



## Original Articles

## Co-occurrence patterns and assembly processes of abundant and rare bacterioplankton in plain river network areas of eastern China

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## ABSTRACT

In the context of anthropogenic impacts on riverine ecosystems globally, understanding the response of bacterioplankton to anthropogenic stress is important for human and environmental health. Bacterioplankton communities are critical for maintaining ecosystem stability, but little is known about their co-occurrence networks and assembly processes in intense human-impacted plains river networks. By applying cooccurrence networks, variance partitioning, and null model analysis, we investigated the mechanisms of interaction and assembly of abundant (>1% relative abundance) and rare (<0.01%) taxa at 32 sites in river networks along an urbanization gradient (urban, suburban, and agricultural areas). Our results show that interactions between the bacterioplankton communities were more complex in urban areas than in other areas, and that environmental factors (primarily fluoride, nitrate nitrogen, and dissolved organic carbon) as well as spatial factors (i.e., Moran's Eigenvector Maps) explained most of the variation in bacterioplankton communities. Abundant taxa showed stronger spatial turnover than rare taxa, indicating that spatial factors played a greater role in the assemblage of abundant taxa. Land use types, especially impervious surfaces, had a unique influence on rare taxa, but contributed less to community change than other factors. In addition, rare taxa were mainly influenced by deterministic processes, whereas abundant taxa were more influenced by stochastic processes, especially in agricultural areas. These findings suggest that the shares of abundant and rare taxa mediate disturbances in local environmental conditions in anthropogenic river network areas, while deterministic processes play a greater role in shaping bacterioplankton communities. Overall, our study provides important insights for environmental monitoring and management in areas of intense human activity, emphasizing the need to consider both abundant and rare taxa when assessing the impact of human activities on riverine ecosystems.

## 1. Introduction

The plain river network area is dominated by plains and features a densely distributed water network with a high population density, a high urbanization level, and a long history of agricultural cultivation (Ren et al., 2022). As a result, it inevitably leads to significant industrial and agricultural as well as domestic drainage inputs to the river (Chen et al., 2018b; Shu et al., 2020; Yan et al., 2019). This is not only directly

changing the water chemistry of water bodies, but also directly imports pathogenic microorganisms, etc., causing serious impacts on the species composition and ecological balance of aquatic ecosystems (Wu et al., 2022; Xu et al., 2018; Zhao et al., 2021). Bacterioplankton are an important part of aquatic ecosystems, and they play an important role in river biogeochemical cycles (Falkowski et al., 2008), degradation of pollution (Mo et al., 2021), and are sensitive indicators of changes in their ambient environment (Liao et al., 2020). Therefore, investigating the characteristics of bacterioplankton in rivers strongly disturbed by

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Nomenclature	
<i>Index of Notations and Abbreviations</i>	
<b>Biological analysis</b>	
ASV	Amplicon Sequence Variant
ddH <sub>2</sub> O	double-distilled water
dNTPs	deoxynucleoside triphosphates
rDNA	ribosomal genes
PCR	Polymerase Chain Reaction
<i>Indices</i>	
B	Levins' niche breadth index
βNTI	weighted beta nearest taxon index
GDP	gross domestic product
RC	Raup-Crick dissimilarity coefficient
<i>Statistical analysis</i>	
FDR	false discovery rate
MEM	Moran eigenvector maps
RDA	Redundancy analysis
VIFs	Variance inflation factors
VPA	Variation partitioning analysis
<i>Water chemical variables</i>	
Cl <sup>-</sup>	chloride
DO	dissolved oxygen
DOC	dissolved organic carbon
EC	electrical conductivity
F <sup>-</sup>	fluoride
NH <sub>4</sub> -N	ammonium nitrogen
NO <sub>x</sub> -N	nitrite and nitrate nitrogen
PO <sub>4</sub> -P	phosphate phosphorus
SO <sub>4</sub> <sup>2-</sup>	sulphate
TN	total nitrogen
TP	total phosphorus
<i>Places name</i>	
WCXY	Wuchengxiyu, an individual hydrodynamic system
NCBI	National Center for Biotechnology Information

human activities is important for understanding the level of anthropogenic stress on aquatic ecosystems.

Bacterioplankton communities are shaped by deterministic and stochastic processes and are decomposed into four processes in Vellend's (2010) conceptual framework of assembly: selection, dispersal, diversification, and drift. The deterministic or niche-based processes are related to selection; the stochastic or neutral processes that influence community composition are related to the rate of dispersal. There have been studies on the assembly processes of bacterioplankton communities in plateau rivers (Wang et al., 2021) and hilly rivers (Zhang et al., 2022), where either stochastic or deterministic processes were dominant. However, relatively few studies have been conducted on the mechanisms of microbial community assembly in plain river network areas. In addition, bacterioplankton communities, including abundant and rare taxa, dynamically adapt to their ambient environment (Guo et al., 2019). There is clear evidence that anthropogenic activities can directly add and remove species and constitute rare species—a large number of rare taxa with low abundance; simultaneously, rare species are derived from the shift of abundant species, i.e., a few high-abundance taxa (Jiao et al., 2017; Mo et al., 2021). Therefore, we hypothesized that rare species in plain river network areas, which are less affected by the dispersal of water bodies, exhibit deterministic processes related to adjacent human activities. One study reported that rare taxa were more susceptible to deterministic processes because of their restricted distribution (Dang et al. 2022); while another study suggested that rare taxa are more susceptible to stochastic processes because they avoid active loss from viral lysis and predation (Wang et al. 2021). These studies do not agree on the mechanisms underlying the assembly processes of abundant and rare taxa, nor do they provide insight into the mechanisms of species interactions.

Network analysis of interactions between taxa (i.e., co-occurrence patterns) provides new insights into the structure of microbial communities (Hu et al. 2017; Wu et al. 2022; Zhang et al., 2022). Network topological properties can be used to identify the relevant substructures within the network by examining the arrangement of nodes and edges to understand ecological cooperation, competition, exploitation, commensalism, and amensalism, thus to better understand the stability of riverine ecosystems (Coyte et al., 2015). On the one hand, the input of domestic sewage and agricultural drainage into the river increases the concentration of pollutants in the river, and species show more cooperation in decomposing the pollutant (Jiao et al., 2017; Mo et al., 2021). On the other hand, due to the allochthonous bacterial input throughout

in sewage, they compete with indigenous species in the river for resources and show competition and predation relationships (Liao et al., 2020; Wu et al., 2022). However, we still do not have a clear understanding of the interactions between riverine microorganisms in the plain river network. We hypothesized that there are more cooperative relationships between species in urban areas than others. Interactions among bacterioplankton taxa are visualized using the co-occurrence network approach (Dang et al. 2022; Wang et al. 2021), but understanding the assembly processes of abundant and rare taxa under the intense human activities remains a challenge.

In the lower reaches of Asia's longest river, Yangtze River, Taihu Lake basin supports >30 million people engaging in agriculture and industry (W.W.F., 2019), providing an ideal system to address the microbial ecology questions under intense human pressure (Kuriqi et al., 2020, Tomczyk et al., 2022). Wuchengxiyu (WCXY, an individual hydrodynamic system) has the most typical plain river network system in the Taihu Lake basin. In this economy-rich and water-rich region, protecting water quality is of fundamental significance to guarantee public drinking water safety, so environmental conditions have been extensively assessed (Niu et al., 2018; Wu et al., 2019; Xu et al., 2018; Zhang et al., 2022), but few studies have been conducted to profile the mechanisms of bacterioplankton community composition. Thus, we sampled water along different gradients of urbanization (urban, suburban and agricultural areas) and aim to 1) characterize the interactions between abundant and rare taxa by co-occurrence networks and 2) provide an analyses framework to extend the understanding of ecological processes driving bacterioplankton communities. Our findings may serve as an important insight into bacterioplankton communities in highly urbanized riverine areas.

