

# Homogenisation of water and sediment bacterial communities in a shallow lake (lake Balihe, China)

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## Abstract

1. Planktonic and benthic bacterial communities hold central roles in the functioning of freshwater ecosystems and mediate key ecosystem services such as primary production and nutrient remineralisation. Although it is clear that such communities vary in composition both within and between lakes, the environmental factors and processes shaping the diversity and composition of freshwater bacteria are still not fully understood.
2. In order to assess seasonal and spatial variability in lake bacterial communities and identify environmental factors underpinning biogeographical patterns, we performed a large-scale sampling campaign with paired water and sediment sample collection at 18 locations during four seasons in Lake Balihe, a subtropical shallow fish-farming lake in mid-eastern China.
3. Pelagic and benthic bacterial communities were distinctly different in terms of diversity, taxonomic composition and community structure, with Actinobacteria, Bacteroidetes, Cyanobacteria and Alphaproteobacteria dominating lake water, and Acidobacteria, Bacteroidetes, Chloroflexi, Gammaproteobacteria and Deltaproteobacteria dominating sediment. Nevertheless, these two communities had stronger spatial concordance and overlap in taxa during spring and autumn seasons. Together, the main drivers of both the spatial and temporal variations in Lake Balihe bacterial communities were identified as water temperature, turbidity, nitrogen and phosphorus availability, and thermal stratification controlled by wind-mixing and activity of the dense farmed fish populations. Notably, populations affiliated with Firmicutes, known to be abundant in fish gut microbiome, were especially abundant in the summer season and locations where high fish biomass was found, suggesting a potential link between fish gut microbiome and the pelagic bacterial communities.

[Correction added on 23 November 2022, after first online publication: The copyright line was changed.]

Meifang Zhong and Eric Capo are joint first authors.

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4. Our findings demonstrated seasonal homogenisation of pelagic and benthic bacterial communities linked to marked shifts in a set of seasonally-driven environmental variables including water temperature and nutrient availability.

#### KEYWORDS

16S rRNA gene, environmental factors, fish farming, shallow lakes, subtropical zone

## 1 | INTRODUCTION

Bacteria play an important role in lake ecosystems where they influence food webs, water quality and biogeochemical cycles (Cotner & Biddanda, 2002). The diversity and composition of bacterial communities living in pelagic and benthic lake compartments already have been studied extensively with cultivation-independent methods (Kara et al., 2013; Rösel et al., 2012; Szabó et al., 2011; Tšertova et al., 2013). Lake pelagic bacterial communities exhibit strong seasonality in both abundance and composition, largely driven by shifts in water temperature and inputs of allochthonous matter. By contrast, benthic bacterial communities appear more stable and less impacted by seasonal change. Earlier studies determining the potential coupling between bacterial communities in sediment and the overlying water column focused mainly on interface reactions (Rusch et al., 2001), nutrient cycling (Hopkinson, 1985), co-existing taxa (Zhang et al., 2021) or the distribution of faecal indicator bacteria or other specific groups of interest (Gao et al., 2011). Meanwhile, there is, to our knowledge, no systematic study of either how environmental conditions influence the spatial and temporal coupling of pelagic and benthic communities, or how such linkages change over the annual cycle.

In shallow lakes, characterised by low water depths (e.g., a few metres), strong interactions between the water column and underlying sediments can influence physical, chemical and biological processes much more strongly than in deeper lakes (Herb & Stefan, 2005). The diversity and composition of bacterial communities in shallow systems are known to be strongly affected by nutrients availability (e.g., nitrogen [N] and phosphorus [P]; Tang et al., 2015), water temperature, thermal stratification (Kimura et al., 2016), mixing induced by strong winds (Tang et al., 2010) and phytoplankton population dynamics (Kolmakova et al., 2019; Paver & Kent, 2010). In addition, anthropogenic impacts can exert significant local effects on microbial communities in these systems (Song et al., 2012; Song & Wang, 2015; Wang et al., 2020). In Lake Baiyangdian (China), sewage discharge and aquaculture have, for example, been shown to modify the composition of the resident bacterial community (Wang et al., 2020). The impacts of aquaculture are exacerbated in shallow lakes as they present conditions that are conducive for fish farming with a naturally rich supply of food for the fish and shallow depths that allow for easy harvesting. Therefore, shallow fish-farming lakes are common, especially in China (Jia et al., 2013). Fish farming can have a strong impact on water quality (Wu et al., 1994), submerged macrophytes (Francová

et al., 2019) and planktonic food webs (Borges et al., 2010; Koksvik & Reinertsen, 1991). Furthermore, as a consequence of their movement within the lake and often flexible feeding modes, fish can provide important linkages between littoral, benthic and pelagic zones (Zanden & Vadeboncoeur, 2002).

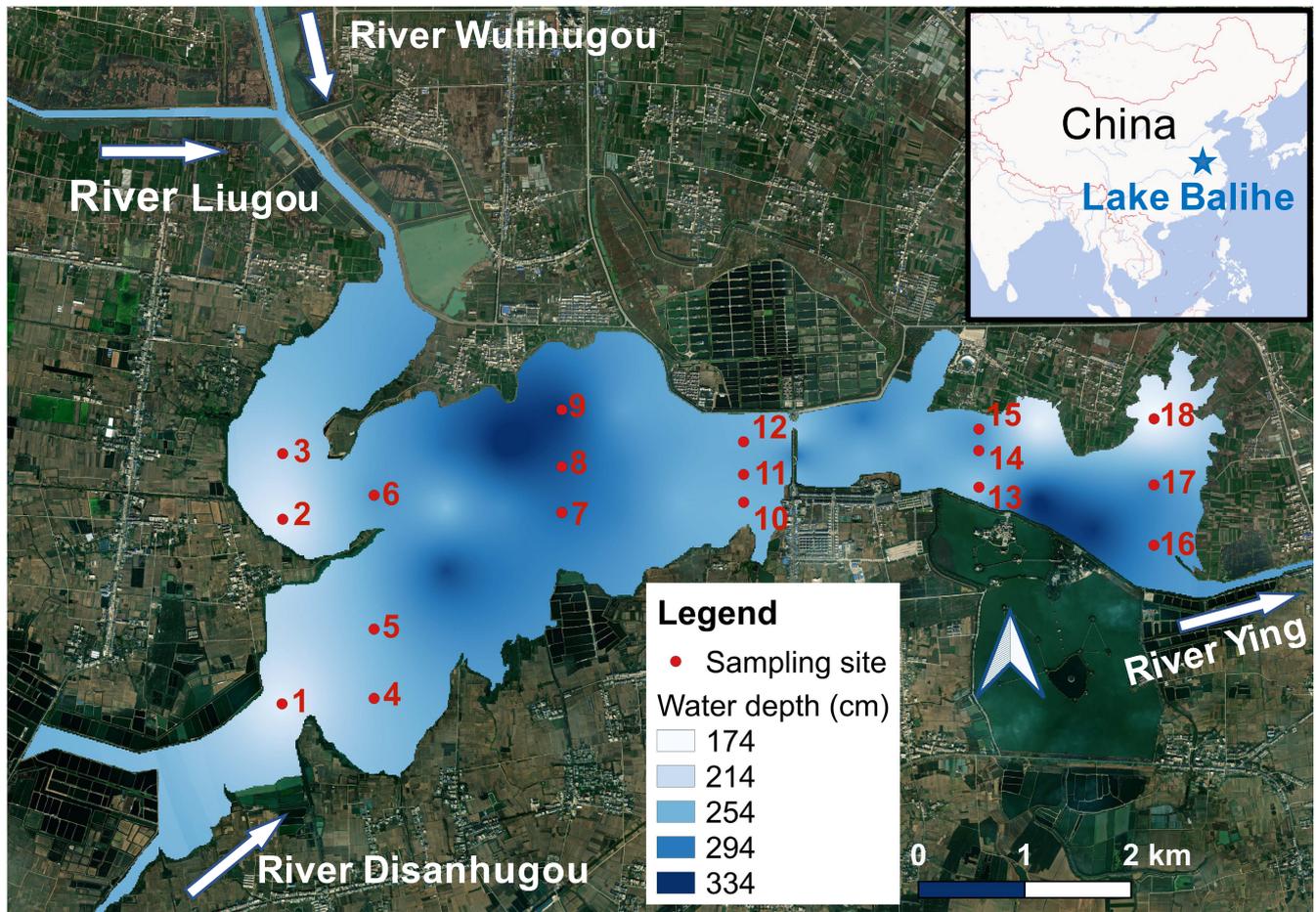
Lake Balihe is an important aquaculture resource in northwest Anhui Province and forms the centre of the Balihe Provincial Nature Reserve. It has been a fish-farming lake since 1958 and is divided into an upstream and a downstream basin by a dike-bridge that connects the north and south banks of the lake (Figure 1). The upstream part receives a higher external load of nutrients (N and P) than the downstream part, although the entire lake is eutrophic (Zhong et al., 2018). Even so, there have not been any algal blooms observed since the launch of a water-quality monitoring programme (August 2016), and the entire lake has maintained a “fair” ecosystem health status based on the planktonic index of biotic integrity value (Zhang, Duan, et al., 2019) and water-quality parameters (He et al., 2019; Lan et al., 2019; Zhang, Zhong, et al., 2019; Zhong et al., 2018).

