters organic matter inputs and sedimentary conditions, thereby inducing divergence in bacterial communities composition and metabolic functions. Early research on mangrove bacteria primarily focused on community assembly, biogeochemical cycles, plant–microbe interactions, bioremediation, microbial resources, and responses to global environmental changes [3,6,11], as well as their involvement in compound decomposition and energy conversion [12]. In addition, salt-tolerant endophytic bacteria isolated from mangrove plants were studied for their tolerance to and detoxification potential of heavy metals [9].

Although previous studies have broadly documented the ecological functions of mangrove sediment bacteria and their responses to environmental variation. Most investigations have tended to focus on generalized microbial patterns across mangrove ecosystems [6–9]. Many regional studies lack targeted comparative analysis of bacterial communities variations between intertidal flats and vegetated zones within the same mangrove reserve. In addition, existing research often provides isolated descriptions of microbial community characteristics or individual sediment environmental factors, without systematically associating bacterial community distribution patterns with key physicochemical indicators (e.g., salinity (Sal), pH, total nitrogen (TN), total phosphorus (TP), total organic carbon (TOC), and biogenic silica (BSi)) under vegetation-driven habitat differentiation. The lack of fine-scale, site-specific comparisons between paired intertidal flats and vegetated zones limits our holistic understanding of how mangrove vegetation shapes sediment bacterial assemblages and their environmental adaptive strategies. Targeted field surveys focusing on habitat divergence in typical conserved mangrove regions are therefore urgently needed to complement current research perspectives.

High-throughput 16S rRNA gene amplicon sequencing provides detailed information on bacterial community structure and function, making it particularly suitable for investigating variations in bacterial communities in sediments from representative ecological regions [10]. Owing to these advantages, this approach has been extensively applied to explore bacterial communities in mangroves and their rhizosphere sediments [13]. In recent years, the application of advanced techniques (such as metagenomics, metabolomics, and high-resolution spatial modeling) has enabled deeper insights into the metabolic potential, interspecific interactions, and fine-scale responses to environmental gradients of mangrove microbial communities, significantly expanding our understanding of this complex ecosystem [14]. As vital functional groups in mangrove sediments, bacteria act as the core drivers of carbon, nitrogen, sulfur, and phosphorus cycling [4]. They sustain ecological stability, pollutant purification, and blue carbon sequestration, and strongly determine the ecosystem's resistance to natural disturbances and human activities.

Global research has extensively explored biological drivers of bacterial communities in mangrove sediments. These studies have preliminarily clarified how biological factors regulate the structure and function of bacterial communities [11], and have also laid a fundamental theoretical foundation for relevant research. However, current studies still have prominent limitations. Limited sampling coverage and spatial scales hinder systematic exploration of the biogeographic distribution patterns of bacterial communities [15]. Furthermore, the core environmental factors regulating bacterial communities also remain unclear. Most existing studies only focus on the impact of individual environmental factors and lack analyses of the synergistic effects of multiple environmental variables [16]. Further research in this field can improve the theoretical system of wetland microbial ecology and biogeochemical cycling and can also provide reliable scientific evidence for mangrove ecological restoration and blue carbon sequestration.

To address this gap, we conducted a spatially extensive survey across representative mangrove habitats in the Northern Beibu Gulf, a region harboring some of China's most distinctive and well-conserved mangrove forests. We employed 16S rRNA gene amplicon sequencing to analyze bacterial communities from both intertidal flats and vegetated zones across multiple locations. Specifically, we (1) characterized bacterial community composition and functional potential in mangrove sediments; (2) compared bacterial diversity and community structure between intertidal flats and vegetated zones within the same sites to assess how vegetation influences sediment physicochemical conditions and niche availability, and (3) explored the effects of bacterial communities on major sediment physicochemical properties (Sal, pH, TN, TP, TOC, and BSi). We aim to provide a mechanistic understanding of the forces that structure mangrove sediment bacteria. Ultimately, this work offers critical insights for predicting ecosystem trajectories and informing conservation strategies in the context of ongoing environmental change.

2. Materials and Methods

2.1. Sample Collection

The Beibu Gulf is a semi-enclosed gulf located in the northwestern part of the South China Sea. It is bounded by the Leizhou Peninsula and Hainan Island to the east, the Guangxi Zhuang Autonomous Region to the north, and Vietnam to the west. This study focuses on the Qinzhou, Fangchenggang, and Beihai regions of Guangxi, which constitute an important maritime corridor between China and the Association of Southeast Asian Nations and represent a key node in China's Belt and Road Initiative. The Northern Beibu Gulf has a typical subtropical maritime monsoon climate, with an average annual temperature of approximately 23.36 °C and an average annual precipitation of 1903.7 mm [17]. Owing to its favorable ecological conditions and abundant natural resources, this region is one of China's important areas for ecological conservation. Hydrologically, the study area has well-developed freshwater runoff systems that sustain stable water and nutrient supplies for coastal mangrove ecosystems. A series of seasonal and perennial rivers, represented by the Qinjiang River, Maoling River, and Nanliu River, flow into the sea across the coastal zones of Qinzhou, Fangchenggang, and Beihai, forming extensive mangrove wetland clusters at large-scale river estuaries [18]. Beyond natural river runoff, dense artificial drainage ditches and irrigation channels are widely distributed in the study region's coastal aquaculture zones and tidal flat reclamation areas. These artificial water infrastructures act as vital secondary freshwater input pathways, modulating the Sal of mangrove tidal flats and further shaping the spatial distribution and growth status of local mangrove communities.

Mangrove areas in Qinzhou, Beihai, and Fangchenggang were selected as experimental sites. Within each site, two habitats, the intertidal flats (i) and vegetated zones (v), were chosen for sampling (Figure 1). Intertidal flats refer to bare intertidal areas without

continuous coverage of mangrove vascular plants. Their sediment surfaces are only covered by microalgal biofilms with negligible plant roots, litter, and woody vegetation, and vegetation coverage within 1 m × 1 m quadrats is less than 5%. In contrast, vegetated zones are intertidal habitats covered by stable mangrove stands including *Avicennia marina*, *Aegiceras corniculatum*, and *Bruguiera gymnorrhiza*, with quadrat vegetation coverage exceeding 10% and abundant underground mangrove roots, fallen debris, and plant debris observed in sediment profiles.

Sampling locations A, located in Qinzhou Shajing (21.84° N, 108.59° E), was dominated by *Aegiceras corniculatum*; B located in Fangchenggang Sanjiaoing (21.71° N, 108.51° E) was dominated by *Avicennia marina*; C located in Fangchenggang East Bay (21.63° N, 108.37° E) was dominated by *Avicennia marina*; D in Beihai Nanliu River (21.60° N, 109.03° E) was dominated by *Aegiceras corniculatum*; and E in Beihai Dandou Sea (21.55° N, 109.67° E) was dominated by *Bruguiera gymnorrhiza*. The distance between mangrove vegetated zones and adjacent intertidal flats was 20–40 m. The specific vegetation characteristics are shown in Table 1. Sampling was conducted in summer, from July to August 2024.

This study selected five typical mangrove wetlands in the Northern Beibu Gulf as sampling sites. Two paired habitat types, including intertidal flats and mangrove vegetated zones, were established at each site, with a horizontal distance of 20–40 m between the two adjacent habitat plots to eliminate the interference of regional background environmental differences. To ensure sampling representativeness and reduce random errors caused by micro-spatial heterogeneity of surface sediments, three sampling points were evenly arranged in a triangular pattern within each habitat plot, with a spacing of no less than 5 m between individual points, and one sediment replicate was collected at each sampling point. Overall, each of the five sampling sites contained two habitat plots with three biological replicates per habitat. In total, 30 valid sediment replicate samples were collected from 10 habitat plot groups. This reasonable spatial layout and sufficient biological replicates guaranteed the accuracy and reliability of subsequent statistical analyses of sediment bacterial communities and physicochemical variables. Surface sediments (0–20 cm) were collected using a five-point sampling method at each site. Approximately 200 g of the homogenized sediment was collected from each site for further processing. This depth was selected because it represents the most microbially active layer of mangrove sediments, receiving substantial organic matter inputs and supporting key biogeochemical processes [5]. After homogenization, sediment samples were placed in sterile self-sealing bags and transported to the laboratory on ice. Plant roots and visible debris were removed, and each sample was divided into two subsamples. One subsample was stored at −80 °C for sediment bacterial diversity analysis, while the other was freeze-dried for sediment physicochemical property analysis.

Table 1. Overview of Mangrove Vegetation Characteristics.

Sampling Site	Dominant Mangrove Species and Vegetation Characteristics	Region	Distance Between Habitats (m)
v-A	<i>Aegiceras corniculatum</i> , evergreen shrub, 2–6 m in height; small fleshy leaves with rapidly decomposing litter	Qinzhou	25
v-D		Beihai	40
v-B	<i>Avicennia marina</i> , evergreen tree, 3–10 m in height; with finger-shaped pneumatophores, salt-enriched leaves, and fast litter decomposition	Fangchenggang	20
v-C			22

V-E	<i>Bruguiera gymnorhiza</i> , a large evergreen tree, 7–20 m in height; with knee-shaped pneumatophores, leaves with high tannin and crude fiber content, and slowly decomposing litter	Beihai 35
-----	---	-----------

