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RESEARCH ARTICLE

Influence of water temperature and water depth on macrophyte–bacterioplankton interaction in a groundwater-fed river

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Abstract

Biotic interactions shape the community structure and function of ecosystems and thus play an important role in ecosystem management and restoration. To investigate how water temperature (related to the season) and water depth (related to spatial patterns of river morphology) affect macrophyte–bacterioplankton interactions in a groundwater-fed river, we conducted the structural equation modeling on datasets grouped by hydrological conditions. In addition to direct effects on macrophyte growth and/or bacterioplankton development, water temperature and water depth could both regulate the role of different nutrients (inorganic and organic) on affecting these biological indicators. Deeper water depth intensified the positive relationship between macrophytes and bacterioplankton, while higher temperature switched the relationship from being positive to negative. Our study provides empirical evidences that abiotic variables, even with relatively low fluctuations, play a critical role in regulating the patterns and strengths of interaction between macrophytes and bacterioplankton.

Keywords Non-trophic interaction · Submerged macrophytes · Microbe · Dissolved organic matter · Nutrient

Introduction

Providing essential ecosystem functions to human well-being, rivers have become increasingly managed to optimize their services provision (Tockner et al. 2011). However, most of earlier ecosystem management approaches have only focused on specific ecosystem services, often leading to conflicts and trade-offs with the protection of biodiversity (Bullock et al. 2011). While the value of biodiversity has been recognized for a long time, the role of biotic interactions becomes more and more appreciated in shaping the structure of communities and regulating many key functional aspects of ecosystems (Barnes et al. 2018). The study of species interactions within an ecosystem can improve our prediction of its responses to

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accelerating environmental changes (Harmon et al. 2009; Tylianakis et al. 2008). Therefore, in addition to be one of the most fundamental issues in ecology (He et al. 2013), it can also play an important role in ecosystem management and restoration (Kollmann et al. 2016). Trophic interactions between the consumer species and resource species and competitions between species that explore the same resource have always been the focal point of ecological research. However, other types of non-trophic interactions (including mutualism, commensalism, neutralism, amensalism, and antagonism) have only recently gained increasing attention in empirical studies (Kéfi et al. 2012), especially in the study of aquatic systems. It has been substantiated that non-trophic interactions can contribute significantly to food web persistence and modulate the functioning of ecosystems (Donadi et al. 2013; Hammill et al. 2015).

Macrophytes as primary producers and microorganisms as key organisms in organic matter decomposition contribute to crucial functions in freshwater ecosystems (Bornette and Puijalon 2009; Finlay et al. 1997). They are tightly related through a range of direct and indirect non-trophic links. For example, dissolved organic carbon (DOC) and nitrogen (DON) derived from macrophytes can subsidize microbial activity and growth (De Kluijver et al. 2015; Stepanauskas et al. 2000). This part of DOC consists mainly of biologically labile, low-molecular-weight compounds and thus plays a prominent role in stimulating bacterioplankton growth (Findlay et al. 1992; Huss and Wehr 2004). Additionally, the growth of macrophytes can create a great variety of microhabitats and niche heterogeneity through alteration of the surrounding pH, light intensity, nutrient availability, water retention time, etc. (Schulz et al. 2003; Švanys et al. 2014; Reitsema et al. 2018), which are reasonably expected to affect microbial communities (Lindström et al. 2005; Warnecke et al. 2005). Previous studies have demonstrated that species composition, structure, and functioning of the microbial community was closely related to the growth and morphology of macrophytes and their C and N content (Levi et al. 2017; Zeng et al. 2012). On the other hand, microorganisms are also able to influence macrophyte growth by assimilating and transforming water column nutrients and thereby altering nutrient availability (Caron 1994; Kirchman 1994). Strong competition between plants and microbial communities for ammonium, nitrate, phosphorus, and other trace elements has been confirmed in many studies (Cantarel et al. 2015; Fourquez et al. 2015; Lamers et al. 2012; Wu et al. 2017).

Although plant–microbe interactions have received considerable attention, in freshwater ecosystems, especially lotic ecosystems, studies that specifically examine the non-trophic interaction pattern between macrophytes and microorganisms and its environmental control are extremely limited. To fill this knowledge gap, we analyzed the spatio-temporal patterns of macrophytes, microorganisms and abiotic variables in a groundwater-fed lowland river. The clean water characteristics and small-scale hydrological variations of this river enable us to explore how small changes in abiotic variables could influence macrophyte–microbe interactions in river systems. Temperature affects the productivity and metabolism of organisms (Brown et al. 2004; Dillon et al. 2010) and hydrologic conditions such as water flow have long been considered a driving force in structuring communities in lotic ecosystems (Schoelynck et al. 2012). Therefore, we predicted that the response of macrophytes and bacteria to water temperature and hydrologic condition could yield different nature and strength of interactions between them. Specially, we hypothesized that (1) the positive macrophyte–bacteria interaction (e.g., mutualism and commensalism) would be weaker or even changes to negative with higher temperature. This is because rising temperature could enhance the growth and reproduction rate of macrophytes and bacteria and, thus, lead to an intensified competition for nutrients between them. (2) The positive interaction strength between macrophytes and bacteria would be intensified at deeper sites due to a more focused water flow into deeper zones could lead an increasing environmental stress on both of them (Chambers et al. 1991; Lau and Liu 1993).

To test these hypotheses, we quantified and compared the relationships between macrophytes and bacterioplankton as well as their relationships with abiotic variables. In this study, we focused on the bacterioplankton, because many bacterial species in the water column can alternate between free-living and attached growth forms (Kiørboe et al. 2003). Additionally, the flow velocity in our research area is relatively low (range 0–0.37 m s^{-1}; mean value 0.18 m s^{-1}); hence, the interaction between bacterioplankton and macrophyte patches can be expected. Heterotrophic bacterioplankton were chosen as an important biotic component as they degrade different organic matter sources, and a large portion of their demand of both nitrogen and phosphorus can be met by direct uptake of phosphate and ammonium from water (Kirchman 1994). We considered different ranges of water temperature which is related to seasonality and water depth which is related to spatial patterns of river morphology and addressed how these two key abiotic factors shape macrophyte–bacterioplankton interactions through influencing the effect of abiotic variables on the two biotic variables. In addition, given that macrophytes are a large contributor of dissolved organic matter (DOM) in aquatic ecosystems (Findlay and Sinsabaugh 2003) and microbes play a critical role in organic matter flux (Logue et al. 2016), we also examined whether DOM quantity and quality is a relevant linkage between macrophytes and bacterioplankton (Thomas 1997).

