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Biodegradable dissolved organic carbon shapes bacterial community structures and co-occurrence patterns **in large eutrophic Lake Taihu**

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ABSTRACT

Interactions between dissolved organic matter (DOM) and bacteria are central in the biogeochemical cycles of aquatic ecosystems; however, the relative importance of biodegradable dissolved organic carbon (BDOC) compared with other environmental variables in structuring the bacterial communities needs further investigation. Here, we investigated bacterial communities, chromophoric DOM (CDOM) characteristics and physico-chemical parameters as well as examined BDOC via bioassay incubations in large eutrophic Lake Taihu, China, to explore the importance of BDOC for shaping bacterial community structures and co-occurrence patterns. We found that the proportion of BDOC (%BDOC) correlated significantly and positively with the DOC concentration and the index of the contribution of recent produced autochthonous CDOM (BIX). %BDOC, further correlated positively with the relative abundance of the tryptophan-like component and negatively with CDOM aromaticity, indicating that autochthonous production of protein-like CDOM was an important source of BDOC. The richness of the bacterial communities correlated negatively with %BDOC, indicating an enhanced number of species in the refractory DOC environments. %BDOC was identified as a significant stronger factor than DOC in shaping bacterial community composition and the co-occurrence network, suggesting that substrate biodegradability is more significant than DOC quantity determining the bacterial communities in a eutrophic lake. Environmental factors explained a larger proportion of the variation in the conditionally rare and abundant subcommunity than for the abundant and the rare bacterial subcommu-

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nities. Our findings emphasize the importance of considering bacteria with different abundance patterns and DOC biodegradability when studying the interactions between DOM and bacteria in eutrophic lakes.

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Introduction

Interactions between dissolved organic matter (DOM) and bacteria play a key role in the biogeochemical cycles of aquatic ecosystems (Mou et al., 2008; Osterholz et al., 2015). DOM consists of various compounds and represents a large fraction of the global carbon pool (Coble, 2007). Bacterial degradation of DOM contributes to bacterial secondary production, nutrient recycling, and greenhouse outgassing, affecting the material circulation and energy flow in water bodies (Bertilsson et al., 2007; Guillemette et al., 2016). DOM quantity and quality are crucial factors shaping bacterial communities (Hur et al., 2011; Muscarella et al., 2019; Ruiz-González et al., 2015). Linkages between bacterial community and DOM composition have been evidenced for numerous systems (Kaartokallio et al., 2015; Logue et al., 2016). For instance, relationships between major bacterial clades and DOM fluorescence components have been established (Amaral et al., 2016; Melo et al., 2020), showing the importance of considering DOM characteristics when studying the interactions between DOM and bacteria.

The effect of DOM on bacterial communities is largely determined by its biodegradability depending on its chemical composition and molecular size (Berggren et al., 2010; Kellerman et al., 2015). Labile proteins and aliphatic compounds are rapidly utilized by bacteria (Guillemette et al., 2016), while the recalcitrant materials can be degraded only by specific groups (Landa et al., 2014). DOM with different biodegradability can cause distinct responses of bacterial diversity, community structure, and metabolism, as reflected in the carbon consumption, growth and respiration rate, as well as enzymatic degradation (Bana et al., 2014; Perez and Sommaruga, 2006; Roiha et al., 2016). Biodegradable dissolved organic carbon (BDOC) refers to the fraction of dissolved organic carbon (DOC) which can be removed by bacteria over a period of bioassay incubations (Hitchcock and Mitrovic, 2015). BDOC is a crucial parameter when examining the biogeochemical role of DOM in regards to global carbon fluxes (Vonk et al., 2015) and is an important component of the microbial loop (Nelson et al., 2011). Although the influence of BDOC on the bacterial community has been evidenced by incubating bacteria with different sources of DOM in lab studies (Guillemette et al., 2013; Perez and Sommaruga, 2006), the relative importance of BDOC compared with other environmental variables in structuring the bacterial communities in natural ecosystems needs further investigation.

Bacterial communities normally consist of a small number of abundant taxa and many rare species, as well as some “occasionally rare and abundant” taxa (Campbell et al., 2011). Taxa with distinct abundance patterns contribute differently to ecosystem function in terms of biomass, biodiversity, carbon flow, and nutrient cycling (Pedros-Alio, 2012). Moreover,

different responses of these subcommunities to environmental changes have been evidenced, for example along elevation gradients (Li et al., 2017), changing in climatic regimes (Liang et al., 2020), algal blooms (Xue et al., 2018; Zhang et al., 2019a), and specific DOM amendment (Li et al., 2019). Moreover, bacteria interact with each other rather than live in isolation, thereby contributing to the overall composition, stability, and biodiversity of microbial ecosystems (Ratzke et al., 2020). Thus, it is important to consider species with different abundance patterns and their interactions when studying the linkages between bacterial communities and DOM. Thanks to high-throughput sequencing techniques and network analyses, rare subcommunities and complex cooccurrence networks between species can now be explored.

We investigated bacterial communities using 16S rRNA gene sequencing and chromophoric DOM (CDOM) characteristics as well as other physico-chemical variables and examined BDOC via bioassay incubations in a large eutrophic lake (Lake Taihu, China). Our objectives were to (i) examine the importance of BDOC for diversity, composition, and co-occurrence patterns of bacterial communities; (ii) compare the responses of abundant and rare bacterial communities with changes in key environmental variables including CDOM and BDOC characteristics. We hypothesized that BDOC is shaping bacterial community composition and co-occurrence patterns, being of particularly importance for the rare community, because rare taxa can include metabolically active species that can become dominant under favorable conditions by acting as bacterial “seed banks” (Lynch and Neufeld, 2015).

1. Materials and methods

1.1. Study sites and sample collection

Lake Taihu is a large eutrophic lake located in the most developed region of eastern China with an area of 2338.1 km². A total of 68 water samples were collected for CDOM optical measurements, including 32 samples collected from the whole lake in August 2018 and 36 samples collected monthly from three sites near the Taihu Laboratory for Lake Ecosystem Research (TLER) from September 2018 to August 2019 (3 × 12) (Appendix A Fig. S1). Forty-seven of the 68 water samples were sequenced for bacterial community analyses, including the 36 monthly samples and 11 samples collected in August 2018 (Appendix A Fig. S1). The 11 samples distributed in the north (with occurrence of cyanobacterial blooms), central (open waters), and east (macrophyte-dominated) regions in Lake Taihu (Appendix A Fig. S1) (Zhou et al., 2018b). The location of TLER was a typical site with the cyanobacteria bloom occurrence, and displayed high spatiotemporal changes due to differences in physicochemical conditions (Huang et al., 2019; Qin et al.,

2018). As there have been numerous studies unraveling the spatiotemporal variability of bacterioplankton communities (Tang et al., 2017; Zhang et al., 2019), we in this study focused on discerning the importance of BDOC on bacterial community composition. Thus, we pooled all BDOC and bacterial results together without considering the spatial or temporal aspects. All samples were collected from the surface water (0.5 m) using 5 L acid-cleaned Niskin bottles and were stored on ice while in the field. The samples were transported to the laboratory and immediately filtered within two hours after collection. Filtrates for physico-chemical variables and CDOM measurements were stored in the dark at 4 °C and measured within two days. Filters for DNA extraction were stored at –20 °C until further processing.

1.2. BDOC measurements

Bioassay incubations for BDOC measurements were performed for all 68 samples. The original samples (100 mL) were first filtered (0.22 µm Millipore filter) to exclude particulate organic matter and bacteria, and then the corresponding original water (2 mL) was added as a bacterial inoculum. Moreover, nutrients were amended to avoid nutrient limitation, increasing ambient concentrations by 80 µmol/L NH₄⁺ and 10 µmol/L PO₄³⁻ (Vonk et al., 2015). All incubated samples were placed at room temperature (20 ± 2 °C) and in the dark for 28 days to ensure adequate degradation following a standard protocol (Abbott et al., 2014; Vonk et al., 2015). All acid-soaked and pre-rinsed (Milli-Q water) brown incubation glass bottles were loosely capped and shaken daily to ensure adequate oxygen supply. At the end of the incubation, DOC concentrations and CDOM absorbance and fluorescence measurements were performed. The proportion of BDOC was calculated as (the initial value – the final value)/the initial value of the corresponding original sample.

1.3. Physico-chemical parameter measurements

Physical variables including temperature, conductivity, and pH were measured in the field using a Yellow Springs Instruments (YSI) 6600 multisensor sonde. Chemical parameters included concentrations of total nitrogen (TN), total dissolved nitrogen (TDN), nitrate (NO₃-N), ammonium (NH₄-N), total phosphorus (TP), total dissolved phosphorus (TDP), orthophosphate (PO₄-P), chlorophyll *a* (Chl-*a*), and dissolved organic carbon (DOC). NH₄-N, NO₃-N, and PO₄-P were determined using a Continuous Flow Analyzer (San⁺⁺, SKALAR, The Netherlands); TN, TP, TDN, and TDP were analyzed using a combined persulfate digestion (Ebina et al., 1983) followed by spectrophotometric measurements; Chl-*a* was determined spectrophotometrically after extraction in 90% hot ethanol (Párista et al., 2002); DOC concentrations was assessed by a TOC-V CPN analyzer (Shimadzu, Tokyo, Japan).

