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Liu, Zhenyuan

2022-10

Liu , Z , Heino , J , Soininen , J , Zhou , T , Wang , W , Cui , Y , Chen , Y , Li , Z , Zhang , J & Xie , Z 2022 , ' Different responses of incidence-weighted and abundance-weighted multiple facets of macroinvertebrate beta diversity to urbanization in a subtropical river system ' , Ecological Indicators , vol. 143 , 109357 . <https://doi.org/10.1016/j.ecolind.2022.109357>

<http://hdl.handle.net/10138/350019>

<https://doi.org/10.1016/j.ecolind.2022.109357>

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Different responses of incidence-weighted and abundance-weighted multiple facets of macroinvertebrate beta diversity to urbanization in a subtropical river system

Zhenyuan Liu^{a,b}, Jani Heino^c, Janne Soininen^d, Tingting Zhou^{a,b}, Weimin Wang^e, Yongde Cui^a, Yushun Chen^a, Zhengfei Li^a, Junqian Zhang^{a,*}, Zhicai Xie^{a,*}

^a The Key Laboratory of Aquatic Biodiversity and Conservation, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China

^b University of Chinese Academy of Sciences, Beijing 100049, China

^c Geography Research Unit, University of Oulu, P.O. Box 8000, FI-90014 Oulu, Finland

^d Department of Geosciences and Geography, University of Helsinki, Helsinki FIN-00014, Finland

^e Central Station for Environmental Monitoring and Assessment, Shenzhen 518049, China

ARTICLE INFO

Keywords:

Biotic homogenization
Richness difference
Replacement
Rare taxa
Deterministic processes
Stochastic processes

ABSTRACT

Urbanization is one of the major drivers of biotic homogenization (i.e., decrease in beta diversity) in freshwater systems. However, only a few studies have simultaneously examined how urbanization affects multiple facets (i.e., taxonomic, functional and phylogenetic) of beta diversity and its underlying ecological drivers in urban river macroinvertebrates. Here, we distinguished the patterns and ecological mechanisms of multiple facets of macroinvertebrate beta diversity weighted by incidence and abundance data in a subtropical river system with a distinct urbanization gradient. We also investigated how total beta diversity patterns stem from replacement versus richness difference among sites. Our results showed that taxonomic and phylogenetic beta diversities weighted by incidence data were primarily driven by replacement of taxa, whereas the richness difference contributed more to multiple facets of beta diversity based on abundance data. Furthermore, multiple facets of beta diversity decreased with urbanization for both incidence-weighted and abundance-weighted data, but the former showed more substantial decreases. Both replacement and richness difference components contributed roughly equally to the decline of incidence-weighted beta diversity. In contrast, the losses of abundance-weighted beta diversity were mainly associated with replacement of taxa. Variation partitioning results revealed that all beta diversity measures based on incidence data were governed primarily by local and land-use variables, whereas spatial variables were more relevant in driving beta diversity weighted by abundance data. Overall, by comparing different facets and components of beta diversity weighted by incidence versus abundance data, we suggest that incidence-weighted data may be more sensitive in portraying the impacts of urbanization on macroinvertebrate diversity. This likely resulted from the fact that incidence-weighted data shows the importance of rare taxa in shaping homogenization induced by urbanization.

1. Introduction

The world is becoming increasingly more urbanized, with the percentage of global urban population being forecasted to increase from 55% in 2018 to 68% in 2050 (United Nations, 2018). Rapid urbanization has become a major threat to river systems, often resulting in the modification of habitat conditions and land-use patterns, deterioration of water quality, and the loss of geo- and biodiversity (Urban et al., 2006; Wiederkehr et al., 2020). One of the major consequences induced

by urbanization is biotic homogenization, which refers to the process of increasing similarity of a set of ecological communities through time (i.e., decline in beta diversity) (McKinney and Lockwood, 1999). Biotic homogenization is primarily driven by the loss of many rare and urban-sensitive taxa (i.e., losers) and the increase of few common urban-adapted species (i.e., winners) (McKinney and Lockwood, 1999), potentially resulting in a reduction of community variation and ecosystem functioning (Gamez-Virues et al., 2015), as well as decrease stability and resilience to environmental changes (Olden and Poff, 2004;

* Corresponding authors.