## 2. Materials and methods

### 2.1. Description of the study area and measurement of water chemistry

River network area widely distributed in the lower reaches of river, dominated by plain. Wuchengxuyu (WCXY) hydrodynamic zone is the most typical plain river network system with an area of 4 016 km<sup>2</sup> among the eight hydrodynamic zones with different flow characteristics in the Taihu Lake Basin. WCXY has a relatively flat topography (elevation: 2.8–6 m) and a high river network density (3.0 km/km<sup>2</sup>). It is located on the south bank of the Yangtze River, the longest river in Asia, and connects to the northern part of Taihu Lake (Fig. 1), making it an

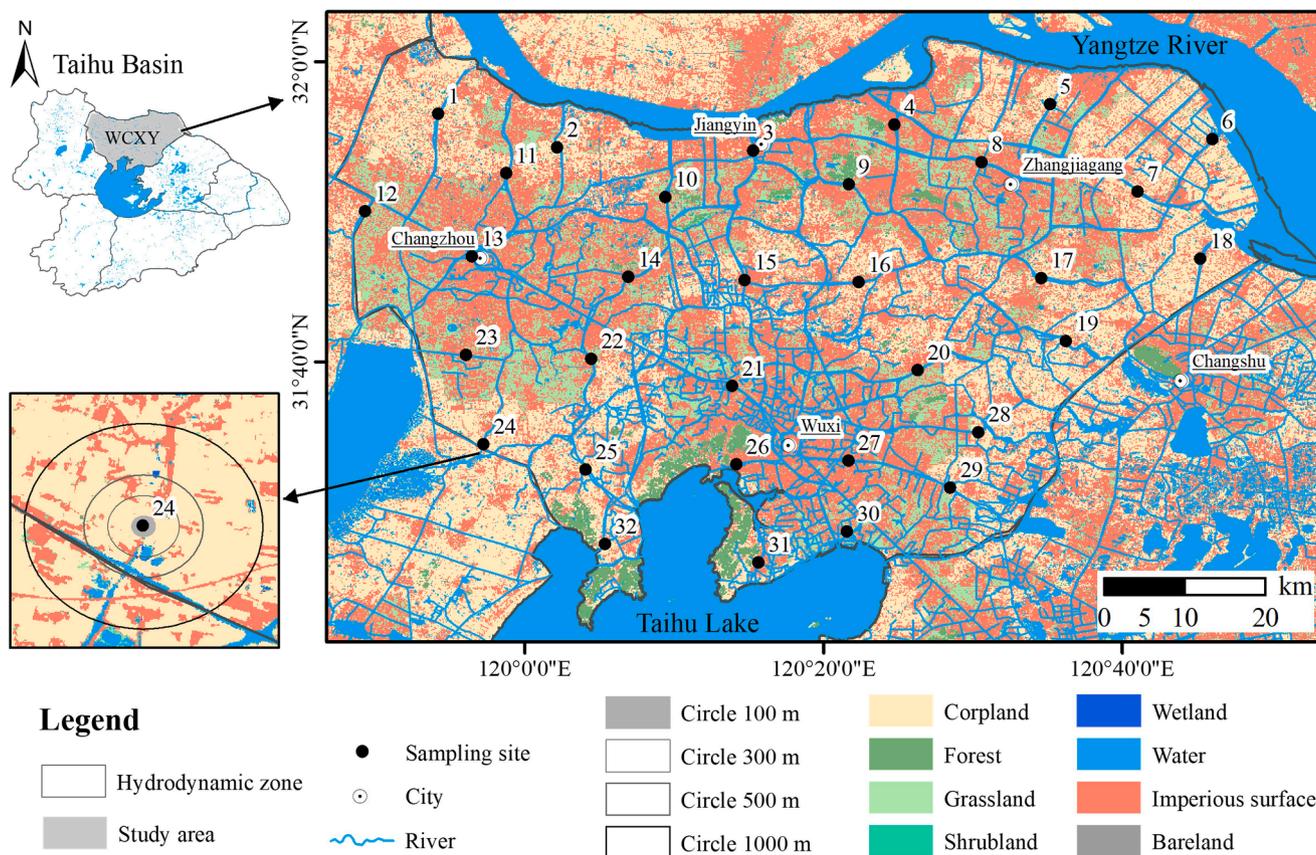


Fig. 1. Study area, sampling sites, land use types, and circular buffer zone.

important hydrodynamic zone for ensuring water quality in the Yangtze River and Taihu Lake. Five highly urbanized cities (Changzhou, Jiangyin, Zhangjiagang, Changshu, and Wuxi) in the WCXY have large populations (average population density of 1 251 people/km<sup>2</sup>) engaged in industry and agriculture and made a large contribution to GDP growth (gross domestic product: 3 445.36 billion RMB) (Fig. S1). Rapid urbanization and industrialization have greatly deteriorated the water quality of river, especially in winter (the worst of time) (Wu et al., 2018). The slow velocity of the rivers contributed to the retention of pollutants, bringing more attention to the comparison of different sites in the plain river network systems (Zhang et al., 2020).

Our sampling design aimed to cover the whole plain river network system. Thus 32 sampling sites were evenly distributed across WCXY based on accessibility (December 2021, Fig. 1 and Table S1). Precipitation and water levels were the lowest of the year, and no extreme weather occurred<sup>1</sup> during the sampling period. There was no evidence of large-scale agricultural activity at this time of year. During such periods of hydrological inactivity (i.e., no rainfall/water flow), it is possible to highlight non-runoff associated river-elevation increase and ignore the intrusion of agricultural non-point source pollution. Thus, it was helpful in confirming our observed and analyzed biological interactions efficiently.

Surface water samples were collected (0.5 m below the surface water approximately) in triplicate at each sampling site from the bridge by sterilizing the water sampler (Suzhou Aire Instruments Co., Ltd., China). Dissolved oxygen (DO), pH, and electrical conductivity (EC) were measured with Y86031 probe (YHequipment Co., Ltd, China) in situ. Three 1 L sterile polyethylene bottles carried the samples in triplicate and then pooled them into one sample. All samples were at the low

temperature of 0–4 °C and transported to an adjacent laboratory for processing within four hours of collection.

Water samples from each site were separated into four 50 ml sterile centrifuge tubes: (1) one for chloride (Cl<sup>-</sup>), sulfate (SO<sub>4</sub><sup>2-</sup>), and fluoride (F<sup>-</sup>), measured by ion chromatography (Dionex ICS2100, United States); (2) one for dissolved organic carbon (DOC), measured by total organic carbon auto-analyzer (Shimadzu TOC-L CPH, Japan); (3) one for ammonium nitrogen (NH<sub>4</sub>-N), nitrite and nitrate nitrogen (NO<sub>x</sub>-N), and phosphate phosphorus (PO<sub>4</sub>-P); (4) one for total nitrogen (TN) and total phosphorus (TP) analysis. (3) and (4) were measured by the continuous flow automated analyzer (San++, Skalar, Netherlands). Except for those analyzed for TN and TP, water samples were filtered through 0.45-μm glass fiber filter (diameter 25 mm, China) were used to filter.

## 2.2. Land use data

Rivers in WCXY have bi-directional currents due to a combination of natural discharge, tidal effects, and anthropogenic management; therefore, a circular buffer zone around each sampling site was considered the most crucial terrestrial land use environment in this study area (Deng, 2019). Buffer distances of 100, 300, 500, and 1000 m were set to determine the most effective buffer zone for the bacterioplankton community. ArcToolbox in ArcGIS (v 10.2) software was used to calculate the proportion of land use types within the four circular buffer zone around the 32 sampling sites.

Land use data with a spatial resolution of 10 m were derived from Sentinel-2 satellite imagery<sup>2</sup> (Fig. 1). After comparing several spatial image classification datasets and images from Google Earth, this land use data accurately reflects the land use within circular buffer zone

<sup>1</sup> <https://jsssl.tjsgsu.gov.cn/>.

<sup>2</sup> <https://data.ess.tsinghua.edu.cn/>.

around each sampling site. Land use data were aggregated into eight categories: cropland, forest, grassland, shrubland, wetland, water, imperious surface, and bareland. For effective and easy analysis of land use data, shrubland and grassland were combined as “Grassland” because of the relatively low proportion of shrubland; wetland and water were combined as “Water” because of the relatively low proportion of wetland; bareland was not considered into further analysis because the proportion was <0.05%. To further effectively compare and analyze the role of human activities in the WCXY, where human disturbance is greater than the environmental gradient, the 32 sampling sites were classified into three types of areas based on the proportion of land use within the circular buffer (Fig. S2), i.e., urban areas (n = 8, No. 3, 4, 13, 14, 15, 21, 27, 31; impervious surface exceeded 70%), suburban areas (n = 10, No. 8, 9, 10, 11, 12, 20, 22, 23, 26, 30; mixed forests and wetland parks), and agricultural areas (n = 14, No. 1, 2, 5, 6, 7, 16, 17, 18, 19, 24, 25, 28, 29, 32; cropland exceeded 50%). This classification was proposed with reference to previous descriptions (Huang and Huang, 2019; Wu et al., 2022; Zhou et al., 2020), combined with our observations in situ.

### 2.3. DNA extraction and sequencing data processing

Samples (1L water) were filtered through a 0.22- $\mu$ m membrane filter (50 diameters, China) to collect microbial cells and through several filters simultaneously to reduce filtration time. Collected samples were stored in sterile centrifuge tubes at  $-80^{\circ}\text{C}$  until DNA extraction.

