RESEARCH ARTICLE

Responses of abundant and rare bacterioplankton to temporal change in a subtropical urban reservoir

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One sentence summary:

Editor: Martin W. Hahn
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ABSTRACT

Investigation of bacterial community dynamics across different time scales is important for understanding how environmental conditions drive community change over time. Bacterioplankton from the surface waters of a subtropical urban reservoir in southeast China were analyzed through high-frequency sampling over 13 months to compare patterns and ecological processes between short (0−8 weeks), medium (9−24 weeks) and long (25−53 weeks) time intervals. We classified the bacterial community into different subcommunities: abundant taxa (AT); conditionally rare taxa (CRT); rare taxa (RT). CRT contributed > 65% of the alpha-diversity, and temporal change of beta-diversities was more pronounced for AT and CRT than RT. The bacterial community exhibited a directional change in the short- and medium-time intervals and a convergent dynamic during the long-time interval due to a seasonal cycle. Cyanobacteria exhibited a strong succession pattern than other phyla. CRT accounted for > 76% of the network nodes in three stations. The bacteria–environment relationship and deterministic processes were stronger for large sample size at station G ($n = 116$) than small sample size at stations C ($n = 12$) and L ($n = 22$). These findings suggest that a high-frequency sampling approach can provide a better understanding on the time scales at which bacterioplankton can change fast between being abundant or rare, thus providing the facts about environmental factors driving microbial community dynamics.

Patterns and processes in alpha- and beta-diversities and community assembly of bacterioplankton differ among different time intervals (short-, medium- and long-time intervals) and different subcommunities (abundant, conditionally rare and rare taxa) in a subtropical urban reservoir, demonstrating the importance of temporal scale and high-frequency sampling in microbial community ecology.

Keywords: bacterioplankton community; rare taxa; high-frequency sampling; temporal dynamics; ecological processes; co-occurrence network

INTRODUCTION

Freshwater bacterioplankton have significant capabilities to response to both natural and human-induced environmental changes at different spatial and temporal scales (Locey and Lennon 2016; Zelaya *et al.* 2019). It is important to investigate the interaction between microbial community and environmental change across various time intervals (short-term vs long-term) to fully understand community assembly of microorganisms in aquatic ecosystems. Seasonal sampling studies relying on relatively long time interval of data collection (e.g. monthly) in general show different seasonal succession patterns in bacterioplankton community composition that occur in lakes and reservoirs (Boucher, Jardillier and Debroas 2006; Ávila *et al.* 2017; Liu *et al.* 2019b; Nyirabuhoro *et al.* 2020). These works illustrate that different environmental variables shape bacterioplankton communities at different sequential scales (Boucher, Jardillier and Debroas 2006; Ávila *et al.* 2017; Nyirabuhoro *et al.* 2020). For example, water temperature, organic nutrients and pH have been connected to seasonal variability in bacterioplankton community (Nyirabuhoro *et al.* 2020). Identifying seasonal dynamics in bacterioplankton community composition at fine time scale have not been widely explored in aquatic habitats (Gilbert *et al.* 2012; Needham *et al.* 2013; Lindh *et al.* 2015).

Groups of closely related individual bacterial populations (operational taxonomic units or OTUs), can cause temporal dynamics over short time scales (e.g. several days to weeks) (Needham *et al.* 2013) and can respond to changes in environmental conditions showing a quick succession of different bacterial taxa (Zelaya *et al.* 2019; Linz *et al.* 2020). This implies that bacterioplankton community sampled in high temporal resolution and influenced by environmental variables can be broken down into responses of each OTU (Lindh *et al.* 2015). Hence, it could be essential to find out whether similar dynamics within bacterioplankton would take place in environment over shorter or longer temporal scales in response to change in environmental conditions (Shade *et al.* 2013; Lindh *et al.* 2015; Linz *et al.* 2020). More importantly, the analyses associated with high-resolution observations over longer time series could help to show the essential features of variations in bacterioplankton community within 1 year, revealing responses of microbial community to environmental disturbances with separate ecological processes (Lindh *et al.* 2015; Xue *et al.* 2018).

In inland waters, bacterioplankton communities usually include a few abundant taxa and many rare or low-abundance ones (Liu *et al.* 2015b; Nyirabuhoro *et al.* 2020). The high-throughput sequencing technologies allowed researchers to explore and identify the rare phylotypes that were difficult to detect with traditional culture-based and microscopic approaches (Liu *et al.* 2015b). At a specific point in space and time, just a few members of abundant taxa generally dominate bacterioplankton community, and they can occur at the same time with a majority of rare taxa (Shade *et al.* 2014; Rivett and Bell 2018). Both abundant and rare bacterioplankton can respond to changes in environmental conditions (Liu *et al.* 2019b; Campbell *et al.* 2011); for example, the rare taxa that can wait for favorable environmental conditions to increase in relative abundance these are called conditionally rare taxa (CRT; Liu *et al.* 2019b; Campbell *et al.* 2011; Shade *et al.* 2014). The ecological importance of the resilience and alteration within these bacterioplankton communities is not well understood, particularly in responding to changes in environmental conditions on various temporal scales. As an example, bacterial community turnover times and percentage change of particular individual populations in aquatic environments may vary over 3–5 days (Yokokawa *et al.* 2004; Fang *et al.* 2019). This shows that spatiotemporal patterns of bacterioplankton may not be easily recognized from observations conducted based on low-frequency sampling.

Microbial community composition, influenced by environmental variables is often considered to be shaped by deterministic processes (Ndayishimiye *et al.* 2020; Nyirabuhoro *et al.* 2020). These ecological processes are also referred to as niche-based processes for the reason that they can produce the competitive interactions among species and changes in community composition (Lindström and Langenheder 2012; Jiao *et al.* 2017). Further, microbial community composition can also be influenced by random changes in demographic characteristics, called neutral-based processes or stochastic processes (Ofiţeru *et al.* 2010; Stegen *et al.* 2012; Chen *et al.* 2019). Both stochastic and deterministic processes are important ecological processes in shaping microbial community structure across space and time (Ofiţeru *et al.* 2010). However, it is still unclear to what extent these two processes work together with each other and influence community assembly at various time scales (Ofiţeru *et al.* 2010; Ndayishimiye *et al.* 2020). Variation partitioning analysis, neutral community model and network approaches offer a set of theories and methods with which to investigate, with greater precision and consistency, the wide range of interactions that are likely to occur among microbial populations in an aquatic environment (Eiler, Heinrich and Bertilsson 2012; Faust and Raes 2012; Mo *et al.* 2018; Chen *et al.* 2019; Liu *et al.* 2019a). In addition, these network methods can not only help better understand species composition, and their interactions in the form of interaction networks, but also in assessing responses of abundant and rare bacterioplankton to temporal change in subtropical reservoirs (Liu *et al.* 2019b).

In this study, the dynamics of bacterioplankton communities in relationship to variations of environmental conditions—at short-, medium- and long-term time scales—have been assessed. Bacterioplankton communities were collected twice a week over 1 year from a subtropical urban reservoir in southeast China, and the bacterial 16S rRNA gene was analyzed to explore the succession patterns within bacterioplankton subcommunities (abundant taxa, conditionally rare taxa and rare taxa) in response to change in environmental variables. It was hypothesized that: (i) Bacterioplankton subcommunities may exhibit distinct temporal patterns at short- and long-term time scales; (ii) Environmental factors influencing bacterioplankton community dynamics may be different across different time intervals and across the three bacterioplankton subcommunities; (iii) The relative importance of deterministic processes driving the community change may be different among different subcommunities. To test our hypotheses, the following objectives were established: (i) Determining the temporal patterns in bacterioplankton community across different time intervals; (ii) Identifying the environmental factors regulating bacterial community dynamics; (iii) Revealing the co-occurrence patterns of bacterioplankton community and the mechanisms underlying their assembly.

MATERIALS AND METHODS

Study area and sampling

Xinglinwan Reservoir is located in Xiamen, southeast China. It has been the subject of long-term monitoring as part of the Xiamen reservoir time-series (XRT), with sampling for plankton typically having occurred twice weekly starting in January 2016. In this study, a total of 150 water samples was collected from three locations in Xinglinwan Reservoir (Figure S1, Supporting Information) from August 2016 to August 2017. The sampling was undertaken at about 9:00 am on Tuesday and Friday in each week. The water samples were first pre-filtered using a 200 μm pore-sized sieve to remove large particles. Then, the water samples (volume: 300−500 mL) were filtered using 0.22 μm polycarbonate membrane (47 mm diameter, Millipore, Billerica, MA) using a vacuum filtration system (filtering time: 30−50 min). The membranes with microbial plankton were packed into sterilized tubes and preserved at −80°C until DNA extraction.

All environmental variables were measured as described previously (Fang *et al.* 2019), and a summary of environmental data is shown in the Figure S2 (Supporting Information). The weather data such as precipitation, air temperature (AiT) and wind speed (WS), which were recorded by China Meteorological Data Service Center (http://data.cma.cn), were obtained from a weather station in Xiamen (ID 59134, 24°28.998′N 118°4.98′E).