In the present study, we used a large-scale sampling approach by collecting paired water and sediment samples at 18 locations across Lake Balihe during four seasonal sampling campaigns (2018–19). A 16S rRNA gene amplicon sequencing approach was used to determine the diversity, composition and structure of both pelagic and benthic bacterial communities. Three main questions were addressed: (1) Does the similarity/dissimilarity between water and sediment bacterial communities change seasonally?, (2) Which processes and environmental factors contribute to seasonal homogenisation of bacterial communities in water and sediment?, and (3) Does fish farming have an impact on the pelagic and benthic bacterial community? Overall, our study provides new knowledge about within-system bacterial community dynamics in subtropical shallow lakes.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site and sample collection

Lake Balihe is a 10 km<sup>2</sup> eutrophic lake located in Fuyang City, Anhui Province, middle-eastern China, where it is found in the transition zone from the warm temperate to subtropical climate zone (Figure 1). Lake Balihe is a fish-farming lake and also famous as a provincial nature reserve. It has a long history of fishing, and an aquaculture industry was established in 1958. Silver carp (*Hypophthalmichthys*



**FIGURE 1** Location of Lake Balihe and distribution of the 18 sampling sites. The data for the water depth in the figure was investigated in summer (July 2019). Water and sediment samples were both collected in each site

*molitrix*) and bighead carp (*Hypophthalmichthys nobilis*) are the most abundant species in the lake. The lake features a 650-m-long dike-bridge which was built in 1989 and dividing the lake into an upstream and a downstream basin. Except for three water apertures in the north, each with a diameter of 3 m, the remaining dike-bridge does not allow water to pass. Seasonal harvesting of big fish individuals and retaining small ones has been the governing principle for the fish-farming operation.

Water and sediment samples from all 18 locations (Figure 1) were collected in four seasons (autumn, November 2018; winter, January 2019; spring, April 2019 and summer, July 2019). Sites 1, 2 and 3 represent the major inflows to the lake, whereas site 15 is the outflow. Sites 4–12 are located in the upstream basin and 13–18 are distributed across the downstream basin. According to previous studies on N and P content, sites 2 and 3 are highly enriched in nutrients, sites 1 and 4–12 are moderately enriched in nutrients, and 13–18 are considered as less enriched in nutrients (Zhong et al., 2018).

Two 1-L water samples were collected from 1 m below the surface at each site using a water-sampling tube; 1 L for biological analyses and 1 L for physicochemical analyses. Water samples were stored in sterilised plastic carboys and processed within 12 hr upon return to the laboratory. For biological analyses, water samples were

pre-filtered through glass fibre filters with 0.7- $\mu\text{m}$  nominal pore size before collecting bacterial cells on sterile 0.22- $\mu\text{m}$  mixed cellulose esters membranes (Membrane Solutions, USA) using gentle vacuum filtration. Filters were immediately stored frozen at  $-80^{\circ}\text{C}$ . For physical and chemical analysis, unfiltered water was used for total N and P analyses, whereas water passed through 0.45- $\mu\text{m}$  acetate membrane filters was used for analysis of total dissolved N (TDN), nitrate ( $\text{NO}_3^-$ ) and other dissolved constituents (see Section 2.2. Datasheet S1).

For each site, two sediment samples were retrieved by a Peterson sampler, one for biological analysis stored in a 50-ml sterilised plastic jar and one for physicochemical analysis stored in a sterilised Ziploc bag. Samples were returned to the lab within 12 hr and stored at  $-80^{\circ}\text{C}$ . After the weight was recorded, sediment samples were dried in dark conditions for estimates of moisture content and downstream chemical analyses. All samples to be used for molecular biology analysis were shipped on dry ice to Novogene.

## 2.2 | Contextual data and chemical analyses

Water temperature (WT), pH, oxidation-reduction potential (ORP), electrical conductivity (EC) and dissolved oxygen (DO) were

measured *in situ* using a multiparameter sonde (YSI Pro Plus). Water depth and transparency were measured by a hand-waving tape measure with a Secchi disk; turbidity was measured with a nephelometer (XinRui WGZ-2B). The analytical methods for factors measured in the laboratory are summarised in Datasheet S1, including water factors: total N (TN), TDN, ammonia N ( $\text{NH}_4^+\text{-N}$ ), nitrate N ( $\text{NO}_3^-\text{-N}$ ), nitrite N ( $\text{NO}_2^-\text{-N}$ ), total P (TP), total dissolved P (TDP), phosphate P ( $\text{PO}_4^{3-}\text{-P}$ ), chemical oxygen demand (COD), Chlorophyll *a* (Chl*a*), arsenic (As), iron (Fe) and aluminium (Al); and sediment factors: TN, TP, TOC,  $\text{NH}_4^+\text{-N}$ ,  $\text{NO}_3^-\text{-N}$ ,  $\text{NO}_2^-\text{-N}$ , NaOH extractable P (NaOH-P), HCl extractable P (HCl-P), organic P (OP), copper (Cu), total mercury (T-Hg), cadmium (Cd), chromium (Cr), lead (Pb), total As (T-As), zinc (Zn), Fe and Al.

Wind, air temperature and precipitation data (Datasheet S2) were downloaded from the website "Reliable Prognosis" (<http://rp5.ru>) from the nearest weather station (station name: Quanhe, Sanquan, Wangyingcun; WMO\_ID: 58203) which is 30km away from Lake Balihe. The weather station recorded the parameters every 3hr. To assess the influence of meteorological parameters on bacterial communities, we extracted one full month of weather data for each season, immediately preceding the sampling day. Wind with a speed  $\geq 3.4$  m/s was considered as strong wind. The wind rose plots visualised by ORIGINPRO 8.5.1 (OriginLab) indicated the main wind direction, velocity and frequency of a certain intensity (Datasheet S3).