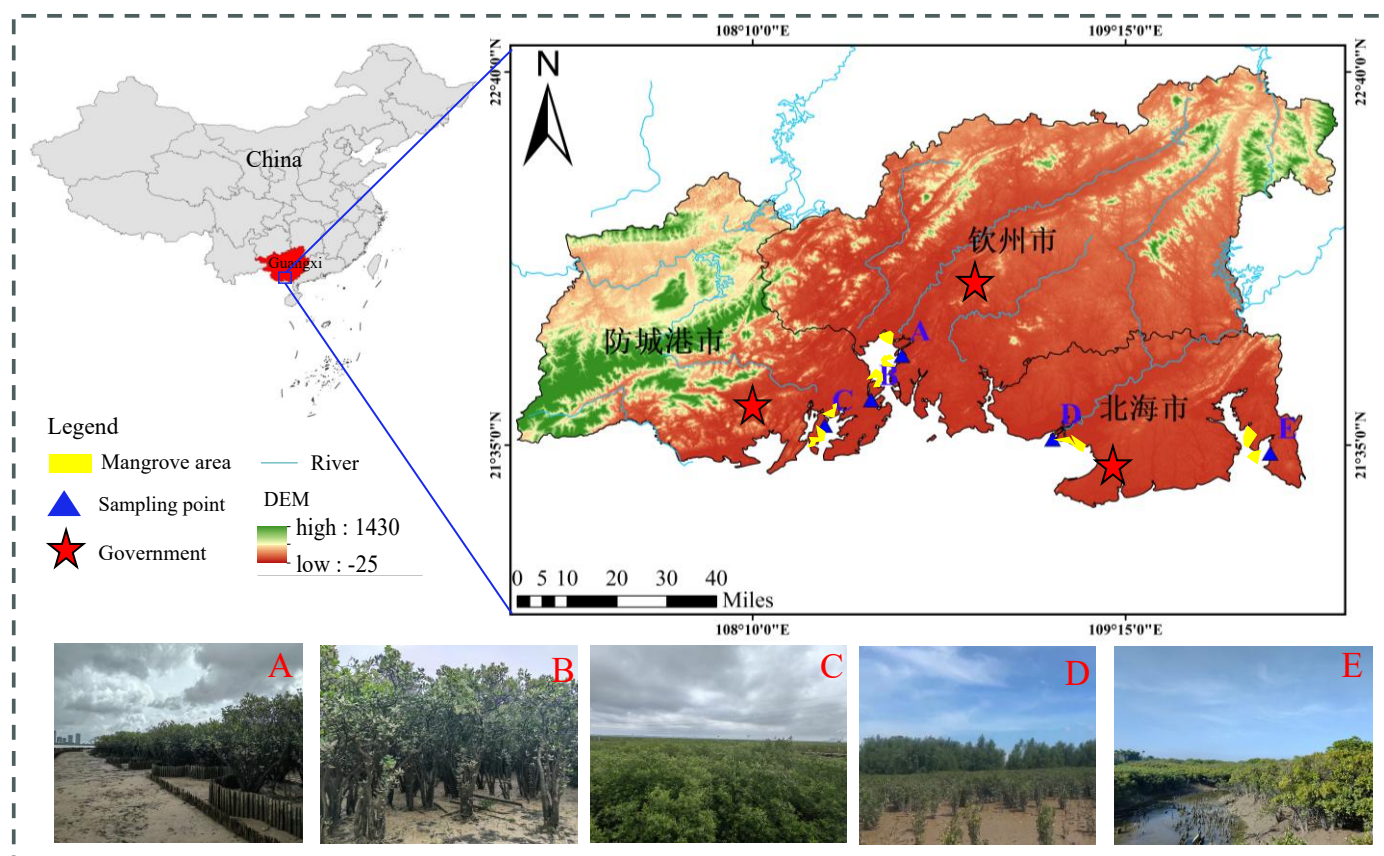


Figure 1. Map of the study area showing the distribution of sampling sites. (A): Shajing Town in Qinzhou; (B): Sanjiaojing Town in Fangchenggang; (C): Eastern Bay of Fangchenggang; (D): Estuary of Nanliu River in Beihai; (E): Dandou Coastal Waters in Beihai. Yellow areas represent mangrove forests, blue triangles indicate sampling points, and five-pointed stars mark the locations of major cities.

2.2. Sample Analysis

Total genomic DNA was extracted from 0.5 g of sediment samples using the TGuide S96 magnetic bead-based sediments DNA kit (Model DP812, Tiangen Biotech (Beijing) Co., Ltd., Beijing, China), following the manufacturer's instructions. The V3-V4 hypervariable regions of the 16S rDNA gene were amplified using the universal bacterial primers 338F (5'-ACTCCTACGGGAGGAGCA-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3') [19,20]. PCR amplification was carried out in a 10 µL reaction mixture containing 2.5–4 ng of genomic DNA, 5 µL of KOD FX Neo Buffer, 2 µL of 2 mM dNTPs, 0.2 µL of KOD FX Neo polymerase, and 0.3 µL each of 10 µM forward and reverse primers. The PCR program consisted of an initial denaturation at 95 °C for 5 min; 25 cycles of denaturation at 95 °C for 30 s, annealing at 50 °C for 30 s, and extension at 72 °C for 40 s; followed by a final extension at 72 °C for 7 min. PCR products were examined, quantified, and normalized using 1.8% agarose gel electrophoresis. Sequencing libraries were constructed and sequenced on the Illumina NovaSeq6000 platform by Biomarker Technologies Corporation (Room 605A, 6th Floor, Building 1, Courtyard 9, Nanfaxin Section, Shunping Road, Nanfaxin Town, Shunyi District, Beijing, 101300, China).

Sediment pH and Sal were measured in situ using a multifunctional salinometer. Sediment Chl-*a* was extracted in a low-temperature and dark environment using organic

solvents, with impurities removed by centrifugation and filtration. The extract absorbance was measured via UV–visible spectrophotometry, and the Chl-*a* concentration was calculated with standard calibration formulas. TOC was determined using a Shimadzu TOC-L analyzer (Shimadzu Corporation, Kyoto, Japan). Samples were pretreated with 1 mol/L hydrochloric acid to remove inorganic carbon before testing. Sediment TN was quantified via the standard Kjeldahl method through digestion, distillation, and titration processes. Sediment nitrite (NO_2^-) was determined by automated spectrophotometry. The extracted supernatant was colorimetrically measured, and its concentration was calculated using standard calibration curves. Sediment TP and inorganic phosphorus (IP) were quantified by alkali fusion combined with molybdenum-antimony spectrophotometry. Samples were completely decomposed via alkali fusion, and the obtained solutions were determined colorimetrically with standard calibration curves [7]. The BSi was extracted by pre-treating 100 mg of ground sediment with 10% H_2O_2 and 1 mol·L⁻¹ HCl, then digesting with 40 mL of 2% Na_2CO_3 at 85 °C for 8 h, collecting 200 µL of supernatant hourly for silicate concentration determination, and total potassium (K) was extracted and determined by flame photometry. After sample digestion and constant volume setting, the emission intensity was measured at the characteristic wavelength of potassium, and the content was calculated using the standard curve method [21,22].

Raw sequencing data were quality-filtered using Trimmomatic v0.33 software. Primer sequences were identified and removed using Cutadapt v1.9.1 software, and paired-end reads were merged using USEARCH v10. Chimeric sequences were detected and removed using UCHIME v4.2. After demultiplexing, operational taxonomic units (OTUs) were clustered at a 97% similarity level, and taxonomic identification of the OTUs was performed by alignment against the SILVA database. Alpha (α) and beta (β) diversity indices were calculated to assess bacterial community diversity and abundance across different mangrove regions. We evaluated the relationships between sediment physicochemical properties and bacterial composition. Pearson correlation analysis was performed using SPSS 20.0. Redundancy analysis (RDA) was conducted using Canoco 5. The β -nearest taxon index (β -NTI) was calculated in R v3.1.1 using the picante v1.8.2 and vegan v2.3-0 packages.

3. Results

3.1. Physicochemical Properties of Sediments

Before statistical comparison, all sediment physicochemical data were tested for normality via the Shapiro–Wilk test and homogeneity of variance via Levene’s test. Independent samples *t*-tests were applied to quantify differences in each parameter between vegetated mangrove zones and intertidal flats. One-way analysis of variance (ANOVA) followed by Tukey’s HSD post hoc test was used to detect regional differences across five sampling sites. All statistical analyses were conducted in R 4.2.1, with the significance level set at $p < 0.05$. All data are presented as the mean $\pm$ standard deviation (SD), $n = 3$ per habitat at each site (Table 2).

The physicochemical properties of sediments differed between vegetated and intertidal flats across the studied regions (Table 2). Vegetated sediments were weakly acidic (mean pH 6.85 ± 0.46 , range 6.39–7.62), while intertidal flat sediments were weakly alkaline (mean pH 7.13 ± 0.57 , range 6.32–7.73). Mean Sal of the intertidal flat was slightly higher in vegetated zones (3.32 ± 2.71 vs. 2.76 ± 2.41), with highest values at Dandou Sea sites (v-E, i-E) and lowest at Nanliu River sites (v-D, i-D). Chl-*a* was lower in vegetated zones (0.16 ± 0.06) than in intertidal flats (0.25 ± 0.13 , $p < 0.05$); the highest Chl-*a* was at i-C in vegetated zones and at i-E (0.45) in intertidal flats.

Our *t*-test results indicated that TP, TN, TOC, and K of intertidal flat were generally higher in vegetated zones (all $p < 0.05$). TP ranged from 11.55 µmol/g (i-A) to 24.81 µmol/g

(v-B). TN ranged from 0.01% (FB-T) to 0.14% (v-E). TOC was highest at v-E (2.21%) and lowest at v-A (0.60%) in vegetated zones, and ranged from 0.10% (i-C) to 1.12% (i-B) in intertidal flats. Mean K was 1.26% in vegetated zones and 1.81% in intertidal flats, ranging from 0.25% (i-C) to 1.85% (v-B). BSi was approximately twice as high in vegetated zones (2.52 $\mu\text{mol/g}$) as in intertidal flats (2.16 $\mu\text{mol/g}$), with the highest BSi at v-E (5.22 $\mu\text{mol/g}$) and the lowest at v-B (1.16 $\mu\text{mol/g}$) in vegetated zones, and from 0.53 $\mu\text{mol/g}$ (i-A) to 2.51 $\mu\text{mol/g}$ (i-D) in intertidal flats. One-way ANOVA confirmed significant spatial differences among the five sampling sites for all measured physicochemical parameters ($p < 0.05$).

Table 2. Physicochemical parameters of the surface sediment samples from the five mangrove sites in Northern Beibu Gulf ($n = 3$, mean $\pm$ SD).