DNA extraction, Illumina sequencing and bioinformatics

Total bacterioplankton DNA was extracted directly from the membrane using the FastDNA SPIN Kit and the FastPrep Instrument (MP Biomedicals, Santa Ana, CA) according to the manufacturer's instructions. The DNA quality and concentration were measured using a NanoDrop 1000 spectrophotometer (Thermo Fisher Scientific, Waltham, MA). The V3–4 hypervariable region of the bacterial 16S rRNA gene was amplified using the primer pair 341F/806R with barcodes following our previous study (Fang *et al.* 2019). PCR products from triplicate reactions per sample were pooled and gel-purified. Gene fragments were sequenced on Illumina MiSeq platform (Illumina Inc., San Diego, CA) using a paired end strategy.

The removal of barcode and primer sequences was carried out and the output data have been made publically available at the GenBank sequence read archive (SRA) under BioProject number PRJNA510463 and accession number SRP173857. Bioinformatic analyses of 16S rRNA gene sequences were conveyed using VSEARCH (Rognes *et al.* 2016). Chimeras were discarded using default settings in VSEARCH from a set of unique sequences to construct biologically corrected sequences. Quality filtered sequences were assigned to OTUs at a 97% sequence similarity threshold. The OTU taxonomies were assigned using the sintax algorithm on query sequences mapped against the Greengenes database (DeSantis *et al.* 2006). Unknown OTUs were removed before the downstream analyses. The resulting OTU tables were subject to subsequent processing with singleton, archaea, chloroplast and mitochondrial sequences removal. Finally, the bacterial sequences were normalized to the same number of sequences 35 000 per sample, and 20 438 OTUs at 97% sequence similarity level were obtained.

The bacterioplankton community was classified into three different taxa categories by setting a local relative abundance threshold of 1% for abundant taxa and 0.01% for rare taxa (Nyirabuhoro *et al.* 2020). Those categories were as follows: (i) abundant taxa (AT), OTUs with relative abundance > 1% at least once in a sample; (ii) conditionally rare taxa (CRT), OTUs with < 0.01% local relative abundance in some samples and $\geq$ 0.01% in others, but never $\geq$ 1%; (iii) rare taxa (RT), OTUs with relative abundance < 0.01% in all samples.

Real-time quantitative PCR

PCR amplification of 16S rRNA genes was performed to prepare the quantitative PCR standard curve (Yu *et al.* 2014). The 50 mL PCR mixture contained 1 μL of the primer set (25 pmol each), 25 μL of 2 × Ex Taq DNA polymerase mix (Takara Bio, Japan), 100 ng of DNA template and ddH$_2$O. The primer set was 341F [5′-CCTACGGGNGGCWGCAG-3′] and 515R [5′-ATTCCGCGGCTGGCA-3′]. PCR was performed in the following thermal cycles: initial denaturation at 94°C for 5 min; 35 cycles at 94°C for 30 s, 51°C for 30 s and 72°C for 60 s; and a final extension at 72°C for 10 min. The purified PCR products were ligated into the pMD18-vector (Takara Bio, Japan) and transformed into *Escherichia coli* DH5α competent cells. The plasmids containing 16S rRNA gene fragments were sequenced using an automated sequencer (ABI3730, Applied Biosystems, Foster City, CA). Successfully inserted plasmids DNA then were extracted using the MiniPrep kit (Qiagen, Germany) and the plasmid concentrations were determined by spectrophotometry using a NanoDrop 1000 (Thermo Fisher Scientific). Standards were prepared with triplicate from linearized plasmid serial dilutions containing between 10^9 and 10^4 16S rRNA gene copies calculated directly from the concentration of extracted plasmid. A standard curve was generated by plotting the threshold cycle values versus log$_{10}$ of the gene copy numbers. The amplification efficiency (E) was estimated using the slope of the standard curve based on the following formula: E = $(10^{-1/\text{slope}})$ −1 (Bustin *et al.* 2009). The efficiency of PCR was between 95 and 105% and R^2 of the standard curve was 0.991 ± 0.002 in this study.

Statistical analyses

The community alpha-diversity was evaluated using six indices (observed OTUs, ACE, Chao 1, Shannon-Wiener, Simpson and Pielou's evenness; Magurran 1988) and they were compared using a the Wilcoxon rank-sum test. Non-metric multidimensional scaling analysis and analysis of similarity (ANOSIM), based on Bray–Curtis similarity, were used to explore the differences in composition of bacterial communities between different months.

To quantify the rate of community variation over time, we employed time-lag regression analysis (Collins, Micheli and Hartt 2000) at three different timescales: short-term (0−8 Δ weeks), medium-term (9−24 Δ weeks) and long-term (25−53 Δ weeks), where delta time Δ stands for the time elapsed between two sampling days. The time-lag analysis has proven to be a useful tool with which to quantify the temporal variation of ecological communities, and it can be considered an extension of autocorrelation analysis for short time series of community data. If the regression line is significant, positive and linear, then it implies that the community is undergoing directional change over time. If the regression line is not significant or the slope is not significantly different from zero, then it implies fluctuation or stochastic variation over time. If the slope of the line is negative, then it implies community composition is becoming more similar to a community-type characteristic of the earlier samples in the time series (Collins, Micheli and Hartt 2000). The fraction of consecutive Bray–Curtis dissimilarity attributed

to the dynamics of each bacterioplankton subcommunity (AT, CRT and RT) was calculated. The dynamics of bacterial community at phylum and genus levels of taxonomic resolution were calculated using relative abundance data in R environment (R Core Team 2019).

To investigate bacterioplankton's responses to environmental conditions, we used Spearman correlation of bacterial abundance (sequence data) against each measured environmental variable, and redundancy analysis and variation partitioning analysis of bacterial community composition (after Hellinger transformation) and significant environmental variables were run in R version 3.6.0 (R Core Team 2019). The redundancy analysis (RDA) was implemented after removing collinearity with threshold of variance inflation factor ($>$ 10). Then we selected the significant environmental variables for explaining the bacterioplankton variations at subcommunity level by forward selection ($P < 0.05$). In variation partitioning analysis, the environmental variables were divided into four groups: weather, physical, chemical and primary producer (chlorophyll-*a*). In addition, the interrelationships between groups of environmental variables in variation partitioning analysis and bacterioplankton communities were evaluated using direct, indirect and total effects determined by partial least squares path modeling analysis (Ndayishimiye *et al.* 2019). The five groups of variables were weather, physical, chemical, primary producer (chlorophyll-*a*) and bacterioplankton subcommunities (AT, CRT and RT).

To analyze the co-occurrence patterns in different bacterioplankton subcommunities (AT, CRT and RT), we performed the network analysis in R environment (R Core Team 2019). In order to simplify complexity of data, only OTUs that present at least in 75% of the samples were kept in our analysis. The relationships between OTUs were calculated using Spearman's rank correlations, and only strong and statistically significant correlations ($|r| > 0.8$, $P < 0.01$) were integrated into the networks, which were visualized and analyzed using Gephi version 0.9.2 (Bastian, Heymann and Jacomy 2009). To characterize the network topology, we calculated the modularity index, degree, betweenness and closeness of different bacterioplankton following our previous study (Xue *et al.* 2018).

The importance of stochastic and deterministic processes in shaping bacterial community was assessed using a community model (Sloan *et al.* 2006) and a null model (Gotelli and Mccabe 2002), respectively. For Sloan neutral community model, the parameters N, m and Nm describe the metacommunity size, immigration rate and dispersal between communities, respectively. The least-square method was employed to determine the best fit distribution curve of the neutral model in R version 3.6.0 (R Core Team 2019). The checkerboard score (C-score; Stone and Robert 1990) was carried out to test the actual distributions for non-randomness of bacterial OTUs. C-score was selected based on the reason that the matrix is relatively unaffected by the minor changes in the data. The sequence-based OTU table was converted into a binary matrix of presence (1) and absence (0), and then analyzed for different combinations (Stone and Robert 1990; Gotelli and McCabe 2002). The standardized effect sizes for C-score were estimated as the difference between the observed index and the mean of the stimulated index over the standard deviation of the stimulated index (Crump *et al.* 2009). C-score was calculated based on a burn-in of 30 000 simulations and using sequential swap randomization algorithm in the package 'EcoSimR' and R version 3.6.0 (R Core Team 2019).

RESULTS

Temporal variation of environmental variables

All measured environmental variables varied over the study period (Figure S2, Supporting Information). The water temperature was low between December 2016 and February 2017 ($15.34-22.51°C$) and high between June and August 2017 ($24.79-35.02°C$). The salinity gradually increased from late 2016 to early 2017 with the highest value (6.10 PSU) in February 2017, then fluctuated and decreased from June to August 2017. Total organic carbon concentrations were low in 2016 and early 2017, but increased to 22.66 mg/L in May 2017. The temporal variation of environmental variables associated with nutrient enrichment showed that Xinglinwan Reservoir was a turbid (low transparency) and eutrophic urban waterbody.

Bacterioplankton community composition and temporal dynamics

In total, stations C, L and G yielded 15 801, 17 363 and 20 336 OTUs, respectively (Table S1, Supporting Information). CRT subcommunities comprised a high proportion of all OTUs (Range: 65.79–67.80%). The bacterial alpha-diversity indices showed a substantial change over time for both RT and CRT subcommunities (Fig. 1). At station G, observed OTUs, ACE and Chao1 were high between August and October 2016 with significant decline between January and April 2017. The values of Shannon, Simpson and Pielou's evenness showed little change over time. The absolute abundance of bacterioplankton 16S rRNA gene varied from 2.66×10^9 to 1.58×10^{11} copies/L in this study (Figure S3, Supporting Information).