Fishing and fry reintroduction data from 2016 to 2019 were provided by the town Balihe government (Datasheet S5). In the summer of 2018, fish were sampled by cast nets with the help of artisanal fishermen. The cast net's radius was 5m, and the spreading radius was about 4m. We carried out two fishing operations, one in the morning of July 19 that included 10 net casts, the other in the afternoon of July 22, also encompassing 10 net casts (Figure S1; Datasheet S6). In the 20 nets, only one caught no fish. In the other 19 nets, most fish were caught at fishing sampling sites 1, 6, 8, 11, 14 and 15. Geographically, sites 1 and 11 were adjacent to the dock with high terrain and buildings nearby; site 8 was near the south bank of the downstream with elevated terrain and two rows of weeping willows; sites 6, 14 and 15 were near the three apertures of the bridge. All of these locations feature waters that experience strong shade in the morning or afternoon. Fish biomass was calculated by using the wet weight of fish divided by the portion of the lake area covered by the cast net.

## 2.3 | DNA extraction, PCR amplifications and sequencing

Total genomic DNA from the combined filters from the water sampling (glassfibre and mixed cellulose esters membrane) or  $\sim 0.5$  g of wet sediment was extracted using the SDS method (Zhou et al., 1996). Agarose gel electrophoresis was used to check the purity and concentration of the extracted DNA (no exact value). Extracted DNA was compared with a standard DNA sample. DNA was diluted to

1 ng/ $\mu\text{l}$  using sterile water in accordance with the original concentration. Then  $\sim 10$  ng DNA extracted from each sample was used to amplify the V3-V4 region of the 16S rRNA gene in a PCR with general bacteria primers 341F (5'-CCTAYGGGRBGCASCAG-3') and 806R (5'-GGACTACNNGGGTATCTAAT-3') and sample-specific barcodes. Each PCR was performed in a total volume of 30  $\mu\text{l}$  containing 15  $\mu\text{l}$  PhusionMaster Mix (2 $\times$ ; New England Biolabs), 3  $\mu\text{l}$  forward and reverse primer (200nM each), 10  $\mu\text{l}$  gDNA (1 ng/ $\mu\text{l}$ ) and 2  $\mu\text{l}$   $\text{H}_2\text{O}$ . The amplification conditions consisted of an initial denaturation at 98°C for 1 min followed by 30 cycles of denaturation at 98°C for 10s, annealing at 50°C for 30s and elongation at 72°C for 30s, and terminated by a final 5-min extension at 72°C. After the PCR, the amplicons were separated and sized by electrophoresis on a 2% agarose gel. The visible band was excised with a razor blade and extracted using a gel extraction kit (GeneJET; Thermo Fisher Scientific). The gene library was constructed with the Ion Plus Fragment Library Kit 48 rxns (Thermo Fisher Scientific). Single-end (400bp) sequencing was performed on the Ion S5TM XL platform.

## 2.4 | Molecular data processing and analysis

The resulting DNA sequences (reads) were processed with the "DADA2" package (Callahan et al., 2016) in R (R Core Team, 2020) to generate amplicon sequence variants (ASVs). Briefly, after quality filtering by DADA2 at position 420, the high-quality reads were clustered into 19,287 ASVs, and then the SILVA v132 database was used to assign taxonomy to these ASVs. Taxonomy is based on NCBI classification. Although certain groups such as Deltaproteobacteria have been reclassified recently (Waite et al., 2020), we kept their previous name to have a homogenised classification of our bacterial communities. A total number of 2,649,760 high-quality DNA reads were obtained with an average of 18,401 reads per sample (range: 6,282–34,736). In total, 5,827 and 15,060 bacterial ASVs were detected in water and sediment, respectively, in which 1,600 ASVs were shared by them. Rarefaction curves (Figure S2) were performed for the 144 samples (72 water samples, 72 sediment samples) using the function *rarecurve* from the "vegan" R package (Oksanen et al., 2009). Three samples with lower estimated richness in rarefaction curves (153 and 155 vs. 891–1,143 for other samples in autumn; 577 vs. 553–828 for other samples in winter) were categorised as outliers by a principal-component analysis (PCoA) plot and were accordingly removed from further analyses. A total of 141 samples were kept for further analyses, including 72 water samples and 69 sediment samples. To make the analyses more robust, low-abundance ASVs (fewer than three samples with counts greater than or equal to 10 reads, samples included both water and sediment samples) were discarded using "DESeq2" package (Love et al., 2014), resulting in a total of 3,157 ASVs corresponding to all samples. All samples were normalised using the *rarefy\_even\_depth* function in the "phyloseq" package (McMurdie & Holmes, 2013) to a minimum sample size of 7,986 reads. The obtained normalised dataset was used for further analysis except for DESeq2 analysis which required un-normalised data (see Section 2.5).

## 2.5 | Data analysis

All statistical analyses were performed using R v3.6.3 and visualised using the “ggplot2” package (Wickham, 2009) unless stated otherwise. Diversity and composition analysis of the bacterial community were performed using phyloseq (McMurdie & Holmes, 2013). Alpha diversity was measured using the function *estimate\_richness* in phyloseq, and the observed ASV and Shannon metrics were used. To examine the similarities and differences in microbial community compositions between water and sediment samples, PCoA analysis was done based on Bray–Curtis dissimilarity distance using the *ordinate* function. To estimate the relative abundance of each bacterial group and the most abundant ASVs in the community, relative abundance stacked barplots were performed at the class and ASV levels using the function *transform\_sample\_counts*. The pairwise Bray–Curtis dissimilarity distance values calculated between co-located pairs of water and sediment molecular sample in each season were examined using the function *distance* and visualised using boxplots. The heatmap of dissimilarity between water and sediment in the whole lake for each season was further visualised by QGIS 3.12.3 (QGIS Development Team, 2020) using Kriging interpolation. To assess the statistical significance of the congruence between water and sediment, Bray–Curtis dissimilarity distance values were calculated independently for water and sediment bacterial communities using the function *vegdist*. Then, the PROTEST permutation procedure analysis (1,000 permutations) was performed using the function *procrustes*. Non-metric multidimensional scaling (nMDS) analysis was utilised for water and sediment. For each of them, a Bray–Curtis dissimilarity matrix was built from the ASVs table and the functions *metaMDS* and *ordisurf* were used to plot the nMDS results and gradients of environmental factors. The *env.fit* function was applied to the Bray–Curtis dissimilarity matrices to evaluate the significance of relationships between bacterial community structure and selected environmental factors and the Pearson coefficient correlations between environmental factors were analysed using function *cor*. The same environmental factors were used to investigate their spatial correlation with the bacterial community using the function *bioenv*. The functions *vegdist*, *procrustes*, *metaMDS*, *ordisurf*, *env.fit* and *bioenv* belong to R/vegan and function *cor* belongs to R/corrplot (Wei et al., 2017).