Sampling Site	pH	Sal (psu)	Chl- <i>a</i> ($\mu\text{g/g}$)	TP ($\mu\text{mol/g}$)	DIP ($\mu\text{mol/g}$)	TN (%)	NO_3^- ($\mu\text{mol/g}$)	TOC (%)	K (%)	BSi ($\mu\text{mol/g}$)
v-A	6.78 $\pm$ 0.3	1.49 $\pm$ 0.005	0.11 $\pm$ 0.02	17.94 $\pm$ 0.2	4.78 $\pm$ 0.02	0.04 $\pm$ 0.01	0.16 $\pm$ 0.01	0.6 $\pm$ 0.06	1.25 $\pm$ 0.11	1.19 $\pm$ 0.15
v-B	6.76 $\pm$ 0.18	2.4 $\pm$ 0.1	0.13 $\pm$ 0.02	24.81 $\pm$ 0.94	14.89 $\pm$ 0.1	0.08 $\pm$ 0.03	0.24 $\pm$ 0.04	0.88 $\pm$ 0.04	1.85 $\pm$ 0.14	1.16 $\pm$ 0.13
v-C	6.39 $\pm$ 0.38	5.6 $\pm$ 0.002	0.25 $\pm$ 0.05	14.14 $\pm$ 0.71	2.84 $\pm$ 0.03	0.06 $\pm$ 0.02	0.27 $\pm$ 0.03	0.89 $\pm$ 0.11	0.83 $\pm$ 0.07	2.73 $\pm$ 0.13
v-D	6.7 $\pm$ 0.14	0.4 $\pm$ 0.001	0.11 $\pm$ 0.02	19.49 $\pm$ 0.15	7.65 $\pm$ 0.12	0.09 $\pm$ 0.02	0.18 $\pm$ 0.02	1.57 $\pm$ 0.14	1.06 $\pm$ 0.23	2.31 $\pm$ 0.09
v-E	7.62 $\pm$ 0.31	6.7 $\pm$ 0.008	0.19 $\pm$ 0.03	19.23 $\pm$ 0.18	11 $\pm$ 0.25	0.14 $\pm$ 0.02	0.24 $\pm$ 0.03	2.21 $\pm$ 0.12	1.32 $\pm$ 0.06	5.22 $\pm$ 0.14
i-A	7.28 $\pm$ 0.06	1.08 $\pm$ 0.001	0.14 $\pm$ 0.01	11.55 $\pm$ 0.26	3.99 $\pm$ 0.3	0.02 $\pm$ 0.01	0.12 $\pm$ 0.03	0.19 $\pm$ 0.04	1.22 $\pm$ 0.08	0.53 $\pm$ 0.16
i-B	6.8 $\pm$ 0.23	2.9 $\pm$ 0.002	0.37 $\pm$ 0.02	22.54 $\pm$ 0.23	14.63 $\pm$ 0.05	0.09 $\pm$ 0.02	0.14 $\pm$ 0.02	1.12 $\pm$ 0.17	1.43 $\pm$ 0.1	1.01 $\pm$ 0.12
i-C	6.32 $\pm$ 0.08	3.7 $\pm$ 0.005	0.23 $\pm$ 0.02	18.57 $\pm$ 0.15	2.51 $\pm$ 0.04	0.01 $\pm$ 0.01	0.18 $\pm$ 0.02	0.1 $\pm$ 0.04	0.25 $\pm$ 0.1	1.76 $\pm$ 0.12
i-D	7.73 $\pm$ 0.27	0.68 $\pm$ 0.002	0.19 $\pm$ 0.02	19.51 $\pm$ 0.17	5.91 $\pm$ 0.03	0.02 $\pm$ 0.02	0.13 $\pm$ 0.01	0.21 $\pm$ 0.01	1.65 $\pm$ 0.09	2.51 $\pm$ 0.13
i-E	7.51 $\pm$ 0.14	6.7 $\pm$ 0.1	0.45 $\pm$ 0.09	16.11 $\pm$ 0.4	6.06 $\pm$ 0.04	0.08 $\pm$ 0.02	0.25 $\pm$ 0.01	1.09 $\pm$ 0.09	1.29 $\pm$ 0.05	2.11 $\pm$ 0.18

Notes: i and v represent the intertidal flats and vegetated zones, respectively. A, B, C, D, and E denote five sampling sites, with three parallel samples set at each site.

3.2. Spatial Distribution, Composition, and Alpha Diversity of Bacterial Communities

Under a 97% sequence similarity threshold, bacterial OTU distributions in mangrove sediments were analyzed across spatial gradients (Figure 2a,b). In intertidal flats, OTU richness was highest at the Nanliu River site (i-D, 2295 OTUs) and lowest at the Dongwan site (i-C, 1469 OTUs). In vegetated zones, the highest OTU richness was at the Sanjiaoqing site (v-B, 2472 OTUs) and the lowest at the Dongwan site (v-C, 1638 OTUs). The Dandou Sea sites (Beihai) showed relatively high OTU richness in both the intertidal (2285) and vegetated (2351) zones, whereas the Shajing sites (Qinzhou) had lower values (1888 and 2068, respectively). Across all regions, 827 OTUs were shared among the intertidal flat, and 1064 were shared among the vegetated zones. Among mangrove species, *Bruguiera gymnorhiza* hosted the highest OTU richness, followed by *Aegiceras corniculatum*, while *Avicennia marina* had the lowest.

A phylogenetic tree (Figure 2c) showed that *Proteobacteria* was the most abundant phylum across all sites, followed by unclassified bacteria. A heatmap of the 20 most abundant phyla (Figure 2d) revealed that at i-D, *Firmicutes* and *Cyanobacteria* dominated, while *Calditrichota* and *Desulfobacterota* were less abundant. *Campylobacterota* dominated at i-B, and *Bacteroidota* at v-B. Lower abundances of *Latescibacterota*, *Acidobacteriota*, and *Chloroflexi* were observed at i-D, i-C, and v-C, respectively. Conversely, higher abundances of *Nitrospirota*, *Gemmatimonadota*, *Chloroflexi*, *Acidobacteriota*, and *Latescibacterota* were found at v-D, i-A, i-B, v-B, v-A, and i-E, showing opposite patterns. Cluster analysis indicated high similarity in bacterial community composition among samples from the same site.

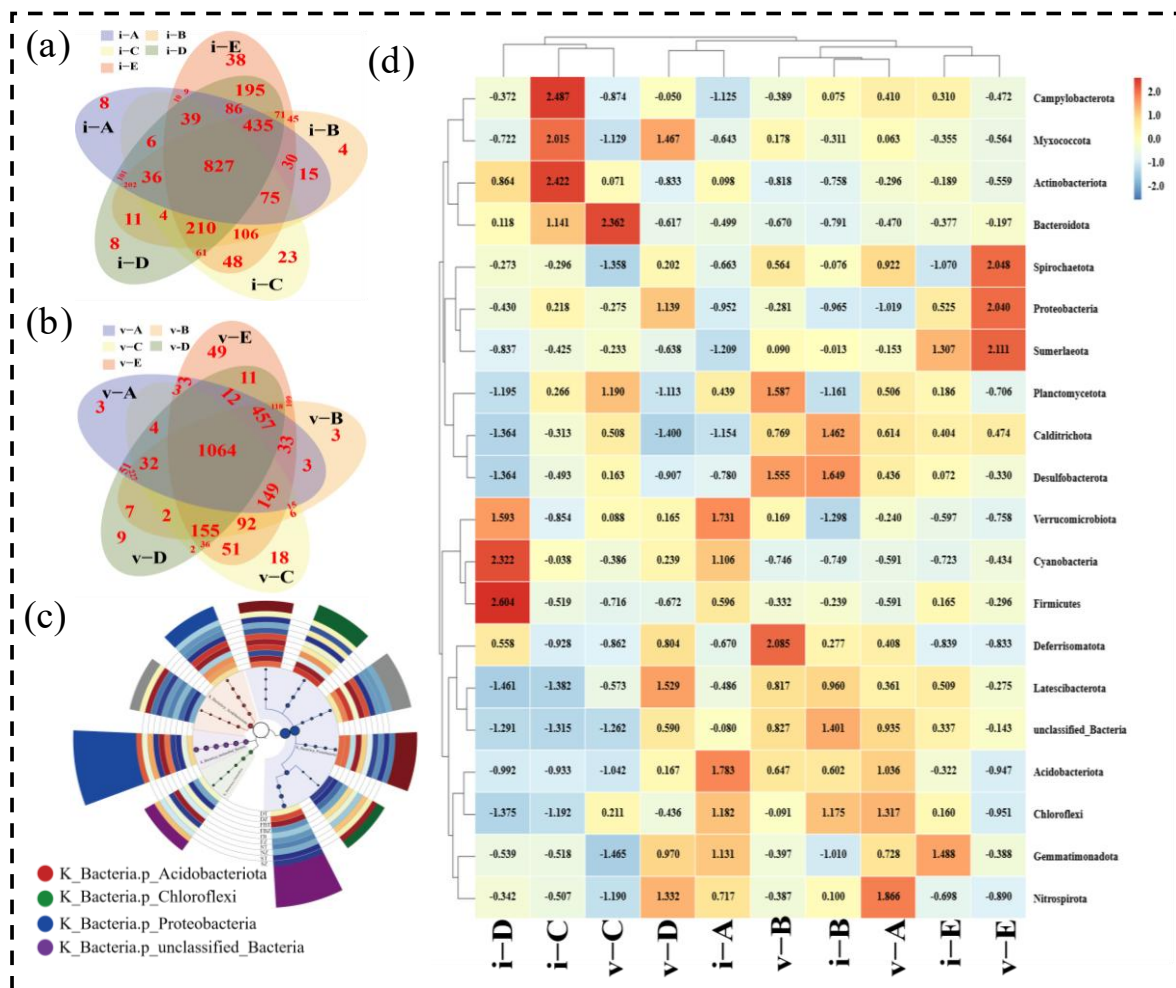


Figure 2. Differences in bacterial communities within mangrove communities across different regions. (a) OTUs in intertidal flats; (b) OTUs in the vegetated zones; (c) Phylogenetic tree diagram of the bacterial community. The color gradient in the outer ring represents the relative abundance differences among subordinate taxa within each phylum. (d) Heatmap of the top 20 bacterial phyla.

Bacterial communities in the intertidal and vegetated zones comprised 40 phyla, 99 classes, 275 orders, 463 families, 748 genera, and 970 species. The five most abundant phyla (relative abundance > 1%; Figure 3) were *Proteobacteria* (33.48%), *unclassified Bacteria* (11.73%), *Bacteroidota* (11.26%), *Acidobacteriota* (8.99%), and *Desulfobacterota* (7.91%), together accounting for 73.39% of total sequences. At the class level, *Gammaproteobacteria* was most abundant (~27% in the intertidal, and ~29% in vegetated), followed by *Bacteroidia* (~11% and ~12%, respectively). At the order, family, and genus levels, unclassified taxa accounted for substantial proportions (~36%, 54%, and 66% of total sequences, respectively), indicating high taxonomic uncertainty and numerous uncharacterized lineages. Notably, unclassified taxa were more abundant in intertidal flats than in vegetated zones, suggesting that greater environmental heterogeneity in intertidal habitats favors the persistence of uncharacterized microorganisms. Alpha diversity (Figure 4a,b): Chao1 richness values ranged from 1811.42 ± 34.01 to 2451.07 ± 15.53 . Significant differences in species richness were observed between vegetated and intertidal flats across different geographical locations ($p < 0.01$). Within the same sampling site, vegetated zone sediments generally showed higher richness than intertidal flat sediments. The v-B site exhibited the highest species richness (mean OTU number 2256.67 ± 22.50) and relatively high ACE and Chao1 indices (2372.10 ± 28.75 and 2393.18 ± 36.91 , respectively). In contrast, the i-C site

had the lowest species richness. Shannon and Simpson indices: among intertidal flat samples, the i-D site showed the highest values (9.74 ± 0.02 and 0.997 ± 0.01 , respectively); among vegetated zone samples, the v-B site showed the highest values. These results indicate that the bacterial communities at the i-E and v-B sites exhibited relatively high diversity and evenness.

