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The different responses of planktonic bacteria and archaea to water temperature maintain the stability of their community diversity in dammed rivers

Na Liu¹, Baoli Wang^{1,2*} , Meiling Yang¹, Wanzhu Li¹, Xinjie Shi¹ and Cong-Qiang Liu^{1,2}

Abstract

Background Planktonic bacteria and archaea play a key role in river nutrient biogeochemical cycling; however, their respective community assembly and how to maintain their diversity are not well known in dammed rivers. Therefore, a seasonal survey of planktonic bacterial and archaeal community compositions and related environmental factors was conducted in 16 cascade reservoirs and corresponding river waters on the Wujiang River and the Pearl River in southwest China to understand the above mechanisms.

Results Deterministic processes dominated bacterial and archaeal community assembly. The structural equation models showed that water temperature can directly or indirectly affect the microbial diversity. Interestingly, planktonic bacterial diversity increased with increasing water temperature, while archaea showed the opposite trend; the overall diversity of bacteria and archaea was no significant changes with changeable water temperature. Abundant microbes had a stronger distance–decay relationship than middle and rare ones, and the relationship was stronger in winter and spring than in summer and autumn.

Conclusions Planktonic bacteria and archaea in dammed rivers had different biogeographic distributions, and water temperature was a key controlling factor. The different responses of planktonic bacterial and archaeal diversity to water temperature could be due to their different phylogenetic diversity. This ultimately maintained the stability of total microbial community diversity. This study reveals the different responses of planktonic bacteria and archaea to water temperature and perfects the theoretical framework for planktonic microbial biogeography in dammed rivers.

Keywords Planktonic bacteria and archaea, Community assembly, Diversity, Water temperature, Cascade reservoirs

Background

Planktonic bacteria and archaea are important components of aquatic ecosystems and play an important role in nutrient biogeochemical cycles (Falkowski et al. 2008;

Newton et al. 2011; Hanson et al. 2012). Microbial biogeography is a discipline that aims to study the temporal and spatial distribution pattern of microbial community (Ansdell et al. 2016). Understanding the controlling mechanisms of planktonic bacterial and archaeal biogeographic distribution will improve the knowledge of their function in aquatic ecosystems (Moitra and Leff 2015; Yang et al. 2016). In 1934, Baas-Becking was the first to propose the microbial distribution hypothesis: everything is everywhere, but the environment selects (Baas-Becking 1934). Microbial biogeography has been rapidly developed with the emergence of high-throughput sequencing

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technology and molecular biology in the twenty-first century and becomes a research hotspot in the field of ecology nowadays (Nio-García et al. 2016; Fierer 2017). Although microorganisms have strong dispersal ability, environmental selection contributes mostly to the temporal and spatial difference in their community structure and then results in their different geographical distribution patterns (Martiny et al. 2006; Zhou and Ning 2017). It is well known that microbial community assembly is controlled by deterministic and stochastic processes (Caswell 1976; Hubbell 2001; Vellend 2010). Deterministic processes, including heterogeneous and homogeneous selection, are based on niche theory and emphasize the influence of environmental factors and microbial species interaction. Stochastic processes, including dispersal limitation, homogenizing dispersal, and drift, are based on the neutral theory and consider that the community assembly is affected by uncontrollable factors (Stegen et al. 2013; Dini-Andreote et al. 2015; Ning et al. 2020).

In microbial communities, only a few species are abundant, and most are rare. Both abundant and rare groups can show similar biogeographical patterns (Chen et al. 2020), but they might have different responses to environmental changes. Abundant species perform the major ecological functions, whereas rare species act as a microbial seed bank and safeguard against environmental changes (Pester et al. 2010). As for microorganisms with middle abundance, there are few reports on their geographical distribution patterns nowadays.

Environmental factors play an important role in shaping microbial community structures. Previous studies have shown that microbial communities in aquatic ecosystems are influenced by different factors such as water temperature (Yuan et al. 2021), salinity (Mo et al. 2021), pH (Liu et al. 2015), and nutrients (Hu et al. 2014). With an increase in salinity in coastal wetlands, deterministic processes gradually dominate planktonic bacterial community assembly, while planktonic archaea are always dominated by stochastic processes (Wang et al. 2021). Nutrients are essential elements for microbial growth, and the abundance of planktonic bacteria in the eutrophic reservoir is thus higher than that in the oligotrophic reservoir (Yue et al. 2021). Water temperature is usually associated with geographical variables such as altitude and solar radiation and can affect the growth and reproduction of microorganisms (Shapiro et al. 2012; Luo et al. 2019). It has been found that water temperature, but not other factors, significantly influences the structure of the planktonic bacterial community in some reservoirs (Chen et al. 2021; Li et al. 2022). In addition, microbial interactions such as mutualism, competition, and parasitism are also the important factors affecting microbial community structure (Wang et al. 2021).

Rivers are transport tubes from land to sea. The rapid development of social economy and the surging population lead to the increasing demand for electric power and promote the rapid development of renewable energy such as hydropower (Wang et al. 2022). Nowadays approximately 70% of the world's rivers have been dammed, and this changes water retention time and material cycling (Grill et al. 2019; Liang et al. 2019) and thus could affect microbial community structure and succession. The changes in environmental factors have been reported to affect the composition of microbial community, but whether planktonic bacteria and archaea respond similarly to these changes is still unclear. In coastal wetlands, salinity has been found to show different effects on the planktonic bacterial and archaeal community assembly (Wang et al. 2020, 2021). Considering that damming can cause discontinuities in river water temperature and its great fluctuations (Yang et al. 2020a, b), we hypothesized that planktonic bacterial and archaeal communities have different responses to water temperature in dammed rivers.

Therefore, we investigated the microbial community composition and the relevant environmental parameters in the 16 cascade reservoirs and their corresponding river waters on the Wujiang River and the Pearl River in southwest China to verify the above hypothesis. The aims of this study are: (1) to explore the geographical distribution patterns of planktonic bacterial and archaeal communities and their influencing factors; (2) to understand the different mechanisms of water temperature on planktonic bacterial and archaeal diversity. This study will perfect the theoretical framework for the planktonic microbial biogeography in dammed rivers.

Methods

Study area and sampling

The Wujiang River, the largest river in Guizhou Province, is a tributary of the Yangtze River with a total length of 1037 km, and has a subtropical monsoon climate. Twelve reservoirs on the Wujiang River, including Hongjiadu (HJD), Dongfeng (DF), Wujiangdu (WJD), Suofengying (SFY), Goupitan (GPT), Silin (SL), Pengshui (PS), and Yinpan (YP) in the main streams, and Pingzhai (PZ), Puding (PD), Yinzidu (YZD), and Hongfeng (HF) in the tributaries (Fig. 1), are surveyed. Surface water samples were collected in the winter (January), spring (April), summer (July), and autumn (October) of 2017 and in the winter (December) of 2019. The Pearl River is the third longest river in China, with a total length of 2320 km. It has a subtropical monsoon climate. In this study, the Dahua (DH), Yantan (YT), Longtan (LT), and Chaishitan (CST) reservoirs on the Pearl River were selected (Fig. 1). Water

SO_4^{2-} , and NO_3^-) were determined by ion chromatography (ICS-5000, Thermo Fisher, USA) with a detection limit of 0.1 mg L^{-1} . Total alkalinity (ALK) was obtained by titration with standard hydrochloric acid. The dissociation constants for carbonic acid were calculated by the temperature and corrected by ionic strength (Maberly 1996; Stumm and Morgan 1983). The concentrations of CO_2 , HCO_3^- , and CO_3^{2-} were calculated using ALK, pH, and corrected dissociation constants. The concentration of dissolved inorganic carbon (DIC) is the sum of CO_2 , HCO_3^- , and CO_3^{2-} concentrations. The data of solar radiation (SR) were obtained from the agrometeorological data (www.wheata.cn), and the monthly average data during the sampling period were selected.