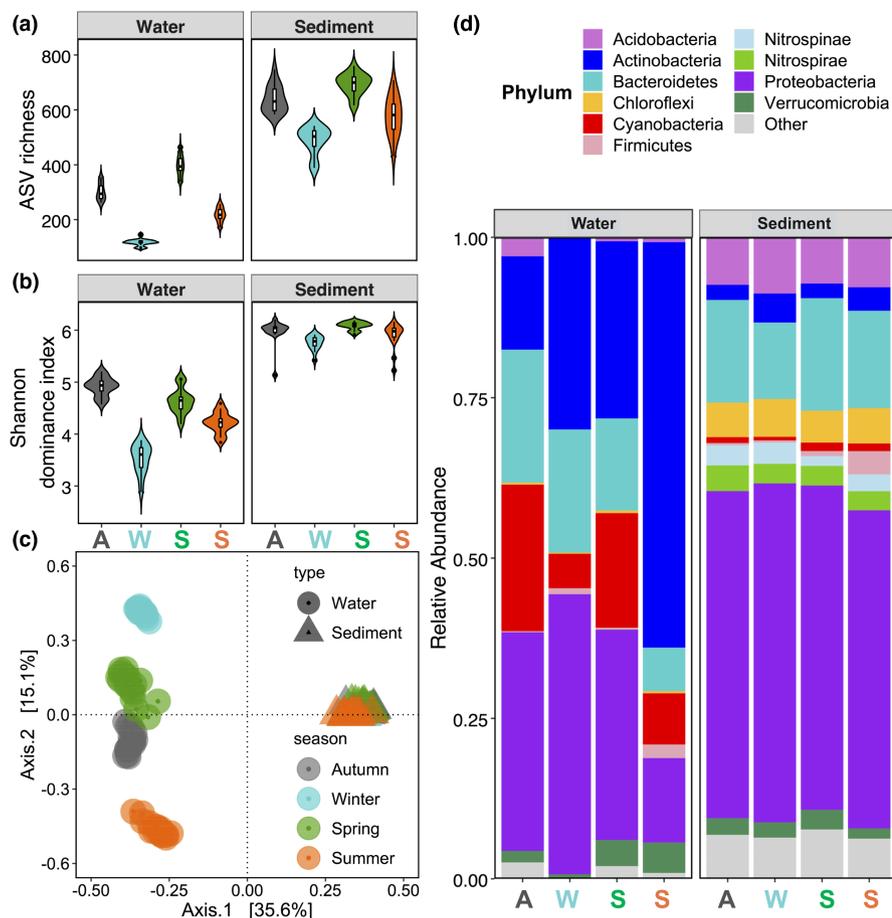
The numbers of shared ASVs between water and sediment bacterial communities in every season and the whole study period was examined using the function *venn\_diagram* from the “VennDiagram” R package (Chen & Boutros, 2011). The enrichment of specific taxa in each of the sample types was detected by DEseq2 (Love et al., 2014). For this we used the non-normalised ASV table which contained 69 water samples (W1811B01, W1811B04 and W1901B07 were removed) and 69 sediment samples. ASVs were considered enriched in water or sediment if they had a  $\log_2$  fold-change of 2 and an adjusted *p*-value of 0.01; otherwise they were considered as shared ASVs. Data from the entire study period were used to build the co-occurrence network.

The co-occurrence network was built to investigate links between water and sediment ASVs in terms of relative abundance. The network was based on the Spearman rank correlation matrix calculated from ASV abundance tables of both water and sediment samples. To reduce the complexity of each network, ASVs that never reached >1% of the total reads in any individual sample were removed. A Spearman rank correlation matrix was computed using the function *corr.test* from the “psych” R package (Revelle & Revelle, 2015) and visualised using the software GEPHI (Bastian et al., 2009). The networks were composed of nodes (ASVs) linked by edges (correlations between individual ASVs based on their relative abundances across the samples). Edges with Spearman rank correlation values <1.2 were removed to simplify the network. The sequences of Firmicutes ASVs in Module 7 of the co-occurrences networks were aligned and consensus identity sequences thus obtained were checked for homology with the NCBI database using the BLAST tool (Johnson et al., 2008). The top 14 nearest cultured homologues were downloaded and their DNA sequences were aligned in EMBL-EBI (<https://www.ebi.ac.uk>) using multiple sequence comparison by log-expectation (MUSCLE).

## 3 | RESULTS

### 3.1 | Environmental conditions

Data obtained from both the time of sampling and collected over the 30-day period preceding the sampling were used in this study to provide a comprehensive framework for a description of links between environmental conditions and lake bacterial communities. During the course of our sampling year—from autumn 2018 to summer 2019—average precipitation values were up to 42 mm in autumn, decreased to 9 mm in winter, rose up to 53 mm in spring and decreased again to 25 mm in summer (Datasheet S2). Average air temperatures (2 m above ground level) changed from 11°C in autumn to 4°C in winter, 17°C in spring and 37°C in summer. Consequently, water temperature followed a similar trajectory with 16, 4, 18 and 32°C for each of the four studied seasons (Datasheet S11). The vertical water temperature difference in autumn, winter and spring was <0.2°C/m (mixed), whereas it was dynamically stratified in summer with a range in temperature differences from 0.1 to 1.3°C/m (Datasheet S12). In the water, the highest N concentration (1.93 mg/L) was found in winter while summer featured the highest TP (0.17 mg/L) (Datasheet S11). High-wind events occurred irregularly in every season (Figure S7). Overall, spring had the most frequent and strong wind events with two days with wind speed up to 20.8 m/s (Datasheet S4). Additionally, wind directions appear to have been more random in spring and summer while mostly facing south in autumn and winter (Figure S8). Every year, fish with weights >2.5 kg—mostly bighead carp and silver carp—are harvested in winter (commonly in January). In January 2018, the biomass of removed fish accounted for 3,150 tons (3.15 t/ha) (Datasheet S5). A few days after fish removal, 58.75 tons (0.06 t/ha) of bighead carp and silver



**FIGURE 2** Alpha diversity, beta diversity and community composition in water and sediment among four seasons. Violin plots showing the observed species (a) and Shannon dominance (b) in water and sediment for each season, showing that sediment has higher observed species and higher Shannon index in every season. PCoA based on Bray–Curtis dissimilarities showing the separation between microbial communities (c). Stack bar charts (d) showing the water and sediment community compositions on phyla level in each season: A, autumn; W, winter; S, spring; S, summer

carp fry were reintroduced into the lake. In July 2018, the biomass of silver carp and bighead carp was estimated using cast nets to be 0.76 t/ha (Datasheet S6). Typically, after growing in summer and hoarding fat in autumn, the fish biomass reached a maximum value of 3.65 t/ha before fish removal in January 2019.

### 3.2 | Distinct bacterial communities in the water and the sediment

Lower richness was found in the number of bacterial ASVs (i.e., taxa) in water (95–456 ASVs) compared to sediment samples (389–752 ASVs) (Figures 2a, S14; Datasheet S7). Likewise, water bacterial communities had lower values of Shannon dominance index (2.9–5.2) than sediment (5.2–6.2) (Figure 2b; Datasheet S7). PCoA plots based on Bray–Curtis dissimilarities revealed distinct water and sediment bacterial communities in terms of community structure (Figure 2c). Pairwise boxplot (Figure S5C) and heatmap (Figure S13) based on Bray–Curtis dissimilarity also indicated high dissimilarities (0.9–1) between water and sediment samples in every season. Overall, water samples were dominated by Actinobacteria, Bacteroidetes, Cyanobacteria and Alphaproteobacteria whereas sediment samples were dominated by Acidobacteria, Bacteroidetes, Chloroflexi and Gammaproteobacteria and Deltaproteobacteria (Figures 2d, 3; Datasheet S8).

Based on the number of ASVs across the entire study period, the sum of ASVs specific to water and sediment was greater than the shared portion and where the former accounted for 68.6% of the total ASVs and 44% of the total number of DNA reads (Figure 4a). A similar trend was detected in the DEseq2 analysis that identified which ASVs were “enriched”—i.e., abundant ASVs in terms of DNA reads proportion—in water or sediment samples; higher numbers of ASVs were found enriched either in water and sediment samples compared to neutral ASVs from both the seasonal and the whole study year’s perspective (Figure 4b; Table 1; Datasheet S10). ASVs affiliated to Proteobacteria, Actinobacteria, Bacteroidetes and Cyanobacteria were enriched (i.e., from two- to 24-fold higher) in water compared to sediment samples. ASVs affiliated to Proteobacteria, Bacteroidetes, Nitrospirae and Acidobacteria were enriched in sediment samples (Table 1). Considering the 10 ASVs with the highest absolute  $\log_2$  fold-change value at each season (9.7–24.3) (Figure S3; Datasheet S10), most of them were found to be enriched in planktonic samples. These latter planktonic ASVs were mainly affiliated to Cyanobacteria (e.g., ASV3, order Chloroplast), Bacteroidetes (e.g., ASV7239, genus *Flavobacterium*), Actinobacteria (e.g., ASV7, genus *CL500-29\_marine\_group* and ASV367, genus *hgcl\_clade*) and Gammaproteobacteria (e.g., ASV210, genus *Polynucleobacter*). In sediment samples, most of the over-represented ASVs were affiliated to Gammaproteobacteria (e.g., ASV303, family Burkholderiaceae), Deltaproteobacteria (e.g., ASV18, genus *Desulfatiglans*) and Firmicutes (ASV4101, genus *Streptococcus*).