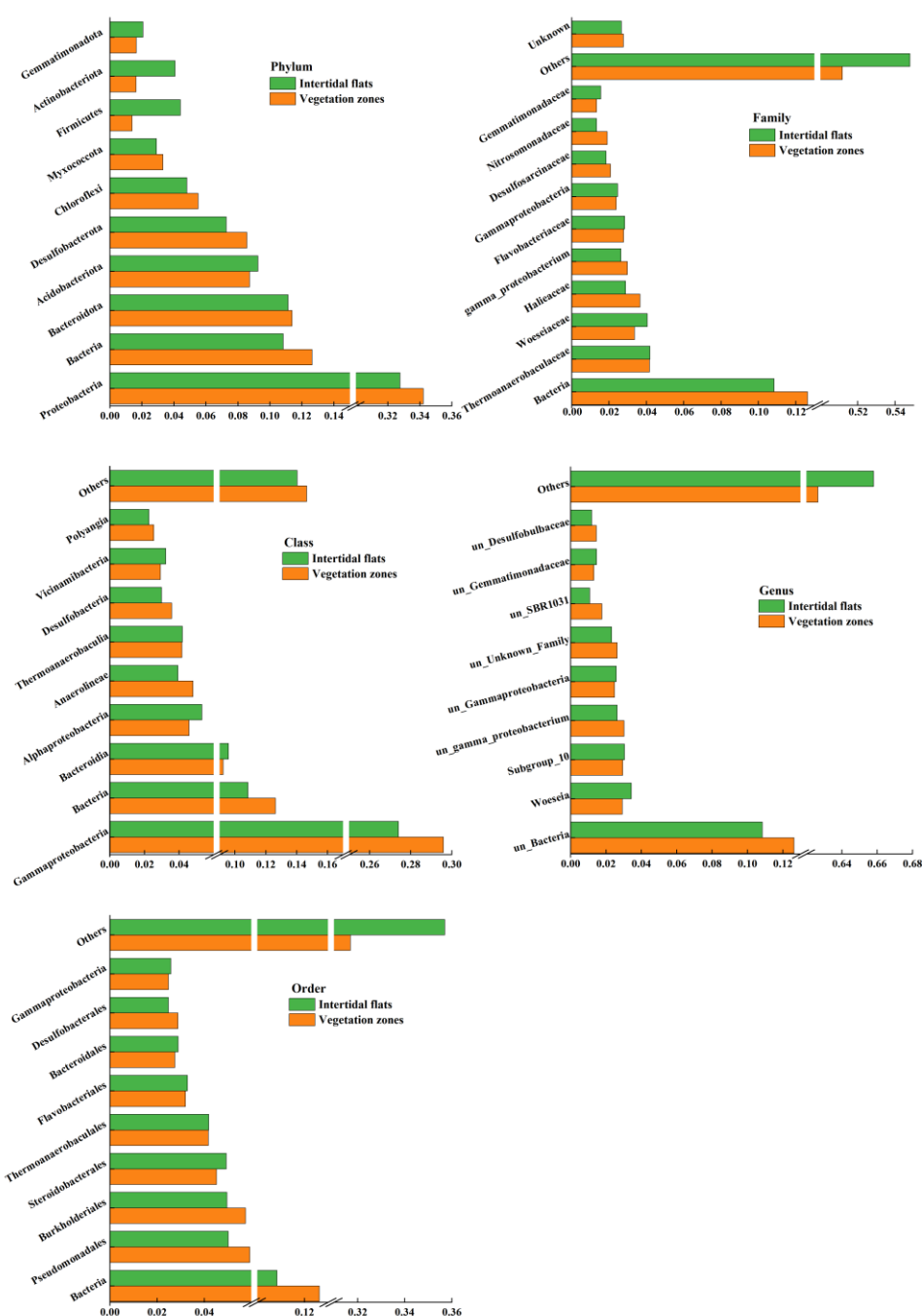


Figure 3. Distribution of the predominant bacteria at different taxonomic levels (phylum, class, order, family, and genus). The predominant taxa (1% relative abundance and ranked among the top 10) in each level are shown.

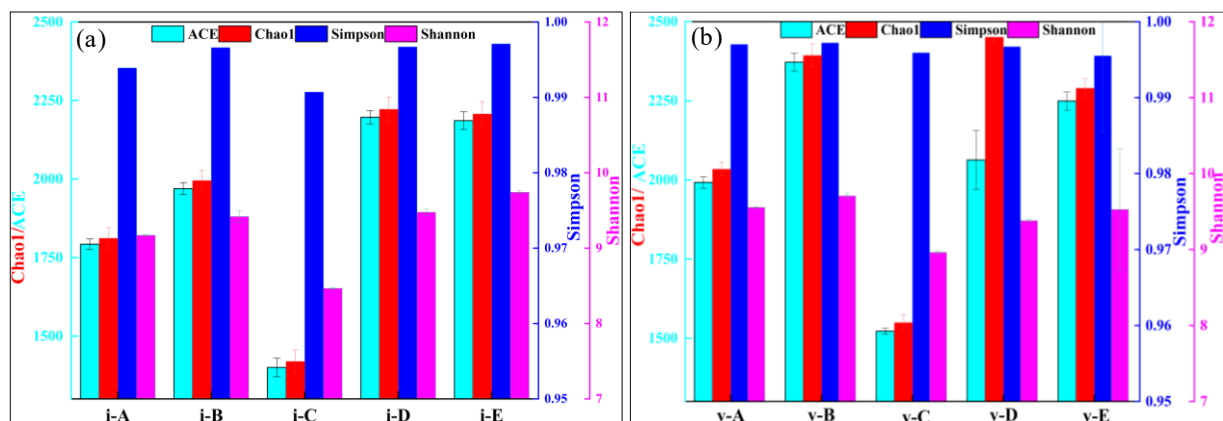


Figure 4. Indices of bacterial diversity and richness of mangrove sediments from each sampling site in (a) the vegetated zones and (b) the intertidal flats.

3.3. Changes in Community Structure and Species Composition of Mangrove Sediments

PCoA (Figure 5a,c) illustrated that PC1 and PC2 explained 67.15% and 70.67% of the total community variation in bare intertidal flats and vegetation zones, respectively, sufficiently capturing the spatial differentiation of sediment bacterial communities. PERMANOVA confirmed highly significant inter-site community differences within both habitats ($p = 0.001$). Samples from bare intertidal flats were more scattered, with clear separation between sites A and D; in contrast, sites E and C clustered tightly in vegetated zones, demonstrating that vegetation mitigates the spatial heterogeneity of bacterial assemblages. *Proteobacteria* dominated both habitats (37–45% relative abundance), followed by *Bacteroidota* and *Acidobacteriota*. Functional phyla, including *Desulfobacterota* and *Nitrospirota*, exhibited distinct abundance patterns across the two habitat types (Figure 5b,d). UPGMA dendrograms (Figure 5b,d) showed that sites B and E in bare flats had a Bray–Curtis dissimilarity of only 0.2–0.3, while sites C and D displayed dissimilarity close to 0.6. In vegetation zones, samples from E and C converged at high similarity, presenting weaker overall community divergence relative to bare flats. Collectively, horizontal spatial gradients structured sediment bacterial β -diversity, and vegetation reshaped community dispersion and taxonomic composition by altering sediment microenvironments.

Beta-diversity distance matrices (Figure 6a,b) revealed high similarity within the i-C series and between the i-A/i-D series in intertidal flats, while i-E/i-B showed pronounced differentiation. In vegetated zones, the v-C and v-E series showed strong compositional similarity, whereas the v-D and v-A series displayed marked differences. NMDS ordination (Figure 6c, stress= 0.0345) and PERMANOVA ($R^2 = 0.043$) indicated that habitat type explained a modest but significant proportion of variation. β -NTI boxplots (Figure 6d) showed deterministic processes only in the N-T group (β -NTI > 2.5); most other groups fell within −2 to 2, indicating stochastic assembly, with high dispersion in v-C and lower dispersion in i-A.

Functional prediction using PICRUSt2 and KEGG showed that primary metabolic pathways were highly stable across all sites (Figure 7), with Metabolism accounting for 80–85% of sequences, followed by Genetic Information Processing (~5–8%) and Environmental Information Processing (~4–6%). Only minor site-specific fluctuations were detected within the dominant Metabolism category, underscoring the functional stability of mangrove sediment bacterial communities despite spatial variation in composition and assembly processes.

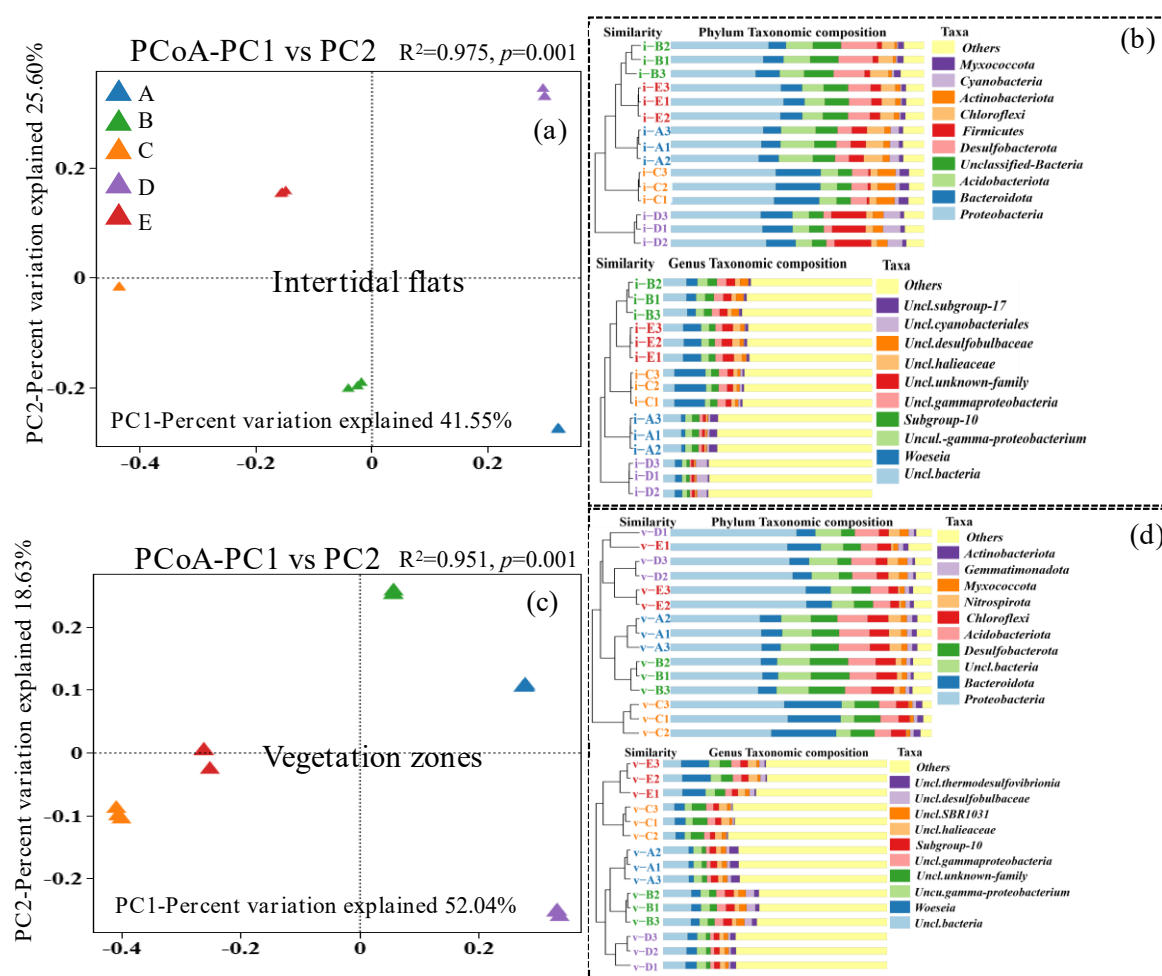


Figure 5. Beta diversity patterns of sediment bacterial communities along horizontal gradients in intertidal flats and vegetation zones. Notes: Principal coordinate analysis (PCoA, panels (a,c)) was conducted using Bray–Curtis dissimilarity at the OTU level to reveal community differentiation among samples, with PERMANOVA (R^2) and p values displayed for each habitat. Panels (b,d) show integrated UPGMA hierarchical clustering trees and taxonomic composition barplots at the phylum and genus levels, illustrating inter-sample community dissimilarity. Numbers 1, 2, and 3 correspond to three biological replicates per location; letters A-E represent the five independent sampling sites, where (a,b) refer to bare intertidal flats, and (c,d) refer to vegetated zones.

