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Urbanization reduces resource use efficiency of phytoplankton community by altering the environment and decreasing biodiversity

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ABSTRACT

Urbanization often exerts multiple effects on aquatic and terrestrial organisms, including changes in biodiversity, species composition and ecosystem functions. However, the impacts of urbanization on river phytoplankton in subtropical urbanizing watersheds remain largely unknown. Here, we explored the effects of urbanization on phytoplankton community structure (i.e., biomass, community composition and diversity) and function (i.e., resource use efficiency) in a subtropical river at watershed scale in southeast China over 6 years. A total of 318 phytoplankton species belonging into 120 genera and 7 phyla were identified from 108 samples. Bacillariophyta biomass showed an increasing trend with increasing urbanization level. The phytoplankton community shifted from Chlorophyta dominance in rural upstream waters to Bacillariophyta dominance in urbanized downstream waters. Furthermore, phytoplankton diversity and resource use efficiency (RUE = phytoplankton biomass/total phosphorus) were significantly decreased with increasing urbanization level from upstream to downstream. Phytoplankton RUE exhibited a significant positive correlation with species richness, but a negative correlation with phytoplankton evenness. The variation in environmental factors (turbidity, total nitrogen, NH_4^+-N, total phosphorus, PO_4^{3-}-P and percentage urbanized area) was significantly correlated with phytoplankton diversity and RUE. Overall, our results revealed the influence of urbanization on phytoplankton community structure and ecosystem function was due to its altering the environmental conditions. Therefore, human-driven urbanization may play crucial roles in shaping the structure and function of phytoplankton communities in subtropical rivers, and the mechanism of this process can provide important information for freshwater sustainable uses, watershed management and conservation.

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Introduction

Urbanization is the process of anthropogenic transformation of wildlands or agricultural lands to the built environment where people live and work (Seto et al., 2012), thus leading to changes of land use and environment conditions, and altering both aquatic and terrestrial ecosystems within, surrounding, and even at great distances from urban areas (Paul and Meyer, 2001; Grimm et al., 2008; Uchida et al., 2021). These changes were largely attributed to anthropogenic activities and water quality changes induced by altering water supply, drainage and constructing impervious surface (Kaye et al., 2006; Wenger et al., 2009). In riverine ecosystems, many studies have found that changes in community assemblage, species diversity, and biotic integrity among the different trophic levels (diatoms, invertebrates, and fishes) were severely influenced by urbanization-related activities (Urban et al., 2006; Wenger et al., 2009; Li et al., 2020). Phytoplankton (algae as primary producers) are a key component of the aquatic food webs (Reynolds, 2006), and play a crucial role in energy flow and nutrient cycling in aquatic ecosystems (Cardinale et al., 2002). Phytoplankton biomass, diversity, and community composition can reflect the states of water quality and ecology due to their sensitive response to environmental conditions (Padisák et al., 2006; Yang et al., 2012; Zhang et al., 2021). Previous studies about the effects of urbanization on algae mainly focused on rivers and lakes in Europe and the United States, especially benthic diatoms (Chessman et al., 1999; Duong et al., 2012; Saros and Anderson, 2015).

Urbanization-driven increasing of surface runoff and decreasing infiltration of precipitation (Paul and Meyer, 2001; Grimm et al., 2008) can affect the structure and function of aquatic ecosystems (Vitousek et al., 1997; Yang et al., 2012; Uchida et al., 2021). Recently, correlation between land use types change and diversity and community composition of freshwater phytoplankton have been reported (Katsiapi et al., 2012; Isabwe et al., 2018). The anthropogenic activities are one of the important drivers affecting the phytoplankton diversity because they can change the supply of available nutrients, increase water temperature, decrease light availability, control physical transport processes, and alter hydrodynamic conditions (Reynolds, 2006; Padisák et al., 2006; Yang et al., 2012; Sailley et al., 2015). Over the past three decades, a rapid and large-scale urbanization has been experienced in southeast China on an unprecedented scale, and a vast rural-to-urban migration of hundreds of millions of people has expanded existing cities (Zhu et al., 2011). This expansion increased water/soil pollutions and habitat fragmentation; with a substantial influence on aquatic physical structure and ecosystems, including direct or indirect loss of biodiversity, change in communities and altering ecosystem functioning (Zhu et al., 2011; García et al., 2013; Best, 2019). To date, however, the way in which urbanization-driven land use change alter phytoplankton community structure and ecosystem functioning in river at watershed scale is poorly understood, especially in subtropical regions.

Resource use efficiency (RUE), is an ecological concept that quantifies ecosystem function by measuring the proportion of supplied resource and converted biomass by organisms (Ptacnik et al., 2008; Hodapp et al., 2019). Phytoplankton diversity might be one of the best predictors for phytoplankton RUE because they have ability to grow within limiting resources (Ptacnik et al., 2008; Striebel et al., 2009), higher phytoplankton diversity (species richness) can result in a more efficient use of the available resources, and produce greater amounts of biomass than the same system at lower levels of diversity (Cardinale et al., 2002). Several studies have shown that RUE of phytoplankton communities increased with increasing taxonomic richness (Ptacnik et al., 2008) and significantly decreased with phytoplankton evenness in lakes and reservoirs (Filstrup et al., 2014, 2019). Further, the positive effects of local biodiversity on ecosystem functioning may arise through higher niche partitioning or niche occupancy because it can enhance RUE in ecosystems by niche partitioning (Loreau et al., 2001; Cardinale, 2011). Ecosystems are likely to sustain species that are highly productive in local environmental conditions; and consequently, increased biodiversity may promote ecosystem functioning through complementary effects (Loreau et al., 2001; Cardinale, 2011; Hodapp et al., 2016). Although the positive biodiversity-ecosystem functioning relationship has been observed in different types of aquatic ecosystem (Loreau et al., 2001; Filstrup et al., 2014, 2019; Yang et al., 2021), but how this relationship is affected in riverine ecosystems by urbanization at watershed scale is largely unknown.

Several studies indicated that phytoplankton RUE will directly be influenced by human-driven environmental change (Steudel et al., 2012; Hodapp et al., 2016). For example, Steudel et al. (2012) found that the positive effects of biodiversity on ecosystem functioning decreased with increasing environmental stress intensity. Furthermore, increased disturbance frequency can result in higher RUE of phytoplankton in subtropical reservoirs (Yang et al., 2021). A recent study indicated that the higher richness and abundance of antibiotic resistance genes in the downstream waters were closely associated with urbanization level along the Houxi River, subtropical China (Peng et al., 2020). However, the effect of urbanization-driven environmental change (especially land use) on phytoplankton RUE in subtropical rivers at watershed scale or along rural-urban gradient remains unknown. In this study, we used phytoplankton RUE as a measure of ecosystem functioning in an urbanizing subtropical river (Houxi River), Xiamen City, Southeast China. We first hypothesized that urbanization may decrease the phytoplankton diversity and increase phytoplankton biomass along the river. Second, we expected that urbanization may significantly alter phytoplankton community composition along the rural-urban gradient by altering the environmental conditions. Third, urbanization may significantly reduce the phytoplankton RUE from rural upstream to urban downstream waters.