DNA extraction was performed on 32 samples using E.Z.N.A.<sup>®</sup> Soil DNA Kit (Omega Bio-Tek, United States) according to manufacturer’s protocol. All DNA samples were quality-checked using NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, United States). The extracted DNA samples were amplified by forward primer 338F(5'-ACTCCTACGGGAGGACAGCAG-3') and reverse primer 806R(5'-GGACTACHVGGGTWTCTAAT-3') to amplify the V3-V4 gene fragments of 16S rDNA, i.e., Polymerase Chain Reaction (PCR, ABI GeneAmp<sup>®</sup> 9700, United States). The amplification program was as follows: pre-denaturation at  $95^{\circ}\text{C}$  for 3 min, 27 cycles (30 s at  $95^{\circ}\text{C}$ , 30 s at  $55^{\circ}\text{C}$ , and 45 s at  $72^{\circ}\text{C}$ ), stable extension at  $72^{\circ}\text{C}$  for 10 min, and then stopped after cooling down to  $10^{\circ}\text{C}$ . PCR reaction system:  $5\times$  *TransStart* FastPfu buffer, 4  $\mu\text{L}$ ; 2.5 mM deoxynucleoside triphosphates (dNTPs), 2  $\mu\text{L}$ ; forward and reverse primers (5  $\mu\text{M}$ ),  $2\times 0.8$   $\mu\text{L}$ ; *TransStart* FastPfu DNA Polymerase, 0.4  $\mu\text{L}$ ; 10 ng template DNA make up 20  $\mu\text{L}$  using double-distilled water ( $\text{ddH}_2\text{O}$ ). The size of the amplicons was verified by 2% agarose gel electrophoresis. Sequencing data were generated by Illumina MiSeq platform PE3000 and uploaded to NCBI Sequence Read Archive (accession number: SRP356578).

MiSeq sequencing had paired-end sequence data. First, sequences were merged and quality filtered to denoising using fastp (v 0.19.6) and FLASH (v 1.2.11) software, respectively (Magoč and Salzberg, 2011; Chen et al., 2018a). Further process was needed to remove error profiles that occurred in the process of quality filtering by the method of DADA2 (Callahan et al., 2016). Real sequence information (ASV, Amplicon Sequence Variant) could be obtained, and an ASV abundance table was constructed. Classify-sklearn (Naive Bayes) was implemented to perform taxonomic assignment of ASVs in Qiime2 program and SILVA release 138 (Bolyen et al., 2019).

Abundant and rare taxa were clarified by previous method: abundant taxa consisted of ASVs with relative abundance >1% within one sample; rare taxa consisted of ASVs with relative abundance <0.01% within one sample (Mo et al., 2018). We further referred to the database of potential pathogens summarized by previous studies to determine the impact of allochthonous inputs (Fang et al., 2018; Liu et al., 2018; Shu et al., 2022).

### 2.4. Network analysis

The co-occurrence network was used to identify the complex

interactions among the bacterioplankton communities based on their strong correlation between identified ASVs (Newman, 2006). All robust correlations determined by pairwise comparisons of genus abundance form a correlation network. Each node represented one genus and each edge represented a strong and significant correlation between nodes. Corrections for multiple comparisons were performed for Spearman’s rank correlations using the “WGCNA” (v 1.72–1) package (Langfelder and Horvath, 2008). All *p*-values for multiple testing using the false discovery rate (FDR) correction control procedure in the “multtest” (v 2.54–0) package (Benjamini and Hochberg, 1995). Based on the correlation coefficients and the FDR-adjusted correlation *p*-values, we constructed co-occurrence networks. Co-occurrence events were identified with statistically robust correlations ( $p < 0.05$ ,  $|r| > 0.75$ ) (Junker and Schreiber, 2011). The topological properties of the network include degree (connections to other nodes), betweenness centrality, closeness centrality, eigenvector centrality clustering coefficient, path distance, density, and modularity (Bastian et al., 2009). Obtained networks were visualized in Gephi (v 0.9.2).

### 2.5. Statistical analysis

ASV abundance data were normalized to the smallest sequence number. Normality of the data was assessed using the Shapiro-Wilk test before analyzing the significant differences of the data among the three types of regions. Data that did not follow the normal distribution after transformation were analyzed using the nonparametric Kruskal-Wallis rank sum test ( $p < 0.05$ ). Unless otherwise stated, all statistical analyses were performed in R (v 4.1.3) (R Core Team, 2019).

A detailed description of statistical analysis procedure was provided in (Zhao et al., 2021), which use multiple functions to select variables and avoid strong co-variation. We followed Lai et al. (2022) to extent this procedure i.e., by using variation partitioning analysis (VPA) to examine the respective role of environmental and spatial factors on bacterioplankton communities. This analysis used the “varpart” function to partition community variation in “rdacca.hp” (v 1.0–8) package (Lai et al., 2022). The procedure is as follows.

Environmental and spatial factors were used as explanatory variables to explain the turnover of the planktonic bacterial community. Geographic distance was calculated with the “geosphere” (v 1.5–14) package to identify the spatial turnover rate of the community (Hijmans, 2021). The spatial locations of the sampled sites were analyzed using Moran eigenvector maps (MEM) to produce a set of orthogonal spatial eigenvectors as spatial factors, calculated using the “dbmem” function of the “adespatial” (v 0.3–16) package (Dray et al., 2006). Prior to MEM, the positions of the 32 sampling sites were transformed in Cartesian coordinates by the “geoXY” function in the “SoDA” (v 1.0–6.1) package (Chambers 2022).

Redundancy analysis (RDA) was performed to determine the relationships between abundant taxa and environmental factors, i.e., water chemistry and land use, with CANOCO 4.5 software (Ter Braak and Smilauer, 2002). Prior to RDA, spearman correlation analysis determined the correlation between the water chemistry for co-linearity. Variance inflation factors (VIFs) were then used to evaluate multicollinearity of multiple regression models for water chemistry and sequentially exclude water chemistry with VIFs >3. Bioenv analyses were performed to identify how well environmental factors explained the bacterioplankton communities. Both VIFs and Bioenv were calculated by the “vegan” (v 2.5–7) package (Clarke and Ainsworth, 1993).

The most important environmental factors of bacterioplankton communities were identified by Bioenv and RDA to construct a matrix of water sample properties for the VPA. This was the statistical analysis procedure. In VPA, the conditional effect of water chemistry was considered as deterministic processes and other parts as stochastic processes (Shu et al., 2020). To further discern the relative contribution of deterministic and stochastic processes in shaping the bacterioplankton communities, Null modeling methods were used (Stegen

et al., 2013). These methods coupling phylogenetic signal in habitat with randomization procedures (Stegen et al., 2015). To quantified phylogenetic information within each sample, weighted beta nearest taxon index ( $\beta$ NTI) was calculated in combination with the Bray-Curtis-based Raup-Crick (RC) dissimilarity coefficient using the “vegan”, “ape” (v 5.6–2), and “picante” (v 1.8.2) package. A mean  $\beta$ NTI value less than  $-2$  or greater  $+2$  across all pairwise comparisons suggest deterministic processes while a value between  $-2$  and  $+2$  is considered to signify the influence of stochastic assembly; homogenizing dispersal dominated the assembly process of communities with RC values varying less than  $-0.95$ ; dispersal limitation dominated the assembly process of communities with RC values greater  $+0.95$ ; drift processes dominated the assembly process of communities with RC values between  $-0.95$  and  $+0.95$  (Zhou and Ning, 2017). Phylogenetic distance between taxa approximates their ecological niche difference, which was relied on to infer relative influence of ecological process. Levins’ niche breadth (B) index was calculated to present habitat specialization of abundant and rare taxa in three types of areas with “spaa” (v 0.2.2) and “EcolUtils” (v 0.1) package (Levins, 2020).

### 3. Results

#### 3.1. Taxonomic compositions

The rarefaction curves reached saturation levels (Fig. S3), and 373 622 high-quality reads were clustered into 4 339 ASVs in 32 water samples. Species accumulation curves indicated a near-saturation of species recovery at each sampling site (Fig. S4). The taxonomic assignment of these representative ASVs revealed bacterial taxa from 40 phyla, 117 classes, 282 orders, 467 families, and 847 genera. At phylum level, Proteobacteria was dominant (44.5%), followed by Actinobacteria (28.1%), Bacteroidota (14.1%), Cyanobacteria (7.0%), Campilobacterota (1.6%); these top 5 phyla constituted 95.3% of the total ASVs (Fig. 2A). A high proportion of 80.43% of ASVs (3 489 ASVs) were rare taxa — 0.76% of the average relative abundance per sample; a low

proportion 0.37% of ASVs (16 ASVs) were abundant taxa — 71.92% of the average relative abundance per sample (Fig. 2B). The proportion of the abundant (mean = 72.84%, 69.7%, 72.97%) and rare taxa (mean = 0.89%, 0.89%, 0.58%) had no significant difference among three types of areas (Fig. 2B and Fig. S5). Abundant taxa consisted of 3 phyla and 13 genera, not covering any potential pathogens (Fig. 2C and D; Table S2); potential pathogens were observed only in rare taxa accounting for 0.86%–28.48% of the sites (Fig. S6A).