1.4. CDOM absorbance, fluorescence, and parallel factor analysis (PARAFAC)

The filtrate after passing pre-combusted 0.22 µm Millipore membrane filters were used for CDOM absorbance and flu-

orescence measurements. CDOM absorbance was measured over the 200–800 nm range (1 nm increments) in a 5 cm quartz cell via a Shimadzu UV-2450 PC UV-vis recording spectrophotometer. CDOM fluorescence excitation-emission matrices (EEMs) were obtained applying an F-7000 fluorescence spectrophotometer (Hitachi High Technologies, Tokyo, Japan) with a 700-V xenon lamp (a scanning speed of 2400 nm min⁻¹). PARAFAC was utilized to decompose each EEM into a series of trilinear components with a residual array (Murphy et al., 2008; Stedmon et al., 2003). Information about the measurements, calibration, and PARAFAC modelling was detailed in Zhou et al. (2017). The specific ultraviolet absorbance of DOC at 254 nm (SUVA) is defined as the ultraviolet absorbance at 254 nm normalized for DOC concentration, indicative of the aromaticity of CDOM molecules (Spencer et al., 2012; Weishaar et al., 2003). The index of recent autochthonous contribution (BIX) is defined as the ratio of CDOM fluorescence at 380 nm to that at 430 nm, both excited at 310 nm, with high values (>1) corresponding to an increased contribution of freshly released autochthonous CDOM (Huguet et al., 2009). A six-component model was validated by PARAFAC modelling in our study (Appendix A Fig. S2).

1.5. DNA extraction, PCR, sequencing, and sequences processing

Water samples (~ 200 mL) were filtered through 0.22 µm Millipore membrane filters for bacterial community analysis. DNA extraction from the filters was implemented using FastDNA Spin Kit for Soil (MP Biomedicals, USA) according to the manufacturer's protocol. The V4 region of bacterial 16S rRNA gene was amplified using primers 515F (5'-GTGYCAGCMGCCGCGGTAA-3') and 806R (5'-GGACTACN VGGGTWCTAAT-3'). Information about PCR amplification and purification is detailed in (Zhou et al., 2018a). Purified amplicon pools were pair-end sequenced (2 × 250) on an Illumina HiSeq platform. Sequenced paired-end reads were processed by USEARCH (v11.0.667) (Edgar, 2013), including merging paired reads, stripping primers, filtering low-quality reads, generating representative-amplicon sequence variants (ASVs) and identifying taxonomy. Denoising of amplicon reads including chimera filtering was performed using the *unoise3* command (Nearing et al., 2018). The representative ASVs were classified based on the SILVA database (release 123) to identify the taxonomy of each ASV. The processed dataset was subsampled to the sequencing depth of the lowest sequence count sample (27,073 reads per sample). To compare changes in bacteria with different abundance patterns, all ASVs were classified into four groups – Abundant taxa (AT) are those with a relative abundance ≥ 0.01% in all samples and ≥ 1% in at least one sample; <0.01% in at least one sample but never ≥1% in any sample are rare taxa (RT); ranging from 0.01% to 1% in all samples are moderate taxa (MT); ranging from rare (< 0.01%) to abundant (≥ 1%) are conditionally rare and abundant taxa (CRAT) (Xue et al., 2018). All the sequences used in this study are available from the NCBI Sequence Read Archive (SRA) under accession number PRJNA686185.

1.6. Co-occurrence network analysis

The network was constructed by calculating pairwise Spearman rank correlations (ρ). ASVs were selected by occurrence frequency ($> 20\%$) to simplify the dataset. Valid co-occurrences with $|\rho| > 0.75$ and p -value < 0.05 were incorporated into networks. The p -values were further adjusted with a multiple testing correction by the Benjamini-Hochberg method to avoid obtaining false-positive results (Benjamini and Hochberg, 1995). Random networks with equal numbers of nodes and edges of the real networks were generated based on Erdős-Rényi random networks (Erdős and Rényi, 2011). Network properties including average degree, average path length, average clustering coefficient, network diameter, and modularity are detailed in (Deng et al., 2012). Network properties calculation, module detection, and visualization were conducted using the interactive platform Gephi (WebAtlas, Paris, France). Module-based eigengene analysis is a useful tool to study the relationships between modules and environmental factors (de Menezes et al., 2015), and each module is represented by its singular value decomposition of abundance profile called module eigengene (Langfelder and Horvath, 2007). Eigengene values of all modules were calculated using the “WGCNA” packages in R (Langfelder and Horvath, 2008).

1.7. Relationships between the bacterial community and environmental factors

As the longest gradient lengths of detrended correspondence analysis (DCA) were < 3 , redundancy analysis (RDA) was performed to investigate the relationships between bacterial communities and environmental variables. ASV data were transformed using Hellinger's transformation (Legendre and Gallagher, 2001), and environmental parameters were log-transformed and normalized before RDA analysis. Environmental variables were then selected by removing variables with high variance inflation factor (VIF) > 10 to avoid collinearity among factors, and a forward selection was conducted to determine the significant factors influencing bacterial community structures ($p < 0.05$) (Blanchet et al., 2008; Mo et al., 2018). Mantel tests were performed between BDOC and community dissimilarities and module structures.

1.8. Other statistical analyses

To help reveal the influences of environmental factors on bacterial community structures, habitat niche breadth was calculated as the average of Levins' niche breadth values from all members occurring in one community (Jiao et al., 2020; Levins, 1968). A higher Levins' niche breadth value for a given ASV represents its wide habitat niche breadth. A bacterial group with a wider niche breadth value is considered more metabolically flexible at the community level and appears to contain more habitat generalists (Jiao et al., 2020). Alpha-diversity indices including Chao 1 (a species richness estimator), Pielou's evenness, and the Shannon index were calculated for all sites. Beta-diversity was examined using abundance-based Bray-Curtis dissimilarities. All statistical analyses, including mean values, standard deviations, cor-

relation calculations, and Wilcoxon tests, were carried out using R 3.6.3.

2. Results

2.1. PARAFAC components and BDOC

The PARAFAC model-derived six components (Appendix A Fig. S2) were identified by comparison to the Open-Fluor database (Murphy et al., 2014). The component C1 (Ex/Em = $< 230/436$ nm) resembles humic-like DOM; C2 (250(340)/476 nm) represents terrestrial humic-like fluorophores (Shutova et al., 2014) and is associated with soil-derived fulvic acids (Osburn et al., 2016); C3 ((250)310/388 nm) represents microbial humic-like fluorophores (Osburn et al., 2016); C4 ($< 230(285)/340$ nm) includes tryptophan-like fluorophores (Stedmon and Markager, 2005a); C5 ($< 230(270)/300$ nm) represents tyrosine-like fluorophores (D'Andrilli et al., 2019), and C6 (275/316 nm) is also associated with red-shifted tyrosine-like fluorophores (Yamashita et al., 2011). The tryptophan-like C4 (ranging from 31.8% to 48.7%) and the tyrosine-like C6 (22.7%~46.5%) were predominant in the samples, followed by C1 (4.0%~22.8%), C5 (2.3%~12.9%), C3 (0.9%~10.3%), and C2 (0.7%~4.7%).

The proportion of BDOC (%BDOC) was significantly positively related to the DOC concentrations (Pearson's $r = 0.55$, $p < 0.001$), BIX ($r = 0.52$, $p < 0.001$), and the relative abundance of tryptophan-like C4 ($r = 0.51$, $p < .001$), and significantly negatively related to SUVA ($r = -0.59$, $p < 0.001$) ($n = 68$) (Fig. 1). Overall, the fluorescence intensities of protein-like C4-C6, as well as C1, had decreased after 28 days bio-incubations, while the fluorescence intensities of terrestrial and microbial humic-like C2 and C3 had increased, suggesting that protein-like CDOM is preferable substrates for bacterial consumption (Fig. 2). Accordingly, the fluorescence intensities of C4 showed the most notable decrease after bio-incubations.

2.2. Composition and co-occurrence network of bacterial communities

The subsampled dataset (27,073 reads per sample) comprised 1272,431 reads and 5491 ASVs. Twenty-two ASVs (0.4%) containing 29.8% of all reads were classified as AT; 5336 ASVs (97.2%), representing 34.3% of all reads, were RT; 128 ASVs (2.3%) were affiliated to CRAT, covering 35.2% of all reads; 5 ASVs were MT. AT consisted of the phyla of *Proteobacteria* (*Betaproteobacteria*, *Gammaproteobacteria*, *Alphaproteobacteria*), *Actinobacteria*, *Verrucomicrobia*, *Cyanobacteria*, and *Bacteroidetes* (Appendix A Table S1). Additionally, *Planctomycetes* was a major phylum (relative abundance $> 0.5\%$) for RT and CRAT, and *Firmicutes* and *Deltaproteobacteria* were major phyla/classes for RT (Appendix A Table S1). Overall, the mean value of habitat niche breadths of CRAT (9.0 ± 0.4) was lower than that of AT (20.6) and RT (10.4 ± 0.7) (Appendix A Table S1).