1. Materials and methods

1.1. *Study area*

The Houxi River (about 25 km long) is located in Xiamen City, Fujian Province, southeast China (Fig. 1), and drains an area of approximately 205 km^2. This area has a subtropical humid

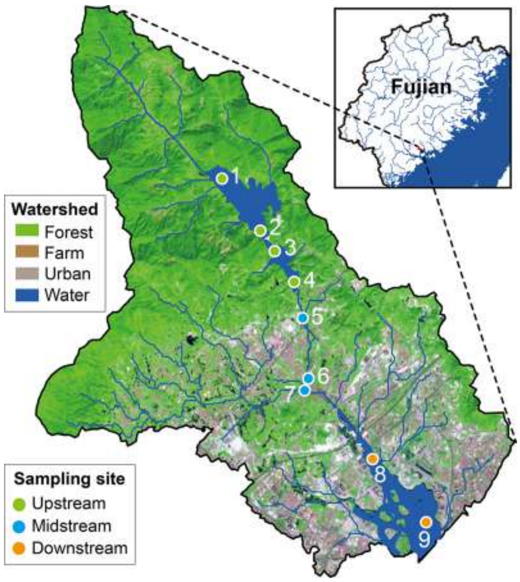

Fig. 1 – The map showing Houxi River watershed and nine sampling sites in Xiamen City of Fujian Province, southeast China. Four main categories of land use are indicated. Sampling sites 1, 2, 3, 4, 8, and 9 are lentic water (standing-water) habitats, while sampling sites 5, 6, 7 in midstream are lotic water (running-water) habitats.

monsoon climate with an annual mean temperature of 20.7°C and a mean annual precipitation of 1335.8 mm (Zhu et al., 2019). The Houxi River watershed has a rural-urban gradient from upstream to downstream (Peng et al., 2020). In this study, the Houxi River was divided into three parts according to the urbanized level: (1) upstream (non-urban region) covers drinking water reservoirs (Shidou and Bantou reservoirs) for > 100,000 people; (2) midstream (urbanizing region) is a stream, which flows through villages and small towns; (3) downstream (urbanized region) is a landscape reservoir (Xinglinwan Reservoir) with both recreational and aesthetic importance for Xiamen City (Peng et al., 2020). Four sampling sites of upstream section (Sites 1–4) are located in two reservoirs (Shidou and Bantou reservoirs), watershed area of these reservoirs is about 67.3 km^2. Three sampling sites of the midstream are located in urbanizing region (Sites 5–7). The remaining two sampling sites are located in the urbanized region (Sites 8 and 9). The whole river system, especially midstream and downstream regions, is strongly impacted by human activities including wastewater discharge (Fig. 1).

1.2. *Sampling and environmental variables*

Field sampling took place in January and July at nine stations along the Houxi River from 2013 to 2018 (Fig. 1). In total, 108 samples were collected and the sampling events were established based on the annual rainfall patterns which cause low- and high-water flows in cold and warm months, respectively. We measured a total of 14 environmental variables (**Appendix A Table S1**) in this study.

Water temperature, pH, dissolved oxygen, turbidity, electrical conductivity, salinity, and oxidation-reduction potential were measured *in situ* using a Hydrolab DS5 water quality analyzer (Hach Company, Loveland, CO, USA). Total nitrogen and total phosphorus were measured spectrophotometrically after digestion. The concentrations of ammonium nitrogen (NH_4^+-N), nitrate nitrogen (NO_3^--N), nitrite nitrogen (NO_2^--N), and phosphate phosphorus (PO_4^{3-}-P) were measured according to standard methods as described in our previous study (Yang et al., 2017). We measured water flow velocity of surface water in the river using a SonTek FlowTracker (Handheld-ADV® YSI, San Diego, CA, USA).

Phytoplankton samples (n = 108, water volume = 2.5 L) were taken from surface waters at nine stations along the Houxi River. Samples were immediately fixed with 1.5% acidic Lugol's solution and kept in the dark conditions at a room temperature until further processing (Lv et al., 2014).

1.3. *Land use data collection*

The data of land use changes for Houxi River watershed between 2013 and 2018 were extracted from Landsat 8 images which were downloaded from the data sharing infrastructure of the earth system science in China (https://www.geodata.cn/). The watershed boundaries and the river system were delineated using digital elevation model in ArcGIS version 10.4 (ESRI, Redlands, CA, USA). Four main categories of land use were used (**Appendix A Table S1**): forest areas (forest and grassland); agricultural areas (dry land and paddy fields) although some small-scale agricultural activities also take place within the forest; percentage urbanized areas (urban areas, rural settlements, and roads); and water areas. The percentage of each land use category was computed by ArcGIS version 10.4.

1.4. *Phytoplankton analysis*

Phytoplankton were identified and counted in chambers using an inverted microscope (Motic AE31, Xiamen, China) under 400 × magnification (Lv et al., 2014). Cells, colonies, and filaments were identified to the lowest possible taxonomic level based on taxonomic illustrations and descriptions of freshwater algae by Hu and Wei (2006). More than 500 specimens were counted for each sample (Lv et al., 2014; Yang et al., 2017). Biovolume was measured and estimated based on standard geometric formulae (Hillebrand et al., 1999) and abundance-data were converted to fresh weight based on measurements of species-specific cell volumes, using a specific weight factor of 1 mg/mm^3 (Wetzel and Likens, 2000).

1.5. *Phytoplankton resource use efficiency*

The phytoplankton functioning was estimated from resource use efficiency (RUE) in this study. Total phosphorus (TP) was used as the basis for phytoplankton RUE given the importance of phosphorus limitation in most freshwater ecosystems (Ptacnik et al., 2008; Sterner, 2008). It is noteworthy that RUE is not equivalent to the rate of biomass production since it relies on an estimate of standing stock, and we quantified phytoplankton RUE by the ratio of phytoplankton biomass to TP following previous study (Ptacnik et al., 2008).

1.6. Statistical analyses

The Shapiro-Wilk normality test showed a non-normal distribution of phytoplankton biomass and environmental variables. Thus, environmental variables, with an exception of pH, were log (x+1)-transformed and normalized; while biotic data were square root-transformed. We separately analyzed upstream (Shidou and Bantou reservoirs); midstream (river); downstream (Xinglinwan Reservoir) data sets in order to assess the variations in phytoplankton biomass and diversity along the Houxi River. Four biodiversity indices, namely species richness, Shannon-Wiener diversity, Simpson diversity and Pielou's evenness, were investigated. The Mann-Whitney U test was performed to identify significant differences between and within groups of samples. The effect of phytoplankton diversity on RUE and biomass was determined by linear regression analysis.

The non-metric multidimensional scaling (NMDS) based on Bray-Curtis similarity of phytoplankton biomass was used to investigate the variations in phytoplankton community. The analysis of similarities (ANOSIM) test was employed to assess the significant differences in community composition between the three habitats (upstream, midstream, and downstream), six years (2013, 2014, 2015, 2016, 2017, 2018), and two seasons (dry and wet), respectively. The Global R value indicates the degree of separation among groups, whereas negative value indicates no separation. In order to identify phytoplankton taxa that contributed to the community dissimilarity, we used the similarity percentage (SIMPER) analysis. Further, Mantel test based on Spearman rank correlation was used to determine the relationships between community structure (biomass and diversity) or RUE and environmental variables. We used a heatmap to show the relationships among environmental variables and the analyses were performed by using the *vegan, corrplot* and *dplyr* packages in R version 3.6.0 (R Core Team, 2020).

The longest gradient length was < 4 standard deviations in detrended correspondence analysis, thereby suggesting that redundancy analysis was the appropriate ordination technique to examine the relationship between phytoplankton community (species biomass data) and environmental variables. Environmental factors with a variance inflation factor (VIF) < 10 were selected and phytoplankton community composition data were subjected to Hellinger-transformation (Legendre and Gallagher, 2001). Redundancy analysis was performed by using the package *vegan* in R version 3.6.0 (R Core Team, 2020). To acquire the independent contribution of each environmental variable to the total variability of phytoplankton communities, we also performed Hierarchical Partitioning (HP) analysis based on the package *rdacca.hp* in R version 3.6.0 (Lai and Peres-Neto, 2020). We did not consider the significant testing for independent contributions in HP analysis because predictor (or groups of predictors) relative importance is usually considered as an exploratory framework for interpreting regression rather than an inferential tool. Finally, we used partial least squares path modeling (PLS-PM) to show the linkage between phytoplankton community structure (e.g., biomass and diversity), functioning (e.g., RUE), environment variables and urbanization level (represented by the percentage urbanized area). The non-significant paths were removed. The goodness-of-fits (GoF) was computed using partial least squares path modeling in the package *plspm* in R version 3.6.0 (R Core Team, 2020).

