



Differences in bacterial community composition, structure and function between sediments in waterways and non-navigable channels in a plain river network area

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Abstract

Bacterial communities greatly help maintain the balance of river ecosystems and are highly sensitive to changes in environmental conditions. Plain river network areas (PRNs) are characterized by dense river networks, low-lying terrain, and slow water flow, where the bottom sediment is frequently disturbed by ship navigation due to the limited water depth and width of waterways, providing a unique ecological niche for bacterial growth. Hence, understanding how bacterial communities in PRNs respond to changes in hydrodynamic conditions, physicochemical parameters, and pollutants under ship navigation is essential to maintaining the stability of inland waterway ecosystems. The Taihu Lake Basin, a typical PRN, was selected to explore the differences in bacterial community composition, structure and function between sediments in waterways (WS) and non-navigable channels (NS). The results indicate that the sediment from NS possessed more diverse and complex bacterial communities than WS. NMDS and ANOSIM analyses further verified the significant differences in bacterial community structure between WS and NS. Combined with LEfSe, we observed the highly differential taxonomy between WS and NS from phylum to order. Moreover, a comparison of beta diversity dissimilarity indices revealed that although species replacement dominated both the WS and NS beta-diversity patterns, species loss caused the differences in the overall beta diversity between them. Variance partitioning analysis revealed that physicochemical parameters (clay content, pH, ORP, and others) and ship traffic volume (STV) were the main driving factors for bacterial community distribution between WS and NS, while pollutants (heavy metals, perfluoroalkyl acids, and others) had a relatively minor influence. PICRUSt2 analysis revealed that the changes in pH, ORP, and STV under ship navigation might inhibit the bacterial ability to metabolize carbohydrates. The results reveal the comprehensive effects of ship navigation disturbance on sediment bacterial communities in the PRN and contribute to further understanding of inland waterway ecosystems.

Keywords Bacterial community · Hydrodynamic action · Pollutants · Beta-diversity pattern · Function prediction · Metabolism

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Introduction

Bacteria play a vital role in biogeochemical processes and nutrient cycling (Chen et al. 2022; Wang et al. 2016; Winter et al. 2007) via assimilation and mineralization as a fundamental dynamics of river ecosystems (Paudel Adhikari et al. 2019; Zhang et al. 2020a). As an indispensable carrier and media in river systems, sediment provides diverse habitats for bacterial growth (Behera et al. 2020b). Meanwhile, surface sediment represents one of the most active regions of bacterial activity that can be used to reflect the changes in functional characteristics of river water environments under the influence of external conditions (Tšertova et al. 2013). However, the composition and activity of bacterial

communities are highly sensitive to changes in environmental conditions (Wang et al. 2021b), and as a result, the attributing factor to these changes can be confounded by the diversity and differences in influencing factors (Shade et al. 2012; Steven et al. 2008). Human activity is reported to be one of the crucial factors attributed to changes in river sediment characteristics and composition (Behera et al. 2021b; Su et al. 2018), which would further affect the assembly of bacterial community structure in river ecosystems (Paudel Adhikari et al. 2019; Zhang et al. 2020a). Effects of common human activities such as water conservancy projects and urban river construction on sediment bacterial community diversity and structure have been investigated (Gao et al. 2021; Li et al. 2019b; Zhang et al. 2020b), while the role of inland waterway transport has received little attention.

Inland waterway transport plays a vital role in cargo transportation because of its large capacity, low cost, and low energy consumption. Plain river network areas (PRNs) are characterized by dense river networks, low-lying terrain, and slow water flow, making the inland water transportation industry highly developed (Li and Hua 2021; Ma et al. 2021). However, due to the limited water depth and width of most waterways in PRNs, benthic sediment is frequently disturbed by ship navigation, providing a unique ecological niche for bacterial growth (Behera et al. 2021a). Contrary to rivers without ship navigation, the propeller jets and ship-induced waves in the waterway provide complicated hydrodynamic conditions with axial, radial, and tangential velocities (Donal et al. 2013; Lam et al. 2011, 2013), which directly affect the physical structure and composition of bacteria (Cheng et al. 2019b). Meanwhile, the turbulent flow caused by ship navigation disrupts the equilibrium state of the sediment–water interface, changing the physicochemical parameters of sediment and triggering pollutants released from bottom sediment to overlying water (Cheng et al. 2019a; Xu et al. 2018), and ultimately affecting the environmental conditions for the survival of bacterial communities. Previous studies have shown that the changes in sediment physicochemical parameters can significantly affect the diversity and composition of microbial communities. For example, Rath et al. (2019) observed large bacterial community differences along with the shifts in pH and salinity. Yao et al. (2022) studied the sediment of a eutrophic river and found that phosphorus and pH were the key factors dominating the bacterial community structure. In addition, studies on the effects of pollutants (e.g., toxic metals and organic pollutants) on microbial communities have also been widely reported. Due to the increasingly frequent human activities, multitudinous pollutants have been discharged into rivers and accumulated in sediment through complex effects (Behera et al. 2020a), which inevitably have affected the microbial community in sediment (Rout et al. 2022). Cr (chromium) and Mn (manganese) significantly negatively

affect microbial alpha diversity, and their contributions have been quantified (Li et al. 2020a). Furthermore, organic pollutants, such as perfluoroalkyl acids (PFAAs) and polycyclic aromatic hydrocarbons (PAHs), have exhibited non-negligible impacts on microbial communities due to their unique chemical properties by changing gene expression and microbial activity (Liu et al. 2021b; Qiao et al. 2018; Wu et al. 2021b). However, whether ship navigation in PRNs affects bacterial community structure and the relative contributions of hydrodynamic conditions, physicochemical parameters and pollutants to the process remain unknown.

Identifying bacterial community patterns that may reveal different processes is crucial for understanding bacterial community structures and their causes (Baselga 2010). Beta diversity has been defined as the extent of change in community composition among sites (Whittaker 1960), which is used to characterize bacterial community patterns (Simpson 1943). Indeed, overall beta diversity stems from one or a combination of biological phenomena: nestedness and spatial turnover (Baselga 2010; Wang et al. 2021a). Nestedness reflects a non-random process of species gain or loss, which occurs when the biota of sites with smaller numbers of species are subsets of the biota at richer sites (Baselga 2013). In contrast, spatial turnover implies the occurrence of the replacement of some species by others across geographic zones as a result of environmental filtering, competition, and historical constraints (Legendre 2014; Leprieur et al. 2011). Although the two biological phenomena can in combination contribute to overall beta diversity, their relative importance may vary across habitats and biological groups (Si et al. 2015; Wang et al. 2021a). In particular, inland waterways where bacterial habitats may become fragmented due to ship navigation disturbance lead to higher ecosystem vulnerability (Si et al. 2015). However, the relative contribution of species turnover and nestedness to bacterial community patterns under ship navigation disturbance remains unclear. Therefore, partitioning the overall beta diversity into separate components would further reveal the ecological processes underlying the biodiversity in inland waterways.