16S rRNA sequencing

The total DNA of sample was extracted by E.Z.N.A.TM Water DNA Kit (OMEGA, United States) according to the manufacturer's protocols. The concentration and purity of DNA were determined by Multiskan GO (Thermo Fisher, United States). The V4 region of 16S rRNA sequencing for archaea and bacteria was performed on Illumina NovaSeq 6,000 platform at Meige Technology Co., Ltd., Guangzhou, China. The 515F (GTGCCAGCMGCCGCGGTAA) and 806R (GGACTA CHVGGGTWTCTAAT) were used as primers for bacteria. The Arch340F (CCCTAYGGGGYGCASCAG), Arch1000F (GGCCATGCACYWCYTCTC), Uni519F (CAGYMGCCRCGGKAAHACC), and Arch806R (GGA CTACNSGGTMTCTAAT) were used as primers for archaea (Li et al. 2022). Raw fastq data were quality-filtered using Trimmomatic (Bolger et al. 2014) to remove contaminating adaptors, low quality ends of reads, and short length reads (<200 bp). The overlapping paired-end reads with sequence mismatching <5 bp and alignment similarity >90% were merged using FLASH (Magoc and Salzberg 2011). Operational taxonomic units (OTUs) were clustered in UPARSE software at 97% consistency level (Edgar 2013). Singleton and doubleton OTUs representing sequencing errors were removed, and the representative OTUs with the highest occurrence frequency were assigned using Greengenes2 (Lan et al. 2012). To equalize sequencing depth, each sample was rarefied to the minimum sequencing depth (the minimum number of bacterial and archaeal reads is 83,126 and 72,619, respectively), and sequence normalization was performed using MOTHUR v.1.33.3 (Schloss et al. 2009). Bacterial and archaeal raw data obtained have been deposited in NCBI SRA database with the accession numbers of SRR8892916, SRR8892914, PRJNA874581, PRJNA874587, PRJNA874586, PRJNA874582, PRJNA907135, and PRJNA907132. The microbes were classified into three groups: abundant OTUs were OTUs

of a mean relative abundance of $\geq 0.1\%$; rare OTUs were OTUs of a mean relative abundance of $< 0.001\%$; and the rest were middle OTUs (Additional file 1: Table S3) (Mo et al. 2021).

Analysis for planktonic bacterial and archaeal community assembly

The Infer Community Assembly Mechanisms by Phylogenetic-bin-based null model (iCAMP) was used for quantitative analysis of planktonic bacterial and archaeal community assembly processes. The observed taxa were divided into different bins based on their phylogenetic relationships, and then it was quantified for the proportions of each ecological process (i.e., heterogenous selection, homogenous selection, dispersal limitation, homogenizing dispersal, and drift) (Ning et al. 2020). In this method, beta Net Relatedness Index indicated phylogenetic diversity, and modified Raup–Crick metric indicated taxonomic β -diversities (Stegen et al. 2013; Ning et al. 2020). The analysis was calculated using the R software (4.2.1) “iCAMP” package.

Data analysis

Community dissimilarities of planktonic bacteria and archaea based on Bray–Curtis distance were calculated using the “vegan” package. Principal coordinates analysis (PCoA) and analysis of similarities (ANOSIM) were used to analyze the differences in community composition among samples with “vegan” package. Random Forest was conducted to identify the key environmental factors affecting the deterministic processes and analyzed using the “rfPermute” package. Spearman's correlation was used for analyses between the variables, and Mantel test was used for understanding the relationship between microbial community composition and environmental factors according to the correlation coefficient r and significance-level p -values of the two matrices. They were calculated using the core function in the “linkET” and “corrplot” packages. Non-parametric variance decomposition based on Bray–Curtis distance was performed using permutational multivariate analysis of variance (PERMANOVA) to assess the contribution of environmental factors to microbial community structure. The alpha diversity indexes (i.e., Shannon–Wiener index, richness index, and phylogenetic diversity) were conducted with the “picante” package. The structural equation model (SEM) is used to determine the direct and indirect relationship between the variables (Rosseeel 2011). The SEM model was constructed using “lavaan” package. All the computational analysis was done on R software (4.2.1 version). The linear fitting analysis was performed using Origin2021 Student Edition.

Results

Physical and chemical parameters

The average WT, pH, DO concentration, and SR in the Wujiang River and the Pearl River were 19.03 °C, 7.91, 8.93 mg L⁻¹, and 8.83 × 10⁶ J m⁻² d⁻¹, respectively. In general, the average WT was higher in the mainstream than in the tributaries, with a gradual increase from upstream to downstream; while the average pH, DO concentration, Chl a concentration, and SR were lower in the mainstream than in the tributaries and higher in summer than in winter (Additional file 1: Figs. S1–3). The average concentrations of DIP, DIN, DSi, and DIC in the Wujiang River and the Pearl River were 2.73 μmol L⁻¹, 0.22 mmol L⁻¹, 0.04 mmol L⁻¹, and 2.62 mmol L⁻¹. The DIP concentration in the upstream was higher than in the downstream for the Wujiang River, whereas that in the Pearl River showed the opposite tendency. The concentrations of DIN and DSi in the Wujiang River and the Pearl River fluctuated significantly in the upstream and were greater in summer than in winter. The concentration of DIC was no regular variation trend from upstream to downstream. The above parameters showed obvious seasonal variations (Additional file 1: Figs. S1–3, Table S2). The average Chl a concentration and F_v/F_m of phytoplankton in the Wujiang River and the Pearl River were 5.40 μg L⁻¹ and 0.61, with a range from 0 to 71.98 μg L⁻¹ and from 0.27 to 0.79, respectively. The average Shannon–Wiener indexes of planktonic bacteria and archaea in the Wujiang River and the Pearl River were 5.29 and 1.52, with a range from 2.67 to 7.82 and from 0.25 to 4.47, respectively (Additional file 1: Fig. S4).

Spatiotemporal distribution of planktonic bacteria and archaea

A total of 24,054 OTUs in planktonic bacteria and 5311 OTUs in planktonic archaea were obtained, and all OTUs were clustered into 50 bacterial phyla and 9 archaeal phyla. The top two bacterial phyla were Proteobacteria and Actinobacteria (Fig. 2). The dominant phylum from upstream to downstream changed from Actinobacteria to Proteobacteria in winter and spring. In summer and autumn, the relative abundance of planktonic bacterial groups did not change significantly. The top two planktonic archaeal phyla were Thaumarchaeota and Nanoarchaeota. In general, the spatiotemporal variation in planktonic archaeal community structure was less obvious than that in planktonic bacterial community structure (Fig. 2). The planktonic archaeal community composition in the HF and CST reservoirs was significantly different from that in the other reservoirs: the relative abundance of Thaumarchaeota decreased significantly, while that of Nanoarchaeota and Crenarchaeota

increased. Both of bacteria and archaea exhibited obvious distance–decay relationships, and the relationship of planktonic bacteria was strong in winter and spring (Fig. 3). In detail, middle and rare planktonic bacteria and abundant planktonic archaea showed significant distance–decay relationships (Additional file 1: Table. S4); while the relationships for abundant bacteria and all archaea were not significant in the Wujiang River in winter (Fig. 3b), and in the Pearl River in summer these for middle and rare archaea were not significant (Fig. 3c). PCoA analysis showed that the distribution patterns of planktonic bacterial communities in summer were different from that in other seasons; while planktonic archaea showed discrete patterns (Fig. 4; Additional file 1: Figs. S5–7).

Planktonic bacterial and archaeal community assembly and the influencing factors

The iCAMP analysis showed that deterministic processes dominated the assembly of planktonic bacteria and archaea (Fig. 5a). For planktonic bacteria, the proportion of stochastic processes increased from winter to autumn. From abundant groups to rare groups of bacteria and archaea, the contribution of stochastic processes to community assembly increased gradually. Random Forest showed that WT was a key factor in general in deterministic processes although there were differences in key influencing factors for different groups or/and different regions (Fig. 5b; Additional file 1: Fig. S8). In the Wujiang River, WT, pH, DO, DSi, DIC, SR, and Chl a were the main influencing factors for the planktonic bacterial community composition (Fig. 5b; Additional file 1: Fig. S8a), whereas WT, DIN, and DSi were the main influencing ones for planktonic archaeal community composition (Additional file 1: Fig. S8b). In the Pearl River, WT, DIP, DSi, and SR were the main influencing factors for planktonic bacterial communities, while WT and SR were the main influencing factors for planktonic archaeal communities (Additional file 1: Fig. S8c, d). In addition, WT had a high contribution to the abundant, middle, and rare group's assembly and was one of their most important influencing factors (Additional file 1: Fig. S9).