Material and methods

Study area and sampling sites

The Fischa River is a tributary of the Austrian part of Danube River, with a catchment area of about 550 km^2 (Fig. 1). It originates southeast of Vienna and flows for 35 km before joining the Danube River. While the western branch of the Fischa River originates in a mountainous area, characterized by floods during spring and winter, the eastern branch is fed by groundwater and has its sources in the lowlands of Lower Austria (Vitvar et al. 2007). In this area, the river is characterized by a very stable hydrological and temperature regime and low concentrations of phosphate and suspended matter (Table S1). Our field survey and sampling was conducted in a lowland branch of the Fischa River close to the village of Pottendorf (47.91° N, 16.39° E), in a study stretch of *c.* 500 m length (Fig. 1). Water temperatures of > 7 °C, also during winter time, support the year-round establishment of macrophytes in this river. More than 90% of the river bed is covered by macrophyte vegetation in this stretch. The dominant macrophyte species is *Berula erecta* (Huds.) Coville and accounts for 99% of the macrophyte biomass. *B. erecta* is a perennial plant that can grow fully submerged or as an emergent species in shallow waters (Preston and Croft, 1997; Fig. 1). In our study area, almost all the individuals grow submerged during the whole year. We selected 10 cross-section transects with *c.* 50 m intervals (T01–T10 in Fig. 1), and at each transect, we selected three sampling points: close to the left bank, in the middle of the river and close to the right bank (Fig. 1).

Sampling procedure

Samples were collected monthly from May 2017 to October 2017, and every sampling was taken in the same time frame from 9:00–11:00 am. We collected samples twice in May to have a better understanding of the background data in the river section. We conducted the sampling survey from downstream to upstream (from T01 to T10 in Fig. 1) to avoid the influence of the suspended sediment by sampling disturbance on the quality of the samples taken downstream. Water temperature was measured in situ using a portable meter (Hach Lange HQ40d, 20 cm below the water surface) at the upstream and downstream transect. We also monitored the daily variation of water temperature at a 30-min interval using automatic data logging units (onset HOBO Pendant 64K, at upstream transect). One fixed cross-section downstream of the stretch was chosen to measure flow velocity and depth using a portable meter (Hach FH950) at 1 m intervals. Undisturbed water samples (~ 120 mL) were collected from within macrophyte patches (before biomass sampling) using a self-designed siphon sampler at the three sampling points per transect. Water depth and the height of macrophytes were measured in situ at the same sampling points. Macrophyte shoots (above-ground biomass) were collected from one 0.5 m × 0.5 m quadrat randomly placed once within each transect. All samples were stored in a cooling box (4~6 °C) and brought to the laboratory

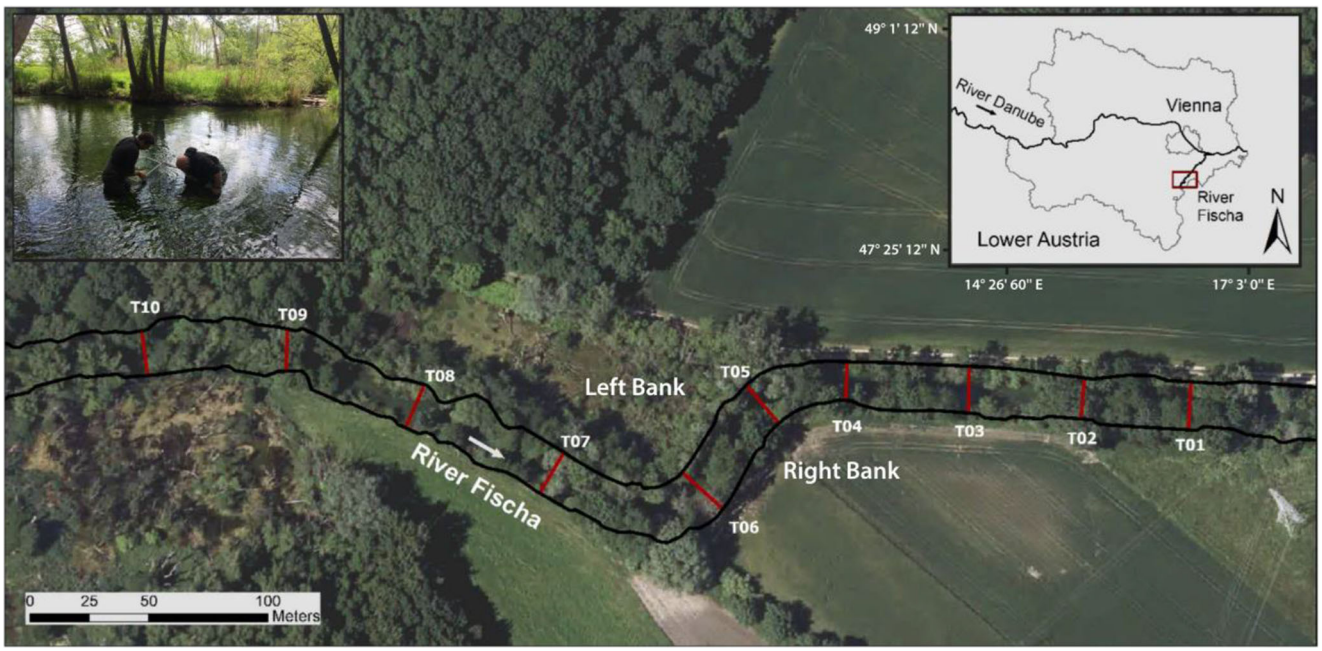

Fig. 1 Location and photo of study sites along the Fischa River in Lower Austria; red lines indicate sampling transects; dark lines show the river bank line; white arrow indicates flow direction

within 3 h after field sampling and then processed further or analyzed immediately.

Chemical analyses

A first fraction of each water sample was filtered through pre-combusted (at 450 °C) Whatman GF/F filters (0.7 μm mesh size). The concentration of ammonium nitrogen (NH_4–N), nitrate (NO_3–N), nitrite (NO_2–N), and ortho-phosphate (PO_4–P) in the filtrate was determined using continuous flow analysis (Alliance Instr., APHA 2005). An unfiltered fraction of each water sample was digested to analyze total phosphorus (TP) according to standard methods (APHA 2005). DOC was measured using a total organic carbon analyzer (Sievers 900, GE Analytical Instruments, USA) and optical properties of DOM were determined by a Hitachi F-7000 fluorescence spectrophotometer within 24 h (Baker 2002). Fluorescence index (FI) was calculated by the ratio of emission wavelengths at 470 nm and 520 nm, obtained at excitation wavelength of 370 nm (Cory and McKnight 2005). The FI has been widely used to distinguish DOM mainly derived from microbial vs. terrestrial higher plant material and determine the degree of degradation of DOM (McKnight et al. 2001). Biological index (BIX) as an indicator for the presence of autochthonous (microbially derived) DOM was calculated by the ratio of emission intensity at 380 nm divided by 430 nm at an excitation wavelength of 310 nm (Huguet et al. 2009).