E-mail addresses: jq_zhang@ihb.ac.cn (J. Zhang), zhcxie@ihb.ac.cn (Z. Xie).

<https://doi.org/10.1016/j.ecolind.2022.109357>

Received 26 June 2022; Received in revised form 15 August 2022; Accepted 21 August 2022

Available online 26 August 2022

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Olden et al., 2004). Biotic homogenization can be seen in different facets of biodiversity, including taxonomic, functional and phylogenetic facets (Olden and Rooney, 2006). Beyond the most studied facets, i.e., taxonomic homogenization, functional and phylogenetic homogenizations should also be considered because the responses of species to environmental changes are not random, but are associated with certain functional traits that may display higher-order phylogenetic affinities (Olden and Rooney, 2006).

Lotic macroinvertebrates are key regulators of organic material processing and nutrient flows (Cummins, 1974), and can be considered indicators of urban river ecological conditions (Rosenberg and Resh, 1993). To date, empirical studies of macroinvertebrate community homogenization induced by urbanization have focused on taxonomic and functional facets of biodiversity (Barnum et al., 2017; Liu et al., 2022; Talaga et al., 2017). To our knowledge, however, no empirical study has tested whether urbanization leads to phylogenetic homogenization in addition to taxonomic and functional homogenizations and what are the underlying drivers.

Phylogenetic homogenization represents increasing similarity of evolutionary lineages among two or more ecological communities (Nowakowski et al., 2018; Sol et al., 2017), and it could occur when altered river conditions favor certain closely related taxa from a given lineage (Nowakowski et al., 2018). Further, the decline of phylogenetic distinctiveness may imply that the whole ecosystem is more vulnerable to disturbances, because remaining less evolutionarily distinct species may exhibit relatively limited resistance to environmental stressors (Cadotte et al., 2012). Additionally, previous studies have shown that phylogenetic homogenization may not necessarily be concomitant with taxonomic and functional homogenizations (Swenson, 2011). For example, the frequent turnover of different species within the same clade of the phylogeny tree along environmental gradients could lead to a low phylogenetic replacement, but higher species replacement (Swenson, 2011). Therefore, studying phylogenetic beta diversity in conjunction with taxonomic and functional facets could be a key to better understand the impacts of urbanization on biotic homogenization of lotic macroinvertebrate (Olden et al., 2018).

In addition to focusing on multiple facets of beta diversity, comparative studies on beta diversity weighted by incidence versus abundance data are mostly lacking (Anderson et al., 2011; Baselga and Chao, 2016). Generally, incidence-weighted measures lay particular emphasis on rare taxa as they consider only the identities of species, whereas abundance-weighted measures emphasize abundant taxa because they are suited to detect community differences among sites that are due to changes in species abundances (Heino, 2014; Koleff et al., 2003; Zhao et al., 2021). Prior studies have indicated that abundant and rare taxa typically have distinct ecological strategies, habitat preferences or functional traits (e.g., dispersal ability) (Heino and Grönroos, 2014; Siqueira et al., 2012). In this case, ecological processes and mechanisms shaping beta diversity based on abundance-weighted data may be distinct from those weighted by incidence data (Heino, 2014; Hu et al., 2018). On one hand, rare taxa are typically characterized by narrower niche breadths and more restricted habitat preferences than abundant taxa (Jousset et al., 2017; Siqueira et al., 2012). Thus, beta diversity weighted by incidence data should be mainly driven by replacement and be more strongly controlled by environmental filtering (e.g., local and land-use variables) than stochastic effects (Leitao et al., 2016). Alternatively, abundance-weighted beta diversity may be affected mainly by dispersal-related processes. Some typical urban-adapted taxa, such as aquatic oligochaetes have been characterized by strong drift ability (Cellot and Juget, 1998), or have higher local abundances which can potentially lead to more frequent dispersal events (Heino et al., 2017). In addition, considering that abundant taxa may be better able to persist in any given site, one can assume that priority effects may be dominant in shaping abundance-weighted beta diversity (Pandit et al., 2009; Zeni et al., 2020). However, some studies also suggested, overall, the opposite. Rare taxa may be strongly driven by

demographic stochasticity because of their small population sizes (Chase et al., 2005), whereas abundant taxa could be more strongly influenced by environmental filtering because they typically inhabit core ecological niches (Umana et al., 2015).