#### 3.2. Distribution of diversity and co-occurrence patterns in bacterioplankton communities

Diversity of rare taxa with lower abundance was significantly higher than abundant taxa (Fig. 3A). Abundant taxa in urban areas had lower mean number of observed species than those in other areas, while rare taxa in urban areas had higher mean number of observed species than those in other areas. Although there were no significant differences in number of observed species among three types of areas, the values showed significant differences between agricultural areas and urban/suburban areas for potential pathogens (Fig. S6B).

Interactivity with bacterioplankton community was visualized by co-occurrence network and had significant differences between the different type of areas as measured by the number of degree, betweenness centrality, closeness centrality, and eigenvector centrality (Fig. 3B and Table 1). Co-occurrence network in urban areas was much more complex, with significantly higher betweenness centrality values than other areas (576.75 vs. 328.64/338.93) (Fig. S7). Network had more degree (37.40 vs. 15.27) and eigenvector centrality (0.19 vs. 0.13), less closeness centrality (0.33 vs. 0.53), and path distance (3.06 vs. 4.45) in urban areas than the agricultural areas.

#### 3.3. Environmental and spatial factors associated with bacterioplankton communities

From 100–1 000 m distance (Fig. S2), the percentage of forest, water,

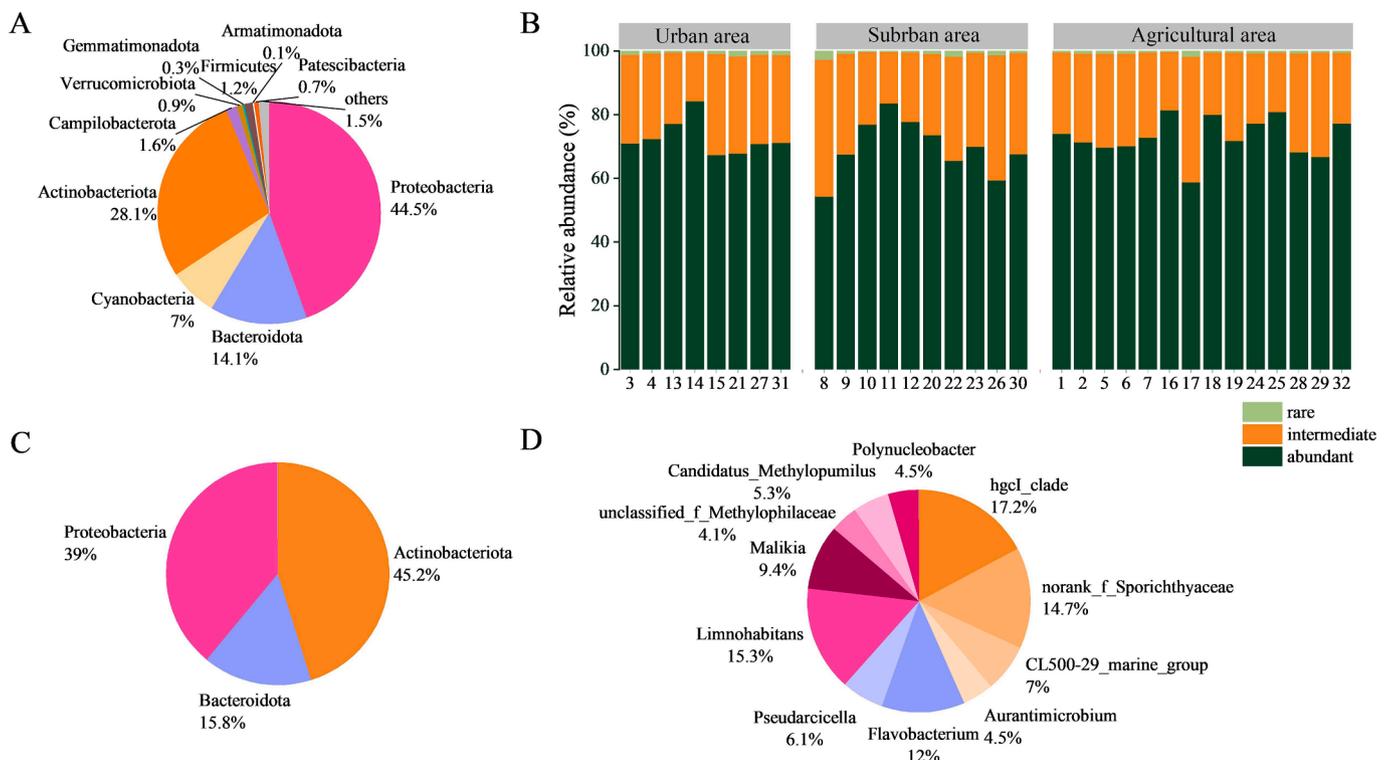
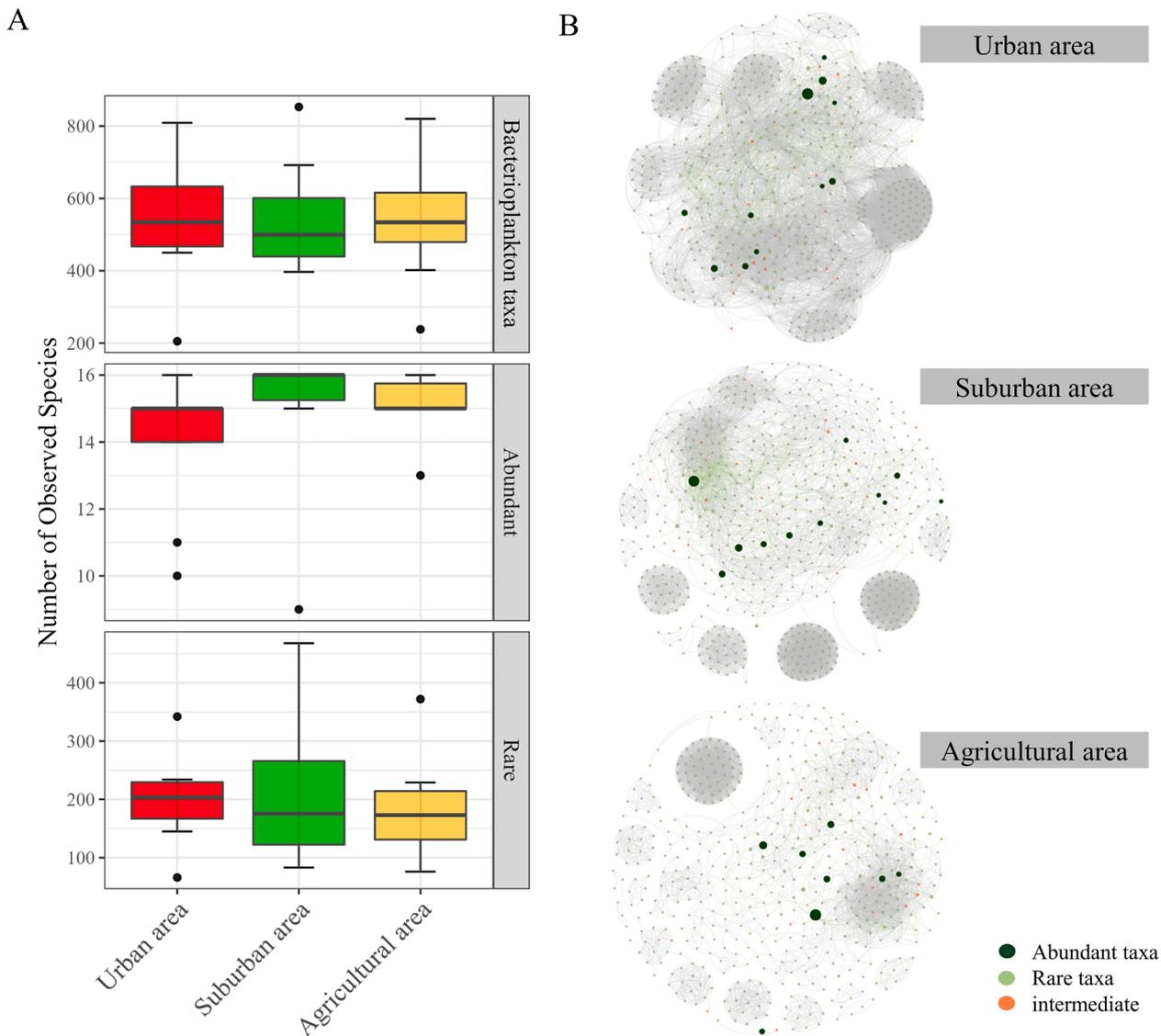


Fig. 2. Composition and distributions of abundant and rare taxa. Composition of bacterioplankton communities at phylum level (A). Distribution of abundant and rare taxa at 32 sampling sites (B), and abundant taxa composition at phylum level (C) and genus level (D).