**FIGURE 3** Histograms showing (a) the top 20 class abundances and (b) the top 20 ASVs in each water and sediment from the four seasons. For both (a) and (b), blank bars correspond to missing data because of no PCR product

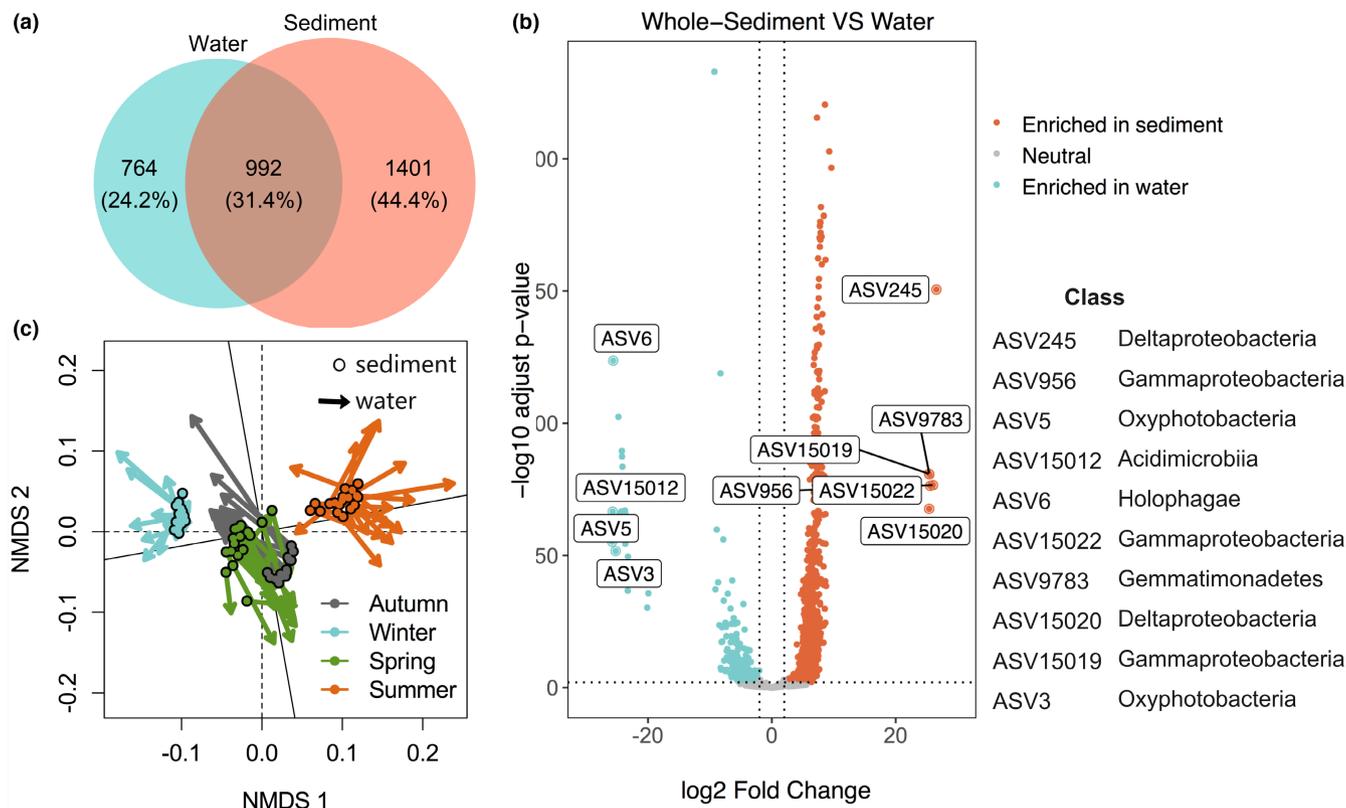
### 3.3 | Seasonal changes in water and sediment bacterial communities

In terms of community composition (Figure 2d) and structure (Figure 2c), the water bacterial community differed notably between seasons whereas the sediment bacterial community remained more stable. Bacterial communities had the lowest ASV richness in winter (water: 117; sediment: 508) and the highest in spring (water: 396; sediment: 688) (Figure 2a). Likewise, the lowest median Shannon index was seen in winter (water: 2.9; sediment: 5.16), with highest levels in autumn 2018 for water (5.19) and spring for sediment (6.19) (Figure 2b).

Distinct bacterial groups were found to dominate water and sediment communities at different times of the year. In autumn, the water had a high representation of Oxyphotobacteria (24%) and Bacteroidia (18%). During the following winter, the community shifted in favour of Alphaproteobacteria (24%), Bacteroidia (20%), Gammaproteobacteria (20%), Actinobacteria (19%), Acidimicrobiia (11%) and Oxyphotobacteria

(5%), which in total accounted for 98.47% of the total community. Subsequently, Oxyphotobacteria (18%) and Alphaproteobacteria (17%) were abundant in spring, and Acidimicrobiia in summer, contributing 46% to the total community. For the sediment bacterial community, Gammaproteobacteria and Bacteroidia were dominant across all seasons, each of them contributing 16%–24% to the total community at all times (Figure 3a; Datasheet S9).

Considering the 20 most abundant ASVs (Figure 3b; Datasheet S13), ASV2 (Alphaproteobacteria, SAR11 clade, subclade III) accounted for 9%, 22%, 13% and 4% of the water community reads in autumn, winter, spring and summer, respectively. ASV3137 (CL500-29 marine group, group acIV-A) was abundant in the summer water samples, representing on average 13% of the total community. In sediment, the ASV2883 (Latescibacteria) and ASV2001 (Ignavibacteria, family BSV26) were abundant across all four seasons with proportions consistently exceeding 5%. ASV15175 affiliated to order *Candidatus* Acidulodesulfobacterales (Sva0485) was highly abundant at sites 15 and 18 (39% and 32%, respectively) in summer.



**FIGURE 4** (a) Venn diagram depicting the number of shared and unique ASVs in water and sediment for the entire study period; (b) the whole period volcano plot obtained from DESeq2 showing ASVs shared or enriched in either sediment or water. (c) Plot of procrustean rotation analysis illustrated the potential seasonal similarities and differences in community structure from water and sediment, the 10 ASVs with the highest  $\log_2$  fold-change were labelled

### 3.4 | Higher similarity between water and sediment bacterial communities in autumn and spring

Water and sediment bacterial communities shared more ASVs in autumn and spring corresponding to a total of 295 ASVs (14% of DNA reads) and 584 ASVs (23.7% of DNA reads) (Figure S4). Pairwise Bray–Curtis dissimilarity boxplots also highlighted that water and sediment communities had higher similarity in their structure in autumn and spring (Figure S5C). A Procrustes analysis revealed significant levels of concordance ( $p < 0.001$ ) between water and sediments samples obtained from specific locations showing links in the diversity and composition of bacterial communities related to their spatial locations in Lake Balihe (Figure 4c). Interestingly, only autumn samples showed a significant level of concordance ( $p < 0.001$ ) when the Procrustes analysis was performed on molecular samples obtained from each season independently. DESeq2 analysis showed that in both autumn and spring, ASVs affiliated with Gammaproteobacteria (e.g., ASV835, family Methylomonaceae in autumn, and ASV9818, genus *Noviherbaspirillum* in spring), Deltaproteobacteria (e.g., ASV931, order SAR324\_clade [Marine\_group\_B] in autumn, and ASV415, order Sva0485 in spring), Bacteroidetes (e.g. ASV338, family AKYH767 in autumn, and ASV2858, species paronense in spring), Actinobacteria (e.g., ASV1027 and ASV7240, genus *CL500-29\_marine\_group* in autumn and spring, respectively) and

Cyanobacteria (e.g., ASV850, genus *Cyanobium\_PCC-6,307* in autumn, and ASV143, genus *Cyanobium\_PCC-6,307* in spring) were most abundant in the pool of ASVs shared between water and sediment (Table 1).