The robust correlation-based co-occurrence network included 676 nodes and 8464 connections (Fig. 3). The real modularity, average path length, and clustering coefficient were all

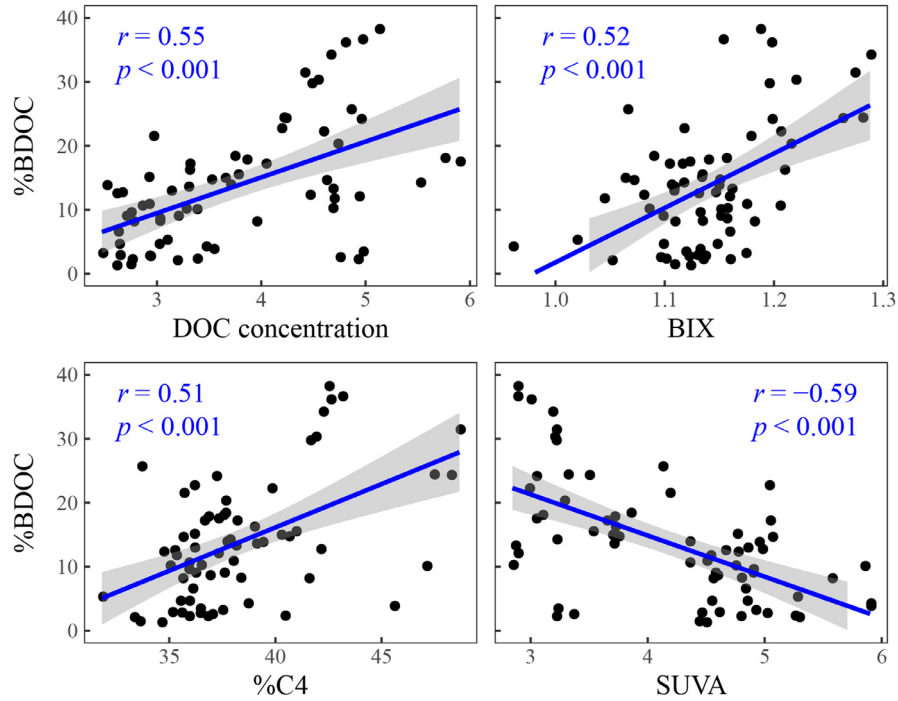


Fig. 1 – Pearson’s correlations (r) between the proportion of biodegradable dissolved organic carbon (%BDOC) and the DOC concentration (mg/L), the biological index (BIX), the relative abundance of tryptophan-like component C4 (%C4), and the specific ultraviolet absorbance at 254 nm (SUVA) ($L\ mg\ C^{-1}\ m^{-1}$).

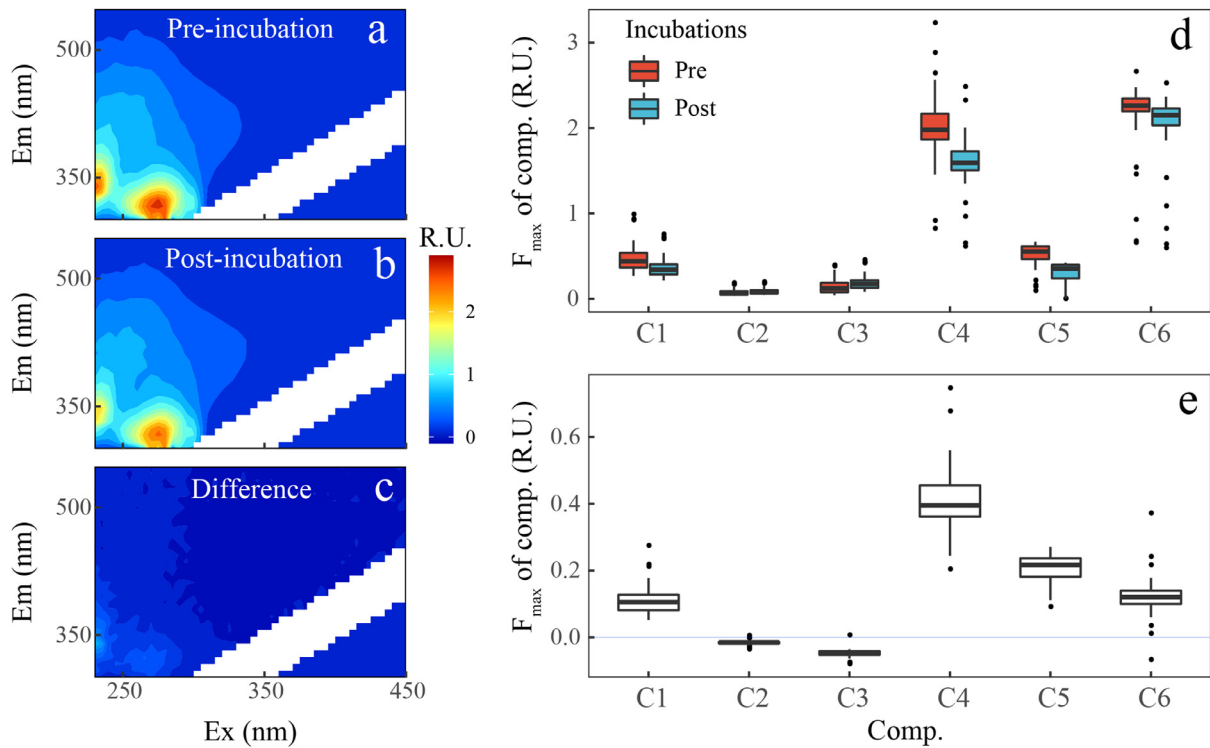


Fig. 2 – The fluorescence excitation-emission matrices (EEMs) spectra of a sample collected from Lake Taihu pre- and post-28 days of bio-incubation (a,b) and difference between the two spectra (Pre-incubation – Post-incubation) (c). Boxplots showing the fluorescence intensities (F_{max}) of six components of all incubated samples pre- and post-28 days of bio-incubation (d) and difference between the two values (Pre-incubation – Post-incubation) (e). Positive values indicate decreased fluorescence intensities after bio-incubations.