The present study focused on a PRN, and five pairs of sampling sites were set in adjacent waterways (WS) and non-navigable channels (NS) with little differences in depth and width. The main objectives were to explore the following questions: (1) What are the differences in sediment bacterial community diversity, composition, and structure between WS and NS? (2) What are the biological phenomena implied by the bacterial community patterns in WS and NS? (3) What are the relative contributions of hydrodynamic conditions, physicochemical parameters, and pollutants to the bacterial community distribution? (4) Would ship navigation disturbance affect the function of bacterial communities in sediment? The results provide theoretical support for the management of inland waterways and advocate further

attention to the sustainable development of inland waterway ecosystems.

Materials and methods

Sampling design

The Taihu Lake Basin is in the core area of the Yangtze River Delta in eastern China, which is densely covered with river networks corresponding to a river density of 3.2 km²/km² (Wu et al. 2018; Yu et al. 2022a, b). Due to the hydrological characteristics of low slope, shallow depth, and complicated connectivity (Li and Hua 2021), most of the waterways in the basin are Grade III and below (Jiangsu Province Waterway Atlas). As a typical PRN, the basin was selected to explore the effects of ship navigation disturbance on the sediment bacterial community. Furthermore, ship traffic would inevitably discharge pollutants such as toxic metals, petroleum hydrocarbons, PFAAs, and antifouling coatings to the waterway due to collision, explosion or breaking (Ali et al. 2022; Prabowo and Bae 2019). Therefore, heavy metals (HMs), PAHs, PFAAs, and organochlorine pesticides (OCPs) were selected as the target pollutants to evaluate their potential role in structuring bacterial communities.

Field sampling was conducted in August 2020. As shown in Fig. S1 and Table S1, the ten sampling sites were divided into five pairs. The water depth and width of WS and NS in each pair were similar (Table S2), and the sampling sites were in close proximity. Specifically, five sampling sites (WS1–WS5) were from Grand Canal, Wangyu River, Wutai Canal, and the Taipu River. The other five sampling sites (NS1–NS5) were in NS, free from the disturbance of ship navigation.

Analysis of sediment physicochemical parameters and pollutants

Three surface sediment samples (approximately 5-cm deep) were collected at each sampling site using a stainless-steel grab sampler and then thoroughly mixed and stored in 50 mL polypropylene centrifuge tubes. All the sediment samples were immediately transported to the laboratory in an ice-cooled box. Samples used for DNA extraction and other analyses were stored at –80 °C and –4 °C in the dark, respectively, until analysis. Physicochemical parameters of sediment samples included ORP, pH, salinity, total dissolved solids (TDS), conductivity, *f*_{oc}, *D*₅₀, clay content, silt content, sand content, total nitrogen (TN), and total phosphorus (TP). Detailed measurement methods and results

of the parameters are provided in Text S1 and Table S1, respectively.

The sediment samples were freeze-dried for 48 h and ground into a fine powder. Then, 1 g dw and 0.5 g dw of the sediment powder were used for HMs and PFAAs extraction (triplicate), respectively. HPLC grade solvents and deionized water were used for sample pretreatment and extraction. Detailed extraction methods of HMs and PFAAs can be found in Text S2. Specifically, eight HMs (Cr, Cd, Ni, Cu, Zn, As, Pb, and Hg) and 13 PFAAs (C4–C14, PFBS, PFHxS, PFOS, PFBA, PFPeA, PFHxA, PFHpA, PFOA, PFNA, PFDA, PFUndA, PFDoA, and PFTeDA) were analyzed in the present study. The abbreviations, full names, molecular structure, and commercial sources of all PFAA and internal standards are summarized in Table S3. Detailed instrumental analyses are provided in Text S3 and Table S4.

The data on PAHs and OCPs were obtained from Zhao et al. (2017), which investigated the residues of PAHs and OCPs from 81 river sediment samples from the Taihu Lake Basin. ArcGIS (ESRI, Cal., USA) and Get-Data Graph Digitizer software were used to extract data. ArcGIS services map matching (geographic registration module) and Get-Data Graph Digitizer extracts data from figures were based on a numerical algorithm (Yu et al. 2022). The extracted data were compared with the existing data in the paper, and the relative standard deviation ranged from 0.14% to 5.76%, indicating that the extracted data were reliable. Finally, the concentrations of PAHs and OCPs in sediment near the desired sampling sites were obtained after careful comparison with the Jiangsu Province Waterway Atlas.

Quality assurance and quality control

To avoid contamination, neither fluorinated substances nor glass was contacted during the field sampling and pre-treated processes. The field blanks and transport blanks were treated, and a procedure blank and solvent blank (methanol) was added to every batch of 12 samples. No target pollutant was detected above the quantification limits in the blank samples. Internal standards were used for the calibration and standardization of target PFAAs. Native compounds were quantified by a standard series of 1–200 µg/L, and the regression coefficients of each PFAA standard curve were greater than 0.99. The limits of detection (LODs) and the limits of quantification (LOQs) were set as signal-to-noise ratios (S/N) of 3:1 and 10:1, respectively (Table S5). Based on the LODs and LOQs, the method detection limits (MDLs) and the method quantification (MQLs) were obtained by a batch of standard

addition tests. The matrix-spiked recoveries of PFAAs (10 ng/g dw) ranged from 82.55% to 127.04% (Table S5).

DNA extraction and sequencing analysis

DNA of each sediment sample was extracted by the ALFA-SEQ Advanced Soil DNA Kit (Guangzhou mCHIP Biotechnology Co., Ltd, China). The regions of the bacterial 16S rRNA gene (V3–V4) were amplified using the 338F (ACT CCTACGGGAGGCAGCA) and 806R (GGACTACHVGGG TWTCTAAT) primers. PCR amplification and Illumina HiSeq sequencing were conducted at Guangdong Magigene Biotechnology Co. Ltd. (Guangzhou, China). The detailed sequencing processes are described in Text S4.