The temporal variability in bacterioplankton community was remarkable in all taxa categories (Fig. 2A), with the difference in communities among groups of samples (i.e. 13 months) was significant (Global R = 0.847, P = 0.001 for AT; Global R = 0.794, P = 0.001 for CRT; Global R = 0.730, P = 0.001 for RT). At phylum level, Proteobacteria and Actinobacteria were dominant with slight temporal variation, while Cyanobacteria fluctuated over time with high (57.18%) and low (5.52%) relative abundances at 239th Julian day of 2016 and 31th Julian day of 2017, respectively (Fig. 2B). At genus level, the temporal change was remarkable for *Synechococcuss* with relative abundance (47.33%) peaking at 239th Julian day of 2016; however, it was lower than $< 1\%$ between 364th Julian day of 2016 and 97th Julian day of 2017 (Fig. 2C).

Both AT and CRT subcommunities were sensitive to sampling time span, with a directional change between $0-8$ and $9-24$ Δ weeks (short-term and medium-term) and with a convergent trend between $25-53$ Δ weeks (long-term). For RT subcommunities, the Bray–Curtis dissimilarity between samples did not greatly change as time-lags increase compared to AT and CRT subcommunities (Fig. 3A). The determination coefficient of community change was the highest ($0.33-0.55$) during the short term in G station (Fig. 3B). RT subcommunities accounted for a large fraction of the community dissimilarity between time points ($36.78-65.50\%$), whereas the fractions of CRT and AT ranged between $22.00-35.22\%$ and $8.25-30.21\%$, respectively (Figure S4, Supporting Information).

Bacterial community-environment relationship

At station C, bacterial abundance was correlated both with turbidity and NO_3-N ($n = 11$, $P < 0.05$). At station L, the bacterial community–environment relationship was highly significant (n
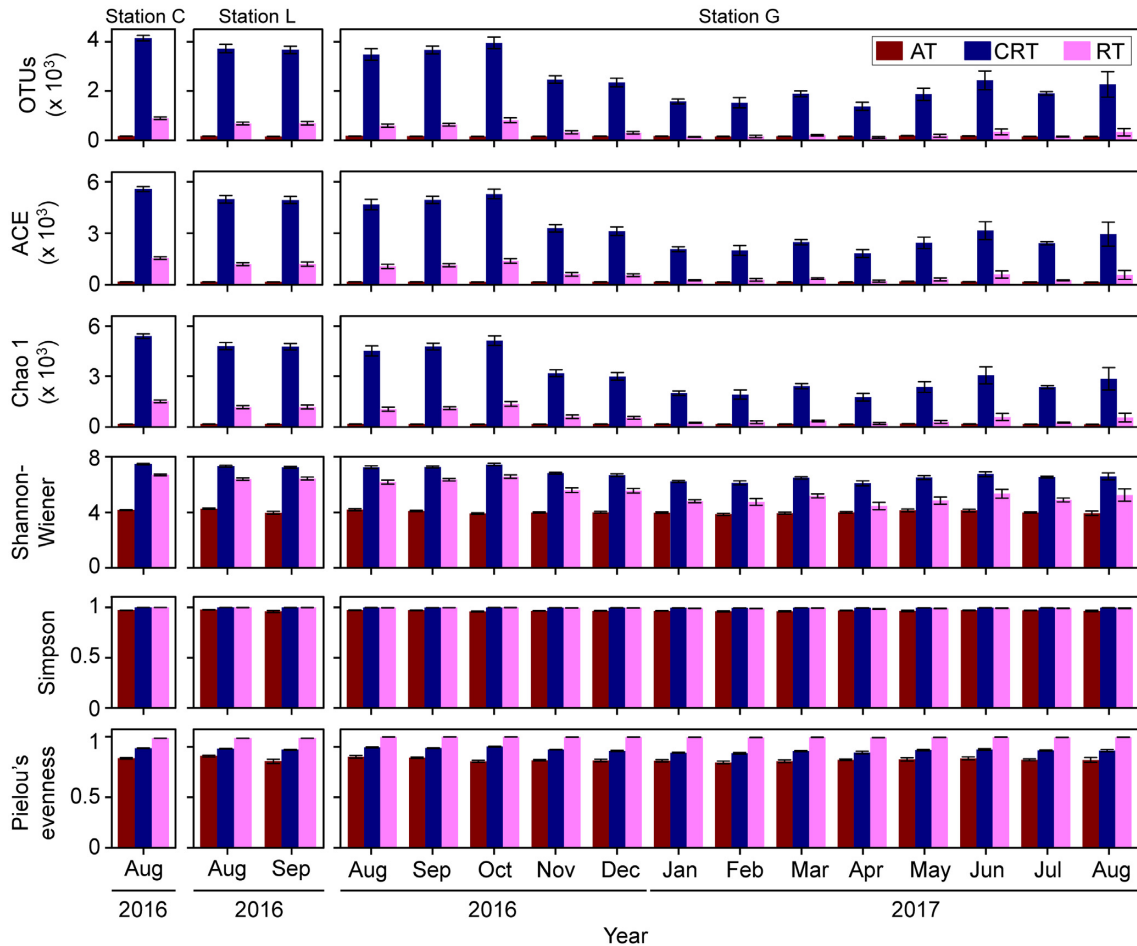
Figure 1. The bacterial community diversity across the study period in Xinglinwan Reservoir. Sampling stations: C, Control point; L, Lianhua; G, Gaota. Taxa categories: AT, abundant taxa; CRT, conditionally rare taxa; RT, rare taxa.

= 22, P < 0.001) for dissolved oxygen, chlorophyll-*a*, precipitation and wind speed. Importantly, all environmental variables exhibited a significant relationship with bacterial abundance at station G (*n* = 116, P < 0.001), with higher correlation coefficients (Table 1) for chlorophyll-*a*, electrical conductivity, salinity and pH at P < 0.001. The Spearman correlation coefficients between environmental variables and bacterial relative abundance showed that the significant correlations were 13, 41, 124 at stations C, L and G, respectively, at phylum level (Figure S5, Supporting Information). At genus level, significant correlations were 38, 41, 118 at stations C, L and G, respectively (Figure S5, Supporting Information). At station G, cyanobacteria were significantly correlated with water temperature (P < 0.001); while cyanobacteria were significantly correlated with precipitation and air temperature at (P < 0.001) at station L (Figure S5, Supporting Information). At genus level, the large variation in *Synechococcus* was strongly linked with water temperature, pH, oxidation-reduction potential and precipitation at station C (P < 0.05). At station L, *Synechococcus* showed a significant correlation with precipitation, air temperature, chlorophyll-*a,* wind speed, water temperature, dissolved oxygen and nitrate nitrogen. At station G, it was strongly connected with water temperature, turbidity, electrical conductivity, salinity, oxidation-reduction potential, total nitrogen, ammonium nitrogen, total phosphorus, phosphate phosphorus and air temperature (Figure S5, Supporting Information).

Water chemistry was an important environmental condition explaining changes in bacterioplankton community composition over time (Fig. 4). Indeed water chemistry explained the highest proportion of community variation in AT subcommunities from stations L and G (18% and 23% based on pure variances, respectively). The pure variances explained by water chemistry were 14 and 16% in CRT subcommunities at stations L and G, respectively. For RT subcommunities, unexplained variances at both stations L and G were great (> 95%). Weather conditions, water physical and chemical variables and primary producers influenced directly and indirectly the bacterial community of Xinglinwan Reservoir (Figure S6, Supporting Information). At station L, water chemistry showed negative effects on AT (−0.59) and CRT (−0.73) subcommunities and positive effect on RT subcommunity (0.27), respectively. At station G, water chemistry exhibited a positive effect on primary producers (0.62−0.75). The direct effects were positive on AT subcommunity (32%) and negative on CRT (−0.26) and RT (−0.28) subcommunities, respectively.