2. Results

2.1. Environmental variables along the urbanization level

Environmental variables in surface waters of Houxi River showed a significant difference (P < 0.05) between the three urbanization levels (i.e., upstream, midstream, and downstream) over six years, except for water temperature and oxidation-reduction potential (**Appendix A Table S1** and **Appendix A Fig. S1**). Dissolved oxygen had the highest value in upstream waters; electrical conductivity and salinity exhibited a higher value in downstream waters; while turbidity and nutrients (TN, NH_4^+-N, NO_3^--N, NO_2^--N, TP, and PO_4^{3-}-P) showed a higher concentration in midstream waters (**Appendix A Table S1**). The forest land area occupied the largest proportion of upstream watershed (90.10% ± 0.00%), whereas higher percentage urbanized area (built area) was found in urbanizing midstream (47.13% ± 0.01%) and downstream areas (58.89% ± 0.01%), respectively (Fig. 1 and **Appendix A Table S1**). Clearly, relatively higher levels of nutrients (mainly nitrogen and phosphorus) in midstream and downstream waters were associated with strong anthropogenic activities and higher percentage urbanized area in the Houxi River watershed.

2.2. Phytoplankton diversity, biomass, community composition, and RUE along the urbanization level

A total of 318 phytoplankton species belonging into 120 genera and 7 phyla were identified in Houxi River. Species richness, Shannon-Wiener diversity, Simpson diversity and Pielou's evenness were significantly lower in the downstream waters than upstream waters (Fig. 2**a**), indicating that phytoplankton diversity significantly decreased with increasing urbanization level. Bacillariophyta, Chlorophyta, Cyanobacteria were the dominant phyla, while Chrysophyta, Cryptophyta, Euglenophyta, and Pyrrophyta accounted for a smaller amount of the biomass (Fig. 2**b**). The phytoplankton biomass exhibited a spatial and temporal variation (**Appendix A Fig. S1d**). The mean phytoplankton biomass in upstream and downstream waters were very similar (14.33 ± 2.86 mg/L in upstream and 14.40 ± 4.10 mg/L in downstream, respectively), but it was about 50% lower in the midstream waters (6.72 ± 0.89 mg/L). Interestingly, Bacillariophyta biomass increased gradually with increasing urbanization level in the Houxi River, while Chlorophyta showed an opposite trend (Fig. 2**b**).

Our NMDS and ANOSIM analyses revealed a significant difference in phytoplankton community compositions between the upstream, midstream, and downstream waters (Global R = 0.653, P < 0.01; Fig. 3**a**), while interannual variation was relatively weak (Global R = 0.238, P < 0.01) and no significant variation was found between dry and wet seasons (Table 1). In terms of the contribution of phytoplankton taxa (phylum and species) to community dissimilarity between upstream, midstream, and downstream waters (Fig. 3**b** and **c; Appendix**

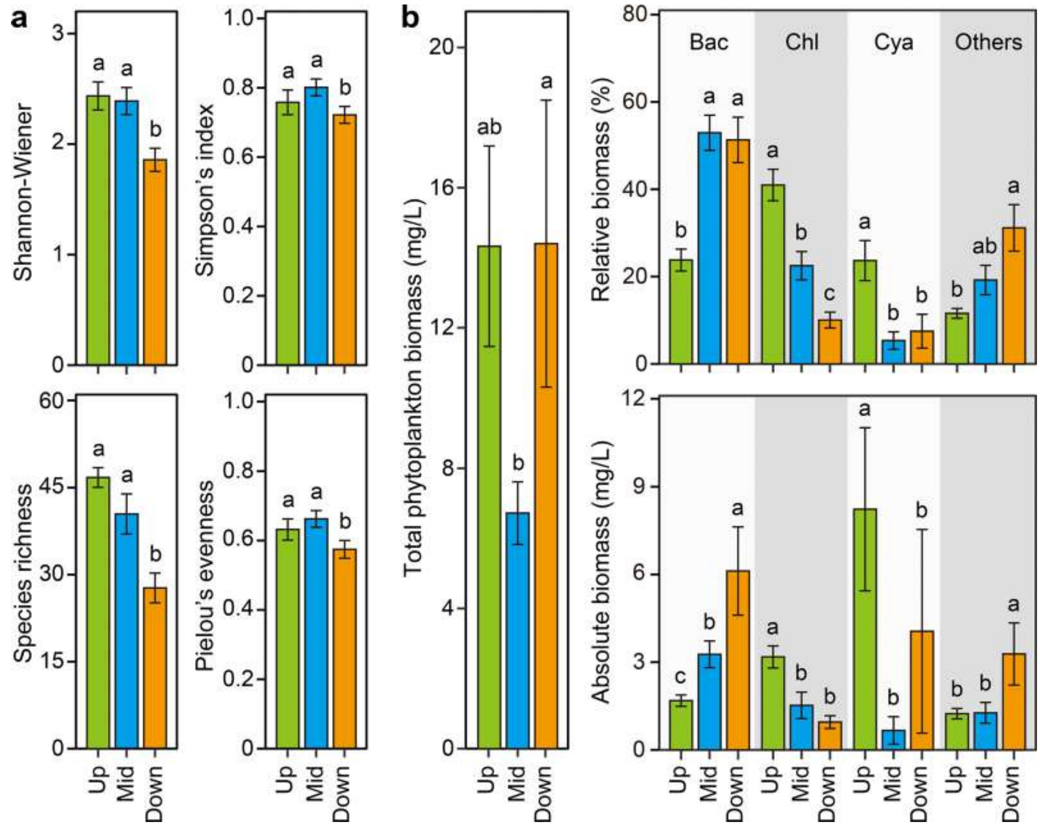

Fig. 2 – Phytoplankton diversity (a) and biomass (b) in Houxi River from upstream to downstream waters. Error bars represent standard error. The different letters above the bar indicate significant difference, the statistical analysis is Mann-Whitney *U* test at *P* < 0.05. Up, upstream; Mid, midstream; Down, downstream. Bac, Bacillariophyta; Chl, Chlorophyta; Cya, Cyanobacteria; Others, other phytoplankton groups including Chrysophyta, Cryptophyta, Euglenophyta, and Pyrrophyta.

Table 1 – Analysis of similarities (ANOSIM) showing changes in phytoplankton community along Houxi River continuum, years and seasons.

Group	Global R	*P*-value
Habitat		
Upstream *vs.* Midstream	0.709	< 0.01
Upstream *vs.* Downstream	0.872	< 0.01
Midstream *vs.* Downstream	0.114	< 0.01
Upstream *vs.* Midstream *vs.* Downstream	0.653	< 0.01
Year		
2013 *vs.* 2014 *vs.* 2015 *vs.* 2016 *vs.* 2017 *vs.* 2018	0.238	< 0.01
Season		
Dry *vs.* Wet	0.007	0.22

Higher *R*-value indicates stronger compositional difference between groups.

A Table S2). Bacillariophyta, Chlorophyta and Cyanobacteria contributed 82.17% of the total community variation at phylum level; while *Cyclotella meneghiniana* (Bacillariophyta) and *Raphidiopsis raciborskii* (Cyanobacteria) contributed 14.97% and 7.49% dissimilarity at species level, respectively. The RUE of total phytoplankton and three dominated phyla (Bacillariophyta, Chlorophyta and Cyanobacteria) in upstream waters was significantly higher than that of midstream and downstream waters (Fig. 4a and **Appendix A Fig. S2a**).