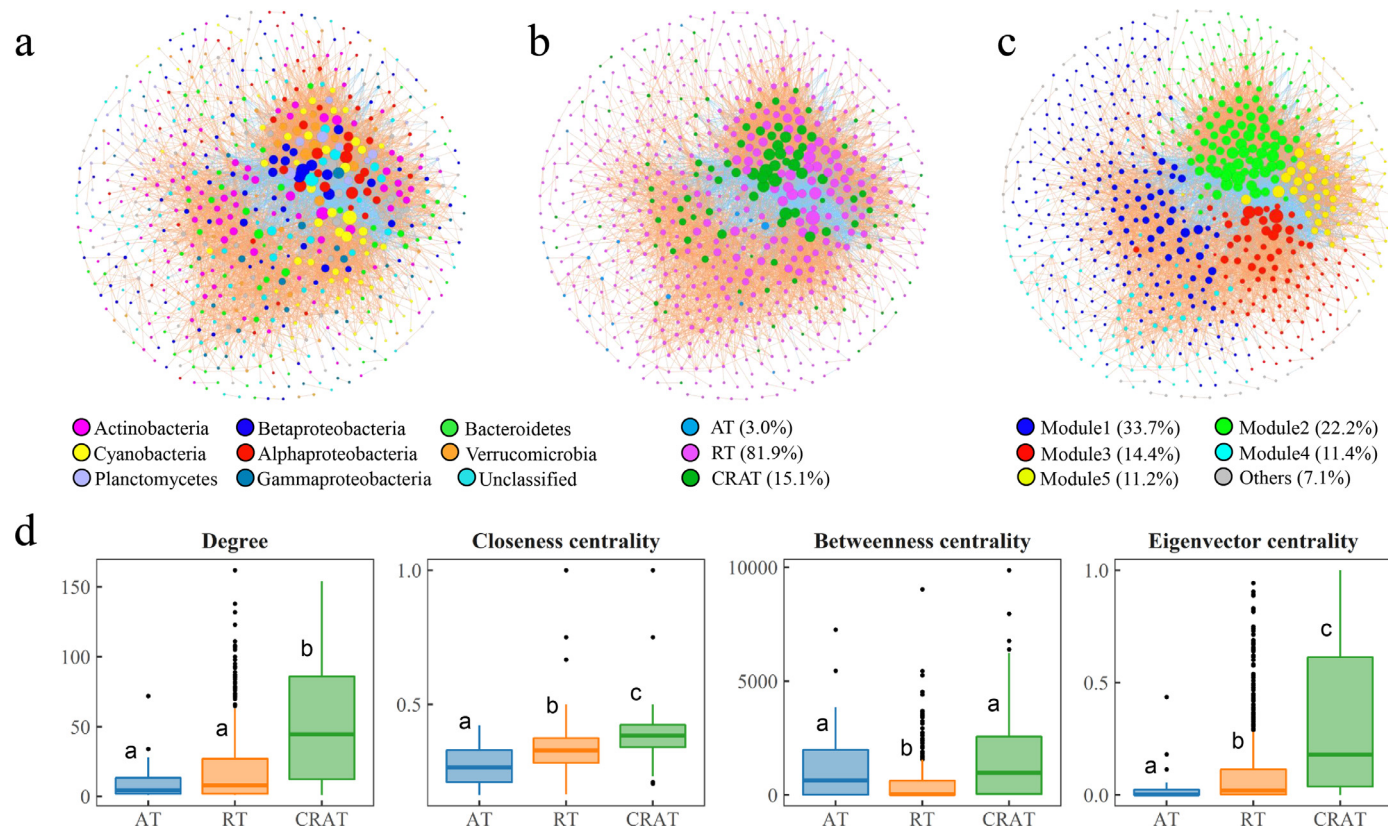


Fig. 3 – Network analysis showing co-occurrence patterns of bacterial communities. Nodes were colored by corresponding phylum/class (a), taxa classification (b), and modules (c). Orange (79.9%) and blue (20.1%) links between nodes represent positive and negative correlations, respectively. Four node-level topological features of taxa with different abundance patterns (abundant taxa (AT); rare taxa (RT); conditionally rare and abundant taxa (CRAT)) (d). Degree represents the number of connections; closeness centrality refers to the average distance of a node to any other node; betweenness centrality is the potential influence of a node on the connections of other nodes; and eigenvector centrality describes the degree of a central node that it is connected to other central nodes. Letters in the boxplots indicate the statistical differences of the four node features among three subcommunities determined by Wilcoxon tests.

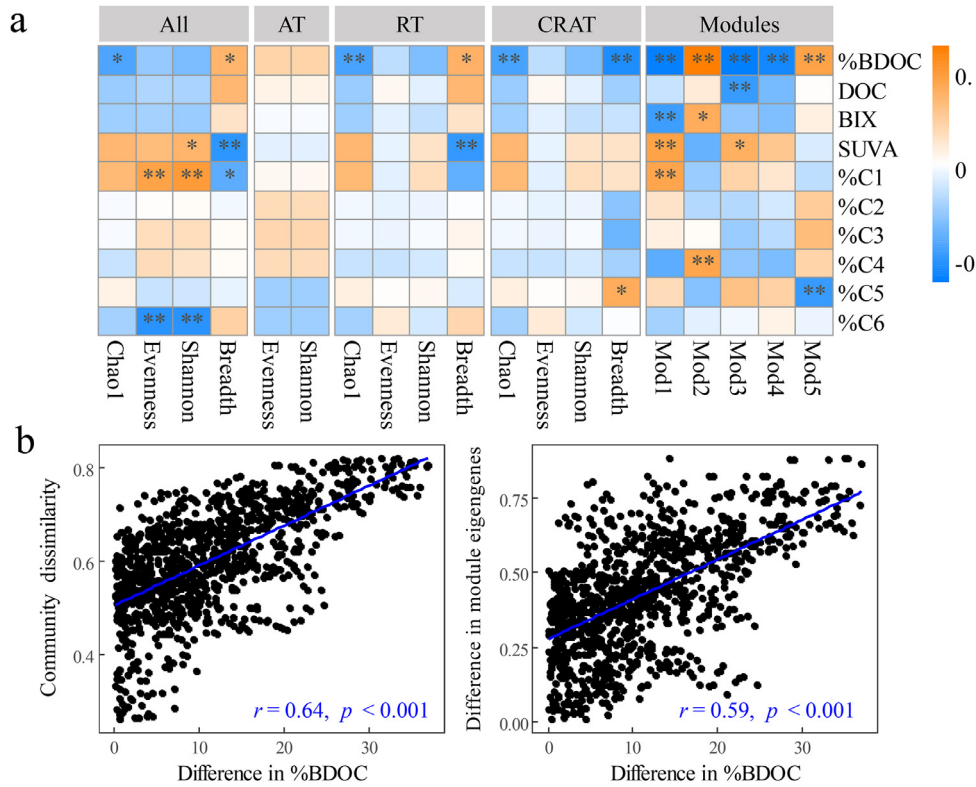


Fig. 4 – Pearson’s correlations between DOM-related parameters with alpha-diversity indices (Chao 1, Pielou’s evenness, and Shannon index) and habitat niche breadth of the whole (All), abundant taxa (AT), rare (RT), conditionally rare and abundant taxa (CRAT) communities, and with module-based eigengenes of the co-occurrence network (a). Mantel tests based on Pearson’s correlations between the difference in %BDOC (Euclidean distance) with the whole community dissimilarity (Bray-Curtis distance) and difference in module eigengenes (Euclidean distance) between pairs of samples (b). %BDOC: the proportion of biodegradable dissolved organic carbon; DOC: dissolved organic carbon; BIX: the biological index; SUVA: specific ultraviolet absorbance at 254 nm; %C1–C6: the relative abundances of fluorescence components C1–C6.

significantly higher than the corresponding random network (Table S2), implying that the network was non-random and had a modular structure. The network was mainly composed of *Actinobacteria*, *Betaproteobacteria*, *Bacteroidetes*, *Cyanobacteria*, *Alphaproteobacteria*, *Verrucomicrobia*, *Planctomycetes*, and *Gammaproteobacteria* (Fig. 3a). The community members of AT, RT, and CRAT tended to co-occur with each other (Fig. 3b). The node-level topological features including degree, closeness, betweenness, and eigenvector centrality of AT, RT, and CRAT were compared (Fig. 3d). All CRAT values were significantly higher than AT and RT values except for a similar betweenness centrality between AT and CRAT (Fig. 3d). The whole network was clustered into five major modules (>10% of all nodes, Fig. 3c). *Actinobacteria*, *Betaproteobacteria*, and *Bacteroidetes* were the most abundant taxa in all modules, whereas *Alphaproteobacteria*, *Verrucomicrobia*, and *Planctomycetes* were mainly clustered into module 2 and module 4. Correlations between module-based eigengenes of different modules showed significant negative correlations between module 1 with module 2 and module 4 and significant positive correlations between module 1 and module 3 (Fig. S3), revealing higher order organizations in the network structure (Deng et al., 2012).

2.3. Associations between BDOC and bacterial diversities and co-occurrence patterns

Correlations of %BDOC and CDOM-related variables versus bacterial diversity indices and module-based eigengenes are shown in Fig. 4. The richness index (Chao 1) of the whole, RT, and CRAT communities showed a significant negative correlation with %BDOC (Fig. 4a), whereas the evenness and Shannon index of the whole community were significantly positively related to the relative abundance of humic-like C1 (%C1). The habitat niche breadths of the whole and RT communities were significantly positively correlated with %BDOC, but a negative correlation was found for the CRAT subcommunity (Fig. 4a). The correlations between module-based eigengenes and environmental variables can be applied to detect the responses of network modular structure to environmental factors. The members of module 2 and module 5 were positively associated with %BDOC or BIX and %C4, whereas module 1, 3, and 4 showed negative correlations with %BDOC or positive correlations with SUVA and %C1 (Fig. 4a). Overall, %BDOC displayed more significant correlations with bacterial diversity indices and module-based eigengenes than DOC and other CDOM-related variables (Fig. 4a). In addition, Mantel’s tests