Macrophyte biomass and coverage

All macrophyte shoots were cleaned with tap water to remove epiphytes, residual roots, and sediments. Then they were dried in paper bags at 70 °C for 5 days and weighed for biomass determination. Coverage (COV) in the quadrant was calculated as the percentage of an area covered with macrophytes. As the macrophyte biomass sample was taken randomly from only one of three water sampling points in each transect, the data size of the biomass samples could not meet the requirement of our further data analysis. We therefore used the product of height × COV percentage as an indicator of the macrophyte biomass. As both height and coverage were measured at all the three sampling points of each transect, the data size of "surrogate-biomass" is three times of that of measured biomass. The positive correlation between biomass and height × COV percentage allowed us to use the "surrogate-biomass" as the representative measure for biomass (Fig. S1).

Bacterioplankton abundance and viability

The remaining fraction of the water sample was fixed with paraformaldehyde in Phosphate-buffered saline (PBS; 0.1 M, pH = 7.4, 0.22 μm filtered) at a final concentration of 1% and stored in the dark for 2–4 h at room temperature. Then the samples were diluted with sterile water and sonicated for 4–6 min (P = 10–100 W), which does not destroy the cell membrane. Afterwards, they were filtered with 20 μm bolting cloth to separate bacterioplankton from bigger particles (Patent CN103926189 B).

To count the abundance of heterotrophic bacterioplankton, the filtered subsamples were stained with SYBR Green I, at a final concentration of 1:10,000, for 20 min in the dark at room temperature (Marie et al. 1997). For bacterioplankton viability, we used LIVE/DEAD BacLight Bacterial Viability Kit (L34856; Molecular Probes, Eugene, OR, USA), according to the manufacturer's instructions (Berney et al. 2007).

All bacterioplankton populations were acquired in a CytoFLEX flow cytometer (Beckman Coulter) and analyzed using the CytExpert software. Bacterioplankton viability was calculated by dividing the density of live cells by the density of total cells (dead and live).

Sub-data processing and statistical analysis

Detailed explanation of the data processing and statistical analyses is presented in the method part of the supplementary information. Briefly, we split the whole dataset into four sub-datasets (n between 101 and 119) using the median value of water temperature and water depth as the boundaries to four subsets: subset high temperature (high-temp, 12.6 °C–14.0 °C), subset low temperature (low-temp, 11.6–12.6 °C), subset deep sites (67.5–130 cm), and subset shallow sites (30–67.5 cm). As Clark et al. (2008) pointed out that while the quantitative limits to these subsets are somewhat arbitrary, it is feasible if the classifications lead to highly interpretable results. Furthermore, according to the median value of water temperature, the subset high-temp represents summer (from 31 May to August), while the subset low-temp represents spring and autumn (beginning of May, September, and October). We conducted multilevel structural equation modeling (SEM, Fig. S2) using the package "lavaan.survey" with the consideration of the temporal survey structure of our study (Rosseel 2012; Oberski 2014) to test multivariate causal hypotheses linking abiotic factors including water depth, water temperature, and nutrients (TN, NH_4–N, NO_3–N, NO_2–N, PO_4–P, DOC, BIX, and FI) to macrophyte biomass (derived from height × COV percentage since there was significant linear relationship between them; Fig. S1), heterotrophic bacterioplankton abundance, and bacterioplankton viability. Given that bacterioplankton abundance could be more likely higher in downstream transects (similar results were found by Goulder (1984)), we also added distance from the most upstream transect (which we defined as zero distance) to the models to capture the spatial autocorrelation in the variable. Compared with other statistical

methods such as factor analysis and multivariate regression, SEM has the advantage that in the model directions can be assigned to several relationships and thus yields multiple explanatory as well as multiple response variables (Grace, 2006). Moreover, it can reveal whether a significant bivariate relationship derives from a significant relationship of these two variables with other variables.

For the four sub-datasets, we identified the significant predictors of DOC, BIX, and FI among the following variables: water temperature, distance, dry biomass, ratio of plant height to water depth, heterotrophic bacterioplankton abundance, and bacterioplankton viability. Predictors included in the final linear regression were decided by the backward stepwise selection based on AIC. Since macrophytes can significantly affect the flow pattern in running waters (Schulz et al. 2003), here we also chose the ratio of plant height to water depth as the explanatory variable in linear regression models.

To test the difference among different sampling times and different sites as well as among the split datasets, a one-way ANOVA followed by LSD post hoc multiple comparisons or a Mann–Whitney *U* test was performed on the variables including water depth and temperature, plant height, the product of plant height and coverage, plant biomass, hetero-bacteria, bacterial viability, NO_3–N, NH_4–N, NO_2–N, PO_4–P, TP, DOC, BIX, and FI. For the height and height × COV variable, we excluded the data whose values were zero.

All the data analysis and graphing were accomplished with R version 3.2.1 (R Core Team 2015).

Results

Macrophyte–bacterioplankon observation patterns

On average, the height of macrophytes increased significantly from May to June (Fig. 2a; LSD $P < 0.05$), but biomass values were almost at the same level during this time period (Fig. 2b) due to the coverage percentage reduction. In the following months, both parameters showed a continuous decline until September and had the same two relatively sharp reductions from June to July and from August to September, which were also observed in water temperature and depth (Fig. S3). The heterotrophic bacterioplankon abundance peaked at the end of May (Fig. 2c; LSD $P < 0.05$) and displayed a slow reduction afterwards. There was no regular temporal pattern in bacterioplankon viability, with a significant higher value in June, September, and October (Fig. 2d; LSD $P < 0.05$).