Co-occurrence patterns of bacterioplankton subcommunities

The co-occurrence networks of bacterial subcommunities (AT, CRT and RT) showed that the potential links between species
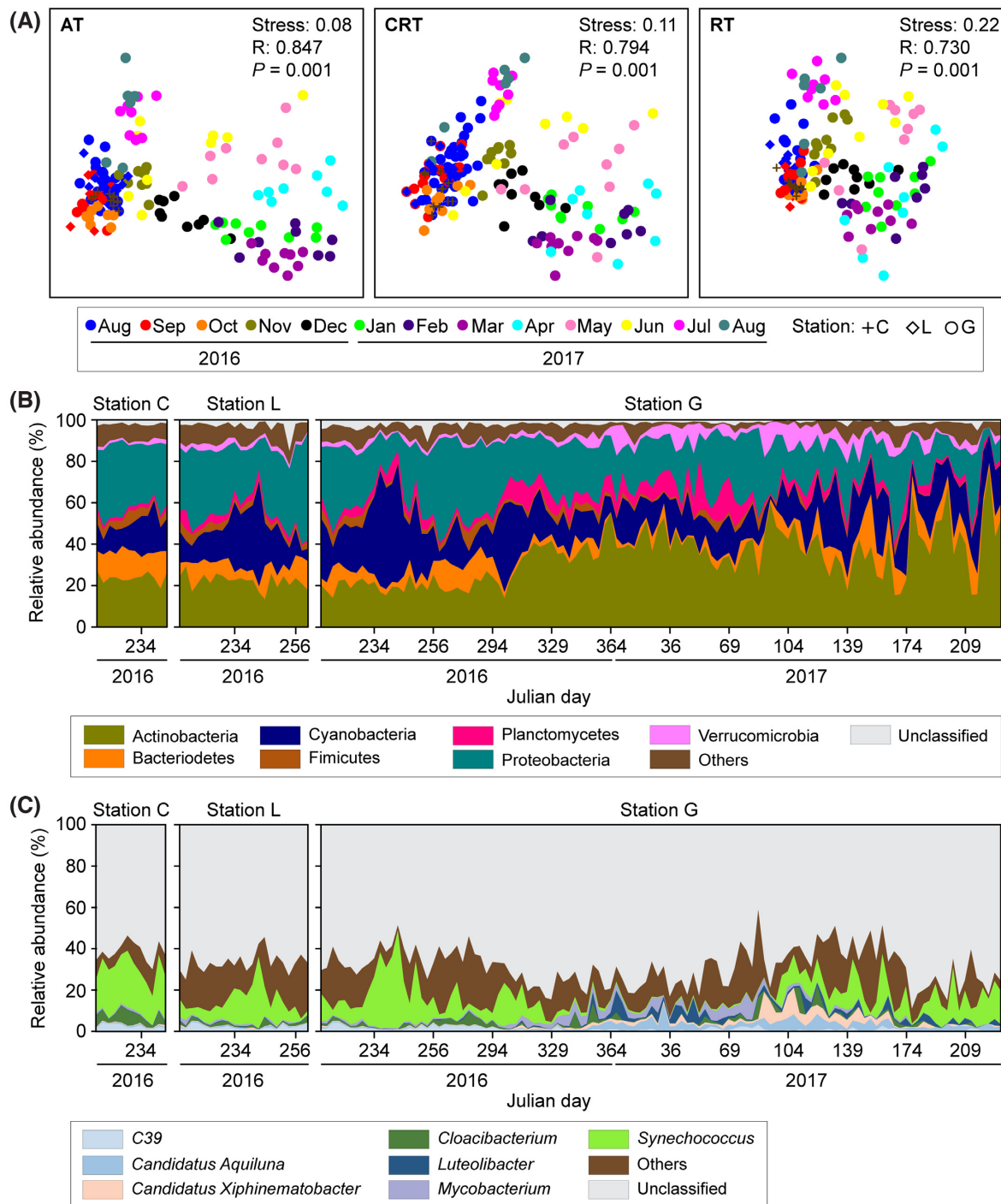
Figure 2. Temporal variation of bacterial community of Xinglinwan Reservoir. (A) Non-metric multidimensional scaling plots based on Bray–Curtis similarity of bacterial communities considering three groups of taxa across time and sampling stations. Sampling stations: C, Control point; L, Lianhua; G, Gaota. Taxa categories: AT, abundant taxa; CRT, conditionally rare taxa; RT, rare taxa. Dynamics of the community at (B) phylum and (C) genus levels of taxonomic resolution.

were organized into complex ecological networks of interacting species over time (Fig. 5 and Table S2, Supporting Information). The networks had 2137, 1109, 824 nodes, and 2700, 1564 and 4047 edges from stations C, L and G, respectively (Fig. 5). Further, six major modules were selected for each station, and their contributions were ranged from 0.56 to 1.73% of nodes (i.e. OTUs) at station C, from 2.98 to 11.45% of nodes (OTUs) at station L and from 6.31 to 17.96% of nodes (OTUs) at station G, respectively (Fig. 5 and Table S2, Supporting Information).

Important phyla that determined the modular structure of networks were Proteobacteria, Bacteriodetes, Actinobacteria, Firmicutes, Cyanobacteria, TM7, Planctomycetes and Verrucomicrobia. The CRT subcommunity contained a great number of nodes (76.79%, 86.65% and 78.76% of stations C, L and G, respectively) in the network compare to AT and RT ones.
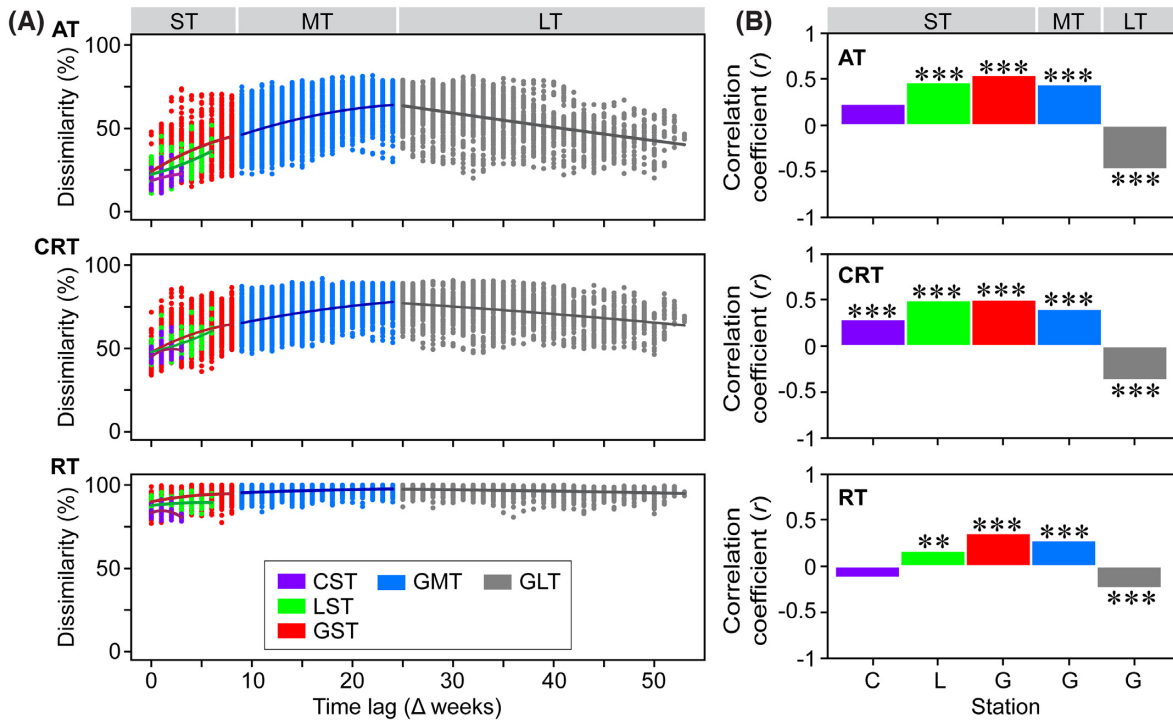
Figure 3. The results of time-lag analysis based on linear regression. (A) The directional change and convergent dynamic in bacterial community composition during short-term or medium-term and long-term periods, respectively. (B) The strength of change in bacterial community composition over time indicated by the correlation coefficient and *P* value. The delta time Δ describes the time elapsed between two sampling days. Sampling stations: C, Control point; L, Lianhua; G, Gaota. Time scales: ST, short-term (0–8 Δ weeks); MT, medium-term (9–24 Δ weeks); LT, long-term (25–53 Δ weeks). Taxa categories: AT, abundant taxa; CRT, conditionally rare taxa; RT, rare taxa. Significant levels: ∗*P* << 0.05i>; ∗∗*P* << 0.01i>; ∗∗∗*P* < 0.001.

Table 1. Spearman's correlations between bacterial abundance and environmental factors.

Environmental variable	Station C			Station L			Station G		
	AT	CRT	RT	AT	CRT	RT	AT	CRT	RT
Water temperature	0.47	− 0.50	− 0.35	**0.47**	**− 0.45**	− 0.50	**− 0.22**	**0.23**	0.05
pH	0.10	− 0.09	− 0.07	0.36	− 0.31	**− 0.58**	**0.70**	**− 0.69**	**− 0.67**
Dissolved oxygen	0.29	− 0.29	− 0.41	**0.51**	**− 0.47**	**− 0.73**	**0.59**	**− 0.58**	**− 0.57**
Chlorophyll-*a*	− 0.17	0.22	0.28	**0.68**	**− 0.67**	**− 0.62**	**0.76**	**− 0.75**	**− 0.73**
Turbidity	− 0.43	0.47	**0.63**	− 0.39	0.40	0.37	− 0.43	0.42	0.42
Electrical conductivity	− 0.07	− 0.01	0.20	**0.52**	**− 0.53**	− 0.29	**0.72**	**− 0.71**	**− 0.71**
Salinity	− 0.03	− 0.07	0.19	**0.51**	**− 0.52**	− 0.27	**0.72**	**− 0.71**	**− 0.71**
Oxidation-reduction potential	− 0.30	0.35	− 0.15	− 0.41	0.40	0.27	**− 0.52**	**0.51**	**0.54**
Total carbon	− 0.08	− 0.01	− 0.06	− 0.23	0.28	− 0.06	**0.55**	**− 0.53**	**− 0.67**
Total organic carbon	− 0.15	0.11	0.00	− 0.30	0.32	0.15	**0.39**	**− 0.38**	**− 0.50**
Total nitrogen	− 0.49	0.41	0.39	− 0.35	0.35	0.37	**0.50**	**− 0.50**	**− 0.42**
Ammonium nitrogen	0.03	− 0.03	0.24	− 0.25	0.22	**0.47**	0.24	− 0.24	− 0.29
Nitrate nitrogen	**− 0.71**	**0.58**	**0.70**	**− 0.47**	**0.51**	0.24	**− 0.52**	**0.50**	**0.66**
Nitrite nitrogen	− 0.05	− 0.04	0.01	**0.50**	**− 0.49**	− 0.39	0.45	− 0.45	− 0.33
Total phosphorus	− 0.27	0.24	0.23	− 0.31	0.33	0.37	**0.48**	**− 0.47**	**− 0.46**
Phosphate phosphorus	− 0.34	0.28	0.41	− 0.17	0.17	0.32	0.28	− 0.28	− 0.25
Precipitation	− 0.42	0.44	0.18	**− 0.72**	**0.75**	0.41	**− 0.56**	**0.55**	**0.54**
Air temperature	0.025	− 0.03	− 0.46	**0.47**	**− 0.47**	− 0.38	− 0.35	0.36	0.19
Wind speed	− 0.31	0.30	− 0.05	**− 0.66**	**0.67**	0.33	− 0.26	0.26	0.28

Values in bold are significant at *P* < 0.05. Taxa categories: AT, abundant taxa; CRT, conditionally rare taxa; RT, rare taxa.
Note that the precipitation and wind speed data are the 7-day accumulation before the sampling day, and the air temperature represents daily average values.