### 3.5 | Summer co-occurrence of firmicutes between water and sediment

A co-occurrence network consisting of 598 nodes (ASVs) linked by 9,319 edges was built from water and sediment samples (Figure 5). A total of six modules were detected in the network. Four modules (0, 1, 2 and 20) were composed mainly of water-enriched ASVs (253 of 364 ASVs), one module (module 39) was composed mainly of sediment-enriched ASVs (135 of 137 ASVs), and the final one (module 7) was composed mainly of neutral ASVs (24 of 30 ASVs). ASVs from module 7 connected the water-ASVs-enriched modules and the “sediment-enriched ASVs” module. This module was composed of 30 ASVs including 12 affiliated with Firmicutes. 11 of the 12 Firmicutes ASVs also were found to be the shared ASVs between water and sediment in summer according to DESeq2 (Table 1), highlighting the ubiquitous distribution of these ASVs in across the lake. Specifically, these ASVs were more abundant in summer samples than in other seasons (Figures 2d, S6), and exhibited a higher

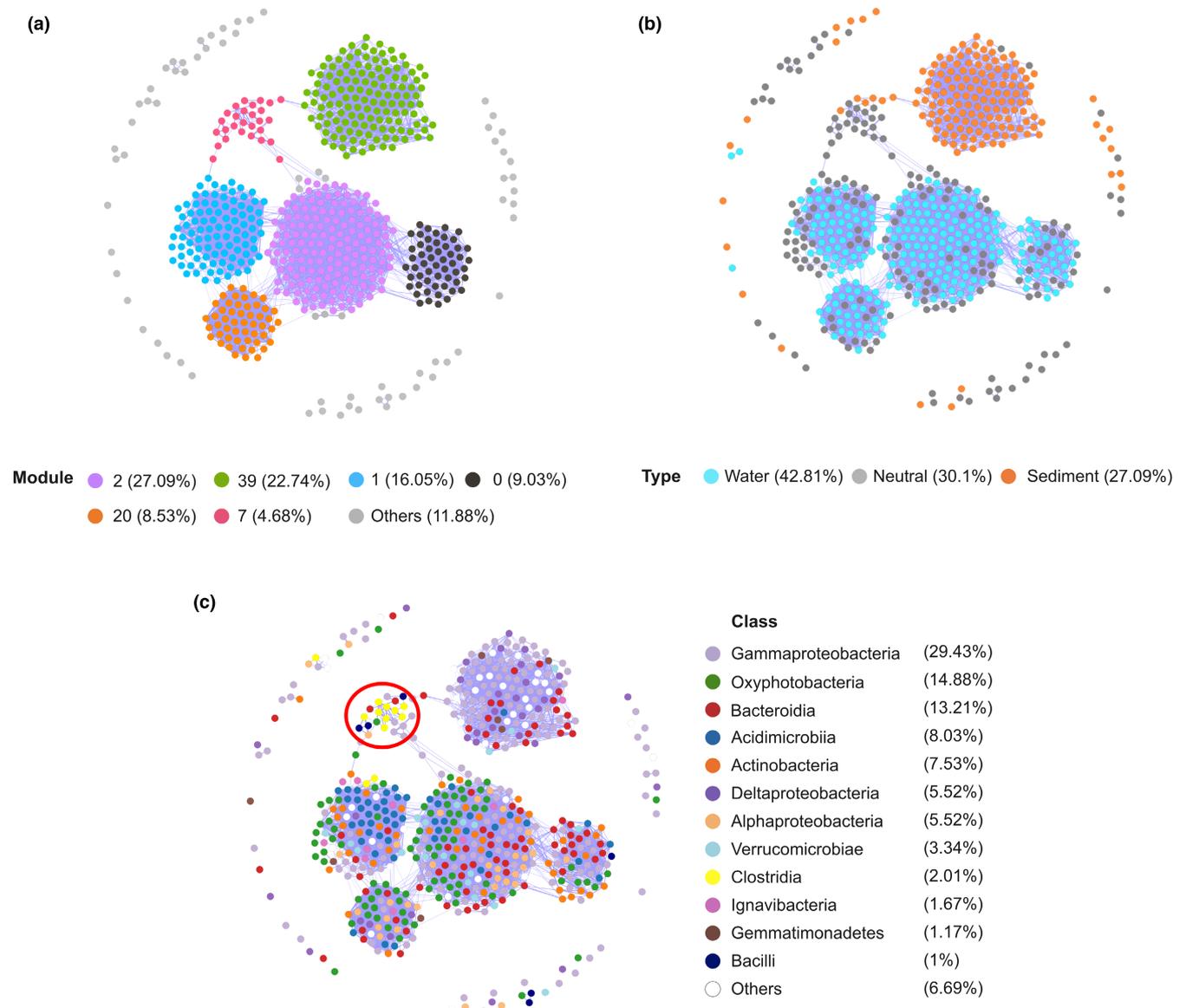
**TABLE 1** DESeq numbers of ASVs and most abundant phyla identified by DESeq2 enriched in different types of samples and their log<sub>2</sub> fold-change ranges in different seasons and the whole study period

Season	Total number of ASVs	Number of ASVs enriched in			Most abundant phyla (number of ASVs and reads) in			log <sub>2</sub> fold-change		
		Water	Sediment	Neutral	Water	Sediment	Neutral	Water	Sediment	Neutral
Autumn	1,164	266 (22.85%)	544 (46.74%)	354 (30.41%)	Bacteroidetes (83 & 20,733), Gammaproteobacteria (49 & 13,436), Cyanobacteria (46 & 27,762), Alphaproteobacteria (29 & 23,620), Actinobacteria (28 & 14,997)	Gammaproteobacteria (134 & 40,089), Deltaproteobacteria (88 & 15,421), Bacteroidetes (112 & 15,607), Nitrospinae (43 & 8,348), Acidobacteria (55 & 7,437)	Gammaproteobacteria (72 & 4,673), Bacteroidetes (65 & 7,201), Deltaproteobacteria (49 & 2,170), Actinobacteria (32 & 38,310), Cyanobacteria (25 & 3,772)	[-23.47, -2.06]	[2.75, 23.43]	[-6.37, 6.90]
Winter	845	117 (13.85%)	460 (54.44%)	268 (31.72%)	Actinobacteria (38 & 39,624), Bacteroidetes (31 & 26,983), Gammaproteobacteria (21 & 17,178), Cyanobacteria (13 & 6,458)	Gammaproteobacteria (108 & 38,131), Bacteroidetes (80 & 13,568), Deltaproteobacteria (77 & 19,132), Acidobacteria (51 & 9,486), Nitrospinae (31 & 7,468)	Gammaproteobacteria (60 & 11,388), Deltaproteobacteria (55 & 3,089), Bacteroidetes (38 & 1874), Actinobacteria (28 & 2,389), Alphaproteobacteria (15 & 1,151)	[-20.50, -4.00]	[4.14, 23.85]	[-6.36, 6.86]
Spring	1,571	368 (29.66%)	643 (40.93%)	560 (35.65%)	Cyanobacteria (68 & 23,362), Gammaproteobacteria (61 & 14,444), Actinobacteria (69 & 38,290), Bacteroidetes (83 & 18,225)	Gammaproteobacteria (156 & 41,718), Bacteroidetes (132 & 20,894), Deltaproteobacteria (109 & 17,548), Acidobacteria (64 & 7,890), Nitrospinae (32 & 6,087)	Gammaproteobacteria (121 & 8,788), Bacteroidetes (98 & 4,983), Deltaproteobacteria (91 & 4,089), Actinobacteria (42 & 2,522), Acidobacteria (41 & 1,511), Cyanobacteria (40 & 3,928)	[-24.25, -2.00]	[2.30, 23.60]	[-6.20, 6.59]