Statistical analyses

To compare the differences in physicochemical parameters, hydrodynamic conditions and pollutant concentrations between WS and NS sediments, the bacterial community diversity, structure, and function in response to the differences were determined. First, the alpha diversity of each sample was calculated in QIIME 2 using the observed species diversity indices based on the OTU analysis. In addition, Spearman correlations were calculated between environmental factors and the alpha diversity of bacteria. Based on the Bray–Curtis distance, non-metric multidimensional scaling (NMDS) analysis was performed in R software (“vegan” package) to determine the dissimilarity of bacterial community structure between WS and NS (Hu et al. 2021). Next, an analysis of similarity (ANOSIM) was conducted to determine whether the differences were significant. The linear discriminant analysis of effect sizes (LEfSe) was used to identify a highly differential taxonomy between WS and NS (Zhang et al. 2019a, 2021b). In this analysis, the non-parametric Kruskal–Wallis rank-sum test was first performed to find the species with significant differences in abundance between the WS and NS. Next, the Wilcoxon rank-sum was used to test the difference consistency among the subgroups of the species obtained in the previous step, followed by linear regression analysis (LDA) to estimate the effect size of each species at log (10) values and visualize taxa in the cladogram.

Furthermore, to reveal the biological phenomena implied by the bacterial community patterns in WS and NS, the Sørensen dissimilarity index (β_{SOR}), Simpson dissimilarity index (β_{SIM}), and the nestedness-resultant dissimilarity index (β_{NES}) of WS and NS were calculated in R-studio (“betapart” package) (Baselga 2010, 2013), respectively. Redundancy analysis (RDA) was conducted in Canoco 5 to elucidate the correlations between bacterial community structure and environmental factors. Variance inflation factor analysis (VIF) was performed to select vital factors before

RDA analysis. Variance partitioning canonical correspondence analysis (VPA) was used to quantify the relative contributions of physicochemical parameters, ship traffic volume (STV), and pollutants to the bacterial communities. A KEGG (Kyoto Encyclopedia of Genes and Genomes) pathway analysis was performed using PICRUSt 2 (phylogenetic investigation of communities by reconstruction of unobserved states) to investigate whether the changes in hydrodynamic conditions might lead to functional differences (Wang et al. 2018; Xu et al. 2020). Finally, the Student’s *t*-test was conducted in IBM SPSS 22 software to test the bacterial metabolic pathways with significant differences characterized at various levels between the WS and NS (Yin and Wang 2021). The Spearman correlations were calculated between the environmental factors and the top 15 bacterial classes.

Results

Physicochemical parameters and pollutants concentrations

The primary river characteristic parameters of WS and NS are provided in Table S2. Five WS, including Grade III and V, correspond to single-line straight waterway widths of 30–55 m and 22–35 m (Inland Waterway Navigation Standards), respectively. The average width of the five NSs is 39.60 m. Additionally, a few differences in water depth between WS (4.22 ± 1.22 m) and NS (3.97 ± 0.46 m) were observed (Taihu Basin Authority of Ministry of Water Resources, Water Information of Jiangsu Province) (Table S2). Furthermore, the physicochemical parameters of the sediment samples collected from each sampling site are listed in Table S1. pH ranged from 6.90 to 7.86, indicating sediment in the study was neutral to slightly alkaline (Chen et al. 2017). Salinity ranged from 0.12 to 0.72 psu (0.44 ± 0.15 psu). In addition, the ORP values of the investigated sediment were between 50.20 and 396.70 mv, with significantly higher ORP values observed in WS (249.48 ± 116.60 mv) ($p < 0.05$), which showed stronger oxidizability than NS (103.90 ± 51.34 mv). The organic carbon content (*foc*) of all sediment ranged from 3.92% to 7.04% ($5.21\% \pm 0.91\%$), with a small range in variation. Sediment from all sampling sites was mainly composed (accounting for more than 70% on average) of silt (2–63 μ m), followed by sand (63–2000 μ m), and clay (<2 μ m), suggesting that the sediment was mainly composed of grains larger than 2 μ m in size. Meanwhile, the sediment grain size distribution between WS and NS exhibited certain differences. The D_{50} , silt content, and sand content of WS sediment were higher than that of NS, whereas the clay content was significantly lower than NS ($p < 0.05$). The TN and

TP concentrations in WS [TN (1671.33 ± 160.36 mg/kg dw) and TP (667.23 ± 116.16 mg/kg dw)] were relatively lower than NS [TN (1727.92 ± 181.30 mg/kg dw) and TP (729.38 ± 149.77 mg/kg dw)].

As for the pollutants, the average concentration of HMs in the studied area followed the decreasing order of: Zn (158.43 ± 46.11 mg/kg dw) > Cr (104.71 ± 20.03 mg/kg dw) > Cu (44.70 ± 18.24 mg/kg dw) > Ni (43.93 ± 12.58 mg/kg dw) > Pb (39.94 ± 12.19 mg/kg dw) > As (16.90 ± 5.03 mg/kg dw) > Cd (0.51 ± 0.16 mg/kg dw) > Hg (0.15 ± 0.07 mg/kg dw) (Table S6). Moreover, the total concentrations of HMs (Σ HMs) in WS ranged from 249.44 to 517.16 mg/kg dw (384.67 ± 88.26 mg/kg dw), and 277.23 to 505.94 mg/kg dw (433.87 ± 80.48 mg/kg dw) in NS. Furthermore, seven PFAAs (PFBA, PFHpA, PFOA, PFDA, PFDoA, PFHxS, and PFOS) were 100% detected among the 13 PFAAs. PFBA, PFOS, PFHpA, and PFOA were identified as the dominant PFAAs, with a proportion of 31.81%, 28.44%, 13.23%, and 12.48%, respectively (Table S7 and Fig. S2). The total concentrations of PFAAs (Σ PFAAs) in all samples ranged from 29.95 to 67.15 ng/g dw, with the median Σ PFAAs in NS being 32.88% higher than that of WS. In addition, the mean concentrations of PAHs and OCPs in WS were 296.38 ± 119.44 ng/g dw and 32.48 ± 6.77 ng/g dw, and those in NS were 325.99 ± 137.96 ng/g dw and 39.98 ± 11.85 ng/g dw, respectively.