Stochastic and deterministic processes shaping bacterial community assembly

The Sloan neutral community model showed that the fit value was 90%, 83% and 46% of explained community variance for AT

subcommunities in stations C, L and G, respectively (Fig. 6A). For CRT, the explained community variance was also high (78%, 80% and 65% in stations C, L and G, respectively). For RT subcommunities, R^2-values were less than zero, indicating no fit to the neutral model.
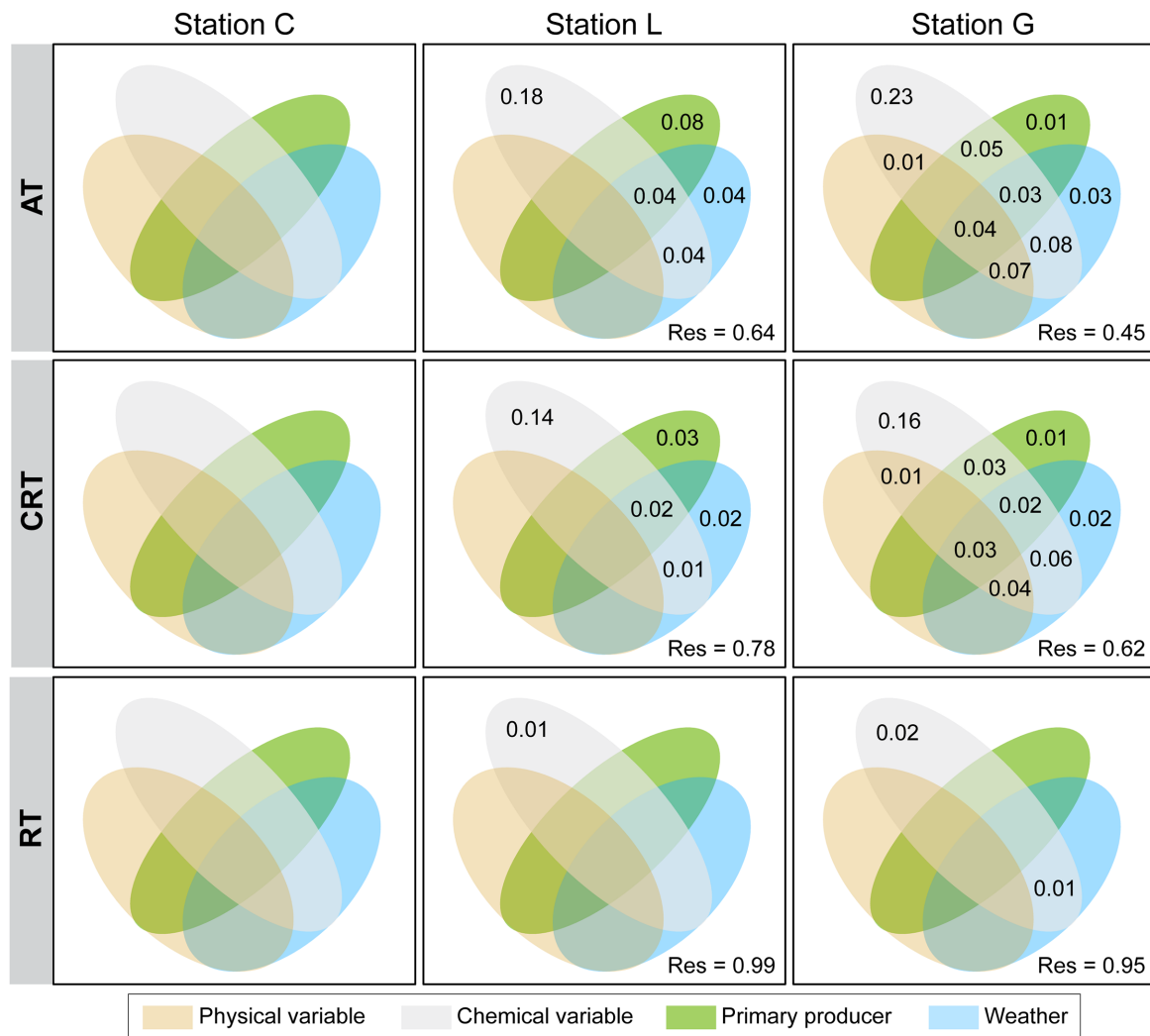
Figure 4. The Venn diagrams showing the results of variation partitioning analysis (VPA) based on bacterioplankton community at subcommunity level (AT, CRT and RT) and four groups of environmental variables (physical, chemical, primary producer and weather). Note that the variances < 0.01 are not displayed for simplicity. Res, residuals. Sampling stations: C, Control point; L, Lianhua; G, Gaota. Taxa categories: AT, abundant taxa; CRT, conditionally rare taxa; RT, rare taxa.

In the null model, C-score revealed non-random patterns of species co-occurrence in the bacterial community (Fig. 6B). High values of observed and simulated C-score were obtained from station G. For AT and CRT, observed C-score values were 19.22 and 19.70, respectively, while simulated ones were 16.44 and 18.40, respectively. At stations C and L, observed and simulated C-score values showed a slight difference except RT subcommunity. AT subcommunities in stations L and G exhibited a marked species segregation (standardized effect sizes were 10.19 and 14.42, respectively), indicating a non-random distribution.

DISCUSSION

Bacterioplankton in freshwaters are an important component of ecosystem structure and function (Liu *et al.* 2015b; Linz *et al.* 2020). Our data clearly show that high-frequency sampling approach can facilitate the identification of a broad range of temporal variations of AT, CRT and RT subcommunities in Xinglinwan Reservoir. This may suggest that clarifying the processes of abundant and rare bacterioplankton dynamics necessitate the use of high-frequency measurement. High-frequency sampling can display the build-up and breakdown of episodic

shifts in the bacterioplankton community that cannot be captured with routine seasonal sampling (Martin-Platero *et al.* 2018). Low-frequency sampling based data have demonstrated the basic patterns of seasonal change and succession of bacterioplankton communities (Avila *et al.* 2017; Nyirabuhoro *et al.* 2020). However, such patterns have not provided a good indication of sharp transition of some microbial taxa (Martin-Platero *et al.* 2018), yet the microbial communities can display rapid responses to environmental variation (Lindh *et al.* 2015) and such interaction may happen at short temporal scale (i.e. days or hours). Therefore, microbial community study based on high-resolution time series was essential to capture both quick changes due to species interactions and elongated series dynamics due to shifts in overall ecological conditions. More importantly, long-term monitoring of bacterioplankton community from high-frequency sampling permits better characterization of the dynamics of AT, CRT and RT subcommunities.
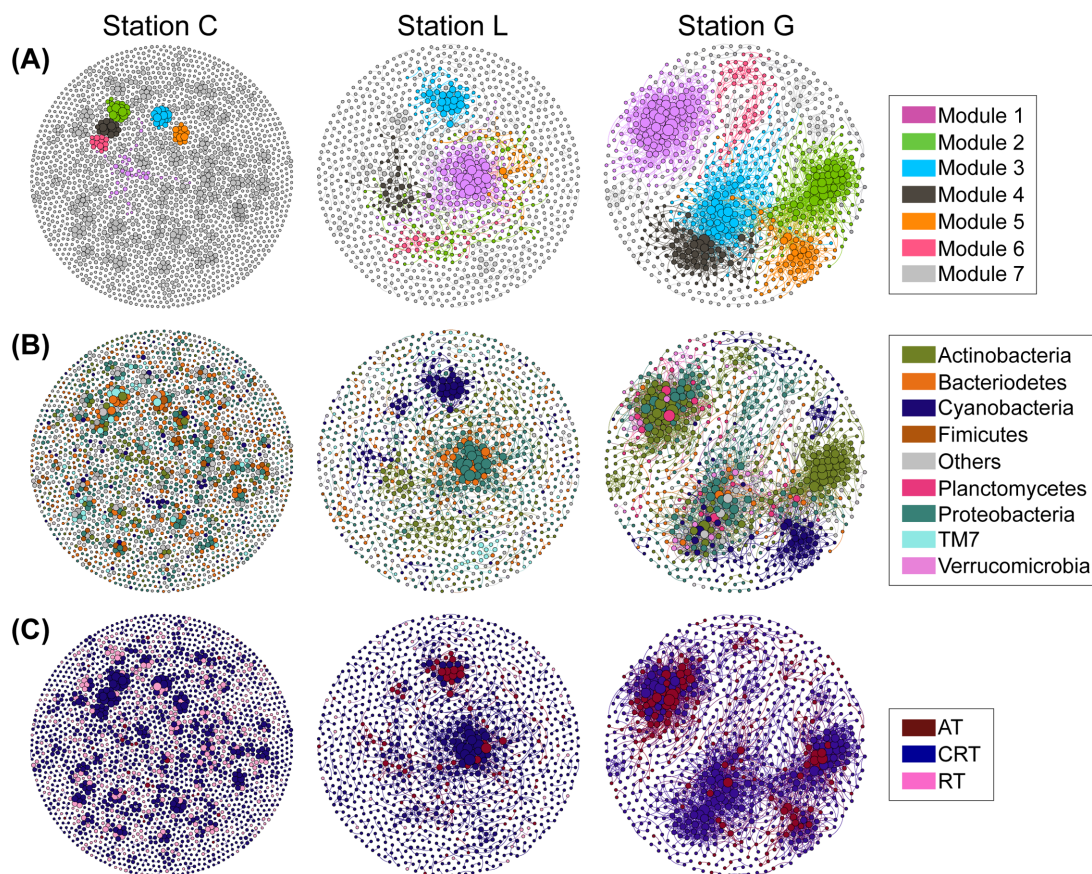
Figure 5. Co-occurrence networks of bacterioplankton communities of Xinglinwan Reservoir. The nodes colors refer to the types of (A) modularity class, (B) phylum and (C) subcommunity, respectively. The size of each node is proportional to the number of connections and only strong and significant correlations ($|r| > 0.8$, $P < 0.01$) are shown. Sampling stations: C, Control point; L, Lianhua; G, Gaota. Taxa categories: AT, abundant taxa; CRT, conditionally rare taxa; RT, rare taxa.