(Continues)

TABLE 1 (Continued)

Season	Total number of ASVs	Number of ASVs enriched in			Most abundant phyla (number of ASVs and reads) in			log <sub>2</sub> fold-change		
		Water	Sediment	Neutral	Water	Sediment	Neutral	Water	Sediment	Neutral
Summer	1,197	180 (15.04%)	504 (42.11%)	513 (42.86%)	Actinobacteria (74 & 91,362), Bacteroidetes (26 & 6,772), Gammaproteobacteria (23 & 5,611), Cyanobacteria (19 & 7,353)	Gammaproteobacteria (103 & 6,405), Bacteroidetes (97 & 16,558), Deltaproteobacteria (81 & 4,287), Acidobacteria (59 & 8,623), Nitrospirae (30 & 7,267)	Gammaproteobacteria (112 & 35,353), Deltaproteobacteria (99 & 19,579), Bacteroidetes (77 & 4,982), Actinobacteria (52 & 2,999), Cyanobacteria (31 & 3,543), Firmicutes (30 & 4,415)	[-23.35, -2.12]	[3.71, 23.30]	[-6.06, 6.59]
Whole	2,857	376 (13.16%)	1,106 (38.71%)	1,375 (48.13%)	Actinobacteria (90 & 166,198), Bacteroidetes (83 & 58,146), Cyanobacteria (60 & 56,303), Gammaproteobacteria (63 & 44,777)	Gammaproteobacteria (254 & 169,053), Deltaproteobacteria (210 & 83,431), Bacteroidetes (204 & 74,129), Acidobacteria (110 & 37,618), Nitrospirae (55 & 30,719)	Gammaproteobacteria (282 & 29,227), Bacteroidetes (237 & 33,603), Deltaproteobacteria (151 & 10,346), Actinobacteria (151 & 33,187), Cyanobacteria (137 & 22,131)	[-25.8, -2.03]	[2.54, 26.58]	[-5.09, 5.54]



**FIGURE 5** Co-occurrence network analysis for the whole year water and sediment ASVs inferred based on the spearman correlation matrix ( $p < 0.05$ ). The results are shown by modules (a), types (b) and class (c). 598 nodes and 9,319 edges formed six modules in the network

proportion in water samples at site 10 (7.2%) and site 17 (6.9%) (Figure 3a). Further identifications of the DNA sequences from these Firmicutes ASVs by BLAST showed 100% sequence identity to sequences from Firmicutes found in human or animal faeces and gut (Datasheet S14).

### 3.6 | Temporal changes in environmental conditions and fish community and their potential impacts on bacterial communities

We evaluated the relationships between the composition of water and sediment bacterial communities and environmental conditions using a suite of statistical tools (Pearson coefficient correlation analysis, *env.fit*, *bioenv*; Datasheet S15; Figures

S9–S12). A total of 15 parameters were significantly correlated to water bacterial community structure ( $p < 0.001$ ) including water temperature, water depth, electrical conductivity, transparency, oxygen, N, P, Al and As concentration. In sediments, the pH, ORP, NaOH-P, Fe, Pb and T-Hg were significantly correlated to the structure of the bacterial community ( $p < 0.001$ ). Amongst those parameters, transparency, N compounds exhibited lower values in the water column in autumn and spring, whereas Pb had high concentrations in sediment during winter. The variation in the structure of the water bacterial community was mainly related to a combination of water temperature, turbidity, TDN,  $\text{NO}_2^-$ -N and TP (correlation 0.86 with the *bioenv* analysis). In sediments, the structure of the bacterial community was linked to concentrations of NaOH-P, OP, Pb, Zn, Fe, pH and ORP (correlation 0.55 with the *bioenv* analysis).

## 4 | DISCUSSION

In line with our initial expectations, bacterial communities in water and sediment from Lake Balihe were clearly distinct in terms of diversity, taxonomic composition and community structure. In terms of differences between seasons and sampling locations, the bacterial community from the water fluctuated more than that of the sediment. We further showed that the water and sediment bacterial communities were more similar in autumn and spring (i.e., had higher taxonomic overlap) than in winter and summer, and had stronger biogeographical concordance. Notably, Firmicutes were found to be more abundant in water and sediment bacterial communities in summer than in other seasons in both water and sediment, and we believe that this may reflect fish dynamics in Lake Balihe.

### 4.1 | Distinct water and sediment bacterial communities: Temporal and spatial patterns

The typically large differences observed between water and localised sediment bacterial communities is likely to be the result of fundamental differences in the local environmental conditions of these contrasting habitats (Hermans et al., 2020; Lindström & Langenheder, 2012; Ren et al., 2019a; Zhang et al., 2021). However, for shallow lakes with frequent and intense mixing events that may increase the exchange of particles and cells between sediments and water, this habitat structuring may be homogenised and less apparent. Nevertheless, the significant dissimilarity between the water and sediment bacterial community composition observed in our work suggest that there is limited exchange between these two lake habitats, a finding in agreement with a previous study for a similar shallow lake (Ren et al., 2019b). Our research also agrees with previous reports of low seasonal variability in sediment bacterial community composition (Moschos et al., 2021; Tšertova et al., 2011; Tšertova et al., 2013) with much stronger seasonal variation in pelagic bacterial community composition (Allgaier & Grossart, 2006; Lima et al., 2016). Compared with sediment communities, the water column is more directly impacted by external episodic disturbances, such as rainfall (Andersson et al., 2014), environmental impacts (Rösel et al., 2012), storms and strong winds (Jones et al., 2008), solar radiation (Pérez & Sommaruga, 2007) and anthropogenic impacts (Zhang et al., 2020). In line with this, dramatic shifts in aquatic bacterial community composition have been demonstrated in response to changes in environmental conditions (Dupont et al., 2014; Wang et al., 2018; Winter et al., 2007). Moreover, the turnover of pelagic bacterial communities is typically fast whereas sediment bacteria represent a much larger biomass and are turned over more slowly (Langerhuus et al., 2012; Pommier et al., 2012). Consequently, the seasonal and spatial variation of the proportion of the dominant bacterial populations in the water is significantly higher than that in

the sediment. Noticeably, in our study the relative abundance of Actinobacteria fluctuated over the year in the water column with shifts in the dominant ASVs, which is in agreement with findings of an earlier study (Warnecke et al., 2005), and may reflect contrasting sensitivity to solar UV, bacterivory or other seasonal drivers of the different subclades of the *acl* lineage. The proportion of Oxyphotobacteria also varied significantly over the year in the water samples as observed previously (Chun et al., 2021; Zhou et al., 2021). In the sediment, Gammaproteobacteria and Bacteroidetes were always dominant in our and previous studies (Brunet et al., 2021; Marshall et al., 2021). In summer, *Candidatus Acidulodesulfobacterales* (Sva0485) were found at large proportions at two sediment sites; this could be explained by the nearby release of fertilisers used to farm lotus and containing sulfate and Fe compounds, both previously being found to enhance the abundance of Sva0485 members (Tan et al., 2019).