There was no regular or similar spatial pattern along the river within the sampling area, for all four biotic variables at the three sampling points (close to the left bank, in the middle of the river and close to the right bank; Fig. 3). A significant difference was only detected between the macrophyte biomass at the "left" and "middle" site (mean value of depth at the

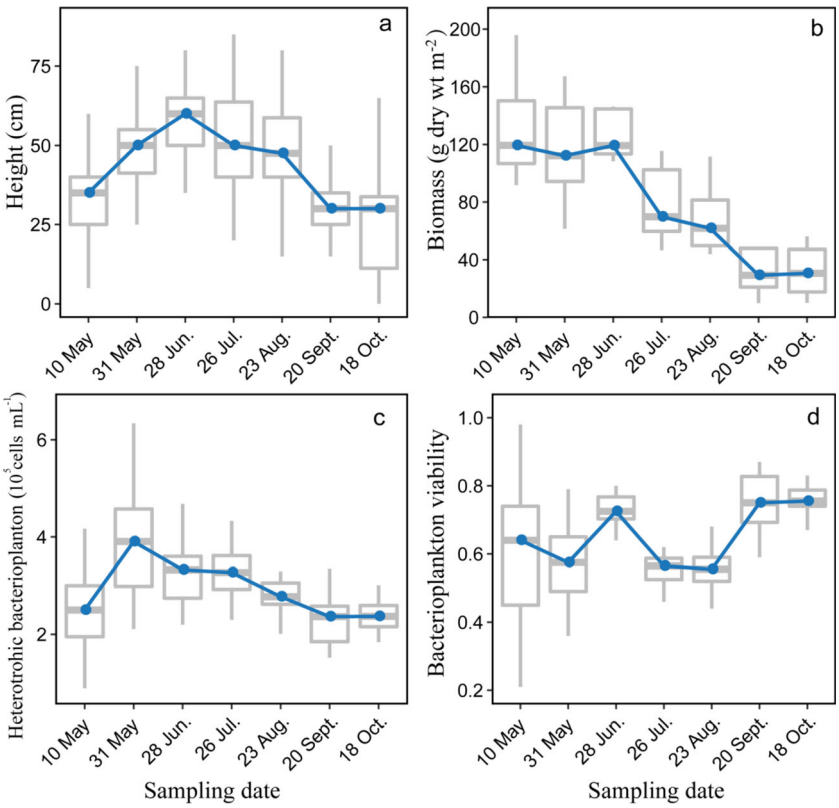

Fig. 2 Boxplots showing the temporal variation of height of macrophytes (**a**), macrophyte biomass (**b**), heterotrophic bacterioplankton abundance (**c**), and bacterioplankton viability (**d**). The median ($n = 30$), lower quartile, upper quartile, smallest observation (sample minimum), and largest observation (sample maximum) are indicated

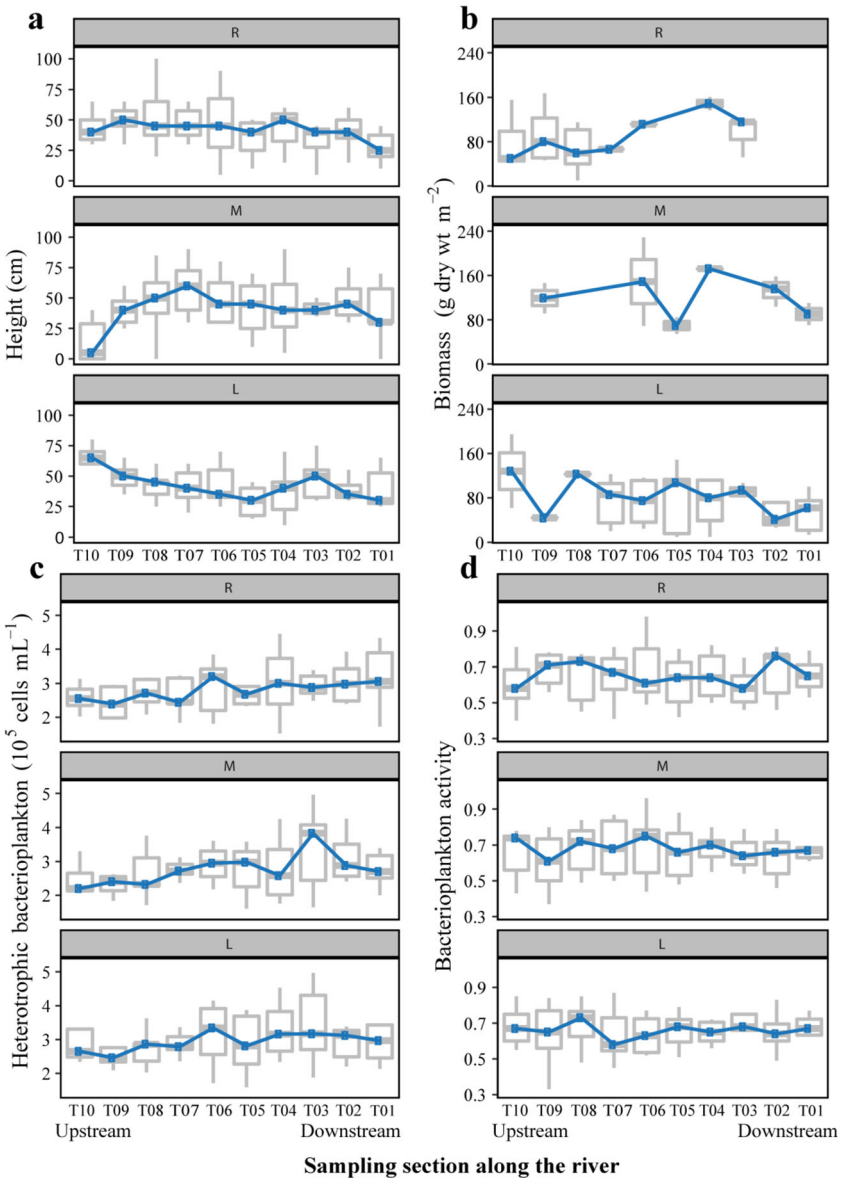

Fig. 3 Boxplots showing the spatial variation of plant height (**a**), macrophyte biomass (**b**), heterotrophic bacterioplankton abundance (**c**), and bacterioplankton viability (**d**). R, M, and L mean the right bank, middle, and left bank of the river (Fig. 1). The median ($n = 7$), lower quartile, upper quartile, smallest observation (sample minimum), and largest observation (sample maximum) are indicated

"right," "middle," and "left" site: 65.6 ± 19.8 cm, 81.7 ± 21.5 cm, and 58.8 ± 19.5 cm, *U* test $P < 0.05$).

Riverine organic matter quality: patterns and its main predictors

The concentration of DOC showed a gradual rise over time and reached the highest value in September with a considerable increase (Fig. 4a; LSD $P < 0.05$). BIX and FI displayed similar temporal changes during most of the sampling season. There was, however, a difference on the26th of July, when the value of BIX had a slight increase but FI showed a decrease compared to that in June (Fig. 4b, c). There was no clear and consistent spatial pattern of DOC, FI, and BIX along the river (Fig. 5). Nevertheless, for all three variables, there was relatively less variation among the 10 sites in the middle of the river compared to that among the sites near banks. Additionally, we found a considerable accumulation of DOC in the all three sites at section T10 (Fig. 5, the DOC concentration difference between T10 and T01 were 0.26 mg L^{-1} (L), 0.07 mg L^{-1} (M), 0.35 mgL^{-1} (R); *U* test $P < 0.05$).