**Fig. 3.** Diversity and co-occurrence networks among different type of areas. Observed species from the urban, suburban, and agricultural areas (A). Co-occurrence networks are colored for abundant and rare taxa from the urban, suburban, and agricultural areas (B). A connection indicates a strong ( $p < 0.05$ ,  $|r| > 0.75$ ) and significant ( $p < 0.01$ ) correlation. The size of each node is genera relative abundance; connecting grey lines represent positive correlation, and green lines represent negative correlation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**  
Topological properties of the bacterioplankton molecular ecological networks at three types of areas.

Network index	Urban area	Suburban area	Agricultural area
Total nodes	561	634	528
Total edges	10 492	7 851	4 030
Negative links	296	579	139
Positive links	10 196	7 268	3 891
Negative/Positive	0.03	0.08	0.04
Average degree	37.40	24.77	15.27
Betweenness centrality	576.75	328.64	338.93
Closeness centrality	0.33	0.54	0.53
Eigenvector centrality	0.19	0.20	0.13
Average clustering coefficient	0.68	0.69	0.71
Average path distance	3.06	3.40	4.45
Graph density	0.07	0.04	0.03
Modularity	0.70	0.78	0.76
Number of modules	9	15	32

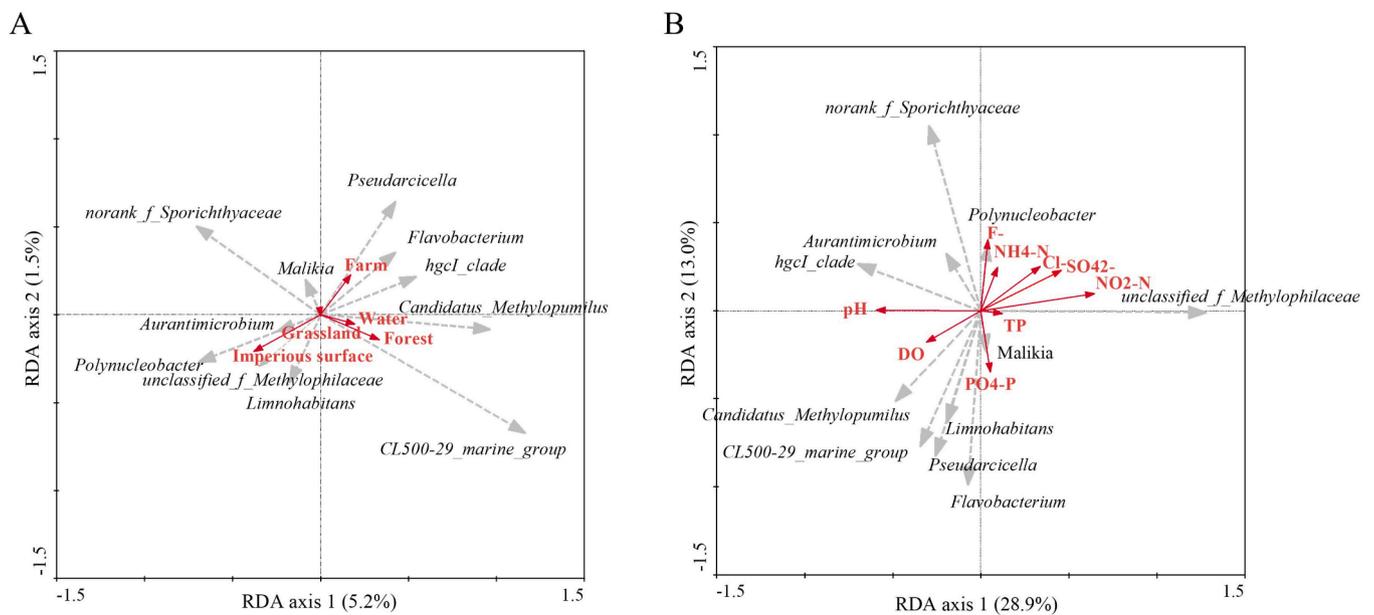
and impervious surface does not substantially increase or decrease, but the correlation with water chemistry variables (such as EC,  $Cl^-$ ,  $SO_4^{2-}$ ,  $F^-$ ,  $NH_4-N$ , and  $NO_2-N$ ) become more significant when near the sampling sites ( $r$ , Table S3). Although water chemistry variables had no significant differences among three types of areas (Table S5), there was also strong evidence for the effect of land use types (Table S3). The highest values (lowest pH, 3.5) were found in urban areas (except for  $NH_4-N$ , TP, and  $PO_4-P$ ), especially No.14, while those variables (highest pH, 8.02) showed the lowest values in agricultural areas.

The best subsets of land use types and water chemistry variables included in all environmental factors were selected as representatives of the land use and water chemistry subsets (Table 2 and Fig. 4). Grassland had the highest correlation with communities within the 100 m buffer zone same as the abundant taxa, while water and impervious surface had the highest correlation with rare taxa within the 1 000 m buffer scale.  $F^-$ , DOC, and  $NO_3-N$  had the highest correlation with bacterioplankton community dissimilarities among sites. DO,  $F^-$ , DOC,  $NO_3-N$ ,  $PO_4-P$  showed the highest correlation with abundant and rare taxa, and they also showed the correlation with each other (Fig. S8). To avoid the impact of collinearity and further identify the most important variables

**Table 2**

Correlations between different combinations of environmental variables and bacterioplankton communities at all, abundant and rare community levels, as indicated by Bioenv analysis.

Environmental variable	Bacterioplankton taxa		Abundant taxa		Rare taxa	
	Combination	correlation	combination	correlation	Combination	correlation
Land use 100 m	<b>Grassland</b>	<b>0.236</b>	<b>Grassland</b>	<b>0.245</b>	Imperious surface	0.140
	Grassland + Imperious surface	0.183	Grassland + Imperious surface	0.192	Water + Imperious surface	0.132
	Grassland + Water + Imperious surface	0.149	Grassland + Water + Imperious surface	0.139	Grassland + Water + Imperious surface	0.120
Land use 300 m	Grassland	0.171	Grassland	0.168	Grassland	0.120
	Grassland + Water	0.154	Grassland + Water	0.149	Water + Imperious surface	0.114
	Grassland + Water + Imperious surface	0.134	Forest + Grassland + Water	0.157	Grassland + Water + Imperious surface	0.107
Land use 500 m	Water	0.126	Water	0.129	Water	0.105
	Water + Imperious surface	0.139	Grassland + Water	0.127	Water + Imperious surface	0.126
	Grass + Water + Imperious surface	0.130	Grassland + Water + Imperious surface	0.095	Forest + Water + Imperious surface	0.123
Land use 1 000 m	Water	0.201	Water	0.188	Water	0.138
	Water + Imperious surface	0.215	Water + Imperious surface	0.151	<b>Water + Imperious surface</b>	<b>0.169</b>
	Forest + Water + Imperious surface	0.228	Forest + Water + Imperious surface	0.139	Forest + Water + Imperious surface	0.167
Water chemistry	DOC	0.570	DOC	0.451	F <sup>-</sup>	0.461
	F <sup>-</sup> + NO <sub>3</sub> -N	0.706	F <sup>-</sup> + NO <sub>3</sub> -N	0.538	F <sup>-</sup> + NO <sub>3</sub> -N	0.571
	<b>F<sup>-</sup> + DOC + NO<sub>3</sub>-N</b>	<b>0.714</b>	F <sup>-</sup> + DOC + PO <sub>4</sub> -P	0.548	F <sup>-</sup> + DOC + NO <sub>3</sub> -N	0.567
	F <sup>-</sup> + DOC + NH <sub>4</sub> -N + NO <sub>3</sub> -N	0.710	DO + F <sup>-</sup> + NO <sub>3</sub> -N + PO <sub>4</sub> -P	0.556	F <sup>-</sup> + DOC + NO <sub>2</sub> -N + NO <sub>3</sub> -N	0.568
	F <sup>-</sup> + DOC + NH <sub>4</sub> -N + NO <sub>2</sub> -N + NO <sub>3</sub> -N	0.703	DO + F <sup>-</sup> + DOC + NO <sub>3</sub> -N + PO <sub>4</sub> -P	0.561	DO + EC + F <sup>-</sup> + NO <sub>2</sub> -N + PO <sub>4</sub> -P	0.578
	F <sup>-</sup> + DOC + TN + NH <sub>4</sub> -N + NO <sub>2</sub> -N + NO <sub>3</sub> -N	0.690	DO + F <sup>-</sup> + DOC + NH <sub>4</sub> -N + NO <sub>3</sub> -N + PO <sub>4</sub> -P	0.568	DO + pH + Cl <sup>-</sup> + F <sup>-</sup> + NO <sub>2</sub> -N + PO <sub>4</sub> -P	0.581
	DO + F <sup>-</sup> + DOC + NH <sub>4</sub> -N + NO <sub>2</sub> -N + NO <sub>3</sub> -N + PO <sub>4</sub> -P	0.685	<b>DO + pH + F<sup>-</sup> + DOC + NH<sub>4</sub>-N + NO<sub>3</sub>-N + PO<sub>4</sub>-P</b>	<b>0.571</b>	<b>DO + EC + F<sup>-</sup> + DOC + NO<sub>2</sub>-N + NO<sub>3</sub>-N + PO<sub>4</sub>-P</b>	<b>0.582</b>
	DO + F <sup>-</sup> + DOC + TN + NH <sub>4</sub> -N + NO <sub>2</sub> -N + NO <sub>3</sub> -N + PO <sub>4</sub> -P	0.683	DO + pH + F <sup>-</sup> + DOC + TN + NH <sub>4</sub> -N + NO <sub>3</sub> -N + PO <sub>4</sub> -P	0.568	DO + pH + EC + F <sup>-</sup> + DOC + NO <sub>2</sub> -N + NO <sub>3</sub> -N + PO <sub>4</sub> -P	0.580