2.3. *Relationships among phytoplankton biomass, diversity, and RUE*

Phytoplankton biomass exhibited a significant negative correlation with phytoplankton evenness at local (upstream, midstream, and downstream) and watershed scales, whereas no significant correlation was found between phytoplankton biomass and species richness ($P > 0.05$) at a watershed scale (Fig. 4b). However, phytoplankton species richness was significantly and positively correlated with phytoplankton biomass in urbanized downstream waters (Fig. 4b).

The phytoplankton RUE exhibited a significant positive correlation with species richness ($r = 0.32$, $P < 0.01$), while it showed a significant and negative correlation with Pielou' evenness ($r = -0.26$, $P < 0.01$) at watershed scale (Fig. 4c). Similarly, the RUE showed a positive correlation with species richness ($r = 0.52$, $P < 0.01$) and a negative correlation with Pielou's evenness ($r = -0.66$, $P < 0.01$) in urbanized downstream waters, respectively (Fig. 4c). In addition, phytoplankton RUE decreased with increasing phytoplankton evenness in the upstream waters. We did not find any significant relationship

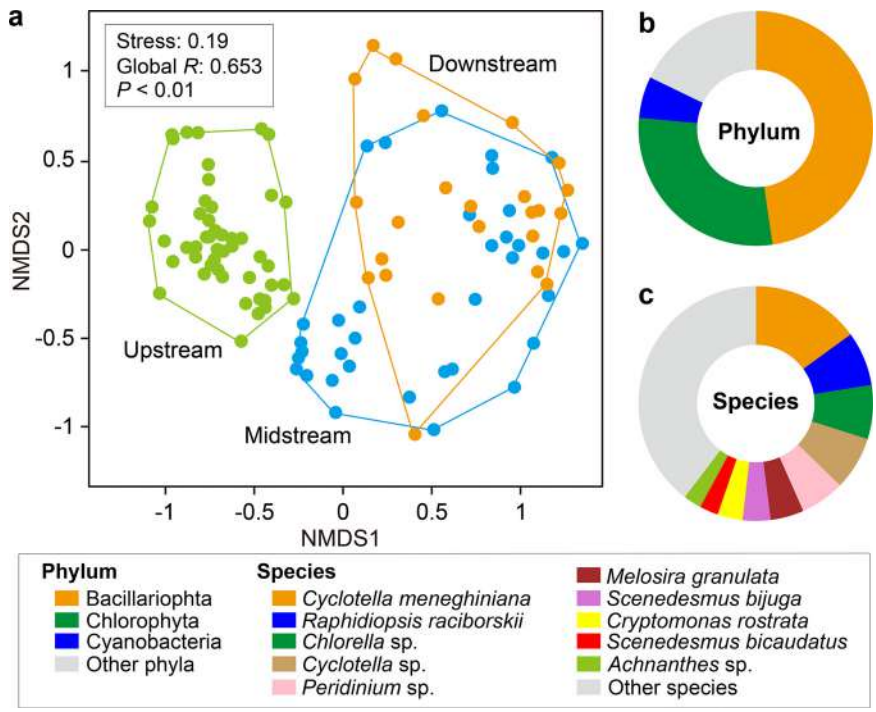

Fig. 3 – Phytoplankton community composition in Houxi River. (a) non-metric multidimensional scaling (NMDS) ordination showing phytoplankton community across the river (non-urban upstream, urbanizing midstream, and urbanized downstream). The contribution in the community dissimilarity at (b) phylum and (c) species levels, respectively. Other phyla including Chrysophyta, Cryptophyta, Euglenophyta, and Pyrrophyta.

between phytoplankton RUE and species richness or Pielou's evenness in urbanizing midstream waters.

2.4. Relationship between phytoplankton communities and environmental variables

The first two axes of redundancy analysis (RDA) showed that land use, nutrients and physicochemical variables only explained 15.5% of overall variation of phytoplankton community at whole watershed (**Appendix A Fig. S3a**). Further, the hierarchical partitioning (HP) analysis indicated that the independent contribution of each of 13 environmental variables explained 24.9% of the total variation in phytoplankton community, with percentage urbanized area explaining the highest variation in phytoplankton community (**Appendix A Fig. S3b**).

Phytoplankton species richness and RUE exhibited more significant responses to 13 environmental variables than phytoplankton biomass and evenness (Fig. 5). Further, percentage urbanized area (i.e., urbanization level), turbidity, and nutrients (including TN, NH_4^+-N, TP, and PO_4^{3-}-P) exhibited a stronger correlation with phytoplankton RUE than species richness. In addition, phytoplankton RUE was strongly negatively related to the water flow velocity (r = -0.56, $P < 0.001$) in Houxi River ecosystem (**Appendix A Table S3**). The water flow velocity also exhibited a significant negative relationship with Chlorophyta biomass (r = -0.29, P = 0.002) and Cyanobacteria biomass (r = -0.30, P = 0.002), while it had a marginally significant correlation with total phytoplankton biomass (r = -0.18, P = 0.064) and Bacillariophyta biomass (r = 0.19, P = 0.055).

Our partial least squares-path model explained 89% of the variation of phytoplankton RUE through urbanization, environmental variables, and phytoplankton community structure (Fig. 6). Urbanization-driven land use showed a weak and negative effect on phytoplankton species richness, while environmental variables had a significant negative effect on evenness. Furthermore, both urbanization and environment had a direct negative effect on phytoplankton RUE. More importantly, urbanization also exhibited an indirect and negative effects on RUE through altering environmental variables and decreasing species richness.

3. Discussion

Urbanization-induced land use change can result in the conversion of natural surfaces to impervious surfaces in terrestrial ecosystem and alter habitat physical structure and hydrological properties in aquatic ecosystems (Paul and Meyer, 2001; Grimm et al., 2008). These changes can considerably affect the water environment conditions by increasing nutrient loads and no-point pollutants from domestic sewage, industries, and agriculture (Kaye et al., 2006; Peng et al., 2020). Phytoplankton are important component of river-reservoir ecosystems and sensitive to environmental change (Yang et al., 2021). Understanding the response of river phytoplankton community structure and functioning to urbanization is critical to human well-being and sustainable management.