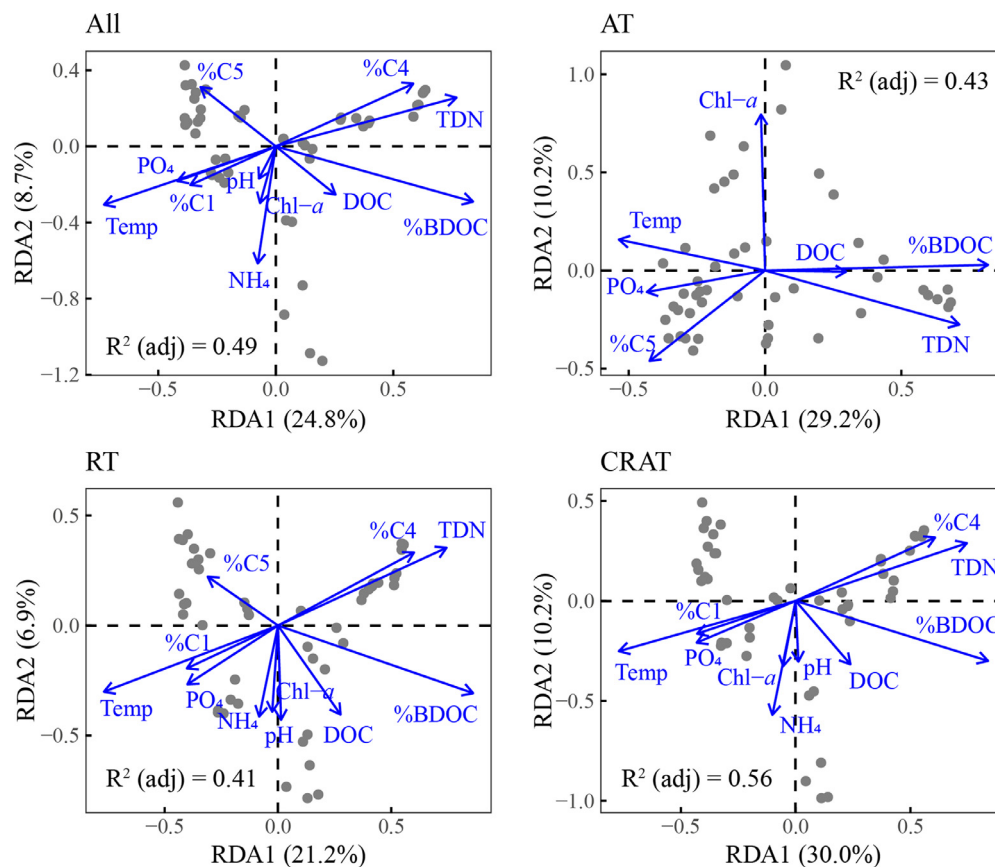


Fig. 5 – Redundancy analysis (RDA) showing the relationships between community structures of the whole (All), abundant (AT), rare (RT), and conditionally rare and abundant (CRAT) taxa with significant environmental factors identified by forward selections. R^2 (adj) represents the adjusted R-square. The arrow length of each variable represents its importance in association with the community structure. %BDOC: the proportion of biodegradable dissolved organic carbon; DOC: dissolved organic carbon; Temp: temperature; Cond: conductivity; TN: total nitrogen; TDN: total dissolved nitrogen; PO_4 -P: orthophosphate; NH_4 -N: ammonia nitrogen; %C1-C6: the relative abundances of fluorescence components C1–C6.

also revealed that the variations of community composition and module structure were strongly associated with changes in %BDOC (Mantel's $r = 0.64$ and 0.59 , Fig. 4b).

2.4. Environmental factors shaping bacterial communities with different abundance patterns

To further explore how BDOC and other environmental variables shaped bacterial communities with different abundance patterns, i.e. AT, RT, and CRAT subcommunities, and the relative importance of BDOC among these environmental variables, redundancy analysis (RDA) was conducted (Fig. 5). Environmental variables explained a higher proportion of variation in CRAT community composition (adjusted $R^2 = 0.56$) than that of AT (adjusted $R^2 = 0.43$) and RT (adjusted $R^2 = 0.41$) (Fig. 5). Significant environmental variables ($p < 0.05$) included temperature, pH, Chl- a , TDN, NH_4 -N, PO_4 -P, DOC, %BDOC, %C1, %C4, and %C5 (Fig. 5). %BDOC had the highest correlation coefficient with the first axis of RDA ordination (RDA1) (Pearson's $r > 0.8$, $p < 0.01$) and showed stronger associations with community structures than other environmental variables including DOC and other CDOM-related variables (%C1, %C4, and %C5) for all subcommunities (Pearson's $r < 0.8$, $p < 0.05$) (Fig. 5).

To examine the relationships between key members of subcommunities with %BDOC and other physico-chemical variables, key taxa were identified based on the co-occurrence network. Key taxa are identified based on the combined score of high mean degree (number of connections of one node), high closeness centrality and low betweenness centrality (Banerjee et al., 2018). The top twenty key taxa (9 RT and 11 CRAT) belonged to the classes of Alphaproteobacteria, Betaproteobacteria, Spartobacteria, Cyanobacteria, Actinobacteria, Verrucomicrobiae, Gammaproteobacteria, and Planctomycetia (Appendix A Table S3; Fig. 6). Additionally, since the degree values of AT were overall lower than that of AT and CRAT (Fig. 3), the top five taxa having the highest degree value were identified as key members for the AT subcommunities (Appendix A Table S3; Fig. 6). %BDOC, TDN, NO_3 -N, temperature, and conductivity were the significant variables associated with the relative abundances of the key taxa (Fig. 6). %BDOC was positively related to the ASVs classified as *Arenimonas*, Actinomycetales, Rhodobacteraceae, Alcaligenaceae, Burkholderiales (2 ASVs), *Sphingorhabdus*, *Gp11a* of Cyanobacteria, Enterobacteriaceae, Rhizobiales, Verrucomicrobiaceae, and Planctomycetaceae (Fig. 6; Appendix A Table S3). All the ASVs except ASV43 (*Arenimonas*) belonged to Module 2 (Appendix A Table S3), likely suggesting similar

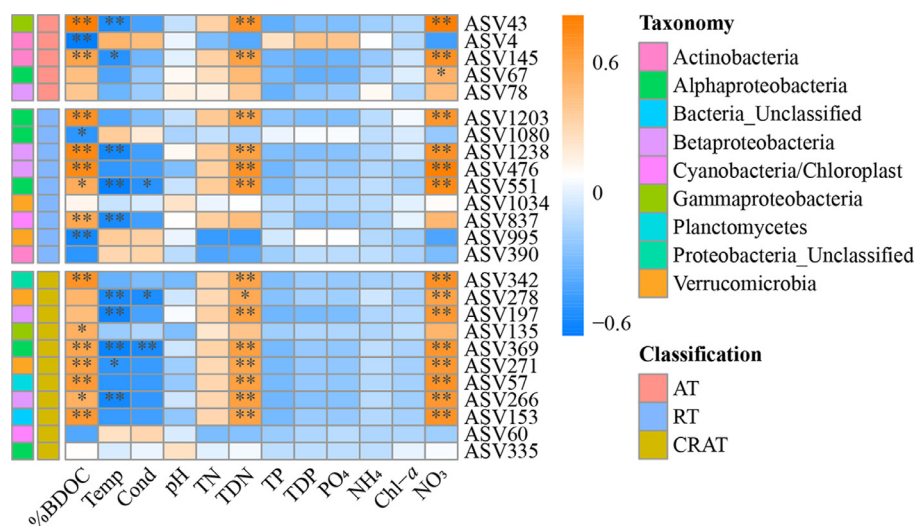


Fig. 6 – Pearson's correlations between environmental factors and the relative abundances of key members of abundant taxa (AT), rare taxa (RT), and conditionally rare and abundant taxa (CRAT) subcommunities. %BDOC: the proportion of biodegradable dissolved organic carbon; Temp: temperature; Cond: conductivity; TN: total nitrogen; TDN: total dissolved nitrogen; PO₄-P: orthophosphate; NH₄-N: ammonia nitrogen.

niche preference/niche overlapping or functional associations among these members.

3. Discussion

Our study revealed strong associations between the proportion of BDOC (%BDOC) and bacterial diversities, module structures of the co-occurrence network, and habitat niche breadths, as well as the relative abundance of key species. Moreover, the effect of environmental variables on bacterial community was most pronounced for the “conditionally rare and abundant” taxa subcommunities.

Our results support the concept that the biodegradability of DOC was highly related to CDOM quantity and chemical properties. Specifically, we found significant relationships between %BDOC and the DOC concentration, BIX, the relative abundance of the tryptophan-like component C4, and SUVA (Fig. 1), as well as the largest drop in the fluorescence intensities of C4 after 28 days bio-incubations (Fig. 2). Protein-like components and BIX are mainly linked to autochthonous production, such as microbial degradation of algae, and high values of BIX indicate presence of freshly released CDOM (Huguet et al., 2009; Song et al., 2019; Yao et al., 2011). These relationships, therefore, demonstrate a high biodegradability of freshly produced protein-like CDOM in Lake Taihu. Our results concur with previous studies showing that high tryptophan fluorescence exhibits dominance of intact or less degraded proteins of recent origin and that the tryptophan-like component is preferentially degraded by bacteria over the tyrosine-like component (Guillemette and del Giorgio, 2011; Stedmon and Markager, 2005b). In addition, domestic sewage is enriched in protein-like components, also contributing to the biodegradability of DOC (Zhou et al., 2021). Furthermore, SUVA, indicative of the aromaticity of DOC (Weishaar et al., 2003), has been found to be negatively correlated with BDOC (Fellman et al.,

2008), suggesting that an increasing proportion of aromatic carbon content of CDOM decreases its biodegradability.