Mantel test indicated that the community composition of planktonic bacteria and archaea was influenced by nutrients (i.e., DIN, DIP, DSi, DIC) in winter and spring but by basic physical and chemical factors (i.e., WT, pH, DO, SR) and nutrients in summer and autumn (Fig. 5c; Additional file 1: Fig. S10). The influence of these factors on the abundant group was stronger than that on the rare one. The results of PERMANOVA analysis showed that the contribution of basic factors to the community assembly was higher than that of nutrients in summer, but the opposite result was observed in other seasons

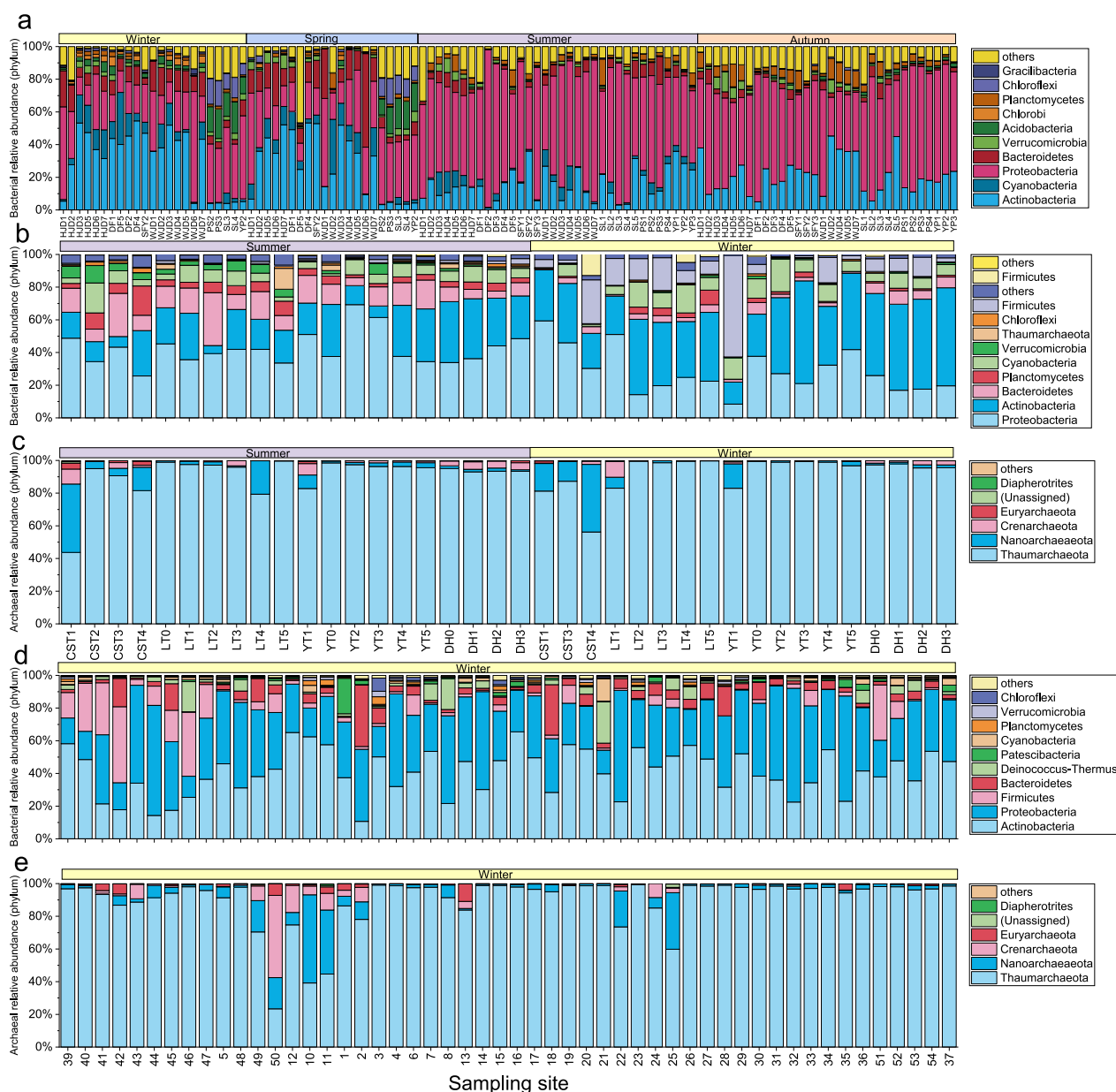


Fig. 2 The compositions of bacterial and archaeal community. Planktonic bacteria of the Wujiang River in 2017 (a); planktonic archaea (b) and bacteria (c) of the Pearl River in 2019; planktonic archaea (d) and bacteria (e) of the Wujiang River in 2019. The X-axis for sampling site is arranged from upstream to downstream

(Additional file 1: Table. S4). The environmental factors contributed less to the community assembly of rare groups. Spearman correlation analysis showed that the impact of environmental factors on community diversity was stronger in summer and autumn than in winter and spring. Environmental factors were significantly correlated with the diversity of planktonic bacteria in summer and archaea in winter, respectively (Fig. 5d; Additional file 1: Fig. S11–12). The SEM model showed that WT not

only directly affected the diversity of planktonic bacteria and archaea, but also indirectly affected them by interfering nutrient variations (Fig. 6; Additional file 1: Fig. S13).

Discussion

Mechanisms controlling planktonic bacterial and archaeal geographical distributions in dammed rivers

There were obvious biogeographical differences for planktonic bacteria and archaea in dammed rivers, and

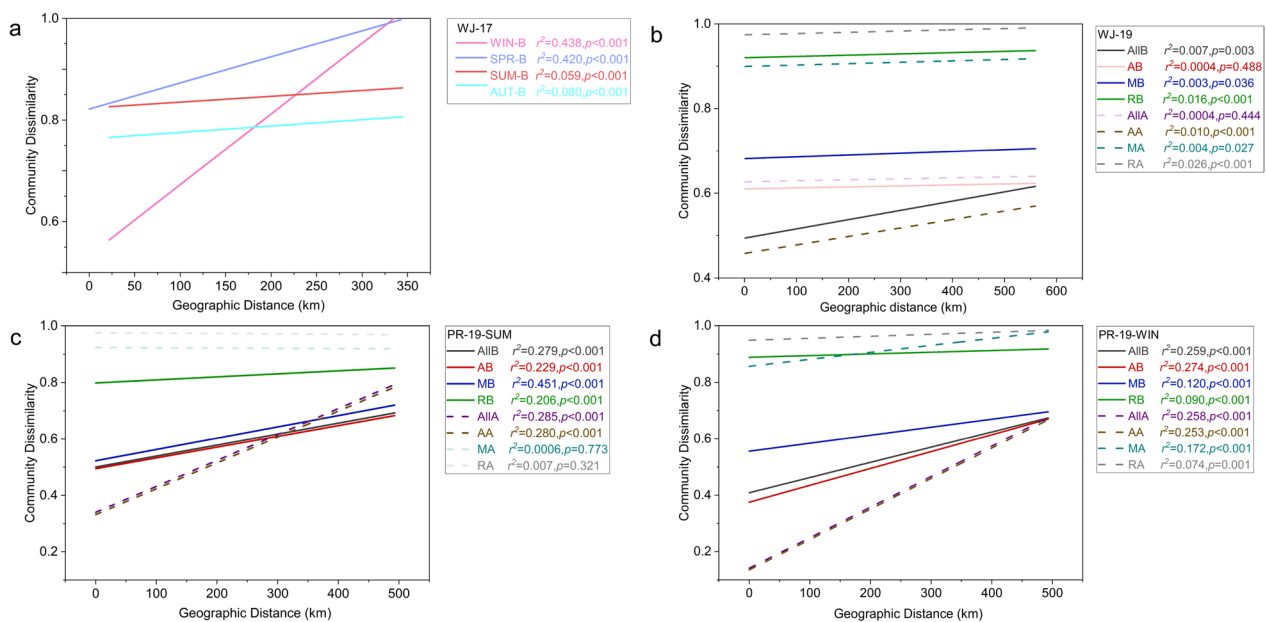


Fig. 3 The regression lines showing the distance–decay relationships. The relationships were for the Wujiang River of 2017 (**a**) and 2019 (**b**) and for the Pearl River in the summer of 2019 (**c**) and in the winter of 2019 (**d**). *WJ* Wujiang River, *PR* Pearl River, *B* Bacteria, *AIIIB* all bacteria, *AB* abundant bacteria, *MB* middle bacteria, *RB* rare bacteria, *AIIA* all archaea, *AA* abundant archaea, *MA* middle archaea, *RA* rare archaea, *WIN* winter, *SPR* spring, *SUM* summer, *AUT* autumn