Temporal variations of bacterioplankton community

We found a similar response to temporal change in all subcommunities but with different trends (Fig. 3). The bacterial community exhibited a directional change in the short- and medium-time intervals (within 24 weeks), whereas it showed convergent dynamics over the long-time interval (25−53 weeks). Our results contribute to understanding the temporal patterns of bacterioplankton community at different time scales and can indicate a seasonal cycle pattern in bacterioplankton community in subtropical reservoir.

The community diversity indices such as observed OTUs, ACE and Chao1 showed the temporal dynamics with the largest contribution of conditionally rare taxa (Fig. 1). This may show that conditionally rare taxa populations contribute more to the community variation and rare taxa can recover and boom in their relative abundance at favorable environmental conditions (Lennon and Jones 2011; Shade *et al.* 2012).

A group of species in the community that consume the same resources in a similar way may exhibit similar shifts in community composition over time (Ndayishimiye *et al.* 2020). Hence, very similar communities within each month and total community that changed dramatically over time (Fig. 2A) may suggest that the communities tend to be more different over a short period of time (< half year) and similar over a long period of time (25−53 weeks). However, although the non-metric multidimensional scaling based on Bray–Curtis distance is routinely used to assess the degree of separation among bacterial communities

(Jiao *et al.* 2017; Xue *et al.* 2018), it cannot truly represent intransitive pairwise similarities in a visualization of RT subcommunity dynamics (Nyirabuhoro *et al.* 2020). A marked difference in Bray–Curtis dissimilarity of many samples of AT subcommunities than in CRT and RT subcommunities (Fig. 2A) may indicate that AT subcommunities were much more sensitive to change in different environmental conditions at fine-time scale (Fig. 4). These differences are possibly associated with distinctive physiology and metabolic function of each bacterioplankton phylotype (Lennon and Jones 2011; Nyirabuhoro *et al.* 2020). Neither Proteobacteria nor Actinobacteria showed a strong response to the temporal change, perhaps because they are core or dominant bacteria in waters and play important roles in biogeochemical cycling of elements (Saarenheimo, Tiirola and Rissanen 2015). A pronounced variation of Cyanobacteria (Fig. 2B) was closely associated with changes in environmental variables (e.g. water temperature, precipitation and air temperature), indicating that the dynamics of Cyanobacteria is largely controlled by environmental conditions specifically a change in temperature (Elliott 2012; Reichwaldt and Ghadouani 2012; Bartosiewicz *et al.* 2019). At genus level, *Synechococcuss* showed a high relative abundance with a pronounced temporal variation over medium- and long-term periods (Fig. 2C). This dominance and variation may indicate the importance of *Synechococcuss* in the ecological health of a reservoir (Cabello-Yeves *et al.* 2017; Mackey *et al.* 2017). The dominance of some genera (e.g. *Synechococcus*) in particular seasons may be attributed to high concentrations of nitrate and nitrite nitrogen because the nutrient can allow rare taxa
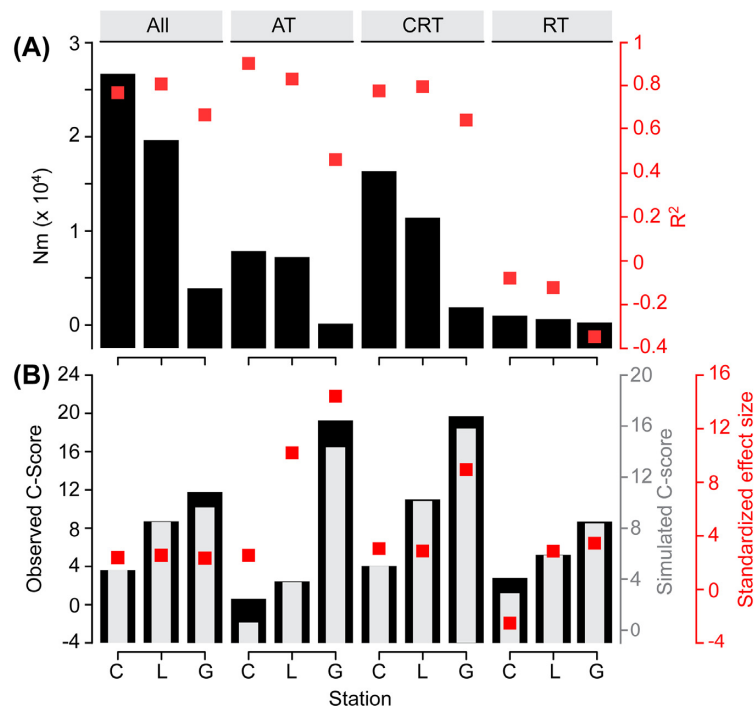
Figure 6. Ecological processes shaping bacterial community assembly in Xinglinwan Reservoir. (A) Stochastic process is shown by fit to Sloan's neutral community model across stations C, L and G from Xinglinwan Reservoir. Nm indicates the metacommunity size times immigration. The positive and negative R^2 values indicate the fit and no fit to the neutral model, respectively. (B) Null model shown by C-score metric. The values of observed C-score > simulated C-score indicate non-random co-occurrence patterns. Standardized effect size < -2 and > 2 indicate aggregation and segregation patterns, respectively. Sampling stations: C, Control point; L, Lianhua; G, Gaota. Taxa categories: AT, abundant taxa; CRT, conditionally rare taxa; RT, rare taxa.

to reproduce abundantly under favorable environmental conditions (Ruiz-González, Niño-García and Del Giorgio 2015).

On short-term time scales, bacterioplankton community revealed trends of indistinct to remarkable temporary variations (Fig. 3A) perhaps due to an extended high-resolution sampling period (Korhonen, Soininen and Hillebrand 2010). The time-lag regression degrees (*r*-values) of all subcommunities were negative and significant at long-term scales (25–53 weeks) (Fig. 3B), possibly due to a resilient status that allows bacterial taxa to recover after environmental disturbances (Liu *et al.* 2015b; Needham *et al.* 2013; Shade *et al.* 2014). Another potential cause of a directional change in the short- and middle-time intervals (within 24 weeks) and a convergent dynamic during the long-time interval (25–53 weeks) might be in high capability of different bacterioplankton taxa or subcommunities to adapt to a changing environment (e.g. seasonal variation in temperature) due to rapid growth rate and evolutionary adaptation (Liu *et al.* 2015a).

Relationship between bacterioplankton community and environment variables

Many studies on rare and abundant bacterioplankton communities have either focused on the community composition in relationship to environmental disturbances or biogeography across spatial scale (Liu *et al.* 2015b; Gilbert *et al.* 2012; Logares *et al.* 2013; Mo *et al.* 2018). However, analyses based on high-resolution sampling at a specific geographical location may come up with

questions about whether temporal dynamics in bacterioplankton communities are controlled by shifts in environmental conditions over time (Lindh *et al.* 2015). This study confirms an influence of environment on bacterioplankton community composition at different time scales (Fig. 4). For example, synchronized shifts in the relative abundance data at phylum and genus levels and different environmental variables (Fig. 2 and Figure S2, Supporting Information) confirmed a close relationship between bacterioplankton community and environmental change. Environmental variables such as nutrients and temperature can shape or disturb bacterioplankton communities (Gilbert *et al.* 2012; Shade *et al.* 2012; Lindh *et al.* 2015). Consequently, a pronounced influence of physical and chemical variables on bacterioplankton community suggests that the environmental variables can lead to an increase or a decline in the abundances of certain bacteria over time (Nyirabuhoro *et al.* 2020).