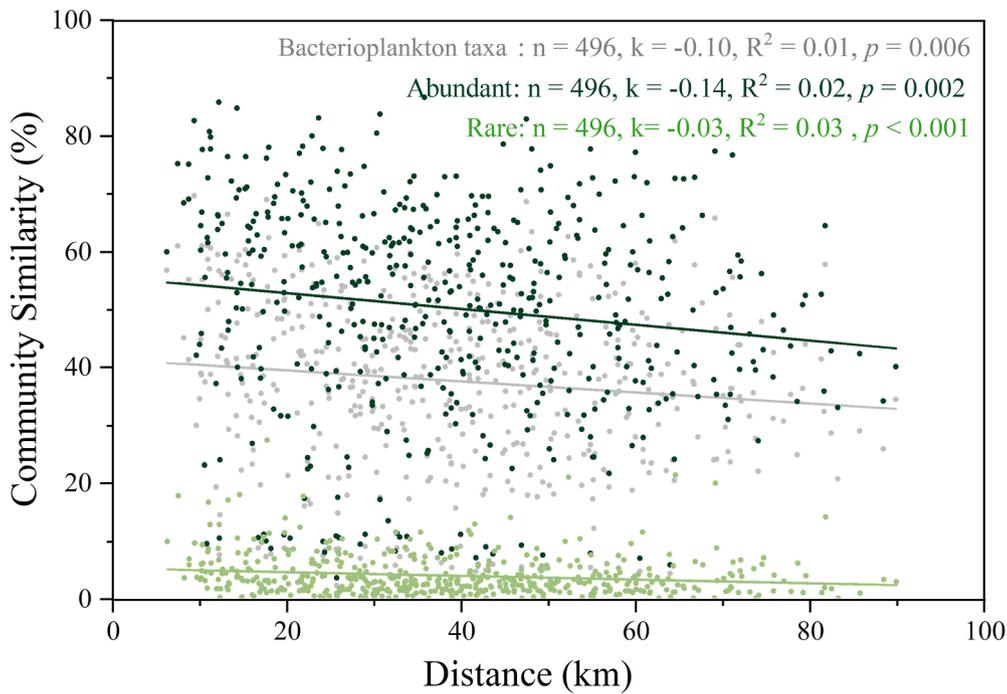


**Fig. 4.** Relationships between bacterioplankton communities and environmental factors. Redundancy analysis (RDA) of abundant taxa composition at the genus level with respect to the land use patterns (A) at 100 m scale around the sampling sites and eight selected water chemistry variables (B) in water; arrows indicate the direction and magnitude of variables.

for abundant taxa, RDA was performed to analyze the relationships between land use, water chemistry, and relative abundance of abundant taxa (Fig. 4). TP, SO<sub>4</sub><sup>2-</sup>, NH<sub>4</sub>-N, Cl<sup>-</sup> correlated with percentage of

abundant taxa significantly ( $p < 0.05$ ), whereas no land use types were correlated percentage of abundant taxa significantly.

Bray-Curtis similarity of bacterioplankton community and



**Fig. 5.** Spatial turnover of the bacterioplankton communities. Pearson correlations ( $r$ ) between bacterioplankton composition similarity (using Bray–Curtis measurement) and geographic distance (in km) at all, abundant, and rare taxa levels with solid lines (least-square linear fit).  $n$ , number of comparison;  $k$ , slope of the curve;  $R^2$ , coefficient of determination for each fitted linear regression.

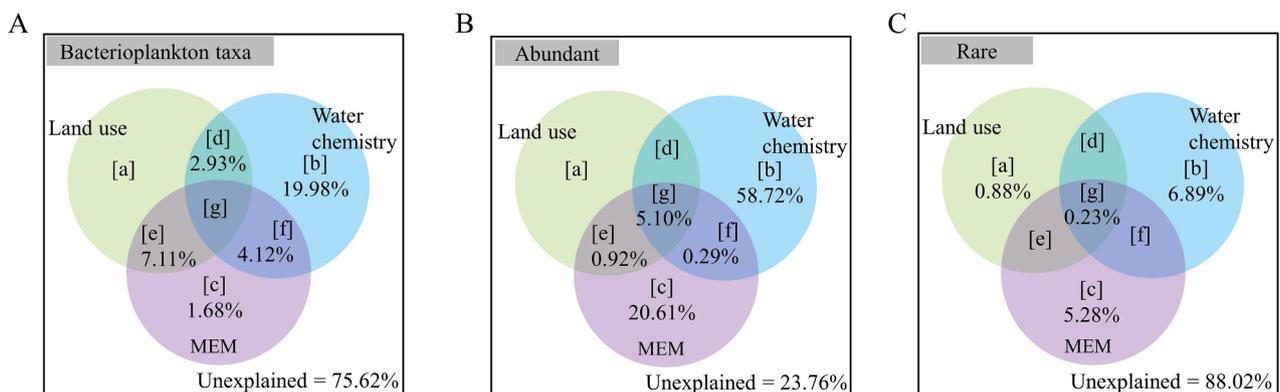
geographical distance had a significant and negative relationship ( $p < 0.01$ ; Fig. 5), indicating community similarity decreased with geographical distance. Abundant taxa were steeper ( $k = -0.14, p = 0.002$ ) than those for rare taxa ( $k = -0.03, p < 0.001$ ), indicating spatial turnover among abundant taxa was greater as geographic distance increased, with a turnover rate of  $-0.14$ .

**3.4. Ecological processes of abundant and rare bacterioplankton in different type of areas**

VPA showed that environmental and spatial factors played significant roles in bacterioplankton communities, especially for abundant taxa (unexplained = 23.76%) (Fig. 6). Interestingly, whole communities have a great unexplained variation (75.62%), which is almost the same as for rare taxa (88.02%). Variation among communities could be significantly explained by environmental factors, but also exhibited

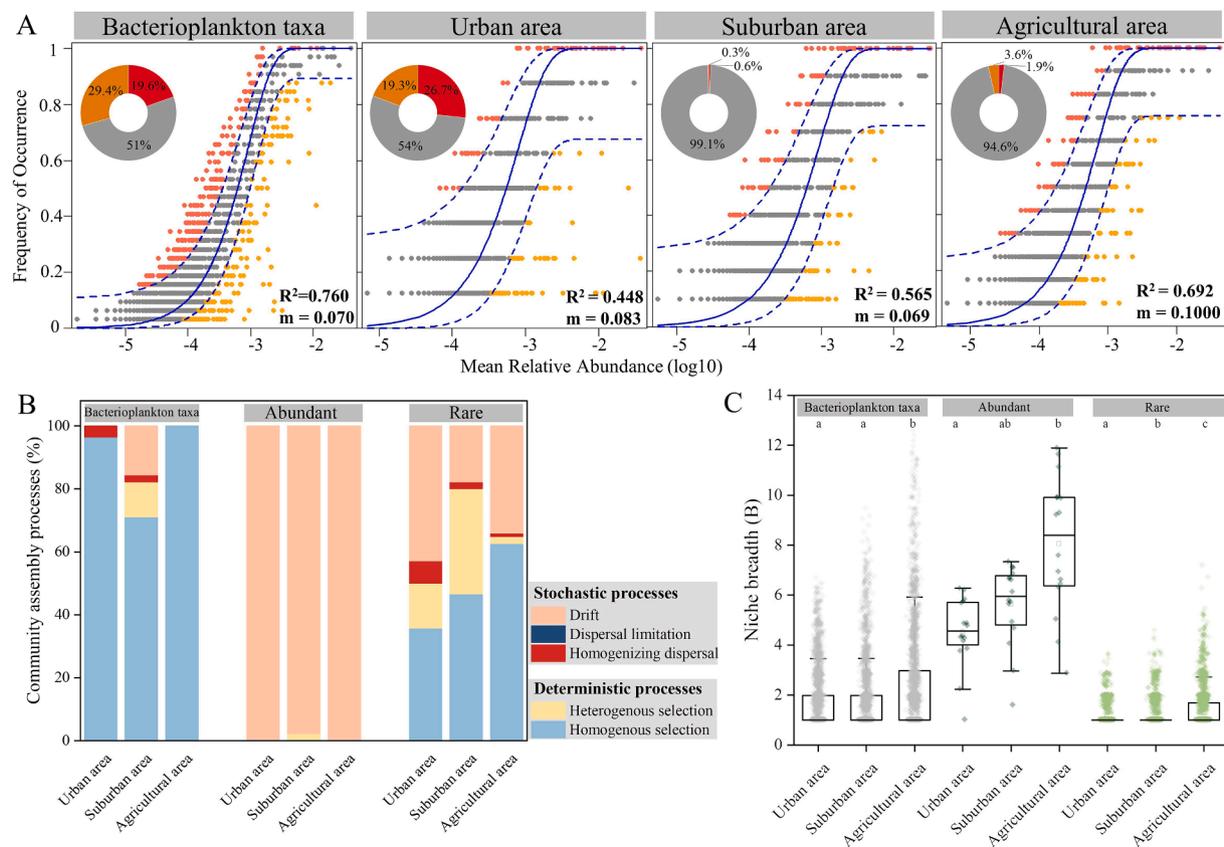
purely spatial factors indicating stochastic processes, with a greater proportion of abundant taxa (20.61%) than rare taxa (5.28%). Land use explained only a minor share of community variation of bacterioplankton community, with pure land use explaining only rare taxa variation (0.88%), while 6.02% of the abundant taxa were explained by the between land use and other factors. These results were also confirmed by analyses performed on level of individual taxa (Table 2 and Fig. 4).