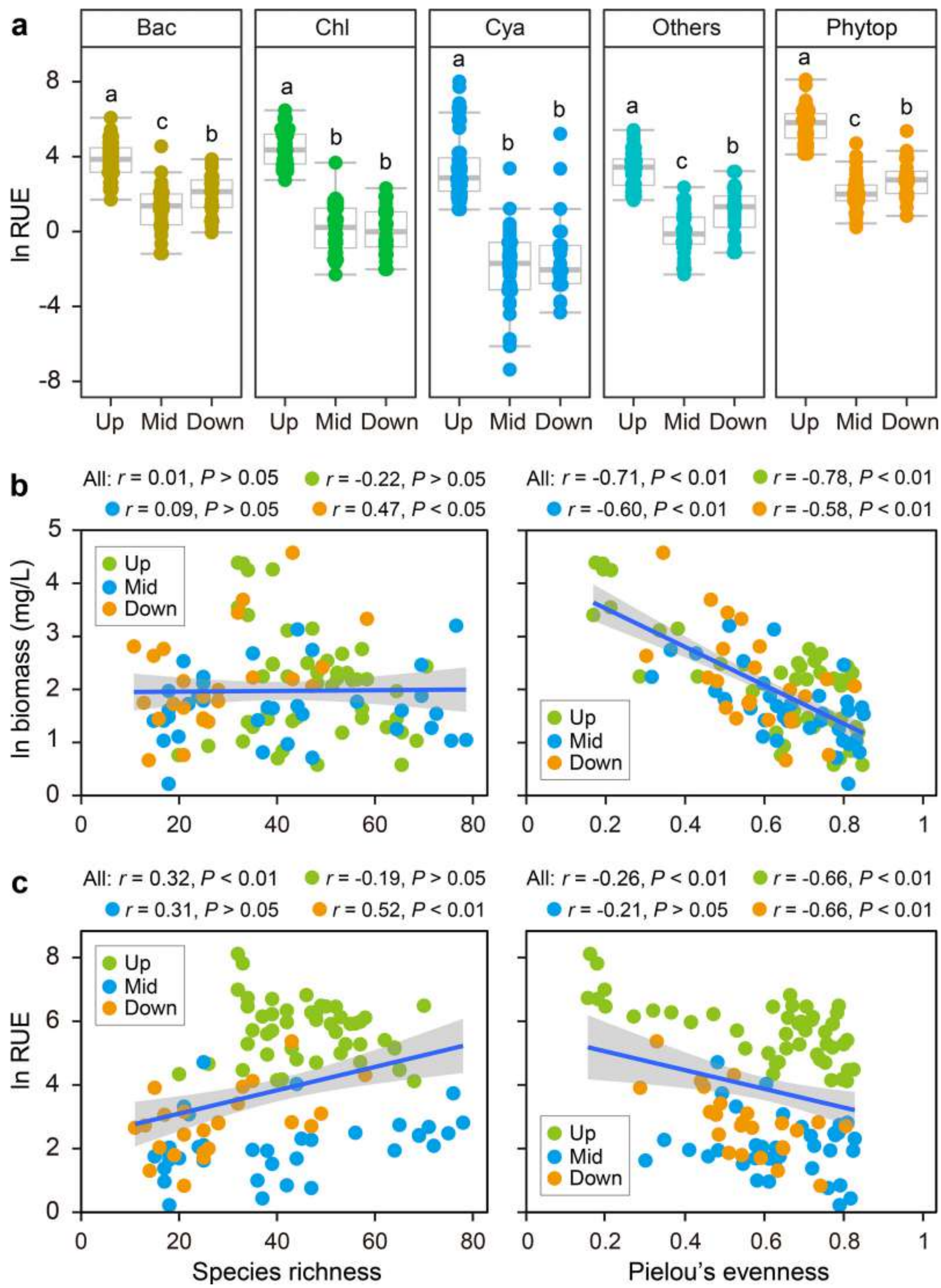

Fig. 4 – Phytoplankton resource use efficiency along Houxi River from rural upstream to urban downstream (a), the relationships between phytoplankton diversity and biomass (b), and relationships between phytoplankton diversity and RUE (c). Phytop, total phytoplankton; RUE, resource use efficiency. The different letters a, b and c indicate significant differences in Fig. 4a, and the statistical analysis is Mann-Whitney *U* test at $P < 0.05$. Pearson correlation coefficients (r) are shown in Figs. 4b and 4c. All indicates all samples; three different colors indicate upstream, midstream, and downstream samples, respectively.

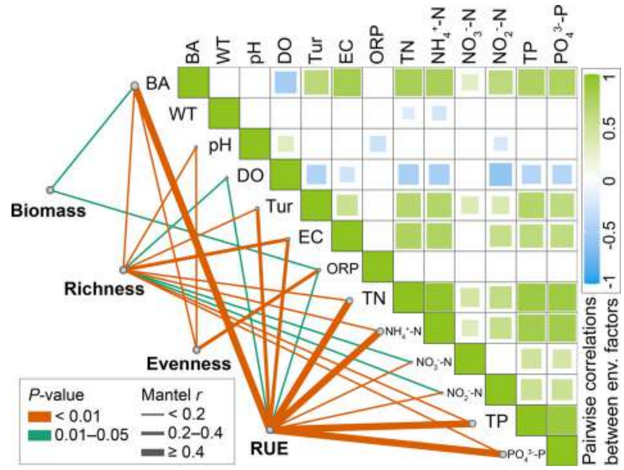

Fig. 5 – Relationships between environmental variables and phytoplankton community structure and function. Pairwise comparisons of environmental factors were displayed with a color gradient denoting Spearman's correlation coefficient at the upper-right. Phytoplankton community was related to each environmental factor by Mantel test at the lower-left. BA, built area percentage; WT, water temperature; DO, dissolved oxygen; Tur, turbidity; EC, electrical conductivity; ORP, oxidation-reduction potential; TN, total nitrogen; TP, total phosphorus; Biomass, phytoplankton biomass; Richness, species richness; Evenness, Pielou's evenness. Only significant Spearman's correlations among environmental variables are shown ($P < 0.05$).

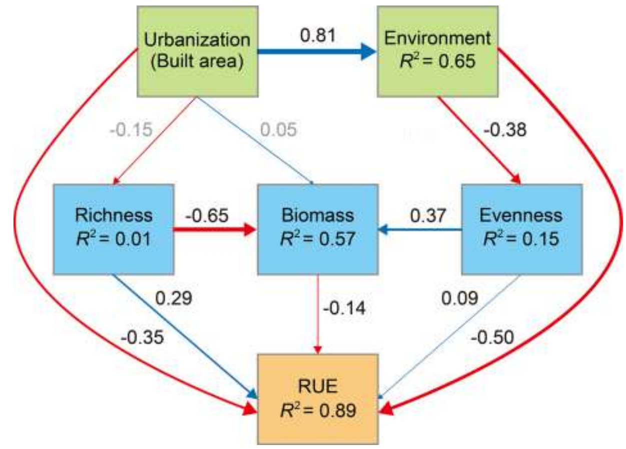

Fig. 6 – Partial least squares path models showing the relationships between urbanization, environmental variables, phytoplankton community structure (i.e., biomass and diversity), and phytoplankton function (i.e., resource use efficiency). Black coefficients indicate a significant relationship ($P < 0.05$), while gray coefficients indicate a non-significant relationship ($P > 0.05$). The goodness of fit index (GoF = 0.62) was used to estimate the prediction performance of models. Blue and red lines indicate positive and negative effects, respectively. Numbers near each arrow indicate partial correlation coefficients associated with each causal relationship. The partial correlation coefficients less than 0.05 were not shown for simplicity. Urbanization represented by built area percentage. Environment included turbidity, TN, NH_4^+-N, TP, and PO_4^{3-}-P.

3.1. *Urbanization reduces phytoplankton diversity*

The significant negative relationship between species richness and percentage urbanized area indicated that urbanization as the important driver of decline in phytoplankton species richness. Previous studies have demonstrated that urbanization can reduce species richness and biotic integrity of invertebrates and fish communities in streams and rivers in the United States (Paul and Meyer, 2001; Mckinney, 2008), however little is known on the effects of human activities on river phytoplankton diversity and function with an exception of diatoms, especially in subtropical regions. The comparison of phytoplankton biomass, composition, and diversity between upstream, midstream, and downstream waters in Houxi River provided additional insight into the effect of urbanization on the structure and function of phytoplankton communities in a subtropical urbanizing watershed. In our study, phytoplankton diversity especially species richness was significantly declined in the urbanized downstream in compare with rural upstream and urbanizing midstream waters along the river (Fig. 2a), indicating that increasing urbanization level can significantly reduce phytoplankton diversity. A recent environmental DNA-based study in the Shaying River, the tributary of the Huai River in temperate China, indicated human land use can explain the decline of the taxonomic and functional diversity of protozoa, fungi, and algae communities (Li et al., 2020). This result is consistent with our finding because phytoplankton species richness decreased with increasing urbanization level in Houxi River. Study on diatom (Bacillariophyta) in Europe and the United States by Chessman et al. (1999) suggested that human activity in a watershed generally increased genus richness through enrichment with alkaline salts. Similarly, the significant negative correlation between percentage urbanized area and phytoplankton species richness (Fig. 5), indicates that phytoplankton communities are susceptible to urbanization-driven disturbances. In our study, a possible reason for lower species richness in the downstream region is strong in environmental stress conditions, caused by pollution from human activities. The effect of pollution on phytoplankton community structure can be translated into environmental filtering (Heino et al., 2017). Therefore, the low species richness in downstream waters may be caused by the combined human activities of sewage discharge, urban runoff, and other anthropogenic contaminants. These results indicate that decline in phytoplankton diversity was closely related to urbanization such as increasing impervious surface cover, housing density and urban population pressure.