Bacterial alpha diversity

After quality filtering, 383,028 high-quality sequences of the bacterial 16S rRNA gene were obtained and assigned to 39,984 OTUs. Diversity information of bacterial communities, including the number of OTUs, Chao1, Shannon, and Simpson indices, are provided in Table S8. The alpha diversity values of bacterial communities between WS and NS were different, with the mean Chao1 (4478 ± 174) and Shannon (10.00 ± 0.20) indices of NS sediment being 1.27 and 1.34 times higher than WS [Chao1 (3520 ± 876) and Shannon indices (7.50 ± 2.10)], respectively. In addition, the mean Simpson index of WS sediment was 20.32 times that of NS.

To further investigate the relationships between bacterial richness, diversity, and environmental factors, Spearman correlation coefficients were calculated (Fig. 1). The results indicate that the STV, Pb, PFBA, clay content, PFHxS, and

Cd significantly affected the bacterial alpha diversity in sediment ($p < 0.05$). Specifically, STV, Pb, PFHxS, and Cd were significantly negatively correlated with the Chao1 and Shannon indices, and positively correlated with the Simpson index. The results revealed that ship navigation disturbance was unfavorable for bacterial alpha diversity and the richness and diversity of bacterial communities decreased with the increase of STV. Meanwhile, the exposure of the bacterial community to Pb, Cd, PFBA, and PFHxS could result in a reduction of alpha diversity. Conversely, clay content was significantly positively correlated with the Chao1 and Shannon indices and negatively correlated with the Simpson index, indicating that the increase in clay content was beneficial to bacterial richness and diversity.

Bacterial community composition and beta diversity

The composition and relative abundance across bacterial communities of different samples at the phylum and order levels are displayed in Fig. S3a–b. Proteobacteria (15.56–87.56%, mean 43.03%) were the dominant phylum in most all sediment samples. The other predominant bacterial phyla in all samples included Chloroflexi (1.08–25.46%, mean 12.38%), Bacteroidetes (1.41–20.77%, mean 11.85%), and Epsilonbacteraeota (0.09–49.71%, mean 7.86%), according to their overall abundance (Fig. S3a). At the order level, the dominant orders included Betaproteobacteriales (6.08–31.05%, mean 17.91%), Campylobacteriales (0.09–49.71%, mean 7.86%), and Anaerolineales (0.30–10.44%, mean 6.60%) (Fig. S3b).

The NMDS analysis based on the Bray–Curtis distance was performed to characterize the beta diversity of bacterial communities and indicated that marked differences in bacterial community structure between WS and NS were observed (Fig. 2). The ANOSIM confirmed the consistency of the results, which further verified that the bacterial community structure in NS sediment was significantly different from that in WS ($R = 0.276$, $p = 0.006$). NMDS analysis suggested that the bacterial community structure in NS showed a tendency to cluster, whereas the bacterial community structure in WS was scattered, indicating that the bacterial community structure in NS sediment was more stable than WS (Fig. 2 and Fig. S3).

LEfSe was then performed to assess the highly differential taxonomy (from phylum to order levels) between the

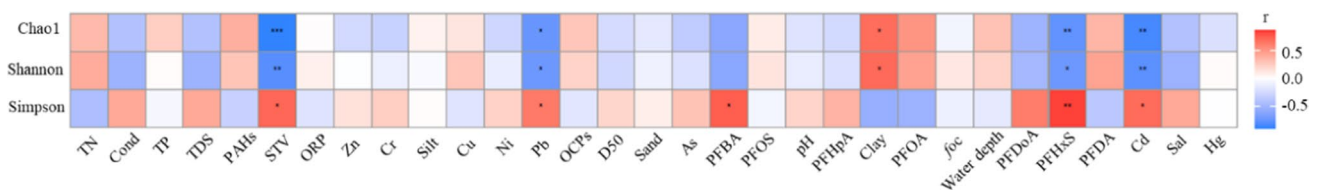


Fig. 1 Heat map illustrates the correlations between environmental factors and bacterial alpha diversity indices (* $0.01 \leq p < 0.05$, ** $p < 0.01$)

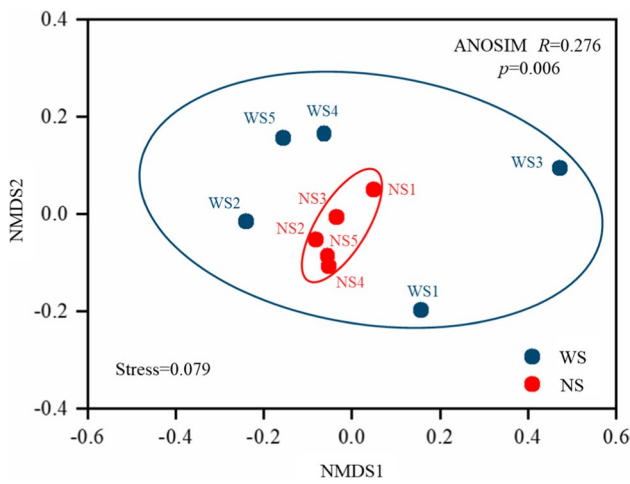


Fig. 2 Non-metric multidimensional scaling (NMS2) ordination of the bacterial community (Bray–Curtis distance). Points close together represent samples with similar bacterial community composition, and the ovals represent the 95% confidence intervals of the grouped samples

samples from WS and NS (Zhang et al. 2019a). The phylogenetic distribution of bacterial lineages is displayed in Fig. 3a, and the LDA values for each lineage are shown in Fig. 3b. LDA values greater than two indicated that species were significantly associated with sediment from the WS (green) and NS (red). The results indicate that 63 differentially abundant taxa were detected between WS and NS, of which 62 were enriched in NS. At the class level, the bacterial taxa significantly enriched in the NS were identified as Gammaproteobacteria, Bacteroidia, Deltaproteobacteria, Lentisphaeria, Hydrogenedentia, Fimbriimonadia, and others, among which Gammaproteobacteria, Bacteroidia, and Deltaproteobacteria belonged to the dominant class. Furthermore, Streptomycetales, belonging to Actinobacteria, exhibited the only significant presence in WS.