Null model was fitted to determine whether stochastic processes could explain the variation of bacterioplankton (Fig. 7A). The Null model was powerful in explaining the bacterioplankton community ( $R^2 = 0.76$ ), but we should note the moderate proportions (49%) of outlying taxa beyond the dashed line, indicating those outside of the model predictions. The fit of the model varied among three types of areas in an order: agricultural areas ( $R^2 = 0.69$ ) > suburban areas ( $R^2 = 0.57$ ) > urban areas ( $R^2 = 0.45$ ). The  $m$  value was higher in agricultural areas



Values < 0 not shown

**Fig. 6.** VPA of contribution of different environmental factors shaping the bacterioplankton communities. All bacterioplankton taxa (A); abundant taxa (B); rare taxa (C). Land use buffer scale and water chemistry variables were chosen from the best subset of environmental variables in Table 2 and Fig. 5 to represent the subset of land use and water chemistry, respectively.



**Fig. 7.** Ecological processes governing bacterial communities turnover and habitat niche breadth comparison. Null model (A) of all bacterioplankton taxa from different type of areas. Red and yellow dots indicated the frequency of ASV occurring more and less than predicted by the model. Blue dashed line indicated the 95% confidence interval around the model prediction. Deterministic and stochastic process (B) in all bacterioplankton communities. Box plots (C) illustrating standardized Levins' niche breadth of bacterioplankton communities in the different types of areas. Data sets in different areas sharing the same letter above the boxes are not significantly different from each other, whereas two data sets with different letters are significantly different (multiple comparisons after Kruskal-Wallis test,  $p < 0.05$ ). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(migration rate: 0.100), suggesting that bacterioplankton in agricultural areas were highly diffused. Overall, bacterioplankton community assemblages had a better fit to neutral model in agricultural areas than in other areas.

Further, community assembly mechanisms were different for bacterioplankton communities with different abundances (Fig. 7B). Deterministic processes (dominated by homogenous selection) were the dominant mechanism shaping bacterioplankton, whereas unlike all community compositional levels, stochastic processes (dominated by drift) explained the abundant taxa. Turnover in rare taxa assembly was driven by different proportions of deterministic processes and a small proportion of stochastic processes. Despite the low-abundance rare taxa (0.37%, Fig. 2B), homogenizing dispersal in shaping rare taxa from three types of areas was same as homogenizing dispersal variability in assembly mechanisms of all community compositional levels. Dispersal accounted for a negligible percentage of the variation in all communities (0%–3.57% for homogenizing dispersal and 0% for dispersal limitation).

Community-level habitat niche breadths showed the same trend that all, abundant and rare taxa had greater niche breadth in agricultural areas than in other areas, and abundant taxa had much greater habitat breadth than rare taxa (Fig. 7C).

#### 4. Discussion

##### 4.1. Co-occurrence networks of bacterioplankton along different gradients of urbanization

We found that a more complex interconnection for bacterioplankton

in urban areas than in suburban and agricultural areas. Microorganisms within specific ecological niches form a complex network of interactions (Faust and Raes, 2012), and abundant and rare species are occupying different ecological niches in the same environment and playing different roles. In urban areas, the network complexity of bacterioplankton communities, with high betweenness centrality (representing microorganisms close to the core of the network, Fig. 3, Table 1), promotes the interconnections between different bacteria taxa in food web and enhancing their coexistence patterns (lower fragmentation) (Widder et al., 2014). According to the network topological properties in urban areas (Table 1), taxa exhibit positive correlation, which suggests effective cooperation. However, this also implies that the network structure was unstable (Coyte et al., 2015) because the negative/positive correlation of the network structure is lowest in urban areas (Table 1), which has the potential for negative taxon association to maintain network stability (de Vries et al. 2018). Rare microbes play a potential role in maintaining ecosystem stability by acting as a diverse pool of taxa. A recent study on lake ecosystems showed that the presence of organic pollutants led to a large increase in rare taxa capable of decomposing them (Wang et al., 2017). The rare taxon Chitinophagaceae (data not show) that contain individual capable of cellulose hydrolysis was more abundant in samples of urban areas, a characteristic of urban rivers (Jeffries et al., 2016). Because the rare taxa contributed a small proportion to the composition (Fig. 2B), the higher (albeit insignificant, Fig. 3A) diversity of rare taxa in urban areas may be attributed to allochthonous bacterial input (i.e., immigration) and a shift from abundant taxa (Pedrós-Alió, 2012; Jiao et al., 2017).

However, some studies have suggested that the higher negative

correlation of network was related to the exogenous pollution, i.e., fragmentation of network structure was found in urban areas (Liao et al., 2020; Wu et al., 2022), which is not consistent with our results. This may be due to the presence of non-point source pollution forming a homogeneous habitat in the Liao et al. (2020) and Wu et al. (2022)'s study area. Of course, this may require more investigation and sampling within a larger area in space. Another reason is that the effect of anthropogenic disturbances on microbial networks can be complex; increased cooperation within communities is expected to increase overall metabolic efficiency, but it does so at the cost of diminished ecological stability (Coyte et al., 2015), while there is a threshold beyond which the network topological properties become more isolated and less complex. Although it is difficult to eliminate heavy pollution through the dynamic equilibrium of abundant and rare taxa, we could observe the interconnection of taxa in threatened rivers through network analysis, suggesting the important role of network analysis in river monitoring.

#### 4.2. Factors impacting assembly processes of abundant and rare bacterioplankton along different gradients of urbanization

We found deterministic processes shaped the bacterioplankton in river network areas, especially for the rare taxa. Determinism was identified as an important ecological process in bacterioplankton communities (Fig. 7B), which was similar to other studies conducted in lowland rivers, estuary reaches, or lakes/reservoirs (Dang et al., 2022; Zhou et al., 2021; Isabwe et al., 2018; Liu et al., 2015). The absence of discharge dynamic at these areas, where microbes gain sufficient time to respond and adapt to local environmental conditions, suggests that the bacterioplankton communities of the plains river network are mainly the result of selection for local environmental conditions. The lower homogeneity and hydrological connectivity of winter habitats limit the distribution of rare taxa, which are more susceptible to deterministic processes and facilitate the observation of point source pollution. In this study, many chemical variables such as DO,  $F^-$ , DOC,  $NO_3-N$ ,  $PO_4-P$  showed correlations with each other (Fig. S8), indicating similar sources. The sources usually contained high nutrient levels and a large number of potential pathogens, which were only observed in rare taxa and were found in the lowest amounts in agricultural areas (Fig. S5). Our results are consistent with studies of other rivers in highly urbanized areas (Bowes et al., 2020; Caporaso et al., 2011). Water chemistry, like  $F^-$ ,  $NO_3-N$ , and DOC, was the main environmental factors impacting the bacterioplankton community (Table 2), which is related to determining processes (competition or predation). Higher levels of  $F^-$ , as well as conductivity in urban areas, could be found in chemical discharge of enterprises (Xu et al., 2018).  $NO_3-N$  could stimulate bacterial growth as an essential nutrient; municipal sewage discharge might be an important origin of DOC (Fang et al., 2020). Thus, nutrient levels were higher in aquatic ecosystems with high proportion of impervious surface (Tables S3 and S5). Similarly, a study in eastern Taihu Lake found that higher levels of polycyclic aromatic hydrocarbons (PAHs) enhancing the strength of species aggregation and facilitative interactions, which was related to anthropogenic inputs from industrial shipping (Yan et al., 2019). Although Chen et al. (2018b) observed pathogens in agricultural areas due to runoff from fertilizer application, given the absence of rainfall and the absence of agricultural activities during the sampling period our results strongly suggested that point source pollution happened in urban areas during the winter and that human activities are an important direct source of rare species, including inputs of potentially pathogenic bacteria.