Our results also showed a major shift in phytoplankton community composition along Houxi River, from Chlorophyta dominance in the rural upstream to Bacillariophyta dominance in the urbanized downstream (Fig. 2b). This shift in community composition could be attributed to the variation in the environmental condition influenced by local or regional land use (Yang et al., 2017; Isabwe et al., 2018). For instance, water quality alternation by increasing nitrogen, phosphorus, and turbidity may promote a selection by single species or a few dominant species that can survive within this stressful environment. Increased turbidity in water can result in a decline in light for phytoplankton growth (Shi et al., 2017), and increasing nutrients enrichment in water can alter community composition in phytoplankton, macroinvertebrates, and fish (Chessman et al., 1999; Weijters et al., 2009; Zhang et al., 2021). When suspended particles and colloidal matter from surface runoff were added to the waterbody the light intensity decreased dramatically, leading to light becoming one of the limiting factors for phytoplankton growth and photosynthesis in urban waters, although the downstream waters had higher nutrient concentrations. Our results indicated the biggest variation in phytoplankton community composition was explained by the percentage urbanized area (**Appendix A Fig. S3b**). This might be attributed to the fact that phytoplankton community composition was influenced by urbanization-driven change in land use types (Katsiapi et al., 2012). We also found that phytoplankton biomass was significantly lower in urbanizing midstream than that of rural upstream and urbanized downstream waters. Normally, Chlorophyta and Cyanobacteria can be impacted by water flow in urbanizing midstream waters because hydrological factors (e.g., flow velocity, discharge, and water retention time) are important to influence phytoplankton biomass and community composition (Tornés et al., 2014; Descy et al., 2017).

In addition, we did find single species bloom in the upstream waters (e.g., cyanobacterial bloom in upstream in 2015), and the bloom event was characterized by lower species diversity and higher biomass. The dominant Bacillariophyta species (especially *Cyclotella meneghiniana*) in urbanized downstream is a common indicator species of sewage-polluted waters (Duong et al., 2012; Doi et al., 2013), thus indicating the existing pollution status in the urbanized downstream in the Houxi River. In our study, only 24.9% of the total variation of phytoplankton community was explained by environmental variables. This might be due to lack of unmeasured variables such as heavy metals and micropollutants which are important in shaping the phytoplankton community. Another possible reason might be due to the microbial interactions that can contribute to changing phytoplankton diversity and community composition (Xue et al, 2018).

3.2. *Urbanization reduces phytoplankton RUE via reducing diversity*

Phytoplankton RUE exhibited a significant positive correlation with species richness (**Fig. 4c**), indicating that species richness acted as a predictor of RUE in phytoplankton community. This relationship supported the coupling of biodiversity and productivity of phytoplankton communities in freshwater lakes and marine systems (Ptacnik et al., 2008; Striebel et al., 2009). Along the rural to urban gradient, we observed that increasing urbanization level could significantly reduce phytoplankton species richness and RUE (**Figs. 2a** and **4a; Appendix A Fig. S2a**). These results were consistent with several theoretical and empirical studies (Hooper et al., 2005; Cardinale, 2011). Ptacnik et al. (2008) reported that increasing genus-level phytoplankton diversity can result in higher RUE. Likewise, a meta-analysis by Cardinale et al. (2006) showed that the effect of decreasing species richness led to biomass (or abundance) decrease of the focal trophic groups, leading to less complete depletion of resources used by that group. Surprisingly, we found that the positive relationship between RUE and species richness became more pronounced in community with lower species richness, indicating the effect of species richness on RUE was stronger for less diverse communities. In addition, phytoplankton RUE exhibited a significant negative correlation with phytoplankton evenness as in previous studies in lakes and reservoirs (Filstrup et al., 2019; Yang et al., 2021). However, inconsistent result was reported in Lake Nansihu, north China (Tian et al., 2017), where species evenness exhibited a significant positive correlation with RUE. This inconsistency may be attributed to sampling different waterbodies under multiple disturbance events (Yang et al., 2021). It is noteworthy that such inconsistent results of the negative correlation between species evenness and RUE were mainly observed in highly eutrophic lakes or reservoirs (Hodapp et al., 2015; Filstrup et al., 2019; Yang et al., 2021).

Previous study indicated that greater numbers of coexisting species with different and complementary niches are predicted to more thoroughly utilize limiting resources than communities with fewer species (Tilman et al., 1997). Cardinale (2011) found phytoplankton communities with more species take greater advantage of the niche opportunities (i.e., niche partitioning) in an environment, and this could allow diverse ecosystems to capture a greater proportion of biologically available resources such as nitrogen and phosphorus. In addition, decline in species richness can result in less occupancy of trophic niches and thus less overall RUE, probably due to the different phytoplankton species having different affinities to a certain form of nutrients (Guedes et al., 2019). Therefore, urbanization-induced species loss can reduce RUE via weakening niche complementary or partitioning of phytoplankton in riverine ecosystems.

Furthermore, a negative relationship between phytoplankton evenness and RUE (**Fig. 4c**) is likely due to the different dominant species of phytoplankton communities (e.g., *Raphidiopsis raciborskii* in rural upstream waters and *Cyclotella meneghiniana* in urbanized downstream waters, respectively). On one hand, *R. raciborskii* is a common bloom-forming Cyanobacteria species with high RUE under certain conditions because of their nitrogen fixation capability in tropical and subtropical deep reservoirs (Filstrup et al., 2014; Tian et al., 2017; Yang et al., 2021). This species can regulate buoyancy by gas vacuoles, and so gaining competitive advantages and inhibiting the growth of other species under limiting nitrogen conditions (Burford et al., 2016), thus allowing this species to grow better than other species under lower resource availability. On the other hand, *C. meneghiniana* dominated the phytoplankton communities in downstream waters probably due to anthropogenic pollution arising from human activities (Saros and Anderson, 2015). These results indicate that certain dominant species, or group of species, which would exhibit specific traits that would give them certain physiological advantages allowing for exploitation resources more efficiently (Filstrup et al., 2019). Overall, our results imply that urbanization-induced species loss can reduce RUE through altering community composition of phytoplankton in riverine ecosystems.