Ecological process underlying biodiversity

The causality underlying the beta diversity is described by one or combinations of two biological phenomena of spatial

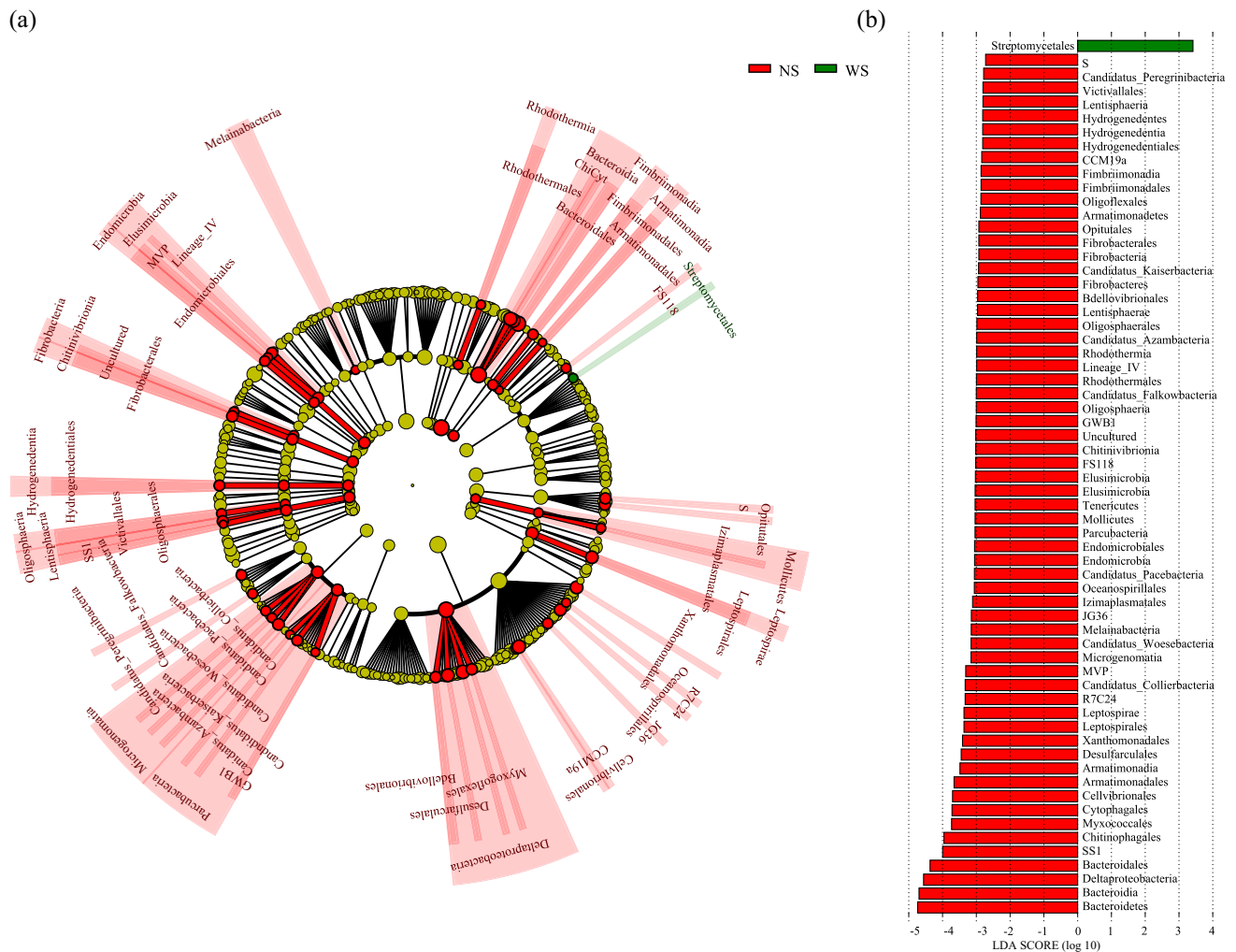


Fig. 3 a The bacterial lineages with significant differences between WS (green) and NS (red) and b LDA values for each lineage

turnover and nestedness, which are evaluated based on the presence and absence of species (Baselga 2010, 2013). To further determine the biological phenomena implied by the bacterial community patterns in WS and NS, the beta diversity dissimilarity indices were calculated, respectively, with results listed in Table S9. For WS, the estimated overall beta diversity β_{SOR} value of the bacterial community among the sampling sites was 0.69, with a substantial contribution from spatial turnover ($\beta_{\text{SIM}}=0.61$) and a small contribution from nestedness ($\beta_{\text{NES}}=0.08$). Similarly, a considerable contribution from spatial turnover ($\beta_{\text{SIM}}=0.59$) and a small contribution from nestedness ($\beta_{\text{NES}}=0.01$) was observed in NS, with the β_{SOR} of the bacterial community at 0.60.

Comparing the dissimilarity indices between WS and NS showed that the overall beta diversity of WS ($\beta_{\text{SOR}}=0.69$) was higher than for NS ($\beta_{\text{SOR}}=0.60$), also indicating the extent of variation in community composition among WS sampling sites was more drastic than NS. Furthermore, analysis of their spatial turnover and nestedness components found that spatial turnover was almost equally important to the WS ($\beta_{\text{SIM}}=0.61$) and NS ($\beta_{\text{SIM}}=0.59$), while nestedness contributed eight times more to the WS ($\beta_{\text{NES}}=0.08$) bacterial community structure than NS ($\beta_{\text{NES}}=0.01$). In comparison, beta-diversity patterns in WS resulted from both species replacements and species loss, while the beta-diversity patterns in NS almost entirely attributed to species replacement only.

Environmental factors affecting bacterial community structure

The RDA was performed to explore the correlations between environmental factors and bacterial community structures (Fig. 4). Based on VIF analysis (Zhang et al. 2019b), STV, clay content, pH, ORP, HMs, PFAAs, OCPs, and TN were selected as the primary explanatory factors affecting the bacterial community in sediment, which could explain 78.24% of the total variation. As shown in Fig. 4, STV ($R^2=0.608$), pH ($R^2=0.596$), and ORP ($R^2=0.486$) had the greatest influences on the bacterial community structure, and other factors—namely, PFAAs, HMs, clay content, and TN—were also strong predictors for bacterial community distribution.

The VPA was next used to determine whether the STV, pollutants (HMs, PFAAs, and OCPs), or physicochemical parameters (clay content, pH, ORP, and TN) contributed more to the bacterial community distribution. The results suggest that the combination of STV, pollutants and physicochemical parameters contributed exceeded 75% to the bacterial community distribution (Fig. 5). Among them, physicochemical parameters and STV were the most important factors, which explained 38.2% and 32.7% of the variation in bacterial communities, respectively, much greater than the role of pollutants (12.2%).