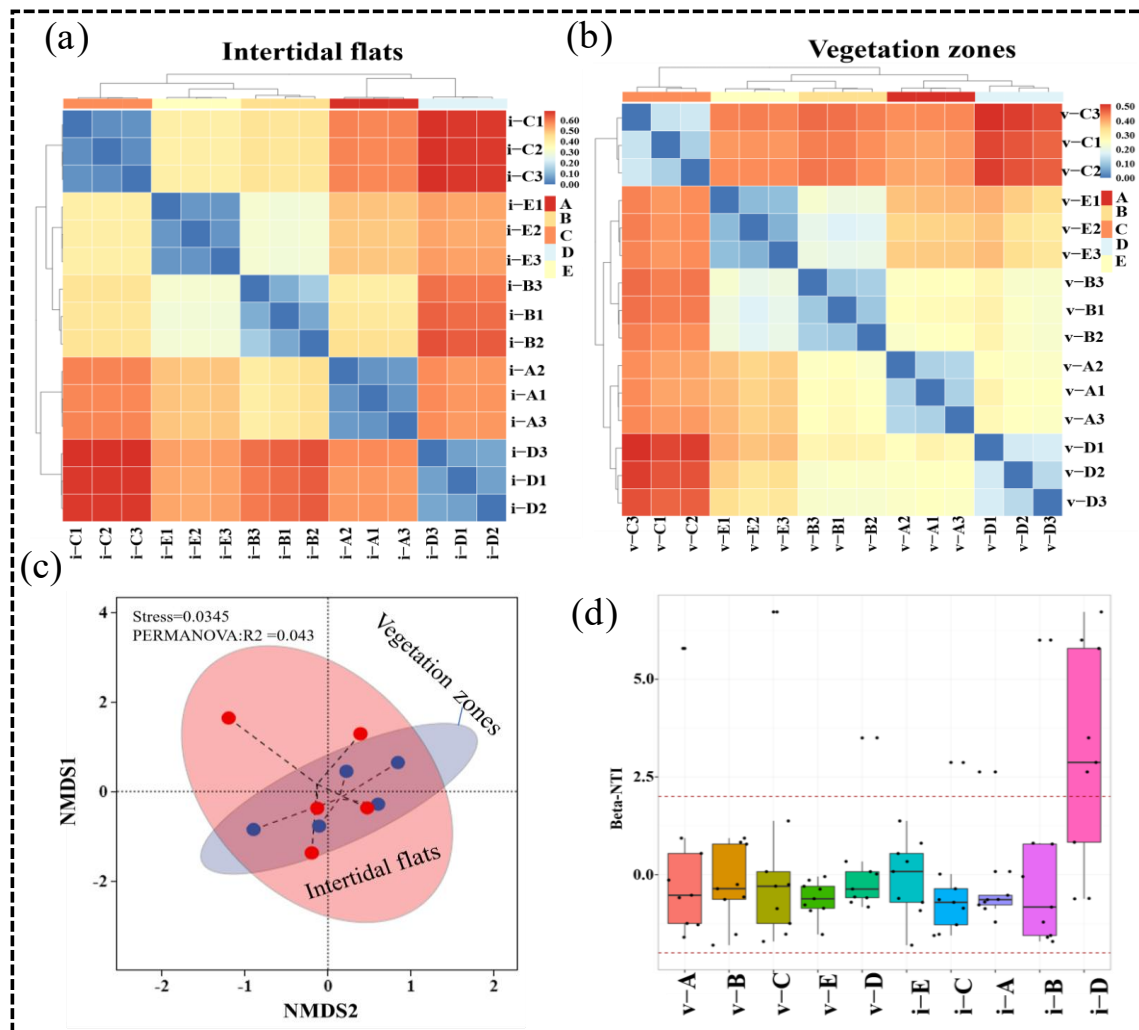


Figure 6. Heatmap showing distances between sediment bacterial samples in (a) intertidal flats, (b) the vegetated zones, and a biplot showing the NMDS of vegetated and intertidal flats, and a boxplot showing the distributions of Beta-NTI for community structure. (c) NMDS ordination separating samples from vegetation zones and intertidal flats; Stress = 0.0345 denotes good ordination fit, and PERMANOVA shows habitat accounts for 4.3% of community variation. Ellipses denote 95% confidence intervals for the two habitat groups. (d) Boxplot of Beta-NTI values for vegetation zone (v-) and intertidal flat (i-) subgroups. Red dashed lines at -2 and 2 are standard thresholds to differentiate deterministic and stochastic assembly processes of bacterial communities.

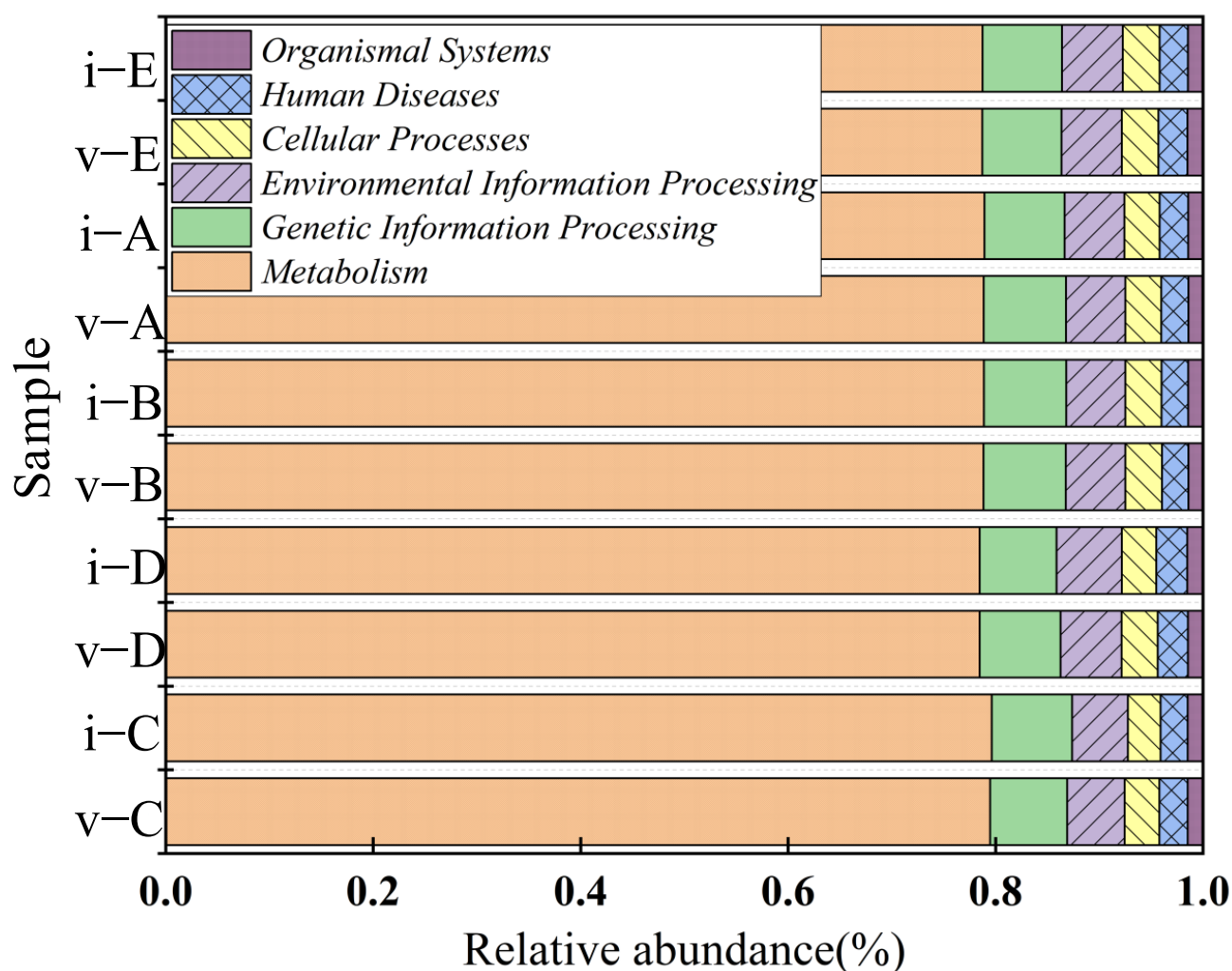


Figure 7. Relative abundance distribution of KEGG functional pathways across different sampling sites.

3.4. Correlation Analysis Between Sediment Physicochemical Properties and Bacterial Community Structure

RDA was performed using Canoco 5 to examine the relationships between sediment physicochemical properties and bacterial community structure (Figure 8). The RDA explained 45.89% and 63.59% of the total variation in bacterial community composition at the phylum (Figure 8a) and class levels (Figure 8b), respectively. This indicated a strong association between environmental variables and bacterial assemblages. At the phylum level, analysis of the top 10 most abundant phyla revealed that *Proteobacteria* and *Myxococcota* were positively correlated with BSi, Sal, and NO_2^- . The sampling site v-E exhibited a distribution pattern closely aligned with *Proteobacteria*. In contrast, i-E showed a strong positive association with TN, indicating that TN is a key environmental driver shaping the bacterial community structure at this site. Sampling sites i-C, v-C, and i-N displayed significant negative correlations with TP, DIP, and K. Additionally, i-B showed a positive correlation with K and was closely associated with *Nitrospirota*, suggesting a potential link between potassium availability and nitrification-related bacterial groups.

At the family level, analysis of the seven most abundant families revealed distinct correlation patterns. *Flavobacteriaceae* exhibited a significant negative correlation with *Nitrosomonadaceae*, indicating potential niche differentiation or competitive interactions between heterotrophic and ammonia-oxidizing bacteria. *Haleaceae* at the i-FB site showed a

strong positive correlation with Sal, highlighting Sal as a key environmental factor influencing the bacterial community structure at this location. The sites v-B, i-B, and v-D were positively correlated with pH and DIP, suggesting that variations in sediment acidity and phosphorus availability play important roles in shaping bacterial communities at these sites. In contrast, bacterial community structures at i-A and v-A showed weak correlations with the measured environmental factors, implying that additional unmeasured variables or stochastic processes may contribute to community assembly in these areas. Notably, *Woeseiaceae* exhibited a positive correlation with BSi, suggesting that this bacterial group may be closely associated with diatom-derived silica dynamics and could play an important role in biogenic silica cycling within mangrove sediment ecosystems.