3.3. *Urbanization reduces phytoplankton RUE via altering environmental conditions*

The relationship between urbanization, environmental variables, phytoplankton diversity and RUE indicated that urbanization significantly reduced phytoplankton RUE through altering the environmental variables (**Fig. 6**). Extensive human settlement in urbanized regions can cause substantial hydrological alterations that influence on aquatic community structure and function (Yang et al., 2017). Further, increased human activities along rivers may not only increase the quantities of nutrients, but also change forms and proportion of nutrients and physicochemical variables, then lead to adverse effects on water quality (Isabwe et al., 2018). Thus, we speculated that change in water quality contributed to lower RUE of phytoplankton through altering the nutrient status. Similarly, we found that the ratio of phytoplankton biomass to suspended solids in rural upstream was significantly higher than in both urbanizing midstream and urbanized downstream waters (**Appendix A Fig. S2b**), indicating that urbanization increased turbidity/suspended solids in waters by surface runoff. Normally, the concentration of suspended particles is one of the controlling factors for phytoplankton biomass or productivity because it can reduce light availability for photosynthesis, consequently affecting phytoplankton RUE (Hodapp et al., 2019). We also observed that percentage urbanized area had a significant and negative effect on phytoplankton RUE as well as land use-driven alternation of the physical conditions (e.g., turbidity) and nutrient concentrations (TN, NH_4^+-N, TP, and PO_4^{3-}-P). Moreover, our results indicated that phytoplankton RUE exhibited a stronger response to water flow velocity than phytoplankton biomass and diversity (**Appendix A Table S3**). In addition, diverse pollutants (e.g., pesticides, antibiotics, hormones, insecticides, and heavy metals) from industries, agriculture, and untreated household sewages might influence the phytoplankton RUE in the midstream and downstream waters (Yang et al., 2021). The positive effects of phytoplankton diversity on ecosystem functioning decreased with increasing environmental stress or multiple disturbances (Steudel et al., 2012; Isbell et al., 2013; Yang et al., 2021). Overall, urbanization-driven land use and environmental changes have multiple effects on phytoplankton communities including changes in community composition, biodiversity and finally ecosystem function.

Urbanization-driven land use affected RUE through the potential pathway mediated by changing environmental conditions (**Fig. 6**). First, phytoplankton diversity and activity in river are mainly influenced by the direct effect of physical-chemical variables and hydrodynamic conditions (Padisák et al., 2006; Isabwe et al., 2018). Second, a decline of RUE could be aggravated by changes in community member interdependence or food web structure, in addition to loss of biodiversity. For example, Li et al. (2020) reported that algal communities were directly affected by invertebrate and protozoa. In addition, multi-trophic communities in rivers jointly play a regulatory role in the process of external stressor changing RUE, this may be related to the niche partitioning (Cardinale, 2011). Therefore, urbanization-induced species loss directly affects the efficiency of utilizing resource of phytoplankton via weakening niche partitioning and altering community composition, while the RUE was substantially reduced by urbanization-driven environmental stresses on phytoplankton cells. Based on our results, we suggest that urban land use should be optimized, riverbank buffer zone should be increased and improved for protecting the water quality and phytoplankton diversity. More importantly, a watershed-based management strategy must be developed for controlling the water pollution and protecting biodiversity, and improving ecosystem service (Yang et al., 2012).

4. Conclusions

By characterizing the relationships between phytoplankton community and urbanization related environmental variables in an urbanizing subtropical river over six years, we found that phytoplankton species richness, biomass and RUE have gradually declined from rural upstream to urbanizing midstream waters, and species richness has significantly declined in urbanized downstream although biomass recovered to the upstream level. Our results indicate land use change is closely related to these changes in phytoplankton community. Urbanization increased Bacillariophyta biomass and reduced Chlorophyta biomass in the Houxi River. Our results also suggest that urbanization reduces resource use efficiency of phytoplankton community through altering the environment and decreasing biodiversity. As biodiversity-ecosystem functioning relationships are still unclear in river ecosystems, this work provides important insights into understanding the role of urbanization in shaping the structure and function of phytoplankton communities in inland waters.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.jes.2021.05.001.

REFERENCES

Best, J., 2019. Anthropogenic stresses on the world's big rivers. Nat. Geosci. 12, 7–21.
Burford, M.A., Beardall, J., Willis, A., Orr, P.T., Magalhaes, V.F., Rangel, L.M., 2016. Understanding the winning strategies used by the bloom-forming cyanobacterium *Cylindrospermopsis raciborskii*. Harmful Algae 54, 44–53.

Cardinale, B.J., 2011. Biodiversity improves water quality through niche partitioning. Nature 472, 86–89.
Cardinale, B.J., Palmer, M.A., Collins, S.L., 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. Nature 415, 426–429.
Cardinale, B.J., Srivastava, D.S., Emmett Duffy, J., Wright, J.P., Downing, A.L., Sankaran, M., et al., 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443, 989–992.
Chessman, B.C., Growns, I., Currey, J., Plunkett-Cole, N., 1999. Predicting diatom communities at the genus level for the rapid biological assessment of rivers. Freshw. Biol. 41, 317–331.
Descy, J.P., Darchambeau, F., Lambert, T., Stoyneva-Gaertner, M.P., Bouillon, S., Borges, A.V., 2017. Phytoplankton dynamics in the Congo River. Freshw. Biol. 62, 87–101.
Doi, H., Katano, I., Negishi, J.N., Sanada, S., Kayaba, Y., 2013. Effects of biodiversity, habitat structure, and water quality on recreational use of rivers. Ecosphere 4, 102.
Duong, T.T., Coste, M., Feurtet-Mazel, A., Dang, D.K., Ho, T.C., Le, T.P.Q., 2012. Responses and structural recovery of periphytic diatom communities after short-term disturbance in some rivers (Hanoi, Vietnam). J. Appl. Phycol. 24, 1053–1065.
Filstrup, C.T., Hillebrand, H., Heathcote, A.J., Harpole, W.S., Downing, J.A., 2014. Cyanobacteria dominance influences resource use efficiency and community turnover in phytoplankton and zooplankton communities. Ecol. Lett. 17, 464–474.
Filstrup, C.T., King, K.B.S., McCullough, L.M., 2019. Evenness effects mask richness effects on ecosystem functioning at macro-scales in lakes. Ecol. Lett. 22, 2120–2129.
García, F.C., Bestion, E., Warfield, R., Yvon-Durocher, G., 2013. Change in temperature alter the relationship between biodiversity and ecosystem functioning. Proc. Natl. Acad. Sci. U.S.A. 115, 10989–10994.
Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J.G., Bai, X.M., et al., 2008. Global change and the ecology of cities. Science 319, 756–760.
Guedes, I.A., Pacheco, A.B.F., Vilar, M.C.P., Mello, M.M., Marinho, M.M., Lurling, M., et al., 2019. Intraspecific variability in response to phosphorus depleted conditions in the cyanobacteria *Microcystis aeruginosa* and *Raphidiopsis raciborskii*. Harmful Algae 86, 96–105.
Heino, J., Soininen, J., Alahuhta, J., Lappalainen, J., Virtanen, R., 2017. Metacommunity ecology meets biogeography: effects of geographical region, spatial dynamics and environmental filtering on community structure in aquatic organisms. Oecologia 183, 121–137.
Hillebrand, H., Dürselen, C.D., Kirschtel, D., Pollingher, U., Zohary, T., 1999. Biovolume calculation for pelagic and benthic microalgae. J. Phycol. 35, 403–424.
Hodapp, D., Hillebrand, H., Blasius, B., Ryabov, A.B., 2016. Environmental and trait variability constrain community structure and the biodiversity-productivity relationship. Ecology 97, 1463–1474.
Hodapp, D., Hillebrand, H., Striebel, M., 2019. “Unifying” the concept of resource use efficiency in ecology. Front. Ecol. Evol. 6, 233.
Hodapp, D., Meier, S., Muijsers, F., Badewien, T., Hillebrand, H., 2015. Structural equation modeling approach to the diversity-productivity relationship of Wadden Sea phytoplankton. Mar. Ecol. Prog. Ser. 523, 31–40.
Hooper, D.U., Chapin III, F.S., Ewel, J., Hector, A., Inchausti, P., Lavorel, S., et al., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75, 3–35.
Hu, H.J., Wei, Y.X., 2006. The Freshwater Algae of China: Systematics, Taxonomy and Ecology. Science Press, Beijing, China.
Isabwe, A., Yang, J.R., Wang, Y.M., Liu, L.M., Chen, H.H., Yang, J., 2018. Community assembly processes underlying phytoplankton and bacterioplankton across a hydrologic change in a human-impacted river. Sci. Total Environ. 630, 658–667.
Isbell, F., Rich, P.B., Tilman, D., Hobbie, S.E., Polasky, S., Binder, S., 2013. Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. Proc. Natl. Acad. Sci. USA. 110, 11911–11916.
Katsiapi, M., Mazaris, A.D., Charalampous, E., Moustaka-Gouni, M., 2012. Watershed land use types as drivers of freshwater phytoplankton structure. Hydrobiologia 698, 121–131.
Kaye, J.P., Groffman, P.M., Grimm, N.B., Baker, L.A., Pouyat, R.V., 2006. A distinct urban biogeochemistry? Trends Ecol. Evol. 21, 192–199.
Lai, J.S., Peres-Neto, P., 2020. *rdacca.hp*: Hierarchical Partitioning for Canonical Analysis. R package version 0.3.0.
Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280.
Li, F.L., Altermatt, F., Yang, J.H., An, S.Q., Li, A., Zhang, X.W., 2020. Human activities’ fingerprint on multitrophic biodiversity and ecosystem functions across a major river catchment in China. Glob. Chang. Biol. 26, 6867–6879.
Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804–808.
Lv, H., Yang, J., Liu, L.M., Yu, X.Q., Yu, Z., Chiang, P.C., 2014. Temperature and nutrients are significant drivers of seasonal shift in phytoplankton community from a drinking water reservoir, subtropical. China. Environ. Sci. Pollut. Res. 21, 5917–5928.
Mckinney, M.L., 2008. Effects of urbanization on species richness: a review of plants and animals. Urban Ecosyst 11, 161–176.
Padisák, J., Borics, G., Grigorszky, I., Soróczki-Pintér, E., 2006. Use of phytoplankton assemblages for monitoring ecological status of lakes within the Water Framework Directive: the assemblage index. Hydrobiologia 553, 1–14.
Paul, M.J., Meyer, J.L., 2001. Streams in the urban landscape. Ann. Rev. Ecol. Syst. 32, 333–365.
Peng, F., Guo, Y.Y., Isabwe, A., Chen, H.H., Wang, Y.M., Zhang, Y.P., et al., 2020. Urbanization drives riverine bacterial antibiotic resistome more than taxonomic community at watershed scale. Environ. Int. 137, 105524.
Ptacnik, R., Solimini, A.G., Andersen, T., Tamminen, T., Brettum, P., Lepistö, L., et al., 2008. Diversity predicts stability and resource use efficiency in natural phytoplankton communities. Proc. Natl. Acad. Sci. USA. 105, 5134–5138.
R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Reynolds, C.S., 2006. Ecology of Phytoplankton. Cambridge University Press, Cambridge.
Sailley, S.F., Polimene, L., Mitra, A., 2015. Impact of zooplankton food selectivity on plankton dynamics and nutrient cycling. J. Plankton Res. 37, 519–529.
Saros, J.E., Anderson, N.J., 2015. The ecology of the planktonic diatom *Cyclotella* and its implications for global environmental change studies. Biol. Rev. 90, 522–541.
Seto, K.C., Guneralp, B., Hutyra, L.R., 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proc. Natl. Acad. Sci. USA. 109, 16083–16088.
Shi, Z., Xu, J., Huang, X.P., Zhang, X., Jiang, Z.J., Ye, F., et al., 2017. Relationship between nutrients and plankton biomass in the turbidity maximum zone of the Pearl River Estuary. J. Environ. Sci. 57, 72–84.