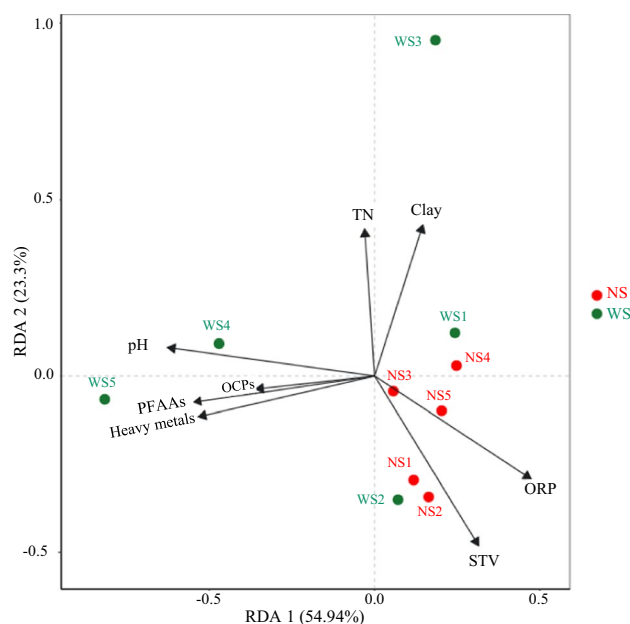


Fig. 4 Redundancy analysis (RDA) shows the relationships between the most significant environmental factors and bacterial community structure in sediment

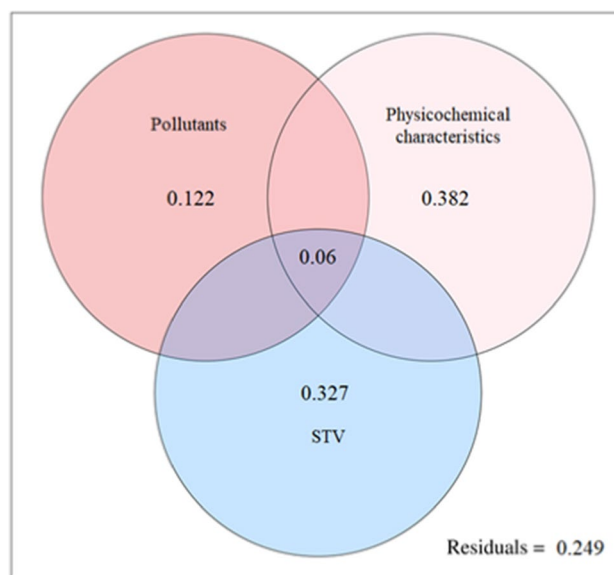


Fig. 5 Variance partitioning canonical correspondence analysis (VPA) illustrates the effects of STV, pollutants (HMs, PFAAs, and OCPs), and physicochemical parameters (clay content, pH, ORP, and TN) on the bacterial communities

Metabolism functional prediction of bacterial community

Among the six categories of biological metabolic pathways in level 1, the relative abundance of genes related to

metabolism was the highest (78.80–79.71%), followed by genetic information processing (12.60–12.79%), cellular processes (4.84–5.59%), and environmental information processing (2.09–2.37%), while the abundances of genes related to organismal systems (0.34–0.35%) and human diseases (0.21–0.28%) were much lower (Fig. 6a).

In comparison, the relative abundance of genes related to metabolism in WS was significantly lower than NS ($p < 0.05$) among the six categories of biological metabolic pathways (Fig. S4), indicating that ship navigation would constrain the metabolic function of bacteria in WS sediment. Subsequently, the distribution of bacterial metabolic function in level 2 was further analyzed (Fig. 6a). The results

suggested that the relative abundances of most sub-functions in WS were lower than in NS, such as the metabolism of cofactors and vitamins, carbohydrate metabolism, and amino acid metabolism that occupied relatively high abundances ($> 10\%$). In particular, the relative abundances of genes related to carbohydrate metabolism, amino acid metabolism, biosynthesis of other secondary metabolites, and transcription in WS were significantly lower than in NS ($p < 0.05$, Fig. 6a). Then, carbohydrate metabolism (12.53%–12.73%) and amino acid metabolism (12.39–12.53%) with relatively higher abundance were selected to take a closer look, and the differences of pathways belonging to these two functions in level 3 between WS and NS were tested. For carbohydrate