Changes in bacterial diversities and community structures along a gradient in %BDOC was also evidenced in our study (Fig. 4). High %BDOC represents more biologically labile and energetically advantageous molecules for bacterial utilization (Trulleyova and Rulik, 2004), whereas low %BDOC indicates dominance of more recalcitrant compounds that may require more complex enzymatic machineries to degrade. Previous studies have shown that the genetic potential for degradation of labile and simple DOM is phylogenetically widespread, while the potential for degradation of complex compounds appears to be restricted to specific clades (Berlemont and Martiny, 2013). This can partly explain the negative correlations between %BDOC and the richness of bacterial communities, as has also found in experimental incubation (Bai et al., 2017), suggesting that refractory substrates with low %BDOC require more bacterial groups equipped with various metabolic capabilities to metabolize. Moreover, this kind of bacteria appeared to be habitat specialists as revealed by changes in habitat niche breadths (Fig. 4a). Habitat niche breadths have been applied to identify to what extent bacterial communities comprise generalists and specialists, with higher values indicating more metabolic flexibility at the community level (Guo et al., 2018; Jiao et al., 2020; Wu et al., 2017). The habitat niche breadth of the whole bacterial community in our study correlated positively with %BDOC and negatively with SUVA and the relative abundance of humic-like C1 (Fig. 4), suggesting that BDOC-rich environments harbor more species with a wide distribution range, whereas the increasing abundance of aromatic substances, especially of the humic-like CDOM, prompts the occurrence of habitat specialists. To further check the associations between substrate quality and bacterial metabolic activities, sequencing technology based on function genes, metagenomics and metabonomics can be applied.

Previous studies have identified water temperature, Chl-*a*, and nutrients (total nitrogen) (Tang et al., 2017; Zhu et al., 2019) as major factors that shaped the spatiotemporal variation of bacterial community composition in Lake Taihu. Considering that %BDOC covaried with other physicochemical variables, we integrated most environmental factors to examine the importance of %BDOC on affecting bacterial community structures (Fig. 5). Our results further found that CDOM quality, including %BDOC and CDOM components, also played key roles in the environmental selection of bacterial communities (Fig. 5). Moreover, much stronger linkages between bacterial community structure with %BDOC than with DOC concentration evidence that the biodegradability of substrates can be more effective in predicting changes in bacterial communities than the quantity of DOC (Fig. 4; Fig. 5). Using the network and module-based eigengene analyses, we further identified the bacterial groups associated with high and low %BDOC conditions. Specifically, members of module 2 and modules 5 were identified as taxa mainly positively correlated with %BDOC (Fig. 3; Fig. 4). For instance, some key taxa belonging to Module 2, such as *Enterobacteriales* and *Burkholderiales*, were positively related to %BDOC (Fig. 6) and have been detected in other resource rich environments (Kiersztyn et al., 2019; Tang et al., 2009; Zhao et al., 2017). A module in the network represents a collection of species that interact strongly among themselves but only with few species in other modules (Olesen et al., 2007; Zhou et al., 2011), and this has proven to be an effective tool for detecting niche partitioning and specific functions of different bacterial groups (Newman, 2006; Zhou et al., 2019). The significant correlations between module-based eigengenes with %BDOC and CDOM fluorescence components (Fig. 4) indicate that niche partitioning of bacterial communities may partly depend on profiles of DOC metabolism, especially the ability to degrade biolabile and refractory organic compounds. Key species with high mean degree, high closeness centrality and low betweenness centrality are generally considered as initiating components in networks, and they are important for community structure and integrity (Banerjee et al., 2018). The observed significant correlations between the abundances of the majority of key taxa with %BDOC (Fig. 6) further support the importance of the biodegradability of substrates in shaping community structures. It is noted that we standardized incubation conditions and thus the importance of potential BDOC was presented in our study, but in reality, the amount of DOC available to the bacterial communities in the lake may be also metabolically limited by nutrient concentrations or thermal constraints (Abbott et al., 2014), which needs further investigation. Moreover, since the correlation-based co-occurrence network cannot provide information about causality (Faust and Raes, 2012), bioassay experiments need to be designed to explore the responses of bacterial groups to the changes of BDOC.

We also revealed different responses of subcommunities with different abundance patterns in response to environmental changes, including differences in %BDOC and CDOM components in the lake. The variation in the CRAT subcommunity composition was more strongly influenced by environmental factors than the AT and RT subcommunities, with the largest proportion being explained by environmental factors in the redundancy analysis (Fig. 5). This can be partly ex-

plained by an overall narrower habitat niche breadth of CRAT than of AT and RT (Table S1), showing that the CRAT subcommunity included more bacteria with a narrow range of distribution. Habitat specialists have been shown to respond more intensively to environment variables than habitat generalists (Pandit et al., 2009). Moreover, the habitat niche breadth of the CRAT subcommunity correlated oppositely with %BDOC (negatively) than the whole and RT communities (positively), indicating that the CRAT subcommunity contained more species preferring a refractory DOC environment. This agrees with previous studies suggesting that rare species act as “seed banks” with metabolic potential and capacity to become dominant under specific conditions (Lynch and Neufeld, 2015; Shade et al., 2014). In the co-occurrence network, RT and CRAT showed relatively higher values of degree and closeness and eigenvector centrality than AT, further emphasizing the importance of considering the rare bacteria and conditionally rare and abundant bacteria in studies of the spatiotemporal dynamics and variations of bacterial communities in response to environmental changes and disturbances.

4. Conclusions

Our results showed that the proportion of BDOC was significantly correlated with the concentration of DOC, BIX, the relative abundance of the tryptophan-like component, and CDOM aromaticity, indicating a strong linkage between autochthonous protein-like CDOM and BDOC in Lake Taihu. BDOC played a significant role in affecting bacterial community diversities, structures, and co-occurrence patterns and was more important than the majority of physico-chemical parameters including DOC. Increasing bacterial richness and decreasing habitat niche breadth with depleted BDOC were observed for the whole and rare bacterial communities, whereas a negative correlation between BDOC and habitat niche breadth of the conditionally rare and abundant bacterial community was observed. Environmental variables explained the largest proportion of variation in the conditionally rare and abundant bacterial community compared with the abundant and rare bacterial subcommunities, together revealing distinct responses of subcommunities with different abundance patterns to environmental changes. Our findings highlight the importance of considering bacteria with different abundance patterns and CDOM quality, including BDOC and CDOM composition, when studying the importance of environmental selection for bacterial communities in eutrophic lakes.

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Appendix A Supplementary data

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.jes.2021.02.011](https://doi.org/10.1016/j.jes.2021.02.011).