In Xinglinwan Reservoir, the influence of environment on bacterioplankton communities is obviously important (Fig. 4). A minor influence of meteorological variables (air temperature, precipitation and wind speed) on bacterioplankton community may suggest that weather conditions led to slight disturbances and shifts in bacterial community directly (Chen *et al.* 2019; Ma *et al.* 2019). The variation of each bacterioplankton subcommunity that could be explained by the environment (water physical and chemical constituents and primary producers and weather conditions) was lower than 55% (Fig. 4). This can be attributed to unmeasured environmental variables and species interactions. For unexplained community variances by environmental conditions, the rare subcommunity (95–99%) was substantially higher than that of abundant (45–64%) and conditionally rare taxa (62–78%). Several reasons may explain this phenomenon. First, the environmental sensitivity might be density-dependent

for bacterioplankton; for example, the low-abundant rare bacteria can be in dormancy status that create the bacterial resistance to environmental change (Lennon and Jones 2011). Second, the large unexplained variances could be due to unmeasured environmental and biological factors (Mo *et al.* 2018). The shift in environmental variables within three stations determines how time affects community composition as different taxa interactions are favored if fundamental conditions change (Figures S2 and S5, Supporting Information). Therefore, bacterial community was strongly responded to change in environmental conditions at station G (Table 1 and Figure S5, Supporting Information). This may suggest that bacterioplankton communities are sensitive to environmental change, but the trends may depend on the sampling time. It is highly impracticable and almost impossible to fully understand the relationship between bacterioplankton community and environment variables if only small sample size and short-term time interval were included in natural waters.

Ecological processes shaping bacterioplankton community assembly

A major challenge in freshwater microbial ecology is to quantify the relative importance of deterministic and stochastic processes controlling the assembly of microbial communities (Ndayishimiye *et al.* 2020). Niche and neutral theories explain that deterministic and stochastic processes can shape microbial community, respectively (Jia, Dini-Andreote and Falcao Salles 2018; Chen *et al.* 2019). Consequently, both deterministic and stochastic processes can regulate the community composition over time, but at different degrees (Roguet *et al.* 2015). In this work, higher R^2-values in a Sloan neutral community model explained a great fraction of the community variation across different bacterioplankton subcommunities (e.g. AT and CRT), suggesting the importance of neutral processes such as migration, births and deaths in a population. Further, higher values of standardized effect sizes (> 2) in the null model indicated a pronounced species segregation or competition in almost all subcommunities (e.g. in AT subcommunity), suggesting that the bacterial community of Xinglinwan Reservoir was not randomly assembled and deterministic processes were mainly at play (Nyirabuhoro *et al.* 2020). This may also be confirmed by a strong link between bacterioplankton dynamics and variability of environmental conditions (Fig. 4 and Figure S6, Supporting Information). The influence of both deterministic and stochastic processes on bacterioplankton communities of Xinglinwan Reservoir may also be connected to environmental changes in the watershed (Isabwe *et al.* 2018). Although the importance of stochastic processes in shaping microbial community assembly in inland waters was low in numerous studies (Chisholm and Pacala 2010; Roguet *et al.* 2015), the stochastic processes can shape the community at different time scales under changing environment (e.g. natural disasters and extreme weather); hence, we cannot ignore the role of stochastic processes in shaping bacterial community of Xinglinwan Reservoir (Fig. 6).

Linking the relative importance of ecological processes with network analyses allow us to better understand the mechanisms shaping the community assembly (Konopka, Lindemann and Fredrickson 2015). The network analyses revealed high connectivity as the sample size increased, with well-connected groups and characterized by higher numbers of modules mostly in CRT subcommunity of station G (Fig. 5 and Table S2, Supporting Information). This interconnected relationship suggests the strong

niche differentiation in closely related species (Xue *et al.* 2018). The topological properties of the networks (Fig. 5) indicated a link between microbial communities and direct connections for specific OTUs, respectively (Barberán *et al.* 2012; Xue *et al.* 2018). In our networks, CRT frequently occupied the central position and exhibited a strong relationship with other taxa in the community, indicating the potential importance of CRT in network interaction or functioning.

Limitations and recommendations for future research

Bacterioplankton community dynamics in Xinglinwan Reservoir was connected to changes in environmental conditions, this may facilitate a better understanding of ecological patterns that can characterize ecosystem integrity and potential in biodiversity conservation and restoration. Environmental change is increasingly shaping the microbial community from local to global scales (Locey and Lennon 2016). A dataset of limited study period using few sampling stations in a waterbody can be a limitation in demonstrating the dynamics of different bacterioplankton subcommunities. For Xinglinwan Reservoir, our results indicated the seasonality of bacterioplankton communities, especially in both alpha- and beta-diversities of AT and CRT (Fig. 1); however our study period was limited to 13 months. Hence, a more prolonged investigation of bacterioplankton and environmental variables could help to evaluate the influence of environment on the community among different years. The abundance of microorganisms may increase or decrease periodically by natural growth or in response to environmental factors such as temperature (Faust *et al.* 2015; Nyirabuhoro *et al.* 2020). For future studies, priority should be given to a larger spatial scale using more reservoirs and generalize our conclusion across a wide range of climate zones.

CONCLUSION

This study presents the temporal dynamics of bacterioplankton from surface waters of a subtropical urban reservoir (Xinglinwan Reservoir) in southeast China, using high-frequency sampling over 13 months. We compared the patterns and processes of bacterioplankton communities across short (0–8 weeks), medium (9–24 weeks) and long (25–53 weeks) time intervals, and revealed the ecological mechanisms controlling their temporal variation and co-occurrence patterns. Marked temporal patterns in beta-diversity were detected in abundant taxa and conditionally rare taxa. Changes in Bray–Curtis dissimilarity of bacterioplankton community revealed a clear directional change in short and medium time intervals (0–24 weeks) and a convergent dynamic over a long time interval (25–53 weeks), respectively. Cyanobacteria showed a strong succession pattern peaking in August with a relative abundance of 57.18% when temperature was high. Microbial co-occurrence networks revealed interspecies associations within AT, CRT and RT subcommunities. The temporal patterns of bacterioplankton community were shaped by both abiotic and abiotic components, but a strong influence was largely connected to changes in water chemistry. Both deterministic and stochastic processes shaped the AT and CRT subcommunities, whereas RT subcommunity may be shaped by more complicated ecological processes. The degree of temporal variation was mainly affected by changes in the relative abundance of bacterioplankton and sampling duration (i.e. sampling time of duration). These findings suggest that there is an urgent need for high-frequency sampling based

study on microbial community for better understanding, modeling and predicting the microbial responses to environmental change in future.

AUTHOR CONTRIBUTIONS

JY conceived the idea and designed the research. PN and XFG performed the laboratory experiments. JY contributed the new reagents and the analytic tools. PN, XFG, JCN, PX, YYM and JY analyzed the data and wrote the manuscript. All authors discussed the interpretation of the results and approved the final manuscript.

ACKNOWLEDGMENTS

SUPPLEMENTARY DATA

Supplementary data are available at FEMSEC online.

FUNDING

Conflicts of Interest. None declared.

REFERENCES

Ávila MP, Staehr PA, Barbosa FAR *et al*. Seasonality of freshwater bacterioplankton diversity in two tropical shallow lakes from the Brazilian Atlantic Forest. *FEMS Microbiol Ecol* 2017; **93**: fiw218.

Barberán A, Bates ST, Casamayor EO *et al*. Using network analysis to explore co-occurrence patterns in soil microbial communities. *ISME J* 2012; **6**: 343–351.

Bartosiewicz M, Przytulska A, Deshpande BN *et al*. Effects of climate change and episodic heat events on cyanobacteria in a eutrophic polymictic lake. *Sci Total Environ* 2019; **693**: 133414.

Bastian M, Heymann S, Jacomy M. Gephi: an open source software for exploring and manipulating networks. *International AAAI Conference on Weblogs and Social Media* 2009. DOI: 10.13140/2.1.1341.1520.

Boucher D, Jardillier L, Debroas D. Succession of bacterial community composition over two consecutive years in two aquatic systems: a natural lake and a lake-reservoir. *FEMS Microbiol Ecol* 2006; **55**: 79–97.

Bustin SA, Benes V, Garson JA *et al*. The MIQE guidelines: minimum information for publication of quantitative real-time PCR experiments. *Clin Chem* 2009; **55**: 611–22.

Cabello-Yeves PJ, Haro-Moreno JM, Martin-Cuadrado AB *et al*. Novel *Synechococcus* genomes reconstructed from freshwater reservoirs. *Front Microbiol* 2017; **8**: 1151.

Campbell BJ, Yu L, Heidelberg JF *et al*. Activity of abundant and rare bacteria in a coastal ocean. *Proc Natl Acad Sci USA* 2011; **108**: 12776–12781.

Chen WD, Ren KX, Isabwe A *et al*. Stochastic processes shape microeukaryotic community assembly in a subtropical river across wet and dry seasons. *Microbiome* 2019; **7**: 138.

Chisholm RA, Pacala SW. Niche and neutral models predict asymptotically equivalent species abundance distributions in high-diversity ecological communities. *Proc Natl Acad Sci USA* 2010; **107**: 15821–15825.

Collins SL, Micheli F, Hartt L. A method to determine rates and patterns of variability in ecological communities. *Oikos* 2000; **91**: 285–293.