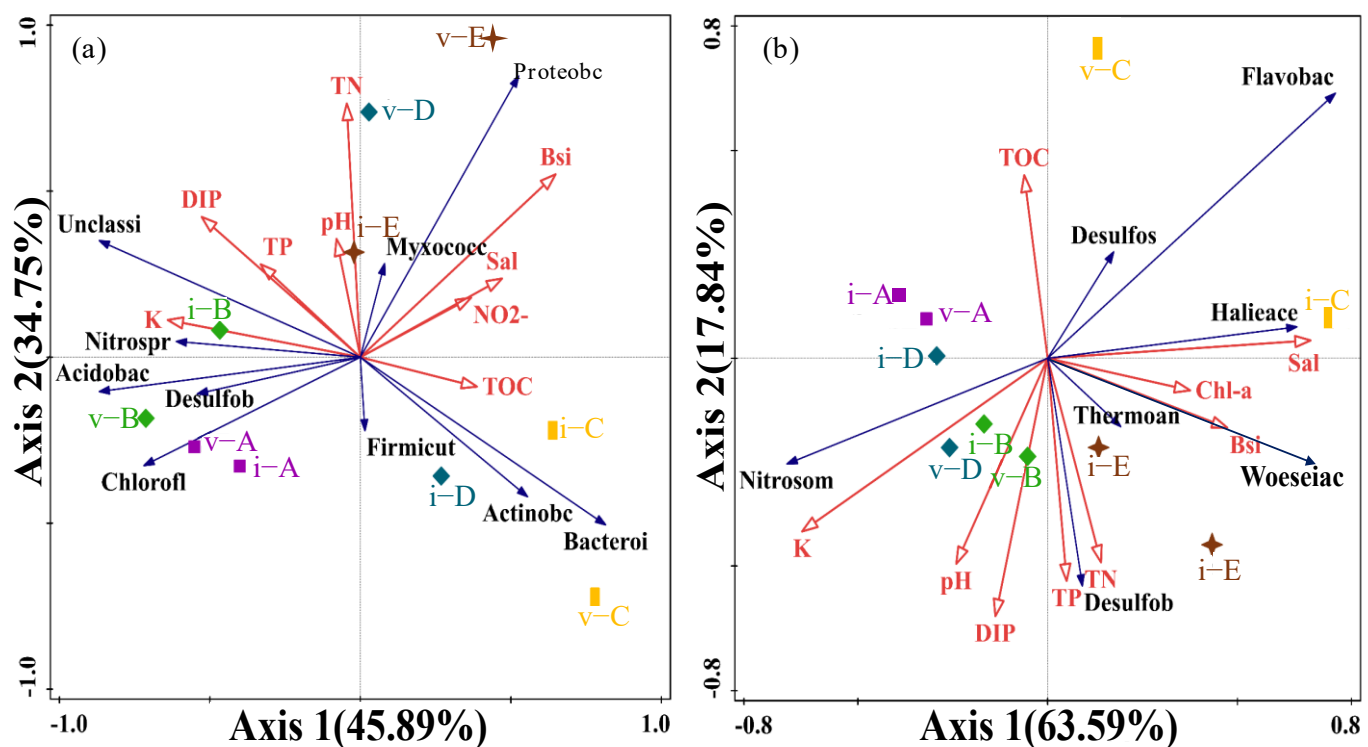


Figure 8. Redundancy analysis (RDA) showing for the relationships between bacterial community composition and various environmental parameters at the phylum (a) and family (b) levels in the mangrove sediments from Northern Beibu Gulf. Shapes of different colors represent sampling sites, red arrows indicate environmental factors, and black arrows denote bacterial names. Notes: Shapes of different colors represent sampling sites, red arrows indicate environmental factors, and black arrows denote bacterial names. In the phylum classification, “Unclassi” represents *unclassified Bacteria*, “Nitrospr” represents *Nitrospirota*, “Acidobac” represents *Acidobacteriota*, “Desulfob” represents *Desulfobacterota*, “Chlorofl” represents *Chloroflexi*, “Firmicut” represents *Firmicutes*, “Actinobc” represents *Actinobacteriota*, “Bacteroi” represents *Bacteroidota*, “Proteobc” represents *Proteobacteria*, “Myxococc” represents *Myxococcota*. In the family classification, “Nitrosom” represents *Nitrosomonadaceae*, “Desulfob” represents *Desulfobulbaceae*, “Flavobac” represents *Flavobacteriaceae*, “Woeseiac” represents *Woeseiaceae*, “Halieace” represents *Haliaceae*, “Thermoan” represents *Thermoanaerobaculaceae*, “Desulfos” represents *Desulfosarcinaceae*.

4. Discussion

4.1. Characteristics of Bacterial Communities in Mangrove Sediments

Numerous studies have shown that bacterial community structure differs significantly across geographically distinct mangrove habitats [23]. At both the phylum and genus levels, the composition of sediment bacterial communities changes in response to variations in mangrove habitat characteristics. Investigations conducted in China, India, and Brazil have consistently identified *Proteobacteria* as the dominant bacterial phylum in mangrove sediments [19,24]. A finding corroborated by the present study, in which *Proteobacteria* was also the most abundant phylum in mangrove sediments of the Northern Beibu Gulf. *Proteobacteria* comprises four major classes, *Alphaproteobacteria*, *Betaproteobacteria*, *Deltaproteobacteria*, and *Gammaproteobacteria* [25]. Among these, *Gammaproteobacteria* and *Alphaproteobacteria* showed relatively high abundances across all sampled mangrove sediments in the Northern Beibu Gulf. With *Gammaproteobacteria* accounting for approximately 40% of the bacterial community in both the vegetated and intertidal flats. Previous studies have shown that *Gammaproteobacteria* and *Alphaproteobacteria* play key roles in carbon, nitrogen, and sulfur cycling in mangrove sediments [26].

Studies of planktonic bacterial communities in marine environments have reported that *Alphaproteobacteria* generally prefer high Sal conditions, a pattern also observed in desert sediment ecosystems [27]. In agreement with these observations, relatively high abundances of *Alphaproteobacteria* were detected at sites i-E and v-C, which exhibited higher Sal levels. However, an exception was observed at i-D, where the abundance of *Alphaproteobacteria* remained high despite comparatively low Sal. This finding suggests that *Alphaproteobacteria* may possess broader Sal tolerance or adaptive flexibility under varying environmental conditions [28]. *Bacteroidia* also constituted a notable proportion of the bacterial communities across the sampling sites, highlighting its important ecological role in mangrove sediments. Members of this class are known to participate in nitrogen and phosphorus metabolism, protein degradation, cellulose decomposition, and the enhancement of plant stress resistance [29]. Overall, the bacterial communities in mangrove sediments exhibited clear differences between intertidal flats and vegetated zones, with distinct community composition patterns across geographical locations. This study further demonstrates significant habitat differentiation of bacterial communities within mangrove ecosystems ($p < 0.05$), manifesting primarily in two ways: (1) Sal fluctuations driven by tidal gradients strongly influence the distribution of dominant bacterial taxa; and (2) variations in vegetation type lead to the selective enrichment of characteristic bacterial groups. Collectively, these findings suggest the strong habitat-filtering effects governing mangrove bacterial community assembly and highlight the close ecological coupling between functional gene expression and local environmental conditions.

Existing studies indicate that within uniform mangrove tidal flats, microscale spatial variation of sediment bacterial communities is low, as tidal flushing homogenizes local sediment physicochemical conditions [30,31]. Clear spatial differentiation of bacterial populations mainly occurs among separate sampling sites, driven by differences in vegetation and hydrological regimes [1]. In this study, we collected three replicate sediment samples at each of the five sampling sites, covering both vegetated and intertidal flats. Owing to constraints imposed by tidal cycles and limited wetland access, we were unable to achieve higher sampling intensity in the field. We acknowledge this relatively low sampling intensity as a limitation of the study and recommend that future investigations increase sampling density to better resolve fine-scale spatial patterns of sediment bacterial populations.

4.2. Dominant Bacterial Community and Their Distribution Differences in Mangrove Sediments

The results demonstrated that *Proteobacteria* were the dominant bacterial phylum in sediments across both intertidal flats and vegetated zones, maintaining a consistently high abundance across all sampling sites. This finding aligns with previous studies conducted in mangrove sediments across various geographic regions worldwide [32,33], which suggest that *Proteobacteria* possess broad ecological adaptability and perform critical functional roles within mangrove ecosystems. Consequently, *Proteobacteria* are recognized as one of the most prevalent bacterial phyla in global sedimentary environments [34]. *Campylobacterota* is commonly associated with seawater-groundwater mixing and plays important roles in sulfur and nitrogen cycling [35]. *Bacteroidota* contributes substantially to host-microbe interactions and global nutrient cycling [36].

The bacterial community distribution exhibited significant geographical heterogeneity among regions. Within the intertidal flats, the Beihai Nanliu River site showed the highest OTU richness, whereas the Fangchenggang East Bay site exhibited the lowest. In vegetated areas, the Fangchenggang Sanjiaojing site displayed the greatest OTU richness, while the Fangchenggang East Bay site again showed the least. These distribution patterns are likely driven by site-specific environmental conditions, geographic settings, and varying degrees of anthropogenic disturbances. In addition, substantial differences in bacterial community structure were observed between the intertidal and vegetated zones within individual sampling sites [6,37]. Intertidal flats showed stronger site-specific community differentiation with wider sample dispersion, while vegetation zones weakened spatial divergence of bacterial assemblages. Though *Proteobacteria* dominated both habitats, functional taxa diverged sharply: *Desulfobacterota* prevailed in bare sediments, whereas *Nitrospirota* were enriched in vegetated zones, indicating that vegetation reshapes sediment bacterial assemblages by altering microenvironmental filtering. Vegetated zones consistently exhibited higher bacterial abundance and diversity than intertidal flats, which may be attributed to vegetation-mediated improvement of sediment conditions and the provision of additional microbial niches.

A considerable proportion of sequences in this study remained unclassified at lower taxonomic levels, representing a large amount of microbial dark matter in mangrove sediments [38]. These poorly characterized yet abundant taxa may possess unique metabolic capabilities and ecological strategies that facilitate their adaptation to the complex and dynamic intertidal environment [39]. Their widespread distribution indicates they play irreplaceable roles in elemental cycling, stress resistance, and community stability. These functions are essential for the long-term sustainability of mangrove ecosystems. Further investigation into these uncharacterized taxa will help uncover novel microbial resources, as well as evolutionary adaptations and ecological functions within mangrove sediments.