Sterner, R.W., 2008. On the phosphorus limitation paradigm for lakes. Int. Rev. Hydrobiol. 93, 433–445.
Steudel, B., Hector, A., Friedl, T., Löfke, C., Lorenz, M., Wesche, M., 2012. Biodiversity effects on ecosystem functioning change along environmental stress gradient. Ecol. Lett. 15, 1397–1405.
Striebel, M., Behl, S., Stibor, H., 2009. The coupling of biodiversity and productivity in phytoplankton communities: consequences for biomass stoichiometry. Ecology 90, 2025–2031.
Tian, W., Zhang, H.Y., Zhang, J., Zhao, L., Miao, M.S., Huang, H., 2017. Biodiversity effects on resource use efficiency and community turnover of plankton in Lake Nansihu. China. Environ. Sci. Pollut. Res. 24, 11279–11288.
Tilman, D., Lehman, C.L., Thomson, K.T., 1997. Plant diversity and ecosystem productivity: theoretical considerations. Proc. Natl. Acad. Sci. USA. 94 (5), 1857–1861.
Tornés, E., Pérez, M.C., Durán, C., Sabater, S., 2014. Reservoirs override seasonal variability of phytoplankton communities in a regulated Mediterranean river. Sci. Total Environ. 475, 225–233.
Uchida, K., Blakey, R.V., Burger, J.R., Cooper, D.S., Niesner, C.A., Blumstein, D.T., 2021. Urban biodiversity and the importance of scale. Trends Ecol. Evol. 36, 123–131.
Urban, M.C., Skelly, D.K., Burchsted, D., Price, W., Lowry, S., 2006. Stream communities across a rural–urban landscape gradient. Divers. Distrib. 12, 337–350.
Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W., et al., 1997. Human alteration of the global nitrogen cycle: sources and consequences. Ecol. Appl. 7, 737–750.
Weijters, M., Janse, J.H., Alkemade, R., Verhoeven, J.T.A., 2009. Quantify the effect of catchment land use and water nutrient concentrations on freshwater river and stream biodiversity. Aquat. Conserv. 19, 104–112.
Wenger, S.J., Roy, A.H., Rhett Jackson, C., Bernhardt, E.S., Carter, T.L., Filoso, S., et al., 2009. Twenty-six key research questions in urban stream ecology: an assessment of the state of the science. J. N. Am. Benthol. Soc. 28, 1080–1090.
Wetzel, R.G., Likens, G.E., 2000. Limnological Analysis. Springer, Berlin, Germany.
Xue, Y.Y., Chen, H.H., Yang, J.R., Liu, M., Huang, B.Q., Yang, J., 2018. Distinct patterns and processes of abundant and rare eukaryotic plankton communities following a reservoir cyanobacterial bloom. ISME J 12, 2263–2277.
Yang, J., Yu, X.Q., Liu, L.M., Zhang, W.J., Guo, P.Y., 2012. Algae community and trophic state of subtropical reservoirs in southeast Fujian. China. Environ. Sci. Pollut. Res. 19, 1432–1442.
Yang, J.R., Lv, H., Isabwe, A., Liu, L.M., Yu, X.Q., Chen, H.H., et al., 2017. Disturbance-induced phytoplankton regime shifts and recovery of cyanobacteria dominance in two subtropical reservoirs. Water Res 120, 52–63.
Yang, J.R., Yu, X.Q., Chen, H.H., Kuo, Y.M., Yang, J., 2021. Structural and functional variations of phytoplankton communities in the face of multiple disturbances. J. Environ. Sci. 100, 287–297.
Zhang, H.H., Zong, R.R., He, H.Y., Liu, K.W., Yan, M.M., Miao, Y.T., et al., 2021. Biogeographic distribution patterns of algal community in different urban lakes in China: insights into the dynamics and co-existence. J. Environ. Sci. 100, 216–227.
Zhu, Y.G., Ioannidis, J.P.A., Li, H., Jones, K.C., Martin, F.L., 2011. Understanding and harnessing the health effects of rapid urbanization in China. Environ. Sci. Technol. 45, 5099–5104.
Zhu, Z.X., Gao, X.F., Peng, F., Chen, H.H., Tang, L.N., Yang, J., 2019. Relationship between water quality and landscape characteristics of the Houxi River watershed in Xiamen City along a rural-urban gradient. Acta. Ecol. Sin. 39, 2021–2033.