Crump BC, Peterson BJ, Raymond PA *et al*. Circumpolar synchrony in big river bacterioplankton. *Proc Natl Acad Sci USA* 2009, **106**: 21208–12

DeSantis TZ, Hugenholtz P, Larsen N *et al*. Greengenes, a chimera-checked 16S rRNA gene database and workbench compatible with ARB. *Appl Environ Microbiol* 2006; **72**: 5069–72.

Eiler A, Heinrich F, Bertilsson S. Coherent dynamics and association networks among lake bacterioplankton taxa. *ISME J* 2012; **6**: 330–342.

Elliott JA. Is the future blue-green? A review of the current model predictions of how climate change could affect pelagic freshwater cyanobacteria. *Water Res* 2012; **46**: 1364–1371.

Fang PJ, Peng F, Gao XF *et al*. Decoupling the dynamics of bacterial taxonomy and antibiotic resistance function in a subtropical urban reservoir as revealed by high-frequency sampling. *Front Microbiol* 2019; **10**: 1448.

Faust K, Lahti L, Gonze D *et al*. Metagenomics meets time series analysis: unraveling microbial community dynamics. *Curr Opin Microbiol* 2015; **25**: 56–66.

Faust K, Raes J. Microbial interactions: from networks to models. *Nat Rev Microbiol* 2012; **10**: 538–550.

Gilbert JA, Steele JA, Caporaso JG *et al*. Defining seasonal marine microbial community dynamics. *ISME J* 2012; **6**: 298–308.

Gotelli NJ, Mccabe DJ. Species co-occurrence: a meta-analysis of J. M. Diamond's assembly rules model. *Ecology* 2002; **83**: 2091–6.

Isabwe A, Yang JR, Wang Y *et al*. Community assembly processes underlying phytoplankton and bacterioplankton across a hydrologic change in a human-impacted river. *Sci Total Environ* 2018; **630**: 658–67.

Jia X, Dini-Andreote F, Falcao Salles J. Community assembly processes of the microbial rare biosphere. *Trends Microbiol* 2018; **26**: 738–747.

Jiao S, Luo Y, Lu M *et al*. Distinct succession patterns of abundant and rare bacteria in temporal microcosms with pollutants. *Environ Pollut* 2017; **225**: 497–505.

Konopka A, Lindemann S, Fredrickson J. Dynamics in microbial communities: unraveling mechanisms to identify principles. *ISME J* 2015; **9**: 1488–1495.

Korhonen JJ, Soininen J, Hillebrand H. A quantitative analysis of temporal turnover in aquatic species assemblages across ecosystems. *Ecology* 2010; **91**: 508–17.

Lennon JT, Jones SE. Microbial seed banks: the ecological and evolutionary implications of dormancy. *Nat Rev Microbiol* 2011; **9**: 119–130.

Lindh MV, Sjostedt J, Andersson AF *et al*. Disentangling seasonal bacterioplankton population dynamics by high-frequency sampling. *Environ Microbiol* 2015; **17**: 2459–2476.

Lindström ES, Langenheder S. Local and regional factors influencing bacterial community assembly. *Environ Microbiol Rep* 2012; **4**: 1–9.

Linz AM, Aylward FO, Bertilsson S *et al*. Time-series metatranscriptomes reveal conserved patterns between phototrophic and heterotrophic microbes in diverse freshwater systems. *Limnol Oceanogr* 2020; **65**: S101–S112.

Liu LM, Chen HH, Liu M *et al*. Response of the eukaryotic plankton community to the cyanobacterial biomass cycle over 6 years in two subtropical reservoirs. *ISME J* 2019a; **13**: 2196–2208.

Liu LM, Yang J, Lv H *et al*. Phytoplankton communities exhibit a stronger response to environmental changes than bacterioplankton in three subtropical reservoirs. *Environ Sci Technol* 2015a; **49**: 10850–10858.

Liu LM, Yang J, Yu Z *et al*. The biogeography of abundant and rare bacterioplankton in the lakes and reservoirs of China. *ISME J* 2015b; **9**: 2068–2077.

Liu M, Liu LM, Chen HH *et al*. Community dynamics of free-living and particle-attached bacteria following a reservoir *Microcystis* bloom. *Sci Total Environ* 2019b; **660**: 501–511.

Locey KJ, Lennon JT. Scaling laws predict global microbial diversity. *Proc Natl Acad Sci USA* 2016; **113**: 5970–5975.

Logares R, Lindström ES, Langenheder S *et al*. Biogeography of bacterial communities exposed to progressive long-term environmental change. *ISME J* 2013; **7**: 937–948.

Ma T, Jiang Y, Elbehery AHA *et al*. Resilience of planktonic bacterial community structure in response to short-term weather deterioration during the growing season in an alpine lake. *Hydrobiologia* 2019, **847**: 535–548.

Mackey KRM, Hunter-Cevera K, Britten GL *et al*. Seasonal succession and spatial patterns of *Synechococcus* microdiversity in a salt marsh estuary revealed through 16S rRNA gene oligotyping. *Front Microbiol* 2017; **8**: 1496.

Magurran AE. *Ecological Diversity and Its Measurement*. Princeton University Press, Princeton, NJ, USA 1988.

Martin-Platero AM, Cleary B, Kauffman K *et al*. High resolution time series reveals cohesive but short-lived communities in coastal plankton. *Nature Commun* 2018; **9**:266.

Mo YY, Zhang WJ, Yang J *et al*. Biogeographic patterns of abundant and rare bacterioplankton in three subtropical bays resulting from selective and neutral processes. *ISME J* 2018; **12**: 2198–2210.

Ndayishimiye JC, Ju LH, Li HK *et al*. Temperature transfer functions based on freshwater testate amoebae from China. *Eur J Protistol* 2019; **69**: 152–164.

Ndayishimiye JC, Nyirabuhoro P, Wang Q *et al*. Effects of natural and anthropogenic changes on testate amoebae communities in an alpine lake over the past 2500 years. *Sci Total Environ* 2020; **721**: 137684.

Needham DM, Chow CE, Cram JA *et al*. Short-term observations of marine bacterial and viral communities: patterns, connections and resilience. *ISME J* 2013; **7**: 1274–1285.

Nyirabuhoro P, Liu M, Xiao P *et al*. Seasonal variability of conditionally rare taxa in the water column bacterioplankton community of subtropical reservoirs in China. *Microb Ecol* 2020; **80**: 14–26.

Ofiţeru ID, Lunn M, Curtis T *et al*. Combined niche and neutral effects in a microbial wastewater treatment community. *Proc Natl Acad Sci USA* 2010; **107**: 15345–50.

R Core Team. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria 2019.

Rivett DW, Bell T. Abundance determines the functional role of bacterial phylotypes in complex communities. *Nat Microbiol* 2018; **3**: 767–772.

Rognes T, Flouri T, Nichols B *et al*. VSEARCH: a versatile open source tool for metagenomics. *PeerJ* 2016; **4**: e2584.

Roguet A, Laigle GS, Therial C *et al*. Neutral community model explains the bacterial community assembly in freshwater lakes. *FEMS Microbiol Ecol* 2015; **91**: fiv125.

Ruiz-González C, Niño-García JP, Del Giorgio PA. Terrestrial origin of bacterial communities in complex boreal freshwater networks. *Ecol Lett* 2015; **18**: 1198–1206.

Saarenheimo J, Tiirola MA, Rissanen AJ. Functional gene pyrosequencing reveals core proteobacterial denitrifiers in boreal lakes. *Front Microbiol* 2015; **6**: 674.

Shade A, Caporaso JG, Handelsman J *et al*. A meta-analysis of changes in bacterial and archaeal communities with time. *ISME J* 2013; **7**: 1493–1506.

Shade A, Read JS, Youngblut ND *et al*. Lake microbial communities are resilient after a whole-ecosystem disturbance. *ISME J* 2012; **6**: 2153–2167.

Shade A, Jones SE, Caporaso JG *et al*. Conditionally rare taxa disproportionately contribute to temporal changes in microbial diversity. *mBio* 2014; **5**: e01371–14.

Sloan WT, Lunn M, Woodcock S *et al*. Quantifying the roles of immigration and chance in shaping prokaryote community structure. *Environ Microbiol* 2006; **8**: 732–740.

Stegen JC, Lin X, Konopka AE *et al*. Stochastic and deterministic assembly processes in subsurface microbial communities. *ISME J* 2012; **6**: 1653–64.

Stone L, Roberts A. The checkerboard score and species distributions. *Oecologia* 1990, **85**:74–79.

Xue YY, Chen HH, Yang JR *et al*. Distinct patterns and processes of abundant and rare eukaryotic plankton communities following a reservoir cyanobacterial bloom. *ISME J* 2018; **12**: 2263–2277.

Yokokawa T, Nagata T, Cottrell MT *et al*. Growth rate of the major phylogenetic bacterial groups in the Delaware estuary. *Limnol Oceanogr* 2004; **49**: 1620–9.

Yu Z, Yang J, Amalfitano S *et al*. Effects of water stratification and mixing on microbial community structure in a subtropical deep reservoir. *Sci Rep* 2014; **4**:5821.

Zelaya AJ, Parker AE, Bailey KL *et al*. High spatiotemporal variability of bacterial diversity over short time scales with unique hydrochemical associations within a shallow aquifer. *Water Res* 2019; **164**: 114917.