For the four sub-datasets, we identified different dominant predictors for DOC, BIX, and FI (Table 1). Water temperature was selected over other biotic and abiotic drivers as the main predictor for organic matter parameters in most datasets. Distance as the main predictor contributed positively to DOC, but negatively to BIX. By comparing the different datasets, bacterioplankton viability as the main predictor of DOC was only identified in the subset high-temp and subset deep sites, whereas the ratio of plant height and water depth presented the opposite pattern and only was found in the subset low-temp and subset shallow sites. In addition, we found

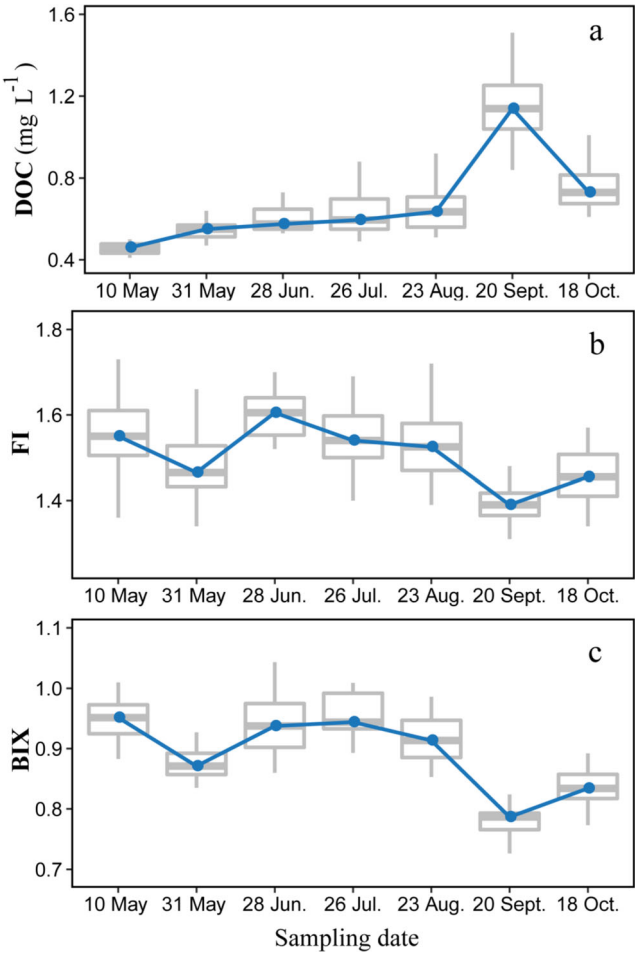

Fig. 4 Boxplots showing the temporal variation of dissolved organic matter (DOC, **a**), fluorescence index (FI, **b**), and biological index (BIX, **c**). The median ($n = 30$), lower quartile, upper quartile, smallest observation (sample minimum), and largest observation (sample maximum) are indicated

heterotrophic bacterial abundance was never selected as a major predictor of organic matter parameters by our linear models.

Structural equation modeling

Our final SEMs fit the data well ($P > 0.05$) and retained only abiotic variables significantly related to macrophyte and/or bacterioplankton (Fig. 6, Fig. S4). Compared with low range datasets, we found that more abiotic variables had direct effects on the three biotic variables in the subset high-temp and subset deep sites (Fig. 6). Besides this, DOC as explaining variable was only included in water depth scenarios. In the subset low-temp, water temperature was the strongest determinant of heterotrophic bacterioplankton abundance, bacterioplankton viability, and macrophyte biomass (Fig. 6b). Strong negative and positive impacts from temperature on the two bacterial parameters were also identified in the subset high-temp, while in the subset low-temp impacts the opposite direction was shown (Fig. 6a, b). Furthermore, in the subset high-temp, water depth had significant positive effects on macrophyte biomass, while no significant effect was identified for temperature. Although the positive effect of distance on heterotrophic bacterioplankton abundance was observed in both temperature subsets, the effect was much stronger in the subset high-temp ($r = 0.48$ vs. $r = 0.12$). For nutrient variables, NO_3–N, NO_2–N, PO_4–P, and TP, in the subset high-temp, their concentration had an effect on one to three biotic variables. In the subset low-temp, only NH_4–N and PO_4–P concentrations had a positive effect on heterotrophic bacterioplankton abundance and macrophyte biomass, respectively. More importantly, we found a negative covariance between bacterioplankton viability and macrophyte biomass as well as between bacterioplankton viability and heterotrophic bacterioplankton abundance in the subset high-temp. In the subset low-temp, there was only a positive covariance between heterotrophic bacterioplankton abundance and macrophyte biomass.

Also, we found that there were considerable differences between the two water depth subsets (Fig. 6c, d). Firstly, in the subset deep sites, the strongest positive relationship existed between heterotrophic bacterioplankton abundance and macrophyte biomass (Fig. 6c). A negative covariance term between bacterioplankton viability and heterotrophic bacterioplankton abundance was identified in the subset shallow sites (Fig. 6d). Secondly, water temperature had a strong effect on heterotrophic bacterioplankton abundance and macrophyte biomass in both cases. In the deep subset, it was the strongest determinant of the two biotic variables, while in the subset shallow sites, it was only the principle determinant of heterotrophic bacterioplankton abundance. For macrophyte biomass, the main determinant was water depth. Moreover, temperature had a negative effect on bacterioplankton viability in the subset shallow sites. Thirdly, in both depth subdatasets, distance and DOC were positively related to heterotrophic bacterioplankton abundance and bacterioplankton viability, respectively, with stronger relationship in the subset deep sites. Finally, the concentration of NO_3–N and TP strongly influenced bacterioplankton viability and macrophyte biomass in the subset deep sites, but their effects were opposite to each other. In the subset shallow sites, only one positive relationship between NO_3–N concentration and bacterioplankton viability was found. However, NO_3–N was also the strongest determinant for bacterioplankton viability.