In traditional ecological theory, variability in environmental conditions across space and time represents habitat heterogeneity, which is thought to determine species diversity and the composition in communities (Cornell & Lawton, 1992; Emily et al., 2017; Tilman, 1999). Van der Gucht et al. (2007) provide evidences that species sorting in response to local environmental factors is a key determinant of the taxon composition of aquatic bacterial communities over a very broad range of spatial scales (<100m to >1,000km) and the main factors controlling bacterial community composition were nutrients (e.g., N compounds) and grazing-related factors (e.g., zooplankton biomass). Likewise, DO and  $\text{NO}_3^-$ -N and  $\text{NO}_2^-$ -N concentrations were found to be highly correlated to variation in bacterial community composition within and across seasons (Shade et al., 2007). Water temperature (Yu et al., 2014) and P concentrations (Ren et al., 2019a) also have been coupled to structural shifts in bacterial communities. In our study, the spatial variability in the water bacterial community appeared to be interactively influenced by water temperature, turbidity, TDN and  $\text{NO}_3^-$ -N, and P concentrations, whereas relationships with environmental parameters measured in sediment and the resident bacterial community in this habitat were less clear and varied less across the yearly cycle or spatially within the lake.

### 4.2 | Environmental factors driving the seasonal changes in homogenisation between water and sediment bacterial communities in Lake Balihe

We further considered stratification, wind mixing and fish activities as potentially strong influential factors driving the seasonal dissimilarity in bacterial community composition and diversity between water and sediment.

Stratification previously has been reported to strongly influence bacterial communities by creating physical barriers and chemical gradients along the depth profile of the water column, in particular at the thermo- and/or chemocline whenever present (Garcia

et al., 2013; Peura et al., 2012). Although such stratification is less apparent or persistent in shallow lakes (mean depths 3–4 m) heating and cooling of shallow water columns frequently cause weak stratification (Phillips, 2005). Lake Balihe is considered to have weak thermal stratification during daytime in summer according to Boegman et al. (2008) who described weak thermal stratification as a gradient of water temperature ( $\Delta T$ ) versus depth ( $\Delta z$ ), i.e.,  $\Delta T/\Delta z = 0.1\text{--}1.5^\circ\text{C}/\text{m}$ . Such thermal stratification slows down the transport of DO and particulates from the upper water column to the lower water column and sediment (Zhang et al., 2015), thus creating heterogeneity in microbial communities along vertical water profiles (De Wever et al., 2005; Liu et al., 2016). DO previously was identified as an important factor shaping the microbial community composition in more stably stratified lakes (Garcia et al., 2013), and although there were small vertical gradients in water temperature in our study, there were strong gradients in DO (0.9–71.8%/m or 0.06–5.08 [mg/L]/m). This detected stratification could explain the higher dissimilarity in bacterial communities in the surface water and the underlying sediments in summer.

Mixing is an important structuring factor for freshwater bacterial communities (Shade et al., 2011) and it has been linked to annual “resetting” of bacterial communities along seasonal trajectories (Nelson, 2009; Shade et al., 2007). In shallow lakes, wind-induced waves are among the most evident and frequent natural disturbances (Shao et al., 2013). Especially in shallow lakes such as Lake Balihe with few rooted macrophytes (vascular plants), mixing can easily reach to the bottom of the lake with enhanced sediment re-suspension as a result (Barko & James, 1998; Herb & Stefan, 2005; Madsen et al., 2001). A previous study reported that in the lake centre of Lake Taihu, moderate wind (3.3–5.0 m/s) could cause strong mixing of the water column and sediment re-suspension during almost two-thirds of the year (Zhang et al., 2003). Sediment re-suspension can be an important mechanism for the exchange of organic matter and attached bacteria between sediments and overlying water (Hopkinson, 1985). In our study, spring was the season with the strongest and most frequent wind events and the shallowest water column (1.67 m on average). In this period, Lake Balihe was readily mixed with great potential for exchange of particle-associated bacteria between water and sediment. Shao et al. (2013) previously reported for a shallow lake that resuspended sediment bacteria remained in the water column for >4 days after wind-driven re-suspension had ceased. The same situation would apply to the autumn in our study when the wind also was frequent and strong. In autumn, yet another factor could have a significant impact on the homogenisation of bacterial communities in the lake—fish migration. With uniform temperatures and oxygen levels in autumn, large quantities of farmed fish are found throughout the lake. After the summer growing season there is a large standing stock of adult fish and we hypothesise that their migration across the lake will mix the water column and resuspended sediment, thus contributing to homogenisation of sediment and water bacterial communities.

### 4.3 | Firmicutes dynamics in Lake Balihe and the potential link to fish farming

In the present study, Firmicutes were relatively abundant both in water and in sediment—in summer more than in the other seasons and especially at the sampling sites where high fish biomass was reported (e.g. site 10). In addition, Firmicutes ASVs shared by water and sediment in summer were prominent features in the co-occurrence network. These Firmicutes ASVs were identical to representatives from gut or faecal bacterial communities. Some earlier studies also showed that several bacterial lineages detected in our study (e.g., genera *Enterococcus* and *Romboutsia*) are found in the fish gut or fish faecal matter (Devriese & Pot, 1995; Geldreich & Kenner, 1969; Li et al., 2018; Ramírez et al., 2018). Moreover, summer is the major feeding and growing season for many subtropical fish species and especially for bighead carp and silver carp (Kolar et al., 2005) found in Lake Balihe. Thus, we suggest that these Firmicutes ASVs may be indicators of fish faecal inputs to the water. It previously was shown that dispersal of microbiomes can be operated across divergent systems and community types (Custer et al., 2022). Faecal bacteria from humans and animals are reported to attach to particles in water column for subsequent sedimentation and burial in sediments (Bai & Lung, 2005; Ferrante & Parker, 1977; Fries et al., 2006; Gao et al., 2011; Thupaki et al., 2013). Consequently, in Lake Balihe where fish faecal inputs are supposedly abundant in summer, the transport of fish faecal bacteria may contribute to the homogenisation of bacterial communities across water–sediment interfaces. This may explain why water and sediment bacterial communities are more similar in those areas (e.g., downstream lake and the places near the bridge and the dock) where fish aggregated in summer. The meta-gut concept proposed by Dutton et al. (2021) addressed the ability of the gut microbiome released from an animal to function outside the host and alter biogeochemical processes mediated by microbes. Their study focused on hippopotamus but may occur for other aquatic species, providing support for the hypothesised fish–microbial links presented in our study.

## 5 | CONCLUSION

In this study, 16S rRNA gene amplicon sequencing, multivariate statistical analyses and ecological networks were used to investigate the spatiotemporal variation of water and sediment bacterial communities in a shallow subtropical fish-farming lake in middle-eastern China. Water and sediment bacterial communities had a higher similarity and a stronger biogeographical concordance in autumn and spring, even though they were distinct from each other. Homogenisation of the water and sediment bacterial communities were related to seasonally-changing environmental factors such as water temperature, turbidity, N and P concentrations and meteorological factors (wind and solar radiation). The large biomass fish-farming activities in the lake also appear to influence resident

bacterial communities of Lake Balihe and this may apply also to other freshwater ecosystems with high fish stocks. Our study contributes to the understanding of bacterial biogeography in lakes and factors affecting the distribution of bacterial communities and provides inspiration for further studies of mixing dynamics and linkages between bacterial communities in water and sediment habitats.

#### AUTHOR CONTRIBUTIONS

MZ, HZ, ZW, WT and TH conceived the study; MZ, ZW, WT and TH conducted field work; MZ and EC performed all data analyses; MZ, SB, EC, HZ and HH contributed to data interpretation; MZ drafted the manuscript with guidance and revisions from SB, EC and HH; and all authors contributed to the final version of the manuscript.

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#### CONFLICT OF INTEREST

The authors declare no conflict of interest.

#### DATA AVAILABILITY STATEMENT

Raw sequence reads were deposited in FigShare (DOI: <https://doi.org/10.6084/m9.figshare.16566498>). Supplementary materials were deposited in FigShare (DOI: <https://doi.org/10.6084/m9.figshare.21353424>).

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