deterministic processes rather than stochastic processes dominated the community assembly processes (Fig. 5a). The respective contribution of deterministic and stochastic processes to planktonic bacterial and archaeal assembly, to some degree, depends on the scale of the study area (e.g., regional or global scale) and the difference in environmental gradients across locations (Hanson and Fuhrman 2012; Morrison-Whittle and Goddard 2015). For example, the CST and HF reservoirs as leading reservoirs had a high eutrophication level (Liang et al. 2019) and thus showed significant different planktonic archaeal community composition from the other reservoirs (Fig. 2b, d). Microbial habitats usually have a larger difference among the tributaries than along the river mainstream, so does microbial community composition. Therefore, planktonic bacterial and archaeal community assembly among the tributaries could show no apparent relationships from each other. The samples of the Pearl River were mainly from the mainstream, while many samples of the Wujiang River were from the tributaries (Fig. 1). This could be the reason why the distance–decay relationship in the Wujiang River was significantly weaker than that in the Pearl River (Fig. 3b, d). In addition, abundant planktonic bacteria and archaea are more sensitive to environmental factors (e.g., WT, DO, and nutrients) than rare ones (Pedrós-Alió 2012; Li et al. 2017a). Therefore, the contribution of deterministic processes to the community formation of abundant

planktonic bacteria and archaea is generally higher than that of middle and rare groups, and the distance decay of rare groups is then much weaker than that of abundant groups (Figs. 3, 5a). Rare species usually have many categories but low abundance in each group; although their biogeographical difference is not obvious, it is known that they have important ecological functions and thus maintain the stability of aquatic ecosystems (Kim et al. 2013; Lynch and Neufeld 2015).

The planktonic microbial community assembly in dammed rivers is firstly constrained by hydrological conditions (Yang et al. 2020a, b), and the species that can adapt to the local environment evolve to be dominant ones, finally resulting in the control of environmental selection on the formation of planktonic bacterial and archaeal communities (Fig. 5). As environmental factors such as light, WT, and nutrient concentrations have obvious seasonal variations (Nyirabuhoro et al. 2020), planktonic bacterial and archaeal community compositions thus show obvious seasonal differences (Fig. 3). Eukaryotic microorganisms in a subtropical river have also been found to have a stronger distance–decay pattern in dry season than in wet season (Chen et al. 2019). In winter and spring, surface runoff to river is small, and river water environment varies little; along the horizontal direction of river flow, dispersal will be a main factor affecting microbial community assembly, and the distance–decay relationship is thus strong. In summer and

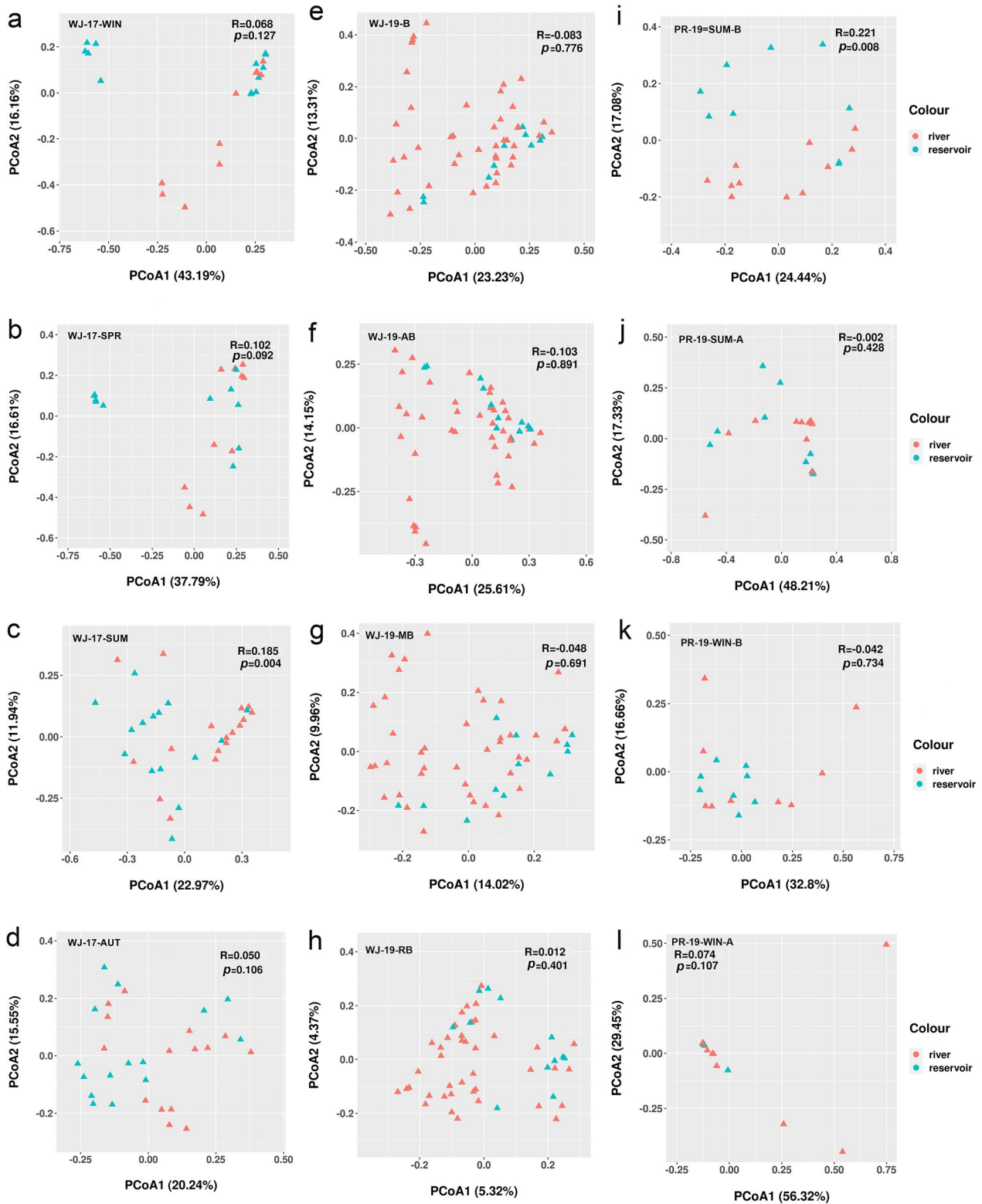


Fig. 4 Principal coordinate analysis (PCoA) of bacterial and archaeal communities. Bacterial community in the Wujiang River in 2017 (a–d) and in 2019 (e–h), and bacterial and archaeal community in the Pearl River in 2019 (i–l). $R > 0$ means the difference between river and reservoir sites more than that between river sites or reservoir sites. Significance level: $p < 0.05$. The other abbreviations are referred to Fig. 3