Discussion

Our study provides evidence for the contribution of abiotic factors to steering interactions between macrophytes and bacterioplankton in running water systems, even at comparable stable environmental conditions. In the study stretch, the

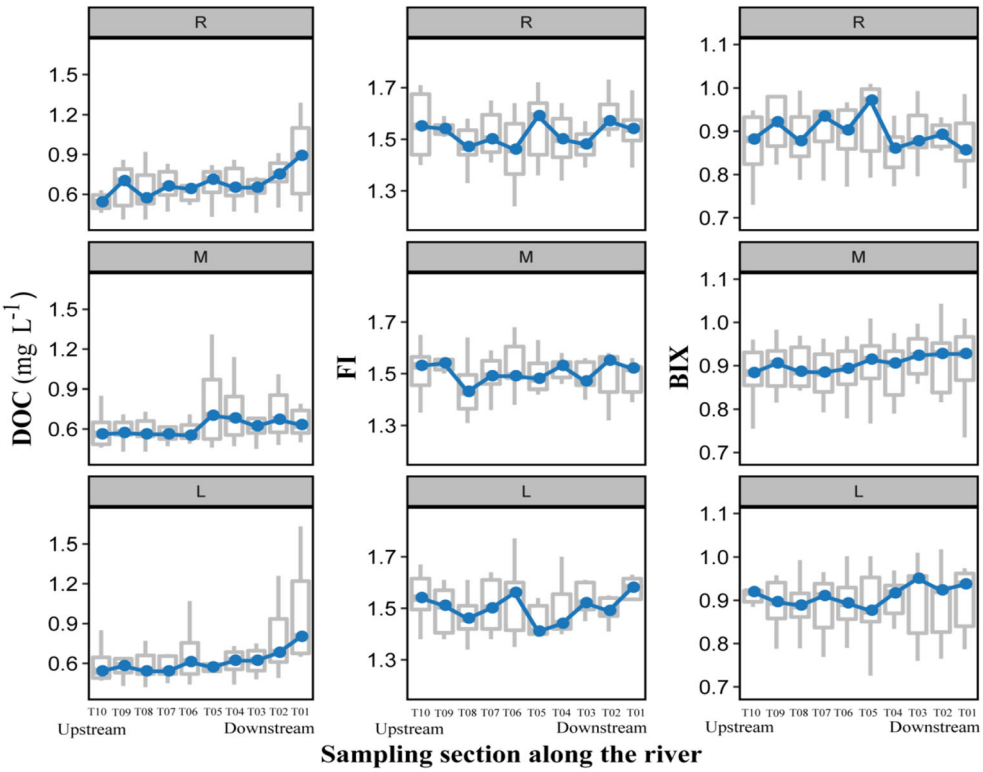

Fig. 5 Spatial variation of dissolved organic matter (DOC), fluorescence index (FI), and biological index (BIX). The median ($n = 7$), lower quartile, upper quartile, smallest observation (sample minimum), and largest observation (sample maximum) are indicated

mean discharge of the whole year (2017) was 0.68 ± 0.08 m^3 s^{-1} and the annual water temperature was below 16 °C, with a mean of 13.3 ± 2.3 °C. As expected, we observed a large difference in patterns and in the strength of abiotic control on macrophytes and bacterioplankton and their interactions at different ranges of water depth and temperature. This occurs despite the comparable low variability, especially for water temperature, which has rather small daily changes and a relatively narrow range of monthly fluctuation (Table S2 and Fig. S3), compared to rivers with less groundwater input or canopy cover (Caissie 2006).

Effect of water temperature and water depth on macrophyte, bacterioplankton, and their interactions

Although we found that a considerable increase in plant height and heterotrophic bacterioplankton abundance occurred with the increment of water temperature and water depth, the temporal and spatial variation of macrophytes and bacterioplankton did not synchronize with any abiotic variable (Figs. S3, S5, and S6). These manifest that macrophyte growth and bacterioplankton development in the river is regulated by multiple factors (Carr et al. 1997; Rubin and Leff 2007). Contrary to the previous observation that submerged macrophyte species could increase growth even when the temperature was up to 28 °C (Barko et al. 1982), the strong effect from water temperature on macrophyte biomass was only detected in the subset low-temp, with values ranging from 11.6 to 12.6 °C. This is because in the subset high-temp macrophyte biomass was controlled by other variables, such as TP and water depth, despite the significantly rising water level (Table S3 and Fig. S3). Submerged macrophytes are generally adapted to increased depth via increasing vertical growth and decrease branch number (Barko and Smart 1981; Maberly 1993). In our study, macrophyte height and biomass was significantly higher in deep sites (Table S3), where the flow velocity was also relatively higher (Fig. S7). However, this is in conflict to the result found by Chambers et al. (1991) that macrophyte biomass decreased with increasing current velocity in the range of 0.01–1 m/s. Our SEMs (Fig. 6c, d) further confirmed the importance of water depth as a controlling factor of macrophytes, yet in the subset deep sites, there was no effect of water depth on macrophyte biomass. This might be due to the dominant species in the river, *B. erecta*, which can only grow to around 100 cm height (Stace 2010). The fact that more nutrient variables were included in the subset deep sites indicates that the strength of bottom–up control increased at deeper sites. Together with the similar differences between the two temperature sub-datasets, these results provided evidence that the influence of nutrients on macrophytes largely depends on hydrologic condition and water temperature (Carr et al. 1997). For example, the negative effect of NO_3–N concentration on macrophyte biomass was found only in the subset deep sites. This phenomenon might be attributed to the amount of nitrogen in sediments assimilated by rooted macrophytes and

Table 1 Predictors of dissolved organic carbon (DOC), biological index (BIX), and fluorescence index (FI) in different datasets

Response variable	Predictor	Estimates	*F* value	df	AIC	*P*(>*F*)	R^2
Temp: median–max (12.64–14.04 °C)							
DOC	Water temperature	*− 0.166*	6.96	1	− 127.14	*0.013*	*0.33*
	Distance	*0.023*	5.97	1	− 128.06	*0.020*	
	Bacterioplankton viability	*0.698*	4.56	1	− 129.43	*0.040*	
BIX	Water temperature	*− 0.112*	5.65	1	− 149.79	*0.023*	0.17
	Distance	− 0.010	2.05	1	− 153.41	0.162	
	Bacterioplankton viability	0.380	2.38	1	− 153.06	0.133	
FI	Water temperature	0.053	2.96	1	− 165.34	0.095	0.14
	Distance	− 0.009	2.17	1	− 166.13	0.149	
Temp: min–median (11.63–12.64 °C)							
DOC	Water temperature	*− 0.747*	30.76	1	− 79.73	*< 0.001*	*0.67*
	Height–depth ratio	*0.370*	6.79	1	− 96.59	*0.015*	
	Bacterioplankton viability	− 0.892	2.94	1	− 100.46	0.099	
	Distance	0.017	2.27	1	− 101.19	0.144	
BIX	Water temperature	*0.288*	43.97	1	− 107.67	*< 0.001*	*0.65*
	Distance	*− 0.015*	5.66	1	− 130.95	*0.025*	
FI	Water temperature	0.138	22.69	1	− 144.16	*< 0.001*	*0.45*
Depth: median–max (67.5–130 cm)							
DOC	Water temperature	*− 0.144*	25.11	1	− 87.28	*< 0.001*	*0.66*
	Distance	*0.020*	5.82	1	− 100.68	*0.026*	
	Bacterioplankton viability	*0.491*	5.87	1	− 100.62	*0.025*	
BIX	Distance	*− 0.023*	4.56	1	− 88.04	*0.044*	*0.27*
	Bacterioplankton viability	− 0.564	4.18	1	− 88.39	0.054	
FI	Water temperature	*0.050*	4.66	1	− 112.52	*0.043*	*0.36*
	Distance	*− 0.015*	5.46	1	− 111.79	*0.029*	
Depth: min–median (30–67.5 cm)							
DOC	Water temperature	*− 0.301*	17.98	1	− 78.50	*< 0.001*	*0.52*
	Distance	*0.032*	5.09	1	− 89.36	*0.032*	
	Height–depth ratio	*0.531*	4.50	1	− 89.94	*0.043*	
	Bacterioplankton viability	0.680	3.34	1	− 91.14	0.078	
BIX	Water temperature	*0.080*	27.74	1	− 157.67	*< 0.001*	*0.47*
FI	Water temperature	*0.063*	2.32	1	− 151.31	*0.006*	*0.35*
	Bacterioplankton viability	− 0.215	8.94	1	− 151.47	0.138	