REFERENCES

- Abbott, B.W., Larouche, J.R., Jones, J.B., Bowden, W.B., Balsler, A.W., 2014. Elevated dissolved organic carbon biodegradability from thawing and collapsing permafrost. *J. Geophys. Res.: Biogeophys.* 119, 2049–2063.
- Amaral, V., Graeber, D., Calliari, D., Alonso, C., 2016. Strong linkages between DOM optical properties and main clades of aquatic bacteria. *Limnol. Oceanogr.* 61, 906–918.
- Bai, L., Cao, C., Wang, C., Xu, H., Zhang, H., Slaveykova, V.I., et al., 2017. Toward quantitative understanding of the bioavailability of dissolved organic matter in freshwater lake during cyanobacteria blooming. *Environ. Sci. Technol.* 51, 6018–6026.
- Bana, Z., Ayo, B., Marrase, C., Gasol, J.M., Iriberrí, J., 2014. Changes in bacterial metabolism as a response to dissolved organic matter modification during protozoan grazing in coastal Cantabrian and Mediterranean waters. *Environ. Microbiol.* 16, 498–511.
- Banerjee, S., Schlaeppi, K., van der Heijden, M.G.A., 2018. Keystone taxa as drivers of microbiome structure and functioning. *Nat. Rev. Microbiol.* 16, 567.
- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate - a practical and powerful approach to multiple testing. *J. R. Stat. Soc. B* 57, 289–300.
- Berggren, M., Laudon, H., Haei, M., Ström, L., Jansson, M., 2010. Efficient aquatic bacterial metabolism of dissolved low-molecular-weight compounds from terrestrial sources. *ISME J.* 4, 408–416.
- Berlemont, R., Martiny, A.C., 2013. Phylogenetic distribution of potential cellulases in bacteria. *Appl. Environ. Microbiol.* 79, 1545–1554.
- Bertilsson, S., Eiler, A., Nordqvist, A., Jørgensen, N.O.G., 2007. Links between bacterial production, amino-acid utilization and community composition in productive lakes. *ISME J.* 1, 532–544.
- Blanchet, F.G., Legendre, P., Borcard, D., 2008. Forward selection of explanatory variables. *Ecology* 89, 2623–2632.
- Campbell, B.J., Yu, L., Heidelberg, J.F., Kirchman, D.L., 2011. Activity of abundant and rare bacteria in a coastal ocean. *Proc. Natl. Acad. Sci. U.S.A.* 108, 12776–12781.
- Coble, P.G., 2007. Marine optical biogeochemistry: the chemistry of ocean color. *Chem. Rev.* 38, 402–418.
- D'Andrilli, J., Junker, J.R., Smith, H.J., Scholl, E.A., Foreman, C.M., 2019. DOM composition alters ecosystem function during microbial processing of isolated sources. *Biogeochemistry* 142, 281–298.
- de Menezes, A.B., Prendergast-Miller, M.T., Richardson, A.E., Toscas, P., Farrell, M., Macdonald, L.M., et al., 2015. Network analysis reveals that bacteria and fungi form modules that correlate independently with soil parameters. *Environ. Microbiol.* 17, 2677–2689.
- Deng, Y., Jiang, Y.H., Yang, Y., He, Z., Luo, F., Zhou, J., 2012. Molecular ecological network analyses. *BMC Bioinformatics* 13, 113.
- Ebina, J., Tsutsui, T., Shirai, T., 1983. Simultaneous determination of total nitrogen and total phosphorus in water using peroxodisulfate oxidation. *Water Res.* 17, 1721–1726.
- Edgar, R.C., 2013. UPARSE: highly accurate OTU sequences from microbial amplicon reads. *Nat. Methods* 10, 996–998.
- Erdős, P., Rényi, A., 2011. On the evolution of random graphs. *T. Am. Math. Soc.* 286, 257–274.
- Faust, K., Raes, J., 2012. Microbial interactions: from networks to models. *Nat. Rev. Microbiol.* 10, 538–550.
- Fellman, J.B.D.A., David, V., Hood, E., Boone, R.D., 2008. Fluorescence characteristics and biodegradability of dissolved organic matter in forest and wetland soils from coastal temperate watersheds in southeast Alaska. *Biogeochemistry* 88, 169–184.
- Guillemette, F., del Giorgio, P.A., 2011. Reconstructing the various facets of dissolved organic carbon bioavailability in freshwater ecosystems. *Limnol. Oceanogr.* 56, 734–748.
- Guillemette, F., Leigh McCallister, S., Del Giorgio, P.A., 2016. Selective consumption and metabolic allocation of terrestrial and algal carbon determine allochthony in lake bacteria. *ISME J.* 10, 1373–1382.
- Guillemette, F., McCallister, S.L., del Giorgio, P.A., 2013. Differentiating the degradation dynamics of algal and terrestrial carbon within complex natural dissolved organic carbon in temperate lakes. *J. Geophys. Res.: Biogeophys.* 118, 963–973.
- Guo, Y., Liu, M., Liu, L., Liu, X., Chen, H., Yang, J., 2018. The antibiotic resistome of free-living and particle-attached bacteria under a reservoir cyanobacterial bloom. *Environ. Int.* 117, 107–115.
- Hitchcock, J.N., Mitrovic, S.M., 2015. After the flood: changing dissolved organic carbon bioavailability and bacterial growth following inflows to estuaries. *Biogeochemistry* 124, 219–233.
- Huang, C., Zhang, Y., Huang, T., Yang, H., Li, Y., Zhang, Z., et al., 2019. Long-term variation of phytoplankton biomass and physiology in Taihu lake as observed via MODIS satellite. *Water Res.* 153, 187–199.
- Huguet, A., Vacher, L., Relexans, S., Saubusse, S., Froidefond, J.M., Parlanti, E., 2009. Properties of fluorescent dissolved organic matter in the Gironde Estuary. *Org. Geochem.* 40, 706–719.
- Hur, J., Lee, B.M., Shin, H.S., 2011. Microbial degradation of dissolved organic matter (DOM) and its influence on phenanthrene-DOM interactions. *Chemosphere* 85, 1360–1367.
- Jiao, S., Yang, Y., Xu, Y., Zhang, J., Lu, Y., 2020. Balance between community assembly processes mediates species coexistence in agricultural soil microbiomes across eastern China. *ISME J.* 14, 202–216.
- Kaartokallio, H., Asmala, E., Autio, R., Thomas, D.N., 2015. Bacterial production, abundance and cell properties in boreal estuaries: relation to dissolved organic matter quantity and quality. *Aquat. Sci.* 78, 525–540.
- Kellerman, A.M., Kothawala, D.N., Dittmar, T., Tranvik, L.J., 2015. Persistence of dissolved organic matter in lakes related to its molecular characteristics. *Nat. Geosci.* 8, 454–457.
- Kiersztyn, B., Chrost, R., Kalinski, T., Siuda, W., Bukowska, A., Kowalczyk, G., et al., 2019. Structural and functional microbial diversity along a eutrophication gradient of interconnected lakes undergoing anthropopressure. *Sci. Rep.* 9, 11144.
- Landa, M., Cottrell, M., Kirchman, D., Kaiser, K., Medeiros, P., Tremblay, L., et al., 2014. Phylogenetic and structural response of heterotrophic bacteria to dissolved organic matter of different chemical composition in a continuous culture study. *Environ. Microbiol.* 16, 1668–1681.