A Previous study showed the abundant taxa were mostly governed by land use (Liao et al., 2017), which is inconsistent with our finding (Fig. 6B). One reason, this is possibly resulting from different environmental context. Our study was conducted in a highly urbanization region with intense human stress, while the previous study was conducted at high altitudes above 1 200 m where bacterioplankton might be more

sensitive to emerging land use practices (Liao et al., 2017). In extreme cases, like intense human stress, microbial dormancy decreases metabolic activities that can persist under unfavorable or harsh local environmental conditions for long periods, such as under long-time human stress (Wang et al., 2021) or long-time oil-contaminated areas (Jiao et al., 2017). Another reason is the season. Large agricultural areas and impervious areas are potential sources of surface water pollution, and changes in suspended particulate matter status in rivers can be strongly linked to land use types and the spatial distribution of microorganisms (AlDahoul et al., 2022; Isabwe et al., 2018; Dila et al. 2018; Song and Li, 2016). Land use, precipitation and associated hydrologic regime can facilitate nutrient export from land use, as found in previous studies investigating spatiotemporal changes in microbes on and after rainfall (Dila et al. 2018; Song and Li, 2016). Extensive agricultural and impervious areas are potential sources of surface water pollution, but nonpoint source pollution is virtually absent in the dry season. Although the contribution of land use was relatively low (0.88%; Fig. 6C), this contribution demonstrated the imprint of impervious surfaces on rare taxa. Despite the importance of environmental factors in our analysis, spatial factors still explained an important part of the variation in the bacterioplankton community, especially for abundant taxa that were affected by stochastic processes (e.g., random births, deaths, and immigration). Variance partitioning analysis identified strong spatial effects for abundant taxa (Fig. 6), but the unexplained variance could not be partially attributed to stochastic processes (Zhou and Ning, 2017), and we further inferred ecological processes using the null model. The higher  $R^2$  (0.76) explained a large fraction of the variance in different bacterioplankton communities (Fig. 7A), indicating the importance of neutral processes, especially in agricultural areas where migration rates were higher than in other areas ( $m = 0.1$ ). This is due to the fact that distance from urban pollution sources make it easy for abundant bacteria to spread spatially. Null model analysis further confirmed that stochastic processes drive more abundant taxa than rare taxa (Fig. 7B). Because environmental factors that directly affect microorganism are less clustered phylogenetically (Langenheder and Lindström 2019). A limitation of the null model is that it underestimates the importance of selection (also known as species sorting). Thus, we should not rely exclusively on inferring the exact proportion of stochastic and deterministic components based on the null model. The complementary information provided by our analytical framework reflects the similar patterns, and our results emphasize the importance of stochastic processes in the construction of rich bacterial communities.

However, contrary results have also been found, with environmental factors being found to explain more variation in abundant taxa than spatial factors in the middle and lower Yangtze River, which stretches over 1 000 km (Bai et al., 2020), and in 2 800 km of plateau rivers (Wang et al., 2021), possibly due to differences in spatial scales (Shi et al., 2018). In plain river network systems with our small sample size scale, local environmental conditions were viewed as fragmented habitats for rare taxa; abundant taxa could disperse to cross the unsuitable landscape by wind dispersal and occupy more ecological niches (Fig. 7). Environmental selection was strong in plain river network, as confirmed by the significant distance decay relationship between abundant and rare species (Fig. 5), with steeper abundance taxa implying greater spatial heterogeneity. Therefore, we infer that stochastic processes leading to community turnover may correspond to water chemistry patchiness at low dispersal velocities in plain rivers (Lilleskov et al., 2004). Stochastic processes are any ecological processes that produce patterns of species diversity, and strong diversification enhances the effects of drift (Chase and Myers, 2011; Zhou and Ning, 2017). In conclusion, our results confirm the importance of shaping the bacterioplankton communities of the plains river network according to the local environmental conditions, and the influence of stochastic processes on abundant taxa cannot be ignored in small-scale gradient research.

Numerous researchers have pointed out the ambiguity of the VPA used to infer ecological processes (Langenheder and Lindström 2019;

Zhou and Ning 2017), i.e., the presence of a large amount of unexplained community variation and ambiguity in the relative importance of the processes controlling community assembly, and thus the use of the Null model approach of (Stegen et al., 2013). Most yielded results that rare taxa have a large proportion of unexplained variability in VPA (Jiao et al., 2017; Mo et al., 2018; Nyirabuhoro et al., 2021; Wang et al., 2020), for which we provide the following reasons. First, unmeasured variables may lead to unexplained variation in rare bacterial communities (Mo et al., 2018). These may include abiotic factors form a known ecological risk in the Taihu basin such as organic compounds that (Yan et al., 2019), heavy metals (Zhang et al., 2020) or biological factors such as aquatic plants and phytoplankton composition (Wu et al., 2019; Xiao et al., 2017). Nevertheless, DO, EC, F<sup>-</sup>, DOC, NO<sub>x</sub>-N, PO<sub>4</sub>-P reported by Bioenv was significantly associated with rare taxa (Table 2, 0.582), and these water chemistry variables reported as important determinants were included in this study. Souffreau et al. (2015) argued that biotic factors like lytic bacterial viruses, bacterivorous protists and zooplankton, which can be indirectly affected through trophic cascades. Second, rare taxa are associated with anthropogenic activities, and the presence of temporal randomness in anthropogenic disturbances may lead microbial communities into unstable trophic states and subsequently transiently affect the bacterioplankton community. Rare taxa shaped by stochastic factors cannot be ignored. Third, rare taxa establish an independent function for responding to disturbance events as a cache or resource pool (Lynch and Neufeld, 2015), suggesting an independent mechanism may be involved in a diverse assemblage of organisms to persist in a community (that is, the reintroduction of organisms to the community) or environmental sensitivity may be related to the density of bacterioplankton (that is, dormancy makes bacteria resistant) (Nyirabuhoro et al., 2021). Thus, the role of rare taxa in ecological processes needs to receive more attention in future research.

## 5. Conclusion

Our study provides a unique perspective on rare and abundant taxa in bacterioplankton communities, coupling them with environmental and spatial data, and intra- and inter-community phylogenetic composition. Furthermore, the findings linked the relative importance of ecological processes to network analysis, allowing us to better understand the mechanisms that shape community assemblages through this analytical framework. This study shows that bacterioplankton communities have a more complex network topology in urban areas than suburban and agricultural areas in a highly urbanized river network north of Taihu Lake, China. Our results confirm that deterministic environmental filtering plays a substantial role in winter river networks and dominates the assemblage processes of rare taxa, while stochastic processes primarily shape the turnover of abundant taxa.

We believe our analysis provides novel insights into the spatial distribution of bacterioplankton communities in urbanized areas, but caution is needed in the interpretation of our results. In the northwest of Taihu Lake, Zhang et al. (2022) found more complex co-occurrence patterns of bacterioplankton during dry season than wet season, reflecting the hydrological condition could change the microbial co-occurrence relationships. Although a previous study observed the relatively stable water conditions in plain river areas (versus that in the upper river areas) (Zhang et al., 2020) and the effect of rainfall-associated runoff on river level fluctuations, the applicability of the findings to wet weather conditions or longer time series needs further studies to evaluate comprehensively co-occurrence patterns of bacterioplankton communities. Further, the large amount of recurring unexplained variation in the structure of the bacterioplankton community suggests that further attention needs to be paid to potential meta-community shaping processes, which may include eco-evolutionary dynamics and priority effects, and alternative approaches to address these processes. Therefore, it is crucial to explore community assembly processes through further development and integration of ecological

niche and neutral theory or experimental tests.

## CRediT authorship contribution statement

**Jun Zhao:** Conceptualization, Methodology, Software, Writing – original draft, Visualization, Investigation. **Thomas Hein:** Writing – review & editing. **Qiqi Yuan:** Investigation, Project administration. **Wang Shu:** Data curation, Writing – review & editing. **Xueying Huang:** Investigation. **Xueli Zhang:** Software, Validation. **Lachun Wang:** Funding acquisition, Supervision.

## Declaration of Competing Interest

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

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2023.110204>.

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