The Akaike information criterion (AIC) was used to estimate Akaike weights; Italic values represent statistical significance

thus leading to nitrogen diffusing from overlying water to pore water (Ambasht 1991).

In the subset high-temp, where more direct effects of nutrients on bacterioplankton were found, a much stronger bottom–up control was revealed during the growing season with warmer temperature. Additionally, the negative effect of temperature on heterotrophic bacterioplankton abundance indirectly supports the assumption that there was a permanent and relatively high rate of grazing and viral lysis in our subset high-temp because of the proliferation of viruses and flagellates (Ram et al. 2005). Therefore, we could infer that in the subset high-temp with temperatures ranging from 12.6 to 14.0 °C, heterotrophic bacterioplankton in river water could be under a strong top–down and bottom–up control simultaneously, as also found by Jardillier et al. (2004) and Šolić et al. (2009). This is consistent with an early report, which inferred that more direct control was from resource supply and removal by bacteriovores and viruses on bacterial production and abundance during summer, and the extent of control was temperature dependent (Shiah and Ducklow 1994). However, this previous study suggested 20 °C as the critical temperature value under which bacterial abundance and water temperature were positively correlated, which contradicts our results that the threshold value could be also found at lower temperature, as in our case around 14.0 °C. We therefore recommend that future research should be conducted in different aquatic ecosystems to explore the cut-off for the temperature control on bacteria, because the survival strategy of bacteria is known to be flexible (Mukamolova et al. 2003; Panikov 1994). The divergent correlation between bacterioplankton viability and

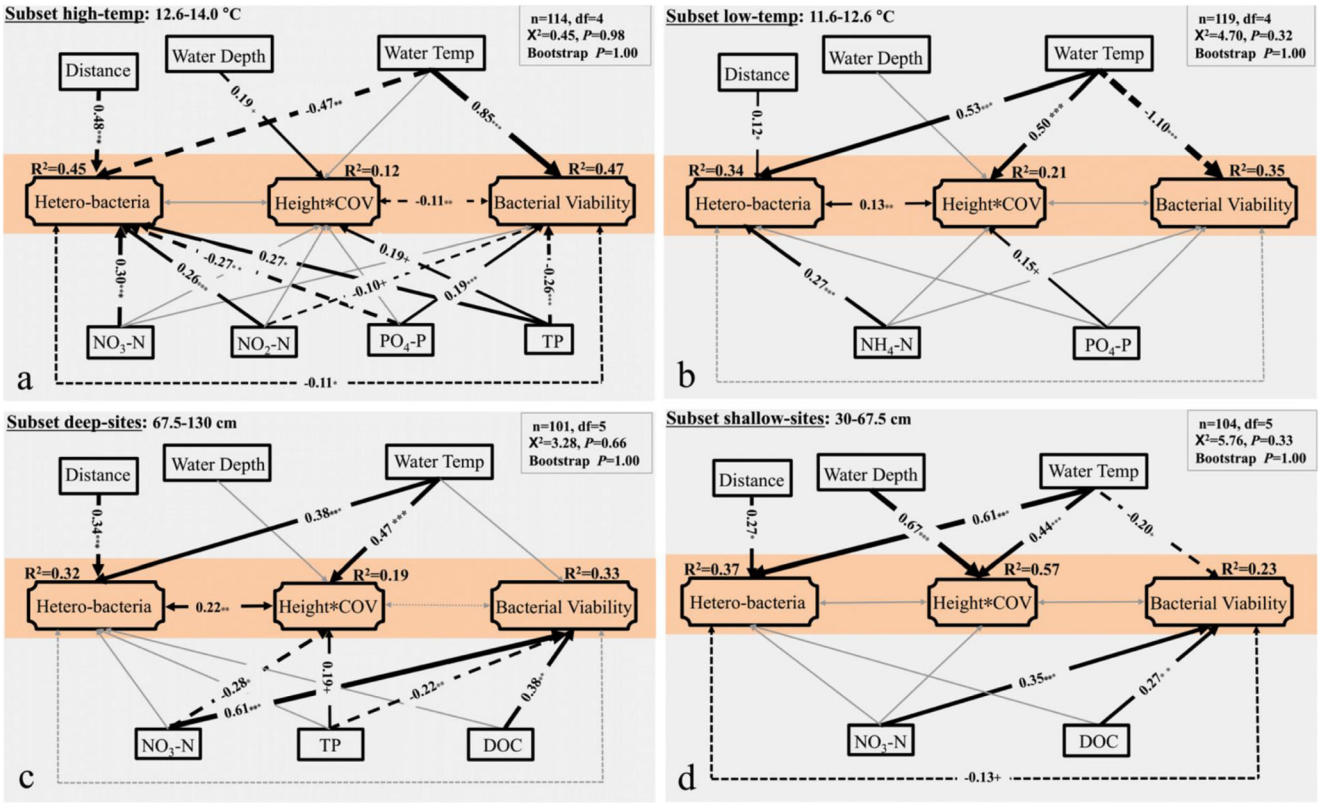

Fig. 6 Structural equation model explaining relationships between bacterioplankton, macrophytes, and abiotic variables for different datasets. Arrows represent direct causal pathways, while double-headed arrows represent paired covariates. **a** Subset high-temperature. **b** Subset low temperature. **c** Subset deep sites. **d** Subset shallow sites. Numbers adjacent to arrows are indicative of the relationship's effect size. The arrow width is proportional to the strength of path coefficients. $^{+}P \leq 0.1$; $^{*}P \leq 0.05$; $^{**}P \leq 0.01$; $^{***}P \leq 0.001$. Continuous and dashed arrows indicate positive and negative relationships, respectively. Black and gray arrows indicate significant and non-significant pathways, respectively. R^2 denotes the proportion of variance explained. df, degrees of freedom; hetero-bacteria: heterotrophic bacterioplankton abundance; Height * COV, plant height × coverage percentage; Temp, temperature; Distance, distance of the transect to the most upstream transect (T10; Fig. 1)