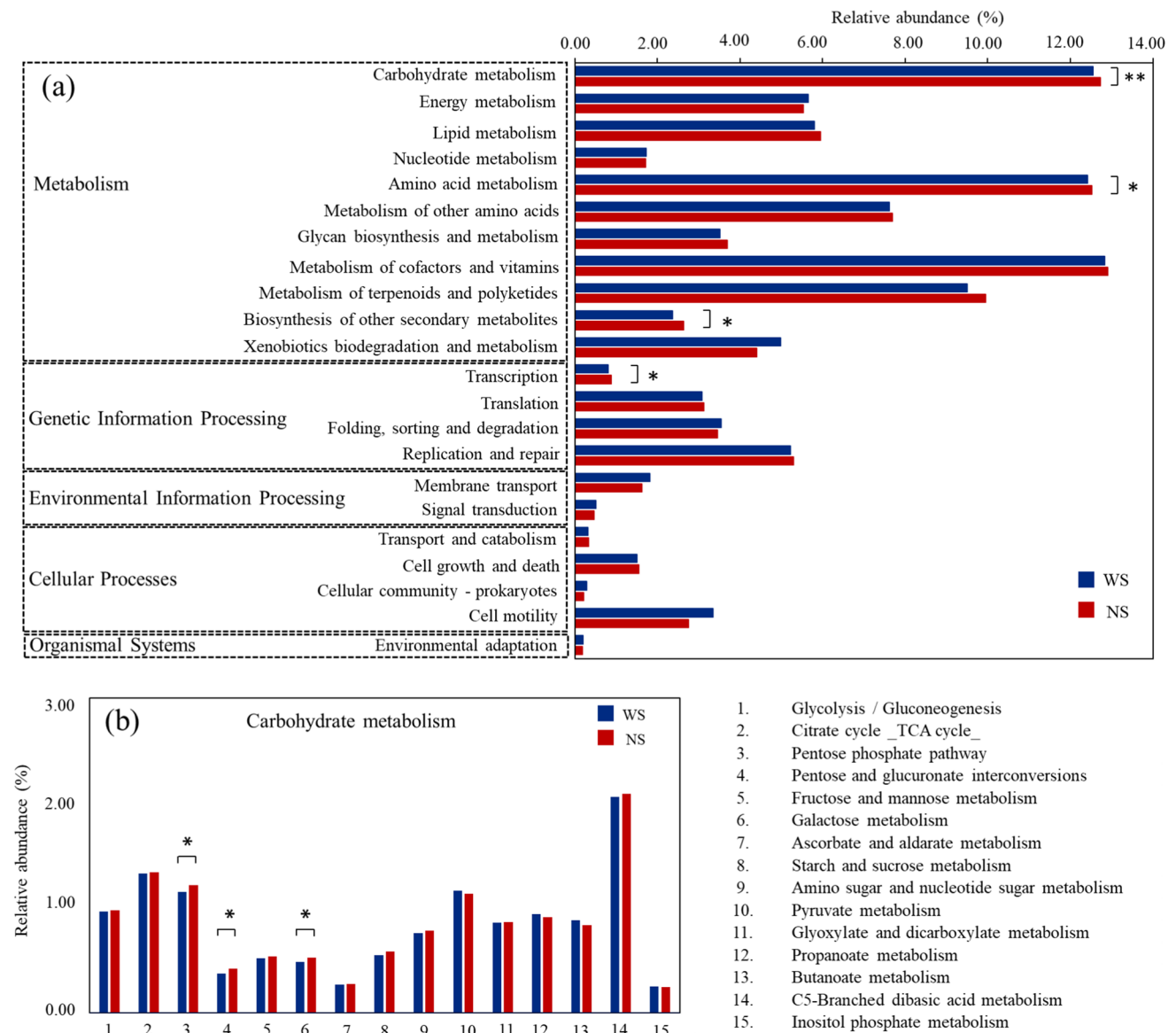


Fig. 6 **a** Relative abundance of metabolic pathways on KEGG categories in level 2; **b** relative abundance of carbohydrate metabolism on KEGG categories in level 3 ($*0.01 \leq p < 0.05$, $**p < 0.01$)

metabolism, the relative abundance of genes related to the pentose phosphate pathway, pentose and glucuronate interconversions, and galactose metabolism in NS sediment were significantly higher than WS ($p < 0.05$, Fig. 6b), indicating that the ability of bacteria in WS sediment to degrade various sugars might be inhibited (Yin and Wang 2021). Spearman correlation analysis showed that the pentose phosphate pathway and galactose metabolism were significantly stimulated by pH ($\rho = 0.652$ and 0.673 , $p < 0.05$), while the pentose and glucuronate interconversions were inhibited by ORP and STV ($\rho = -0.624$ and -0.661 , $p < 0.05$). Furthermore, no significant difference was found between WS and NS concerning amino acid metabolism in level 3.

Discussion

To investigate the dynamic changes of bacterial communities under ship navigation disturbance in the PRN, we compared the differences in diversity, composition and function of bacterial communities between WS and NS sediments. WS sediment is frequently disturbed by ship navigation, whereas NS sediment is free from the disturbance of ship navigation.

The alpha diversity analysis showed there was an uneven distribution in bacterial communities between WS and NS. The Chao1 index reflects the bacterial richness, while the Shannon and Simpson indices represent the bacterial diversity. The Chao1 and Shannon indices of WS were lower than those of NS, while the Simpson index was higher than that of NS (Table S8), indicating that the sediment from NS possessed more diverse and complex bacterial communities than WS. In addition, the bacterial community compositions in NS varied slightly among the different sampling sites, whereas the bacterial community structure in WS showed considerable spatial heterogeneity (Fig. 2). A similar phenomenon was observed in the bacterial community structure of sediment between the inflowing estuary and the central area of Dongting Lake (Zhang et al. 2019a), and they attributed this difference to the combined effects of sediment transport and deposition under different hydrodynamic conditions. Then, LefSe analysis further showed that WS sediment had a unique bacterial community pattern compared with NS. Ship navigation disturbance appears to have an apparent environmental filtering effect on selecting adaptive species in WS sediment. Zhang et al. (2021a) also reported a similar filtering effect of frequent water level fluctuations on the bacteria in riparian zones.

A comparison of beta diversity dissimilarity indices suggested that spatial turnover and nestedness contributed differently to the bacterial community structures, with species replacement dominating the formation of beta-diversity patterns in WS and NS rather than species loss, illustrating the high proportion of endemic bacterial species present in the

study area (Baselga 2010). Wu et al. (2021c) also reported that spatial turnover explained more variation in planktonic bacterial community structure than nestedness. However, although species loss contributed less than species replacement to the WS and NS beta-diversity patterns, it caused a difference in the overall beta diversity between WS and NS, which should also deserve attention. It is generally accepted that both geographic and environmental factors would affect the patterns of bacterial communities (Baselga 2010; Liu et al. 2018). For example, research on the beta-diversity patterns of European longhorn beetles reported an orderly increase in species loss with an increase in geographic distance from southern to northern Europe (Baselga 2010). Liu et al. (2018) also reported the increase in the differences between bacterial communities from the upper reach of the Yangtze River to the river mouth (4300 km). However, the geographic distance between sampling sites in NS and WS was not likely a factor since they were close to each other in each pair (Fig. S1 and Table S1), which was far less distant than the geographical distances that led to the dissimilarities of the river bacterial community composition. Therefore, the effect of geographic distance on the differences in bacterial community structure between WS and NS can almost be ignored. Meanwhile, environmental factors were most likely the dominant contributing factors to the differences observed and appear to be important factors affecting bacterial communities (Wang et al. 2021a; Zhang et al. 2019b). As previously discussed, the hydrodynamic conditions, physicochemical characteristics, and pollutant concentrations in WS sediment differed from NS. Compared to NS, the higher contribution of species loss to the bacterial community structure observed in WS suggested that the local environmental conditions provided by WS sediment might not be conducive to bacterial growth.