In our previous study, we found that increasing levels of urbanization resulted in taxonomic and functional homogenizations of macroinvertebrate communities (Liu et al., 2022). Here, we go beyond our previous study by specifically comparing incidence-weighted and abundance-weighted data and examining the responses of beta diversity of multiple facets (i.e., taxonomic, functional and phylogenetic) and components (i.e., replacement and richness difference) to an urbanization gradient. Specifically, given the distinct properties (e.g., environmental preferences and key functional traits) between abundant and rare taxa (Siqueira et al., 2012), we examined the following three hypotheses. First, the roles of replacement and richness difference components should be different between incidence and abundance data (Marcacci et al., 2021; Zhao et al., 2021). We hypothesized that (H₁) replacement component contributes more to incidence-weighted beta diversity (Zhao et al., 2021), whilst abundance-weighted beta diversity could be more driven by abundance difference (de Siqueira et al., 2021). Second, responses of beta diversity weighted by incidence and abundance data to urbanization should be driven differently by replacement and richness difference components (Knop, 2016; Marcacci et al., 2021). We thus expected that (H₂) the decrease of incidence-weighted beta diversity was mainly driven by richness difference, while the decline of abundance-weighted beta diversity was primarily contributed by replacement (Knop, 2016; Marcacci et al., 2021). Third, incidence-weighted and abundance-weighted beta diversities should be structured by different assembly mechanisms (Hu et al., 2018). We expected that (H₃) deterministic processes (i.e., environmental filtering by local and land-use factors) could play a greater role in shaping incidence-weighted beta diversity, while stochasticity (i.e., dispersal-related factors) should be more strongly associated with abundance-weighted beta diversity (Pandit et al., 2009).

2. Material and methods

2.1. Study area and sampling sites

The current study was carried out in the six rivers (i.e., Maozhouhe River: MZHR; Guanlanhe River: GLHR; Shenzhenhe River: SZHR; Pingshanhe River: PSHR; Dapenghe River: DPHR; Longganghe River: LGHR) of Shenzhen, South China. Shenzhen city covers an area of 1,997 km², with open plains, rolling hills, and mountains being the most dominant topography (Liu et al., 2021; Liu et al., 2022; To et al., 2021). This region has a maximum elevation of approximately 950 m above sea level, with a terrain of high in southeast and low in northwest. Shenzhen city has a subtropical monsoon climate, with an average annual temperature and precipitation are 24 °C and 1,882 mm, respectively (Shenzhen climate bulletin, 2020). Shenzhen city has >310 streams and rivers, with only five major rivers having a watershed area of 100 km² (<https://swj.sz.gov.cn/html>).

Since it was approved as the China's first Special Economic Zone (SEZ) in 1980, Shenzhen has experienced a rapid urbanization process, evolving from an impoverished fishing village into one of the megacities in China (To et al., 2021). On the one hand, the economy of Shenzhen has developed rapidly in the past four decades. For instance, Shenzhen's gross domestic product (GDP) surpassed that of Hong Kong in 2018, hitting a record 2.4 trillion yuan (\$2400 billion) (To et al., 2021). On the other hand, Shenzhen has a total population of 13 million in the end of 2018 (ca. 6,484 per km²) (Shenzhen statistical yearbook, 2020). In the last four decades, Shenzhen's rivers have suffered intensive anthropogenic stressors, such as point and nonpoint sources, land-use change and water pollution (Liu et al., 2021; Qiu et al., 2019), etc. Such disturbances have been evidenced to strongly threaten aquatic biodiversity (Qiu et al., 2019). Thus, the rivers in Shenzhen are considered ideal arenas to

elucidate how rapid urbanization processes mediate community assembly and biodiversity patterns of ecological communities.