water temperature in the two temperature sub-datasets and the significantly different mean values (Table S3) could be explained by different survival strategies of bacterioplankton communities in response to changing environmental conditions (Del Giorgio and Cole 1998; Roszak and Colwell 1987) and the viability of different species of bacterioplankton (e.g., warm-adapted species and cold-adapted species) could show opposite responses to temperature change at different ranges (Houston 1914; Hall et al. 2008).

The varying behavioral and/or physiological responses of individual organisms to multiple environmental variables can lead to changes in interactions (Ushio et al. 2018). Hence, estimating the interaction strength between organisms is an especially complex task from field measurements (Wootton and Emmerson 2005). However, we are still able to carry out an overall assessment of the direction and strength of interspecific interactions through causality analysis (Iriondo et al. 2003; Jassey et al. 2013). Our findings indicate that the nature (positive/mutualism, commensalism; negative/competition, amensalism; uncoupled interaction) and the corresponding strength of relationships between macrophytes and bacterioplankton are changing with water temperature and water depth. These variations should result from different survival strategies of organisms in response to abiotic conditions (Dimkpa et al. 2009; Yang et al. 2009). By synthesizing 135 studies, Compant et al. (2010) found that positive, neutral, and negative effects of increased temperature on beneficial plant-associated microorganisms were equally common and varied considerably with the study system and the temperature range investigated. We found partial supports for our first hypothesis that interaction in subset low-temp changed from positive between heterotrophic bacterioplankton abundance and macrophyte biomass to negative between bacterioplankton viability and macrophyte biomass, together with the strong negative relationship between bacterioplankton viability and heterotrophic bacterial abundance in subset high-temp. Based on the result that bacterioplankton viability decreased but heterotrophic bacterioplankton abundance and macrophyte biomass increased with rising temperature (Table S3), we speculate that there might be amensalism between macrophytes and bacterioplankton during summer. A previous study has reported that macrophyte could release allelochemicals and thus had

an inhibitory effect on bacterial activity (Juan et al. 2014). The second hypothesis postulating the presence of intensified macrophyte–bacterioplankton interaction in deep sites is supported by the strong positive relationship existing between heterotrophic bacterioplankton abundance and macrophyte biomass in the subset deep sites. Their intensified interaction could be attributed to commensalism, because no significant difference in heterotrophic bacterioplankton abundance and bacterioplankton viability between subset deep sites and shallow sites were found (Table S3). Although we can infer the impact of nutrients on macrophyte–bacterioplankton interactions from the different effects of nutrients on macrophyte growth and bacterioplankton development at different ranges of water temperature and water depth, further research is needed to address the underlying mechanisms. How the competition or mutualism for nutrients (like nitrogen and phosphorus) between plant and soil microorganisms change depending on the environmental context has been intensely debated ever since because of their context-dependent relationships (Kaye and Hart 1997; Richardson et al. 2009).

The role of DOM in macrophyte–bacterioplankton interactions

Despite long-standing interest in DOM dynamics in aquatic ecosystems, up to now there is limited evidence about its role in the macrophyte–bacteria interaction. Generally, in addition to the aquatic (autochthonous) DOM, terrestrial inputs can have a considerable contribution to riverine DOM (Stanley et al. 2012). In our study, the water level fluctuated only at longer time scales (Fig. S3), implying that there was remarkable seasonal variation in rainfall and groundwater discharge, which brings exogenous inputs of organic matters. The FI median values (1.39–1.60) further demonstrate that the terrestrially derived source accounted for a large proportion of the DOM (McKnight et al. 2001). Nevertheless, the temporal median values of BIX ranged from 0.83 to 0.95, suggesting that DOM in the river water still had sizable autochthonous components (Huguet et al. 2009). And bacterioplankton was a source of DOC (Kawasaki and Benner 2006; Thomas 1997), because there is a causal link between bacterioplankton viability and DOC (Table S4).

Contrary to our expectation, we found that macrophyte biomass and heterotrophic bacterioplankton abundance were excluded from all models. Moreover, bacterioplankton viability as the main predictor of DOC was only included in low temperature and shallow depth range datasets, while the height–depth ratio was only included in subset high-temp and deep site. These results imply that macrophytes and bacterioplankton could regulate the quality and quantity of DOM in rivers, but only in concert with other environmental variables (Barrón et al. 2012; Farjalla et al. 2006). On the other hand, our SEMs showed positive effects of DOC on bacterioplankton viability, but only in the two depth sub-datasets, despite significantly different mean values of DOC, BIX, and FI between the two temperature sub-datasets (Table S3). In addition, there was no significant interactive effect between macrophyte biomass and bacterioplankton viability. Hence, we came to the conclusion that DOM may be an important linkage between macrophytes and bacterioplankton in a river, but other environmental factors (like water temperature, water flow and nutrients) are more crucial for controlling the interaction between them. Similar conclusion was inferred between bacteria and algae in stream ecosystems where bacteria were associated with algae. Their interaction depends on light, DOC, nutrient concentrations, and other variables, such as temperature and the taxonomic composition of the assemblage (Rier and Stevenson 2002). Given the impact from abiotic variables, more endeavors exploring the role of DOM in mediating macrophyte–bacterioplankton interactions are needed, together with research on the main impacting factors and underlying mechanisms.

Conclusions

Our findings provide empirical evidences that, similar to what has been found for plants and soil bacteria, in river systems abiotic variables play a critical role in regulating the interaction patterns and strength between macrophytes and bacterioplankton. Our results highlight the dynamic interactions between macrophytes and bacterioplankton in a slow-flowing river, even with relatively low variability in water temperature and depth. This implies that even minor climate- and or management-induced (e.g., dredging and channel modification) changes may alter macrophyte–bacterioplankton interactions and, in consequence, affect ecosystem functioning and the provision of key ecosystem services. Additionally, in our study, DOM could not be verified as main mediator of the interaction between macrophytes and bacterioplankton. However, it should be stressed that targeted experiments are required to consolidate this observation.

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