4.3. Variations in Bacterial Communities and Environmental Physicochemical Factors in Mangrove Sediments

RDA analyses indicated that bacterial community assembly driven by niche differentiation influences Sal, pH, BSi, TP, and TN, and its effects differ across sites due to variable environmental filtering [40]. Sal and BSi co-selected for halophilic and silicon-metabolizing taxa (e.g., *Flavobacteriaceae*) in high Sal sites (i-C/v-C), consistent with osmotic stress tolerance and silicon-dependent metabolic pathways [41]. In neutral, nitrogen-rich sites (v-D/i-E), pH and TN promoted nitrifying and myxobacterial groups (e.g., *Proteobacteria*, *Myxococcaceae*), likely via enhanced nitrogen mineralization and optimal enzymatic activity [42]. Conversely, acidic, phosphorus-enriched sites (v-B/v-A/i-A) were dominated by sulfate-reducing and acidophilic bacteria (e.g., *Desulfobulbaceae*, *Acidobacteriaceae*), driven by TP availability and low pH constraints on nutrient solubility. These context-

dependent effects arise from nutrient co-limitation (e.g., N-limitation in v-D vs. P-limitation in v-E) and interactive abiotic pressures, highlighting how environmental gradients shape bacterial community composition across coastal ecosystems. *Proteobacteria* prevailed at site v-E, demonstrating that the environmental features of this sampling site are highly conducive to the growth of *Proteobacteria*.

Proteobacteria was identified as the dominant phylum across multiple regions, including Dongzhaigang (Hainan), Lianjiang, Yunxiao Nature Reserve, the Beibu Gulf, and Bhitarakanika (India) (Table 3), accounting for 46.6–68.9% of the bacterial community. This consistent dominance likely reflects the phylum's high metabolic versatility, enabling adaptation to dynamic intertidal environments. However, the distribution of its metabolic functional genes was strongly influenced by sediment texture (sandy versus muddy), indicating that local geochemical conditions modulate phylum-level functional potential [43]. The regulatory effects of physicochemical factors on bacterial communities varied among regions. For example, in the Gaoqiao mangrove (Lianjiang), TOC and TN showed significant correlations with microbial composition in the mid-tide zone, whereas nitrogen and phosphorus nutrients dominated in the high-tide zone. In the Northern Beibu Gulf, sediment texture indirectly regulated the abundance of carbon-, nitrogen-, and sulfur-metabolism genes by modifying pore structure and redox conditions [7]. In Dongzhaigang, bacterial community composition was mainly controlled by Sal and TOC. These regional differences underscore that environmental drivers must be interpreted within specific hydrological and geographical contexts (e.g., tidal frequency, sediment permeability), rather than assumed to have universal applicability.

At the genus level, notable differences in community composition were observed. In the intertidal flats, *Woeseia* was the dominant genus at site C, while sites B and E exhibited similar genus compositions and relative abundances. In the vegetated zones, *Woeseia* dominated at site E, whereas unclassified Bacteria predominated at site B. The similarity in genus composition among sites C, A, and D suggests that local hydrodynamics may homogenize communities within hydrologically connected zones. The prevalence of *Woeseia*, a chemoheterotrophic genus commonly associated with sulfur cycling, across multiple sites reflects its ecological flexibility and potential role in maintaining biogeochemical functions under fluctuating redox conditions.

Our findings offer practical guidance for mangrove management in the Beibu Gulf. First, the significant variation in bacterial OTU richness across mangrove species (*Bruguiera gymnorhiza* > *Aegiceras corniculatum* > *Avicennia marina*) suggests that restoration projects should adopt species-specific planting strategies: prioritize *Bruguiera gymnorhiza* in zones where enhancing microbial diversity is a goal, while *Avicennia marina* is more suitable for high Sal pioneer zones given its strongly halotolerant rhizosphere communities. Second, the highly consistent metabolic profiles (80–85% metabolism pathways) across all sites indicate high functional redundancy, suggesting that Beibu Gulf mangroves possess inherent resilience to environmental fluctuations. Conservation efforts should focus on maintaining this functional stability by preserving hydrological connectivity and sediment-nutrient regimes. Third, the strong phosphorus-sulfur coupling implies that nutrient input monitoring is critical: elevated TP from aquaculture could stimulate sulfide production, posing risks to mangrove health. It is recommended that buffer zones be established and fertilizer use be regulated in adjacent watersheds. Future research should integrate multi-scale environmental data with machine-learning approaches to predict bacterial community responses under climate change scenarios, which would provide scientific support for carbon sink management in mangrove conservation and restoration.

Table 3. Comparative analysis of mangrove microorganisms, environmental factors, and other research regions.

Study Areas	Dominant Bacterial Species (Phylum Level)	Environment Factors	References
Dongzhai Gang Mangrove Forests, China	<i>Proteobacteria</i>	Sal, TOC, pH, and SO_4^{2-}	[25]
Lianjiang Gaoqiao Mangrove Forests, China	<i>Proteobacteria</i>	Sal, pH, DOC, and TN	[44]
Yunxiao National Mangrove Nature Reserve, China	<i>Proteobacteria</i>	C, S, N	[45]
Bhitarkanika mangrove, India	<i>Proteobacteria</i>	pH, EC, DO	[15]
This study was conducted in China	<i>Proteobacteria</i>	Sal, pH, BSi, TP, TN	

5. Conclusions

This study investigated bacterial communities in mangrove sediments from intertidal and vegetated zones across five locations in the Northern Beibu Gulf. The biogeographical distribution patterns of sediment bacterial communities and their relationships with key environmental drivers were systematically elucidated. The main conclusions are as follows:

- (1) Mangrove sediments in the northern Beibu Gulf harbor highly diverse bacterial communities, with *Proteobacteria* as the dominant phylum, accounting for 37–45% of the total community across sampling sites. Marked geographical variations in bacterial community composition were observed among the study regions. Functional prediction revealed that metabolism-related functions comprised 80–85% of the total relative abundance, with the composition of functional categories remaining highly consistent across all sampling sites.
- (2) Both environmental conditions and geographical settings jointly influence bacterial community distribution and diversity. Distinct differences were detected between the intertidal and vegetated zones within the same site. Overall, the vegetated zone exhibited slightly higher bacterial abundance and diversity, likely due to vegetation-induced improvements in sediment physicochemical conditions and the creation of additional ecological niches.
- (3) Bacterial community structure significantly affects multiple physicochemical factors, including Sal, pH, BSi, TP, and TN. Through alterations in metabolic activity and interspecific interactions, bacteria regulate the environment and indirectly modify these physicochemical properties.

Overall, this study elucidates the biogeographical patterns and environmental drivers of bacterial communities in mangrove sediments of the Northern Beibu Gulf, offering valuable insights into the functional stability and resilience of these ecosystems. Future research should integrate metagenomic and metabolomic approaches to further decipher the functional plasticity of key bacterial taxa and to better evaluate the impacts of anthropogenic activities on mangrove ecosystems. Such efforts will establish a more robust theoretical foundation for microbial regulation and ecological restoration in mangrove conservation programs.

Author Contributions: J.Z. designed the research plan. P.H. conducted validation and field investigation. Z.D. contributed to methodology, conceptualization, and manuscript review and editing. D.L. took part in conceptualization, manuscript review and editing, and project administration. B.Y. completed data visualization. W.S., Z.W., and S.F.D. analyzed the data. H.H. performed manuscript review and editing, supervision, and funding acquisition. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by grants from the Guangxi Natural Science Foundation (No. 2025GXNSFHA069202, 2025GXNSFDA02850005, and GuikeLT2504240009), Natural Science Foundation of China (No. 42166002, 42576261), the Natural Science Foundation of China Shiptime Sharing Project (No. 42349911) for supporting the Beibu Gulf cruise (No. NORC2024-11).

Data Availability Statement: The authors declare that all the data obtained in this work are available in the main text of this article and from the corresponding authors upon request. All raw sequence datasets of 16S rRNA genes from this study have been deposited into the NCBI Sequence Read Archive (SRA) database with accession no. SUB15471118.

Acknowledgments: We thank all colleagues who participated in the sampling, analysis, and testing for their great support for this work.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Behera, P.; Mohapatra, M.; Kim, J.Y.; Adhya, T.K.; Pattnaik, A.K.; Rastogi, G. Spatial and temporal heterogeneity in the structure and function of sediment bacterial communities of a tropical mangrove forest. *Environ. Sci. Pollut. Res. Int.* **2019**, *26*, 3893–3908.
2. Murdiyarso, D.; Purbopuspito, J.; Kauffman, J.B.; Warren, M.W.; Sasmito, S.D.; Donato, D.C.; Manuri, S.; Krisnawati, H.; Taberima, S.; Kurnianto, S. The potential of Indonesian mangrove forests for global climate change mitigation. *Nat. Clim. Change* **2015**, *5*, 1089–1092.
3. Palit, K.; Rath, S.; Chatterjee, S.; Das, S. Microbial diversity and ecological interactions of microorganisms in the mangrove ecosystem: Threats, vulnerability, and adaptations. *Environ. Sci. Pollut. Res. Int.* **2022**, *29*, 32467–32512.
4. Meng, S.; Peng, T.; Liu, X.; Wang, H.; Hu, T.; Gu, J.; Hu, Z. Ecological role of bacteria involved in the biogeochemical cycles of mangroves based on functional genes detected through GeoChip 5.0. *mSphere* **2022**, *7*, e00936-21.
5. Wang, S.; Zhao, Z.; Cheng, R.; Cui, L.; Wang, J.; Rubin-Blum, M.; Zhang, Y.; Liu, B.; Chen, X.; Baltar, F. Phylogenetically and metabolically diverse active carbon-fixing microbes reside in mangrove sediments. *Microbiome* **2025**, *13*, 194.
6. Chen, Q.; Zhao, Q.; Li, J.; Jian, S.; Ren, H. Mangrove succession enriches the sediment microbial community in South China. *Sci. Rep.* **2016**, *6*, 27468.
7. Liu, Y.; Chen, S.; Liang, J.; Song, J.; Sun, Y.; Liao, R.; Liang, M.; Cao, H.; Chen, X.; Wu, Y. Bacterial Community Structure and Environmental Driving Factors in the Surface Sediments of Six Mangrove Sites from Guangxi, China. *Microorganisms* **2024**, *12*, 2607.
8. Gao, C.; Wang, Y.; Li, S.; Lin, X. Salinity-driven shifts in potential ammonia oxidation rates and microbial community dynamics in estuarine mangrove sediments. *Mar. Pollut. Bull.* **2026**, *222*, 118936.
9. Soto-Varela, Z.E.; Orozco-Sánchez, C.J.; Bolívar-Anillo, H.J.; Martínez, J.M.; Rodríguez, N.; Consuegra-Padilla, N.; Robledo-Meza, A.; Amils, R. Halotolerant Endophytic Bacteria *Priestia flexa* 7BS3110 with Hg²⁺ Tolerance Isolated from *Avicennia germinans* in a Caribbean Mangrove from Colombia. *Microorganisms* **2024**, *12*, 1857.
10. Vieira, S.; Adão, H.; Vicente, C.S. Assessing spatial and temporal patterns of benthic bacterial communities in response to different sediment conditions. *Mar. Environ. Res.* **2025**, *204*, 106963.
11. Lee, H.; Heo, Y.M.; Kwon, S.L.; Yoo, Y.; Kim, D.; Lee, J.; Kwon, B.-O.; Khim, J.S.; Kim, J.-J. Environmental drivers affecting the bacterial community of intertidal sediments in the Yellow Sea. *Sci. Total Environ.* **2021**, *755*, 142726.
12. Cadamuro, R.D.; Bastos, I.M.A.D.S.; De Freitas, A.C.O.; Rosa, M.D.S.; Costa, G.D.O.; Da Silva, I.T.; Robl, D.; Stoco, P.H.; Sandjo, L.P.; Treichel, H. Bioactivity screening and chemical characterization of biocompound from endophytic *Neofusicoccum parvum* and *Buergenerula spartinae* isolated from mangrove ecosystem. *Microorganisms* **2023**, *11*, 1599.