A total of 69 wadeable sampling sites belonging to these rivers were sampled in December 2019 (Fig. 1, Supplementary Fig. S1). These sampling sites represented a continuous urbanization gradient from low-level urbanization (LUS), to medium-level urbanization (MUS) and high-level urbanization (HUS) (Liu et al., 2015; Liu et al., 2022). We selected sampling sites based on the two criteria (Czeglédi et al., 2020): 1) to avoid the confounding effect of natural environmental variability, we only choose sampling sites that situate below elevation of 300 m; 2) we excluded some sites that suffered dramatically from other anthropogenic disturbances, such as bridge construction and river reaches being restored. Notably, we here used the percentage of impervious area (i.e., PIA index), a widely-used index of urbanization intensity (McMahon and Cuffney, 2000), to characterize the urbanization gradient. The PIA index was calculated based on the percentage of urban land area of the total area within the buffer zone (i.e., 2 km × 2 km) (Supplementary S1, Table S1). Overall, most of the LUS sites were located in PSHR and DPHR rivers with > 50% forest and < 30% urban land. MUS sites were mainly located in LGHR with > 45% urban land. HUS sites had a much higher percentage of urban land (i.e., >60%) and were mainly located in MZHR and GLHR. Besides, these rivers were also characterized by distinct local environmental conditions, with more degraded water quality and habitat heterogeneity (e.g., increase the concentration of sand and silt) being detected in the sets of MUS and HUS (Supplementary Table S1).

2.2. Macroinvertebrate sampling

In the field, we employed a standardized multi-habitat sampling technique to sample macroinvertebrates (Barbour et al., 1999). Given

the majority of sampling sites in our study area were wadeable, macroinvertebrates were sampled from at least five subsamples along a 100 m reach using a D-frame kick net (30 × 30 cm, 250 μm in mesh size) (Liu et al., 2021; Liu et al., 2022). To collect as many specimens as possible, the main habitats were selected *a priori*, including different substrate (i.e., boulder, cobble, pebble, gravel and sand and silt), riparian zone and submerged macrophytes. In each site, the subsamples were pooled together and sieved using a copper sieve (500-μm) and were subsequently returned to the laboratory within the 24-hour. Specimens were hand-picked out of debris and stored in ethanol (75%) in the laboratory. Specimens were identified to the lowest taxonomical level (usually genus or species) based on relevant taxonomic references and individuals were counted (detailed taxonomic references were provided in the Supplementary S1) (Liu et al., 2022).

2.3. Trait information and taxonomic levels

Twenty-eight categories of eight functional traits were selected (Liu et al., 2022), including voltinism, development, adult life span, body size, occurrence in drift, habit, respiration and trophic groups (Table 1). These traits are known to respond to urbanization gradient, as shown in our previous studies and other reports (Barnum et al., 2017; Liu et al., 2022; Talaga et al., 2017). Trait information was mainly gathered from relevant taxonomic literature and published articles (Supplementary S1).

Due to lack of a true phylogenetic tree involving all the macroinvertebrate taxa sampled in the study region, we employed taxonomic distance between pairs of species based on the path lengths through the Linnean taxonomic trees as a surrogate for true phylogeny (Clarke and Warwick, 1998). While this approach is admittedly only a coarse proxy,