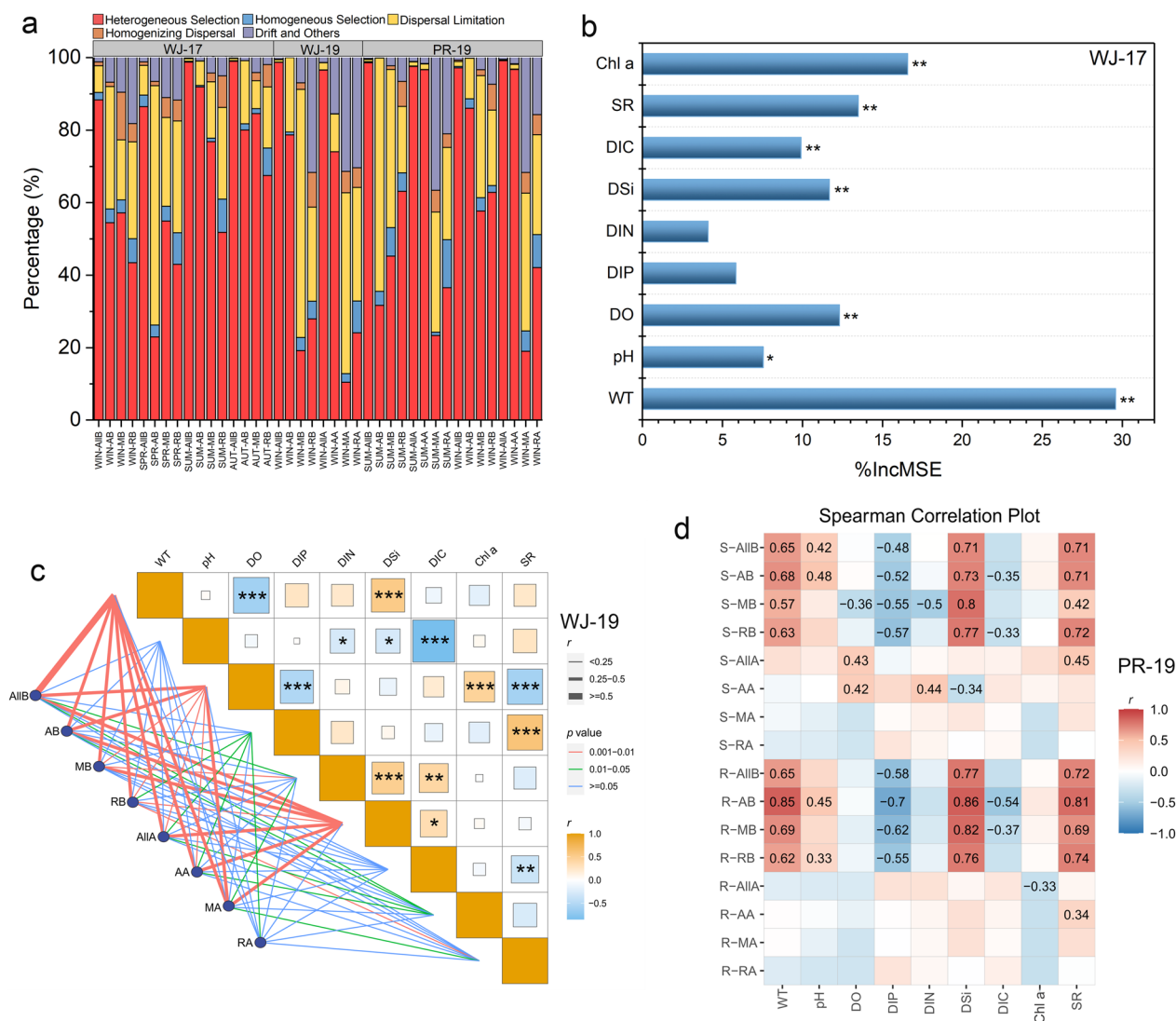


Fig. 5 **a** The assembly processes for different groups of bacterial and archaeal communities. **b** Random Forest analysis for bacterial deterministic process in the Wujiang River in 2017; **c** correlations between the variables in the Wujiang River in 2019. Pairwise comparisons of physical and chemical factors are displayed with a color gradient to denote Spearman's correlation coefficients. Community composition is related to each environmental factor by performing a Mantel test. Significance level: $p < 0.001$ ***; $p < 0.01$ **; $p < 0.05$ *; **d** Spearman correlation between physical and chemical factors and diversity index of planktonic bacteria and archaea in the Pearl River in 2019. S: Shannon index; R: richness index. The numbers represent significant correlation coefficients ($p < 0.05$). The abbreviations are referred to the above text

autumn, river hydrological conditions change greatly, WT and light increase, and nutrient concentrations fluctuate strongly, resulting in a large variation in different local environmental factors (Wang et al. 2015); at that time, environmental selection contributes a lot to the community assembly, and the significant relationships between environmental parameters and planktonic bacterial diversity also support that. In addition, as damming interrupts river continuum, the environmental factors differ significantly between reservoir and river waters (e.g., reservoir waters have long retention time and high

WT), especially in summer; therefore, planktonic bacterial communities at river and reservoir sampling sites were significantly different in summer (Fig. 4; Additional file 1: Figs. S5-7).

Different responses of planktonic bacterial and archaeal diversity to water temperature in dammed rivers

Water temperature is a key factor shaping planktonic bacterial and archaeal communities in dammed rivers. Firstly, WT directly affects the activity of microbial metabolic enzymes (Adams et al. 2010). As different

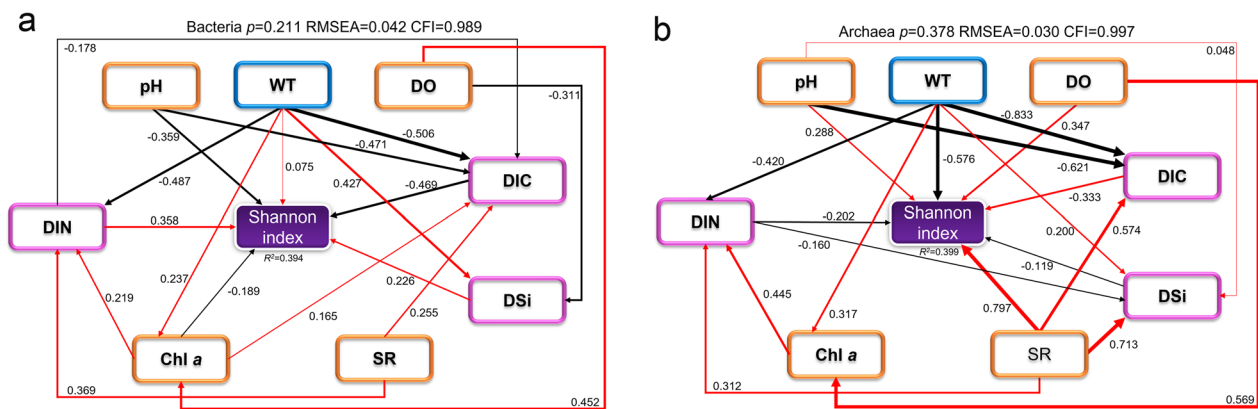


Fig. 6 Structural equation model (SEM) representing the causal relationship between direct and indirect variables on the Shannon index of planktonic bacteria (a) and archaea (b) for all data. The red line: a positive relationship; and the black line: a negative relationship. p , p value for a test of close fit, $RMSEA$ root mean square error of estimation, CFI comparative fit index

biochemical enzymes usually have different optimum reaction temperature at molecular level, and as a response, at cellular level different species of bacteria and archaea have different optimum growth temperature. For example, *Microcystis aeruginosa* is most suitable for 25–30 °C (Lürling et al. 2013), while the optimum temperature of hydrogenotrophic methanogens is 40–50 °C (Blake et al. 2020). Secondly, WT can indirectly affect bacterial and archaeal community composition by influencing other environmental factors. In summer, the high WT will promote the growth of phytoplankton and then accelerate the consumption of CO_2 and the release of O_2 , thus changing water pH and DO concentration (Additional file 1: Fig. S6). Changes in pH and DO concentration can usually result in changes in the structure of the planktonic bacterial and archaeal community (Spitz et al. 2015; Li et al. 2019). In addition, the assimilation of inorganic nutrients by phytoplankton reduces the bioavailable nutrients in the water and then affects the community assembly of bacteria and archaea (Fig. 6; Additional file 1: Fig. S10). Thirdly, WT can affect the community composition by influencing microbial interactions. The significant correlation between the maximum quantum yield per unit biomass of phytoplankton (F_v/F_m : Chl a) and the ratio of archaeal to bacterial community dissimilarity was relative to WT (Fig. 7f), and this suggests that WT may regulate relationships among phytoplankton, bacteria, and archaea although the detailed interaction mechanism is not known yet. It has been reported that phytoplankton and bacteria have a complex coexistence relationship, and this coexistence has a significant impact on the microbial community (Li et al. 2015; Li et al. 2019). In addition, bacterial richness is found decreasing with the increase in temperature, and a larger temperature difference leads to a lower community

composition similarity (Cole et al. 2013). In freshwater lakes, the abundance of planktonic archaea is found higher in summer than in winter (Yang et al. 2016).