The RDA and VPA analyses further revealed that the physicochemical parameters and STV contributed more to the variation in bacterial communities between WS and NS than pollutants (Figs. 4 and 5). In general, hydrodynamic disturbances are the primary physical force affecting bacterial living environments (Cheng and Hua 2016; Jalil et al. 2019). For example, Besemer et al. (2009) reported that the spatial variation of hydrodynamic forces largely explained the change of community composition along with bedforms. In the present study, STV represents the intensity of ship navigation disturbance to a certain extent, providing additional hydrodynamic forces for WS sediment. The riverbed of a waterway is proven to undergo significant changes when subjected to a strong swirling jet flow induced by a rotating ship propeller (Hong et al. 2016; Nadia et al. 2019). Strong shear stress would break the stability of the riverbed and resuspend bottom sediment (Lam et al. 2010), thus forcing the bacterial communities to strip away from the colonized substrate and random diffusion from sediment to overlying

water (Lv et al. 2021; Shen et al. 2015) and leading to the species loss observed in WS sediment. Sediment particle size distribution, which was reported as a driving factor causing the different structures of the microbial community (Zhang et al. 2020b), may further verify the speculation. Generally, smaller particles favor bacterial attachment since they have larger specific surface areas (Gao et al. 2021; Wu et al. 2021a). The significant lower clay content in WS than NS indicated that the erosion caused by ship navigation on WS sediment could carry away fine grained sediment, resulting in the coarse-graining of WS sediment, which was consistent with Grant et al. (2018) and Wei et al. (2016), who found that coarser-grained sediment is deposited in areas with high current velocity. As a result, the bacterial communities originally colonized on clay may be lost in the process, which also explained why the higher contribution of species loss to bacterial community structure was observed in WS than in NS. Meanwhile, the frequent disturbance could alter the degree of bacterial aggregation in sediment (Li et al. 2020b; Shen et al. 2015), subsequently increasing the possibility of bacterial community migration and leading to the distribution of bacterial communities in sediment exhibiting considerable spatial variability. Therefore, the bacterial community structure in WS sediment could be altered under the direct physical disturbance of ship navigation. A similar phenomenon was observed in the study of water diversion-induced changes in sediment bacterial communities (Lv et al. 2021), which reported that water diversion totally altered the natural seasonal changes in bacterial communities.

On the other hand, hydrodynamic disturbances can induce sediment–water interface material exchange (Cheng et al. 2019b; Wang et al. 2015), causing changes in the physico-chemical characteristics of sediment and indirectly affecting the bacterial community. ORP and pH have been considered two of the critical factors that significantly affect the structure and composition of microbial communities (Chang et al. 2014; Meng et al. 2021; Zhang et al. 2021b). In the present study, the mean value of ORP in WS sediment was significantly higher than NS ($p < 0.05$), and the pH was correspondingly lower than NS (Table S1). ORP values can laterally reflect the oxygen content in sediment (Li et al. 2019a), and the significant higher ORP values in WS suggested that ship navigation disturbance might directly accelerate the oxygen exchange rate at the sediment–water interface (Ma et al. 2021), which oxygenates the sediment. This condition was conducive to the decomposition of organic matter, which in turn releases acidic substances (Fang et al. 2021; Mastný et al. 2018) and reduces the pH of WS sediment. Lower pH may be stressful for bacterial growth (Kim et al. 2016); the relatively higher ORP and lower pH conditions in WS sediment might also be responsible for the differences in bacterial communities between WS and NS.

Additionally, HMs and organic pollutants are also important factors affecting the diversity and composition of microbial communities. For example, Yao et al. (2022) reported that HMs dominated the variation of microbial communities in eutrophic rivers and exhibited different effects on bacterial and fungal communities. Several studies indicated that PFAAs would lead to the evolution of bacterial communities with characteristics that resisted toxicity, which had the dual effects of stimulating and inhibiting the growth of the bacterial community (Lu et al. 2020; Qiao et al. 2018). Furthermore, the effects of PAHs and OCPs on microbial communities were also confirmed (Egbe et al. 2021; Liu et al. 2021b; Yan et al. 2019). However, although the concentrations of studied pollutants in WS sediment were relatively lower than those in NS, no significant differences were observed in the mean concentrations of pollutants in sediment between WS and NS ($p > 0.05$). The results may be a function of surface sediment being an important sink for pollutants (Hua et al. 2021), and in turn reflecting the results of the long-term deposition of pollutants in the sediment. Second, Taihu Lake Basin is a typical annular river network with an uncertain flow direction. The sampling sites from WS and NS in each pair were close and affected by approximate external pollution sources. Thus, ship navigation disturbance may trigger the release of these pollutants from sediment in a short time (Ma et al. 2021), but the concentration of pollutants in sediment is generally stable. Therefore, although the pollutants had varying degrees of impact on the alpha diversity of bacterial communities (Fig. 1), they were not the main factor causing the differences in bacterial community structure between WS and NS (Fig. 5).

Predictions of metabolic pathways are essential for understanding the metabolic activity of bacterial communities (Liu et al. 2021a; Wu et al. 2021c). Although the functional predictions of bacterial communities in the present study are putative, this can still provide valuable predictive information for exploring the functional differences of bacteria under ship navigation disturbance. The results of the present study were consistent with previous studies that found that metabolism and genetic information processing are the two dominant functions of bacteria in sediment (Abia et al. 2018; Rajeev et al. 2021). However, the bacterial communities in sediment exhibited considerable variations in functional composition under different hydrodynamic conditions. Notably, ship navigation disturbance might inhibit the carbohydrate metabolism function of bacterial communities in WS by reducing pH and increasing ORP and STV. Therefore, attention should be paid to the possible inhibitory effects of ship navigation disturbance on bacterial metabolism function, especially in plain river networks with dense WS, where the adverse effects of ship navigation disturbance on the bacterial metabolism activities could be greater.

Conclusions

The present study contributes to a better understanding of the dynamic changes of sediment bacterial communities under complex hydrodynamic environments. We found that the sediment bacterial alpha diversity decreased gradually from NS to WS and that the bacterial community structure in WS was less stable than that in NS. Moreover, the underlying factor of the differences in beta diversity between WS and NS was species loss caused by the changes in hydrodynamic conditions and physicochemical parameters in WS sediments. In addition, ship navigation disturbance may inhibit the carbohydrate metabolic function of bacterial communities in WS by reducing pH and increasing ORP and STV. Our study provides a reference for understanding the response of bacterial communities in sediment to ship navigation disturbance in the PRN, although further studies are needed to elucidate how this response changes in different seasons. While inland transport brings great economic benefits, it is important to pay attention to the ecosystem health of inland waterways.

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Data availability The sequenced data can be found in the NCBI Sequence Read Archive (accession number: PRJNA785136).

Declarations

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