- Langfelder, P., Horvath, S., 2007. Eigengene networks for studying the relationships between co-expression modules. *BMC Syst. Biol.* 1, 54.
- Langfelder, P., Horvath, S., 2008. WGCNA: an R package for weighted correlation network analysis. *BMC Bioinformatics* 9, 559.
- Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280.
- Levins, R., 1968. *Evolution in Changing environments: Some Theoretical Explorations*. Princeton University Press.
- Li, H., Zeng, J., Ren, L., Wang, J., Xing, P., Wu, Q.L., 2017. Contrasting patterns of diversity of abundant and rare bacterioplankton in freshwater lakes along an elevation gradient. *Limnol. Oceanogr.* 62, 1570–1585.
- Li, P., Liu, J., Jiang, C., Wu, M., Liu, M., Li, Z., 2019. Distinct successions of common and rare bacteria in soil under humic acid amendment - a microcosm study. *Front. Microbiol.* 10, 2271.
- Liang, Y., Xiao, X., Nuccio, E.E., Yuan, M., Zhang, N., Xue, K., et al., 2020. Differentiation strategies of soil rare and abundant microbial taxa in response to changing climatic regimes. *Environ. Microbiol.* 22, 1327–1340.
- Logue, J.B., Stedmon, C.A., Kellerman, A.M., Nielsen, N.J., Andersson, A.F., Laudon, H., et al., 2016. Experimental insights into the importance of aquatic bacterial community composition to the degradation of dissolved organic matter. *ISME J.* 10, 533–545.
- Lynch, M.D., Neufeld, J.D., 2015. Ecology and exploration of the rare biosphere. *Nat. Rev. Microbiol.* 13, 217–229.
- Melo, M.L., Kothawala, D.N., Bertilsson, S., Amaral, J.H., Forsberg, B., Sarmiento, H., 2020. Linking dissolved organic matter composition and bacterioplankton communities in an Amazon floodplain system. *Limnol. Oceanogr.* 65, 63–76.
- Mo, Y., Zhang, W., Yang, J., Lin, Y., Yu, Z., Lin, S., 2018. Biogeographic patterns of abundant and rare bacterioplankton in three subtropical bays resulting from selective and neutral processes. *ISME J.* 12, 2198–2210.
- Mou, X., Sun, S., Edwards, R.A., Hodson, R.E., Moran, M.A., 2008. Bacterial carbon processing by generalist species in the coastal ocean. *Nature* 451, 708–711.
- Murphy, K.R., Stedmon, C.A., Waite, T.D., Ruiz, G.M., 2008. Distinguishing between terrestrial and autochthonous organic matter sources in marine environments using fluorescence spectroscopy. *Mar. Chem.* 108, 40–58.
- Murphy, K.R., Stedmon, C.A., Wenig, P., Bro, R., 2014. OpenFluor—an online spectral library of auto-fluorescence by organic compounds in the environment. *Anal. Methods* 6, 658–661.
- Muscarella, M.E., Boot, C.M., Broeckling, C.D., Lennon, J.T., 2019. Resource heterogeneity structures aquatic bacterial communities. *ISME J.* 13, 2183–2195.
- Nearing, J.T., Douglas, G.M., Comeau, A.M., Langille, M.G.I., 2018. Denoising the Denoisers: an independent evaluation of microbiome sequence error-correction approaches. *PeerJ* 6, e5364.
- Nelson, C.E., Alldredge, A.L., McCliment, E.A., Amaral-Zettler, L.A., Carlson, C.A., 2011. Depleted dissolved organic carbon and distinct bacterial communities in the water column of a rapid-flushing coral reef ecosystem. *ISME J.* 5, 1374–1387.
- Newman, M.E.J., 2006. Modularity and community structure in networks. *Proc. Nat. Acad. Sci. U.S.A.* 103, 8577–8582.
- Olesen, J.M., Bascompte, J., Dupont, Y.L., Jordano, P., 2007. The modularity of pollination networks. *Proc. Nat. Acad. Sci. U.S.A.* 104, 19891–19896.
- Osburn, C.L., Boyd, T.J., Montgomery, M.T., Bianchi, T.S., Coffin, R.B., Paerl, H.W., 2016. Optical proxies for terrestrial dissolved organic matter in estuaries and coastal waters. *Front. Mar. Sci.* 2, 127.
- Osterholz, H., Niggemann, J., Giebel, H.-A., Simon, M., Dittmar, T., 2015. Inefficient microbial production of refractory dissolved organic matter in the ocean. *Nat. Commun.* 6.
- Pandit, S.N., Kolasa, J., Cottenie, K., 2009. Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. *Ecology* 90, 2253–2262.
- Párista, É., Ács, É., Böddi, B., 2002. Chlorophyll-a determination with ethanol—a critical test. *Hydrobiologia* 485, 191–198.
- Pedros-Alio, C., 2012. The rare bacterial biosphere. *Ann. Rev. Mar. Sci.* 4, 449–466.
- Perez, M.T., Sommaruga, R., 2006. Differential effect of algal- and soil-derived dissolved organic matter on alpine lake bacterial community composition and activity. *Limnol. Oceanogr.* 51, 2527–2537.
- Qin, B., Yang, G., Ma, J., Wu, T., Li, W., Liu, L., et al., 2018. Spatiotemporal changes of cyanobacterial bloom in large shallow eutrophic Lake Taihu, China. *Front. Microbiol.* 9, 451.
- Ratzke, C., Barrere, J., Gore, J., 2020. Strength of species interactions determines biodiversity and stability in microbial communities. *Nat. Ecol. Evol.* 4, 376–383.
- Roiha, T., Peura, S., Cusson, M., Rautio, M., 2016. Allochthonous carbon is a major regulator to bacterial growth and community composition in subarctic freshwaters. *Sci. Rep.* 6, 34456.
- Ruiz-González, C., Niño-García, J.P., Lapierre, J.-F., del Giorgio, P.A., 2015. The quality of organic matter shapes the functional biogeography of bacterioplankton across boreal freshwater ecosystems. *Global Ecol. Biogeogr.* 24, 1487–1498.
- Shade, A., Jones, S.E., Caporaso, J.G., Handelsman, J., Knight, R., Fierer, N., et al., 2014. Conditionally rare taxa disproportionately contribute to temporal changes in microbial diversity. *MBio* 5, e01314–e01371.
- Shutova, Y., Baker, A., Bridgeman, J., Henderson, R.K., 2014. Spectroscopic characterisation of dissolved organic matter changes in drinking water treatment: from PARAFAC analysis to online monitoring wavelengths. *Water Res.* 54, 159–169.
- Song, K., Shang, Y., Wen, Z., Jacinthe, P.A., Liu, G., Lyu, L., et al., 2019. Characterization of CDOM in saline and freshwater lakes across China using spectroscopic analysis. *Water Res.* 150, 403–417.
- Spencer, R.G., Butler, K.D., Aiken, G.R., 2012. Dissolved organic carbon and chromophoric dissolved organic matter properties of rivers in the USA. *J. Geophys. Res.: Biogeogr.* 117.
- Stedmon, C.A., Markager, S., 2005a. Resolving the variability in dissolved organic matter fluorescence in a temperate estuary and its catchment using PARAFAC analysis. *Limnol. Oceanogr.* 50, 686–697.
- Stedmon, C.A., Markager, S., 2005b. Tracing the production and degradation of autochthonous fractions of dissolved organic matter by fluorescence analysis. *Limnol. Oceanogr.* 50, 1415–1426.
- Stedmon, C.A., Markager, S., Bro, R., 2003. Tracing dissolved organic matter in aquatic environments using a new approach to fluorescence spectroscopy. *Mar. Chem.* 82, 239–254.
- Tang, X., Chao, J., Gong, Y., Wang, Y., Wilhelm, S.W., Gao, G., 2017. Spatiotemporal dynamics of bacterial community composition in large shallow eutrophic Lake Taihu: high overlap between free-living and particle-attached assemblages. *Limnol. Oceanogr.* 62, 1366–1382.
- Tang, X., Gao, G., Qin, B., Zhu, L., Chao, J., Wang, J., et al., 2009. Characterization of bacterial communities associated with organic aggregates in a large, shallow, eutrophic freshwater lake (Lake Taihu, China). *Microb. Ecol.* 58, 307–322.
- Trulleyova, S., Rulik, M., 2004. Determination of biodegradable dissolved organic carbon in waters: comparison of batch methods. *Sci. Total Environ.* 332, 253–260.

- Vonk, J.E., Tank, S.E., Mann, P.J., Spencer, R.G.M., Treat, C.C., Striegl, R.G., et al., 2015. Biodegradability of dissolved organic carbon in permafrost soils and aquatic systems: a meta-analysis. *Biogeosciences* 12, 6915–6930.
- Weishaar, J.L., Aiken, G.R., Bergamaschi, B.A., Fram, M.S., Fujii, R., Mopper, K., 2003. Evaluation of specific ultraviolet absorbance as an indicator of the chemical composition and reactivity of dissolved organic carbon. *Environ. Sci. Technol.* 37, 4702–4708.
- Wu, W., Lu, H.P., Sastri, A., Yeh, Y.C., Gong, G.C., Chou, W.C., et al., 2017. Contrasting the relative importance of species sorting and dispersal limitation in shaping marine bacterial versus protist communities. *ISME J.* 12, 485–494.
- Xue, Y., Chen, H., Yang, J.R., Liu, M., Huang, B., Yang, J., 2018. Distinct patterns and processes of abundant and rare eukaryotic plankton communities following a reservoir cyanobacterial bloom. *ISME J.* 12, 2263–2277.
- Yamashita, Y., Kloeppel, B., Knoepp, J., Zausen, G., Jaffe, R., 2011. Effects of watershed history on dissolved organic matter characteristics in headwater streams. *Ecosystems* 14, 1110–1122.
- Yao, X., Zhang, Y., Zhu, G., Qin, B., Feng, L., Cai, L., et al., 2011. Resolving the variability of CDOM fluorescence to differentiate the sources and fate of DOM in Lake Taihu and its tributaries. *Chemosphere* 82, 145–155.
- Zhang, H., Hou, F., Xie, W., Wang, K., Zhou, X., Zhang, D., et al., 2020. Interaction and assembly processes of abundant and rare microbial communities during a diatom bloom process. *Environ. Microbiol.* 22, 1707–1719.
- Zhang, W., Zhou, Y., Jeppesen, E., Wang, L., Tan, H., Zhang, J., 2019. Linking heterotrophic bacterioplankton community composition to the optical dynamics of dissolved organic matter in a large eutrophic Chinese lake. *Sci. Total Environ.* 679, 136–147.
- Zhao, B., Xing, P., Wu, Q.L., 2017. Microbes participated in macrophyte leaf litters decomposition in freshwater habitat. *FEMS Microbiol. Ecol.* 93, fix108.
- Zhou, J., Deng, Y., Luo, F., He, Z., Yang, Y., 2011. Phylogenetic molecular ecological network of soil microbial communities in response to elevated CO₂. *MBio* 2, e00111–e00122.
- Zhou, L., Bai, C., Cai, J., Hu, Y., Shao, K., Gao, G., et al., 2018a. Bio-cord plays a similar role as submerged macrophytes in harboring bacterial assemblages in an eco-ditch. *Environ. Sci. Pollut. Res.* 25, 26550–26561.
- Zhou, L., Zhou, Y., Hu, Y., Cai, J., Liu, X., Bai, C., et al., 2019. Microbial production and consumption of dissolved organic matter in glacial ecosystems on the Tibetan Plateau. *Water Res.* 160, 18–28.
- Zhou, L., Zhou, Y., Tang, X., Zhang, Y., Jang, K.-S., Székely, A.J., et al., 2021. Resource aromaticity affects bacterial community successions in response to different sources of dissolved organic matter. *Water Res.* 190, 116776.
- Zhou, Y., Shi, K., Zhang, Y., Jeppesen, E., Liu, X., Zhou, Q., et al., 2017. Fluorescence peak integration ratio IC: IT as a new potential indicator tracing the compositional changes in chromophoric dissolved organic matter. *Sci. Total Environ.* 574, 1588–1598.
- Zhou, Y., Xiao, Q., Yao, X., Zhang, Y., Zhang, M., Shi, K., et al., 2018b. Accumulation of terrestrial dissolved organic matter potentially enhances dissolved methane levels in eutrophic Lake Taihu, China. *Environ. Sci. Technol.* 52, 10297–10306.
- Zhu, C., Zhang, J., Nawaz, M.Z., Mahboob, S., Al-Ghanim, K.A., Khan, I.A., et al., 2019. Seasonal succession and spatial distribution of bacterial community structure in a eutrophic freshwater Lake. *Lake Taihu. Sci. Total Environ.* 669, 29–40.