However, the total diversity (i.e., Shannon–Wiener index) of planktonic bacteria and archaea did not change significantly with the increase in WT (Fig. 7d). Interestingly, the respective diversity of planktonic bacteria and archaea showed totally different changes with increasing WT (Fig. 7a; Additional file 1: Fig. S14), and their different responses to WT make the overall diversity relatively stable during WT fluctuations. From a phylogenetic perspective, the greater the phylogenetic diversity of planktonic bacteria and archaea, the more complex the phylogenetic relationship (Faith 1992; Véron et al. 2019). With the increase in WT, the phylogenetic diversity increased, the number of abundant species increased, and the α -diversity increased accordingly for planktonic bacteria; but for planktonic archaea all these variables decreased (Fig. 7b). It has been noted that more microbial species are required to maintain functions under higher WT, and the existence and relative abundance of species are related to their optimal growth temperature (García et al. 2018). Bacteria in temperate lakes are found temperature-dependent when temperature is below the threshold value, beyond which other factors regulate their growth (Vrede 2005). In our study, deterministic processes contributed more to the assembly of planktonic bacterial and archaeal community in the warmer waters, and meanwhile the community was more susceptible to environmental disturbances (Fig. 7c; Additional file 1: Fig. S14). In addition, the succession rate of planktonic bacterial community decreased with increasing WT (Fig. 7e), and then the influence of other environmental factors increased. This could be the reason why the relationship between planktonic bacterial and

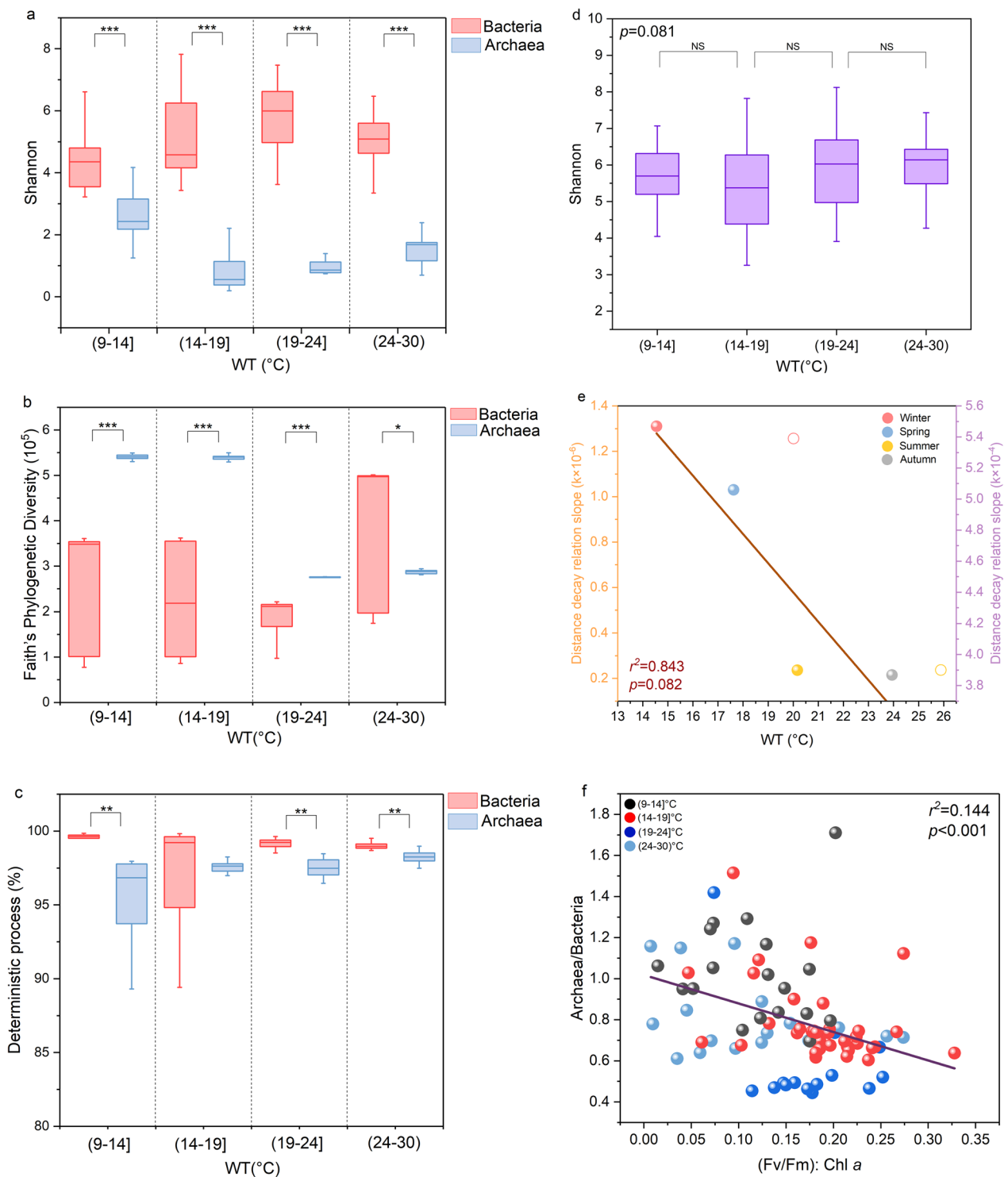


Fig. 7 Variations in Shannon–Wiener index (**a**), Faith’s phylogenetic diversity (**b**), and contribution of deterministic processes (%) (**c**) for bacteria and archaea, respectively, and the Shannon–Wiener index of total bacteria and archaea (NS: Not Significant) (**d**) with water temperature (WT) gradients, each WT gradient is 5 °C. Significance level: $p < 0.001$ ***; $p < 0.01$ **; $p < 0.05$ *. **e** Average WT in the sampling month versus the slope of distance–decay relationship for bacteria in the Wujiang River (left) in 2017 (solid point) and in the Pearl River (right) in 2019 (hollow point), and the regression is only for WJ-17. **f** The ratio of archaeal community dissimilarity to bacterial community dissimilarity versus the ratio of F_v/F_m to Chl a concentration. The abbreviations are referred to the above text

archaeal diversity and environmental factors was more significant in summer and autumn (Figs. 5d; Additional file 1: Fig. S11; S12).

Conclusion

Planktonic bacteria and archaea in dammed rivers had a significant distance–decay relationship, and the relationship was strong in winter and spring. Water temperature was a key factor affecting the planktonic bacterial and archaeal community assembly. The structural equation model showed that WT can directly or indirectly affect microbial diversity. The diversity of planktonic bacteria increased with increasing WT, but that of the planktonic archaea decreased. The phylogenetic diversity of planktonic bacteria and archaea also showed the opposite changes with increasing WT. As such, the overall diversity of planktonic bacteria and archaea did not change significantly with WT variations. This study reveals the different responses of planktonic bacteria and archaea to WT changes and thus perfects the theoretical system for the planktonic microbial biogeography in dammed rivers.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-023-00438-9>.

Additional file 1: Table S1. The detailed information of sampling sites. **Table S2.** The maximum, minimum, and average for physical and chemical parameters of water samples. **Table S3.** OTU numbers of planktonic bacteria and archaea in different groups. **Table S4.** Fitting results of distance–decay relationship. **Table S5.** Permutational multivariate analysis of variance (PERMANOVA) based on Bray–Curtis distance. **Fig. S1.** Physical and chemical parameters of the Wujiang River in 2017. **Fig. S2.** Physical and chemical parameters of the Wujiang River in 2019. **Fig. S3.** Physical and chemical parameters of the Pearl River in 2019. **Fig. S4.** Shannon–Wiener index of bacteria and archaea in the Wujiang River and the Pearl River. **Fig. S5.** PCoA analysis of different groups of bacteria in the Wujiang River in 2017. **Fig. S6.** PCoA analysis of different groups of archaea in the Wujiang in 2019. **Fig. S7.** PCoA analysis of different groups of bacteria and archaea in the Pearl River in 2019. **Fig. S8.** Random Forest analysis for archaeal deterministic processes. **Fig. S9.** Random Forest analysis for different groups of bacterial and archaeal deterministic process. **Fig. S10.** Correlations between physical and chemical factors and community characteristic parameters of bacteria and archaea. **Fig. S11.** Spearman correlation between physicochemical factors and diversity index of planktonic bacteria and archaea. **Fig. S12.** Spearman correlation between physical and chemical factors and diversity index of different groups of bacteria and archaea. **Fig. S13.** Structural equation model representing the causal relationship between direct and indirect variables on the Shannon index of bacteria and archaea. **Fig. S14.** Variations in Shannon–Wiener index, and contribution of deterministic processes for different groups of bacteria and archaea with water temperature gradients.