13. Alzubaidy, H.; Essack, M.; Malas, T.B.; Bokhari, A.; Motwalli, O.; Kamanu, F.K.; Jamhor, S.A.; Mokhtar, N.A.; Antunes, A.; Simões, M.F. Rhizosphere microbiome metagenomics of gray mangroves (*Avicennia marina*) in the Red Sea. *Gene* **2016**, *576*, 626–636.
14. Hussain, N.; Rahman, M.A.; Karim, M.R.; Rana, P.; Islam, M.N.; Muzirafuti, A. High-Resolution Satellite-Driven Estimation of Photosynthetic Carbon Sequestration in the Sundarbans Mangrove Forest, Bangladesh. *Remote Sens.* **2026**, *18*, 401.
15. Palit, K.; Das, S. Community structure, taxonomic diversity and spatio-temporal variation of sediment and water bacteria in Bhitarkanika mangrove ecosystem, India. *Int. J. Environ. Sci. Technol.* **2021**, *18*, 1147–1166.
16. Muwawa, E.M.; Obieze, C.C.; Makonde, H.M.; Jefwa, J.M.; Kahindi, J.H.P.; Khasa, D.P. 16S rRNA gene amplicon-based meta-genomic analysis of bacterial communities in the rhizospheres of selected mangrove species from Mida Creek and Gazi Bay, Kenya. *PLoS ONE* **2021**, *16*, e0248485.
17. Zeng, Z.; Liu, J.; Zhao, X.; Chen, Z.; Chen, Y.; Chen, B.; Shi, M.; He, W. A Circulation Study Based on the 2022 Sino–Vietnamese Joint Survey Data from the Beibu Gulf. *Water* **2024**, *16*, 2943.
18. Xu, C.; Huang, Y.; Yang, B.; Jia, R.; Ning, Z.; Yang, B.; Xie, L.; Yang, L.; Lu, D.; Kang, Z.; et al. Molecular-weight-dependent mixing behavior of organic phosphorus and carbon in a subtropic river-estuary-bay continuum. *Water Res.* **2026**, *296*, 125650.
19. Yao, J.; Zhao, H.; Ye, W.; Ye, Y.; Lin, G. Spatial patterns of total and methane-cycling microbial communities in surface sediments of the eastern Guangdong coast in summer. *Mar. Environ. Res.* **2025**, *211*, 107365.
20. Li, L.; Peng, C.; Yang, Z.; He, Y.; Liang, M.; Cao, H.; Qiu, Q.; Song, J.; Su, Y.; Gong, B. Microbial communities in swamps of four mangrove reserves driven by interactions between physicochemical properties and microbe in the North Beibu Gulf, China. *Environ. Sci. Pollut. Res. Int.* **2022**, *29*, 37582–37597.
21. Sohail, M.I.; Rehman, M.Z.U.; Murtaza, G.; Wahid, M.A. Chemical investigations of Si-rich organic and inorganic amendments and correlation analysis between different chemical composition and Si contents in amendments. *Arab. J. Geosci.* **2019**, *12*, 47.
22. Tanaka, K.; Watanabe, N. Size distribution of alkali elements in riverbed sediment and its relevance to fractionation of alkali elements during chemical weathering. *Chem. Geol.* **2015**, *411*, 12–18.
23. Liu, M.; Huang, H.; Bao, S.; Tong, Y. Microbial community structure of soils in Bamenwan mangrove wetland. *Sci. Rep.* **2019**, *9*, 8406.
24. Nathan, V.K.; Vijayan, J.; Ammini, P. Comparison of bacterial diversity from two mangrove ecosystems from India through metagenomic sequencing. *Reg. Stud. Mar. Sci.* **2020**, *35*, 101184.
25. Zhang, P.; Xie, X.J.; Li, Q.H.; Gan, Z.Y.; Hu, T.; Yang, J.; Deng, Y.M.; Gan, Y.Q.; Zhang, Y.P. Structural Characteristics of Microbial Community in Dongzhai Harbor Mangrove Sediments and Their Response to Environmental Factors. *Earth Sci.* **2022**, *47*, 1122–1135. (In Chinese with English abstract)
26. Andreote, F.D.; Jiménez, D.J.; Chaves, D.; Dias, A.C.F.; Luvizotto, D.M.; Dini-Andreote, F.; Fasanella, C.C.; Lopez, M.V.; Baena, S.; Taketani, R.G. The microbiome of Brazilian mangrove sediments as revealed by metagenomics. *PLoS ONE* **2012**, *7*, e38600.
27. Zhao, S.; Liu, J.-J.; Banerjee, S.; Zhou, N.; Zhao, Z.-Y.; Zhang, K.; Tian, C.-Y. Soil pH is equally important as salinity in shaping bacterial communities in saline soils under halophytic vegetation. *Sci. Rep.* **2018**, *8*, 4550.
28. Bai, Y.; Ren, P.; Feng, P.; Yan, H.; Li, W. Shift in rhizospheric and endophytic bacterial communities of tomato caused by salinity and grafting. *Sci. Total Environ.* **2020**, *734*, 139388.
29. Yang, P.; Zhai, P.; Zhao, X.; Wang, S.M.; Liu, H.L.; Zhang, X. Effects of Arbuscular Mycorrhizal Fungi and Rhizobium Interaction on the Bacterial Community Structure in the Rhizosphere sediments of *Medicago sativa* and PICRUSt Functional Prediction Analysis. *Microbiol. Bull.* **2020**, *47*, 3868–3879. (In Chinese with English abstract)
30. De Santana, C.O.; Spealman, P.; Melo, V.M.M.; Gresham, D.; De Jesus, T.B.; Chinalia, F.A. Effects of tidal influence on the structure and function of prokaryotic communities in the sediments of a pristine Brazilian mangrove. *Biogeosciences* **2021**, *18*, 2259–2273.
31. Gijssman, R.; Horstman, E.M.; Swales, A.; Macdonald, L.T.; Bouma, T.J.; Wal, D.V.D.; Wijnberg, K.M. Mangrove forest drag and bed stabilisation effects on intertidal flat morphology. *Earth Surf. Proc. Land.* **2024**, *49*, 1117–1134.
32. Wang, F.; Guo, R.; Zhang, N.; Yang, S.; Cao, W. Soil organic carbon storages and bacterial communities along a restored mangrove soil chronosequence in the Jiulong River Estuary: From tidal flats to mangrove afforestation. *Fundam. Res.* **2023**, *3*, 880–889.
33. Jiang, C.; Diao, X.; Wang, H.; Ma, S. Diverse and abundant antibiotic resistance genes in mangrove area and their relationship with bacterial communities—A study in Hainan Island, China. *Environ. Pollut.* **2021**, *276*, 116704.
34. Delgado-Baquerizo, M.; Oliverio, A.M.; Brewer, T.E.; Benavent-González, A.; Eldridge, D.J.; Bardgett, R.D.; Maestre, F.T.; Singh, B.K.; Fierer, N. A global atlas of the dominant bacteria found in soil. *Science* **2018**, *359*, 320–325.

35. Huang, L.; Bae, H.S.; Young, C.; Pain, A.J.; Martin, J.B.; Ogram, A. Campylobacterota dominate the microbial communities in a tropical karst subterranean estuary, with implications for cycling and export of nitrogen to coastal waters. *Environ. Microbiol.* **2021**, *23*, 6749–6763.
36. Pan, X.; Raaijmakers, J.M.; Carrión, V.J. Importance of Bacteroidetes in host–microbe interactions and ecosystem functioning. *Trends Microbiol.* **2023**, *31*, 959–971.
37. Rocha, L.L.; Colares, G.B.; Nogueira, V.L.; Paes, F.A.; Melo, V.M. Distinct habitats select particular bacterial communities in mangrove sediments. *Int. J. Microbiol.* **2016**, *2016*, 3435809.
38. Gawali, R.S.; Ajayakumar, A.; Yadav, U. Investigating the role of microbial dark matter in marine & garden soil health and ecosystem resilience. *Int. J. Innov. Sci. Res. Technol.* **2025**, *10*, 726–731.
39. Jansson, J.K.; Hofmockel, K.S. The soil microbiome—From metagenomics to metaphenomics. *Curr. Opin. Microbiol.* **2018**, *43*, 162–168.
40. Capdeville, C.; Pommier, T.; Gervais, J.; Fromard, F.; Rols, J.-L.; Leflaive, J. Mangrove facies drives resistance and resilience of sediment microbes exposed to anthropic disturbance. *Front. Microbiol.* **2019**, *9*, 3337.
41. Mohamed Zubi, W.S.; Mohd, M.H.; Mohamed Nor, N.M.I.; Zakaria, L. Fusarium species in mangrove soil in northern peninsular Malaysia and the soil physico-chemical properties. *Microorganisms* **2021**, *9*, 497.
42. Wang, W.; Wang, N.; Dang, K.; Dai, Y.; Zhang, L.; Li, J.; Liu, Z.; Chen, H.; Zhou, T.; Yang, F.; et al. Long-term nitrogen application decreases the abundance and copy number of predatory myxobacteria and alters the myxobacterial community structure in the soil. *Sci. Total Environ.* **2020**, *708*, 135114.
43. Zhu, D.; Lin, X.; Liu, S.M. Spatio-temporal variation in the potential ammonia oxidation rates and microbial communities of mangrove wetlands with different sediment textures in South China. *Mar. Pollut. Bull.* **2025**, *220*, 118463.
44. Liang, W.Y.; Wang, X.M.; Liu, Q. Characteristics of Microbial Community Structure and Its Correlation with Nutrient Factors in Mangrove Sediments of Gaoqiao, Lianjiang. *J. Guangdong Ocean Univ.* **2024**, *44*, 80–87. (In Chinese with English abstract).
45. Lin, X.; Hetharua, B.; Lin, L.; Xu, H.; Zheng, T.; He, Z.; Tian, Y. Mangrove sediment microbiome: adaptive microbial assemblages and their routed biogeochemical processes in Yunxiao mangrove national nature reserve, China. *Microb. Ecol.* **2019**, *78*, 57–69.

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.