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Author contributions

BW developed the idea, BW and CQL optimized study, NL, WL, XS and MY performed the experiment and field work, NL and BW produced the first draft, and all co-authors contributed to the final version of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The data that support the findings of this study are openly available in NCBI SRA database at <https://www.ncbi.nlm.nih.gov>, reference number SRR8892916, SRR8892914, PRJNA874581, PRJNA874587, PRJNA874586, PRJNA874582, PRJNA907135, and PRJNA907132.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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References

- Adams HE, Crump BC, Kling GW (2010) Temperature controls on aquatic bacterial production and community dynamics in arctic lakes and streams. *Environ Microbiol* 12:1319–1333. <https://doi.org/10.1111/j.1462-2920.2010.02176.x>
- Ansdell M, Hanson CA (2016) Biogeography, microbiota. *Encycl Evol Biol* 1:179–185
- Baas-Becking LGM (1934) *Geobiologie of inleiding tot de milieukunde*. Van Stockum & Zoon, The Hague
- Blake LI, Sherry A, Mejeha OK, Leary P, Coombs H, Stone W, Head IM, Gray ND (2020) An unexpectedly broad thermal and salinity-tolerant estuarine methanogen community. *Microorganisms* 8:1467. <https://doi.org/10.3390/microorganisms8101467>
- Bolger AM, Lohse M, Usadel B (2014) Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics* 30:2114–2120. <https://doi.org/10.1093/bioinformatics/btu170>
- Caswell H (1976) Community structure: a neutral model analysis. *Ecol Monogr* 46:327–354. <https://doi.org/10.2307/1942257>
- Chen W, Ren K, Isabwe A, Chen H, Liu M, Yang J (2019) Stochastic processes shape microeukaryotic community assembly in a subtropical river across wet and dry seasons. *Microbiome* 7:138. <https://doi.org/10.1186/s40168-019-0749-8>
- Chen J, Wang P, Wang C, Wang X, Miao L, Liu S, Yuan Q, Sun S (2020) Distinct assembly mechanisms underlie similar biogeographic patterns of rare and abundant bacterioplankton in cascade reservoirs of a large river. *Front Microbiol* 11:158. <https://doi.org/10.3389/fmicb>
- Chen Q, Chen Y, Yang J, Maberly SC, Zhang J, Ni J, Wang J, Tonina D, Xiao L, Ma H (2021) Bacterial communities in cascade reservoirs along a large river. *Limnol Oceanogr* 66:4363–4374. <https://doi.org/10.1002/lno.11967>
- Cole J, Peacock J, Dodsworth J, Williams A, Thompson D, Dong H, Wu G, Hedlund B (2013) Sediment microbial communities in Great Boiling Spring are controlled by temperature and distinct from water communities. *ISME J* 7:718–729. <https://doi.org/10.1038/ismej.2012.157>
- Dini-Andreote F, Stegen JC, van Elsas JD, Salles JF (2015) Disentangling mechanisms that mediate the balance between stochastic and deterministic

- processes in microbial succession. *P Natl Acad Sci USA* 112:1326–1332. <https://doi.org/10.1073/pnas.1414261112>
- Edgar RC (2013) UPARSE: highly accurate OTU sequences from microbial amplicon reads. *Nat Methods* 10:996–998. <https://doi.org/10.1038/nmeth.2604>
- Faith DP (1992) Conservation evaluation and phylogenetic diversity. *Biol Conserv* 61:1–10. [https://doi.org/10.1016/0006-3207\(92\)91201-3](https://doi.org/10.1016/0006-3207(92)91201-3)
- Falkowski PG, Fenchel T, Delong EF (2008) The microbial engines that drive earth's biogeochemical cycles. *Science* 320:1034–1039. <https://doi.org/10.1126/SCIENCE.1153213>
- Fierer N (2017) Embracing the unknown: Disentangling the complexities of the soil microbiome. *Nat Rev Microbiol* 15:579–590. <https://doi.org/10.1038/nrmicro.2017.87>
- García FC, Bestion E, Warfield R, Yvon-Durocher G (2018) Changes in temperature alter the relationship between biodiversity and ecosystem functioning. *P Natl Acad Sci USA* 115:201805518. <https://doi.org/10.1073/pnas.1805518115>
- Grill G, Lehner B, Thieme M, Geenen B, Tickner D, Antonelli F, Babu S, Borrelli P, Cheng L, Crochetiere H, Ehalt Macedo H, Filgueiras R, Goichot M, Higgins J, Hogan Z, Lip B, McClain ME, Meng J, Mulligan M, Nilsson C, Olden JD, Opperman JJ, Petry P, Reidy Liermann C, Sáenz L, Salinas-Rodríguez S, Schelle P, Schmitt RJP, Snider J, Tan F, Tockner K, Valdujo PH, van Soestbergen A, Zarfl C (2019) Mapping the world's free-flowing rivers. *Nature* 569:215–221. <https://doi.org/10.1038/s41586-019-1379-9>
- Hanson CA, Fuhrman JA, Horner-Devine MC, Martiny JB (2012) Beyond biogeographical patterns: processes shaping the microbial landscape. *Nat Rev Microbiol* 10:497–506. <https://doi.org/10.1038/nrmicro2795>
- Hu A, Yang X, Chen N, Hou L, Ma Y, Yu C-P (2014) Response of bacterial communities to environmental changes in a mesoscale subtropical watershed, Southeast China. *Sci Total Environ* 472:746–756. <https://doi.org/10.1016/j.scitotenv.2013.11.097>
- Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton
- Kim TS, Jeong JY, Wells GF, Park HD (2013) General and rare bacterial taxa demonstrating different temporal dynamic patterns in an activated sludge bioreactor. *Appl Microbiol Biotechnol* 97:1755–1765. <https://doi.org/10.1007/s00253-012-4002-7>
- Lan Y, Wang Q, Cole JR, Rosen GL, Anthony GJ (2012) Using the RDP classifier to predict taxonomic novelty and reduce the search space for finding novel organisms. *PLoS ONE* 7:e32491. <https://doi.org/10.1371/journal.pone.0032491>
- Li J, Zhang J, Liu L, Fan Y, Li L, Yang Y, Lu Z, Zhang X (2015) Annual periodicity in planktonic bacterial and archaeal community composition of eutrophic Lake Taihu. *Sci Rep* 5:15488. <https://doi.org/10.1038/srep15488>
- Li H, Zeng J, Ren L, Wang J, Xing P, Wu QL (2017a) Contrasting patterns of diversity of abundant and rare bacterioplankton in freshwater lakes along an elevation gradient. *Limnol Oceanogr* 62:1570–1585. <https://doi.org/10.1002/lno.10518>
- Li H, Xing P, Wu QL (2017b) Genus-specific relationships between the phytoplankton and bacterioplankton communities in Lake Taihu. *China Hydrobiologia* 795:281–294. <https://doi.org/10.1007/s10750-017-3141-3>
- Li R, Tong T, Wu S, Chai M, Xie S (2019) Multiple factors govern the biogeographic distribution of archaeal community in mangroves across China. *Estuar Coast Shelf S* 231:106414.1–106414.6. <https://doi.org/10.1016/j.ecss.2019.106414>
- Li W, Wang B, Liu N, Yang M, Liu C-Q, Xu S (2022) River damming enhances ecological functional stability of planktonic microorganisms. *Front Microbiol* 13:1049120. <https://doi.org/10.3389/fmicb.2022.1049120>
- Liang X, Xing T, Li J, Wang B, Wang F, He C, Hou L, Li S (2019) Control of the hydraulic load on nitrous oxide emissions from cascade reservoirs. *Environ Sci Technol* 53:11745–11754. <https://doi.org/10.1021/acs.est.9b03438>
- Liu S, Ren H, Shen L, Lou L, Tian G, Zheng P, Hu B (2015) pH levels drive bacterial community structure in the Qiantang River as determined by 454 pyrosequencing. *Front Microbiol* 6:285. <https://doi.org/10.3389/fmicb>
- Luo Z, Liu J, Zhao P, Jia T, Li C, Chai B (2019) Biogeographic patterns and assembly mechanisms of bacterial communities differ between habitat generalists and specialists across elevational gradients. *Front Microbiol* 10:169. <https://doi.org/10.3389/fmicb.2019.00169>
- Lüring M, Eshetu F, Faassen EJ, Kosten S, Huszar VLM (2013) Comparison of cyanobacterial and green algal growth rates at different temperatures. *Freshwater Biol* 58:552–559. <https://doi.org/10.1111/j.1365-2427.2012.02866.x>
- Lynch MD, Neufeld JD (2015) Ecology and exploration of the rare biosphere. *Nat Rev Microbiol* 13:217–229. <https://doi.org/10.1038/nrmicro3400>
- Maberly SC (1996) Diel, episodic and seasonal changes in pH and concentrations of inorganic carbon in a productive lake. *Freshwater Biol* 35:579–598. <https://doi.org/10.1111/j.1365-2427.1996.tb01770.x>
- Magoc T, Salzberg SL (2011) FLASH: fast length adjustment of short reads to improve genome assemblies. *Bioinformatics* 27:2957–2963. <https://doi.org/10.1093/bioinformatics/btr507>
- Martiny JBH, Bohannan BJM, Brown JH, Colwell RK, Fuhrman JA, Green JL, Horner-Devine MC, Kane M, Krumins JA, Kuske CR, Morin PJ, Naeem S, Øvreås L, Reysenbach A-L, Smith VH, Staley JT (2006) Microbial biogeography: putting microorganisms on the map. *Nat Rev Microbiol* 4:102–112. <https://doi.org/10.1038/NRMICRO1341>
- Mo Y, Peng F, Gao X, Xiao P, Logares R, Jeppesen E, Ren K, Xue Y, Yang J (2019) Low shifts in salinity determined assembly processes and network stability of microeukaryotic plankton communities in a subtropical urban reservoir. *Microbiome* 9:128. <https://doi.org/10.1186/s40168-021-01079-w>
- Mo Y, Zhang W, Wilkinson DM, Yu Z, Xiao P, Yang J (2021) Biogeography and co-occurrence patterns of bacterial generalists and specialists in three subtropical marine bays. *Limnol Oceanogr* 66:793–806. <https://doi.org/10.1002/lno.11643>
- Moitra M, Leff LG (2015) Bacterial community composition and function along a river to reservoir transition. *Hydrobiologia* 747:201–215. <https://doi.org/10.1007/S10750-014-2140-X>
- Morrison-Whittle P, Goddard MR (2015) Quantifying the relative roles of selective and neutral processes in defining eukaryotic microbial communities. *ISME J* 9:2003–2011. <https://doi.org/10.1038/ismej.2015.18>
- Newton RJ, Jones SE, Eiler A, McMahon KD, Bertilsson S (2011) A guide to the natural history of freshwater lake bacteria. *Microbiol Mol Biol Rev* 75:14–49. <https://doi.org/10.1128/MMBR.00028-10>
- Ning D, Yuan M, Wu L, Zhang Y, Guo X, Zhou X, Yang Y, Arkin AP, Firestone MK, Zhou J (2020) A quantitative framework reveals the ecological drivers of grassland soil microbial community assembly in response to warming. *Nat Commun* 11:4717. <https://doi.org/10.1038/s41467-020-18560-z>
- Nio-García JP, Ruiz-González C, Giorgio P (2016) Interactions between hydrology and water chemistry shape bacterioplankton biogeography across boreal freshwater networks. *ISME J* 10:1755–1766. <https://doi.org/10.1038/ismej.2015.226>
- Nyirabuhoro P, Liu M, Xiao P, Liu L, Yu Z, Wang L, Yang J (2020) Seasonal variability of conditionally rare taxa in the water column bacterioplankton community of subtropical reservoirs in China. *Microb Ecol* 80:14–26. <https://doi.org/10.1007/s00248-019-01458-9>
- Pedrés-Allió C (2012) The rare bacterial biosphere. *Annu Rev Mar Sci* 4:449–466. <https://doi.org/10.1146/annurev-marine-120710-100948>
- Pester M, Bittner N, Deevong P, Wagner M, Loy A (2010) A 'rare biosphere' microorganism contributes to sulfate reduction in a peatland. *ISME J* 4:1591–1602. <https://doi.org/10.1038/ismej.2010.75>
- Rosseel Y (2011) lavaan: An R Package for Structural Equation Modeling and More v.0.4–9 (BETA) (Ghent University)
- Schloss PD, Westcott SL, Ryabin T, Hall JR, Hartmann M, Hollister EB, Lesniewski RA, Oakley BB, Parks DH, Robinson CJ, Sahl JW, Stres B, Thallinger GG, Van Horn DJ, Weber CF (2009) Introducing mothur: open-source, platform-independent, community supported software for describing and comparing microbial communities. *Appl Environ Microb* 75:7537–7541. <https://doi.org/10.1128/AEM.01541-09>
- Shapiro RS, Cowen LE (2012) Thermal control of microbial development and virulence: molecular mechanisms of microbial temperature sensing. *Mbio* 3:1357–1365. <https://doi.org/10.1128/mBio.00238-12>
- Spiez RL, Williams CM, Roca G, Horner-Devine MC (2015) A dissolved oxygen threshold for shifts in bacterial community structure in a seasonally hypoxic estuary. *PLoS ONE* 10:e0135731. <https://doi.org/10.1371/journal.pone.0135731>
- Stegen JC, Lin X, Fredrickson JK, Chen X, Kennedy DW, Murray CJ, Rockhold ML, Konopka A (2013) Quantifying community assembly processes and identifying features that impose them. *ISME J* 7:2069–2079. <https://doi.org/10.1038/ismej.2013.93>

- Stumm W, Morgan JJ (1983) Aquatic chemistry, an introduction emphasizing chemical equilibria in natural waters. *Ecol Model* 19:227–230. <https://doi.org/10.1021/ed048pA779.1>
- Vellend M (2010) Conceptual synthesis in community ecology. *Q Rev Biol* 85:183–206. <https://doi.org/10.1086/652373>
- Véron S, Saito V, Padilla-García N, Forest F, Bertheau Y (2019) The use of phylogenetic diversity in conservation biology and community ecology: a common base but different approaches. *Q Rev Biol* 94:123–148. <https://doi.org/10.1086/703580>
- Vrede K (2005) Nutrient and temperature limitation of bacterioplankton growth in temperate lakes. *Microb Ecol* 49:245–256. <https://doi.org/10.1007/s00248-004-0259-4>
- Wang Y, Liu L, Chen H, Yang J (2015) Spatiotemporal dynamics and determinants of planktonic bacterial and microeukaryotic communities in a Chinese subtropical river. *Appl Microbiol Biotechnol* 99:9255–9266. <https://doi.org/10.1007/s00253-015-6773-0>
- Wang K, Yan H, Peng X, Hu H, Zhang H, Hou D, Chen W, Qian P, Liu J, Cai J, Chai X, Zhang D (2020) Community assembly of bacteria and archaea in coastal waters governed by contrasting mechanisms: a seasonal perspective. *Mol Ecol* 29:3762–3776. <https://doi.org/10.1111/mec.15600>
- Wang B, Liu N, Yang M, Wang L, Liang X, Liu C-Q (2021) Co-occurrence of planktonic bacteria and archaea affects their biogeographic patterns in China's coastal wetlands. *Environ Microbiome* 16:19. <https://doi.org/10.1186/s40793-021-00388-9>
- Wang B, Yang X, Li S-L, Liang X, Li X-D, Wang F, Yang M, Liu C-Q (2022) Anthropogenic regulation governs nutrient cycling and biological succession in hydropower reservoirs. *Sci Total Environ* 834:155392. <https://doi.org/10.1016/j.scitotenv.2022.155392>
- Yang Y, Dai Y, Wu Z, Xie S, Liu Y (2016) Temporal and spatial dynamics of archaeal communities in two freshwater lakes at different trophic status. *Front Microbiol* 7:451. <https://doi.org/10.3389/fmicb.2016.00451>
- Yang M, Shi J, Wang B, Xiao J, Li W, Liu C-Q (2020a) Control of hydraulic load on bacterioplankton diversity in cascade hydropower reservoirs, Southwest China. *Microb Ecol* 80:537–545. <https://doi.org/10.1007/s00248-020-01523-8>
- Yang X, Li Y, Wang B, Xiao J, Yang M, Liu C-Q (2020b) Effect of hydraulic load on thermal stratification in karst cascade hydropower reservoirs, Southwest China. *J Hydrol-Reg Stud* 32:100748. <https://doi.org/10.1016/j.ejrh.2020.100748>
- Yuan MM, Guo X, Wu L, Zhang Y, Xiao N, Ning D, Shi Z, Zhou X, Wu L, Yang Y, Tiedje JM, Zhou J (2021) Climate warming enhances microbial network complexity and stability. *Nat Clim Chang* 11:343–348. <https://doi.org/10.1038/s41558-021-00989-9>
- Yue Y, Cai L, Tang Y, Zhang Y, Yang M, Wang F (2021) Vertical distribution of bacterial community in water columns of reservoirs with different trophic conditions during thermal stratification. *Front Environ Sci* 9:632089. <https://doi.org/10.3389/fenvs.2021.632089>
- Zhou J, Ning D (2017) Stochastic community assembly: does it matter in microbial ecology? *Microbiol Mol Biol R* 81:e00002-17. <https://doi.org/10.1128/MMBR.00002-17>

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