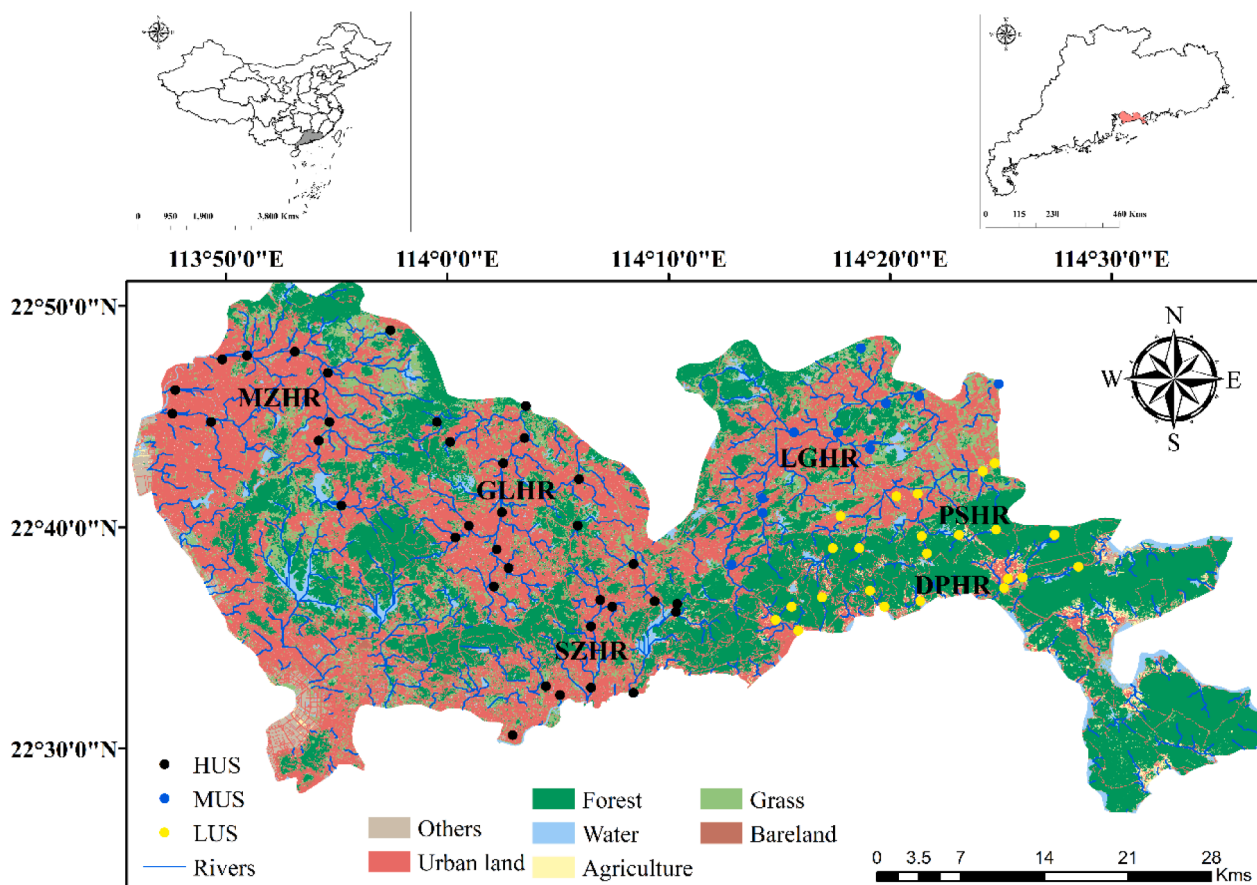


Fig. 1. Locations of the 69 sites in the six study rivers (i.e., Maozhouhe River: MZHR; Guanlanhe River: GLHR; Shenzhenhe River: SZHR; Pingshanhe River: PSHR; Dapenghe River: DPHR; Longganghe River: LGHR) in the Shenzhen city, South China. LUS (i.e., PSHR, DPHR), MUS (i.e., LGHR), HUS (i.e., MZHR, GLHR).

Table 1
Functional traits, trait categories and their codes used in this study.

Trait	Category	Code
Voltinism	Semivoltine	Vol1
	Univoltine	Vol2
	Bi-or multivoltine	Vol3
Development	Fast seasonal	Dev1
	Slow seasonal	Dev2
	Nonseasonal	Dev3
Adult life span	Less one week	Life1
	Less one month	Life2
	More one month	Life3
Body size	Small (<9 mm)	Size1
	Medium (9–16 mm)	Size2
	Large (>16 mm)	Size3
Occurrence in drift	Rare	Drif1
	Common (typically observed)	Drif2
	Very abundant (dominant in drift samples)	Drif3
Habit	Climb	Hab1
	Burrow	Hab2
	Sprawl	Hab3
	Cling	Hab4
	Swim	Hab5
Respiration	Tegument	Res1
	Gills	Res2
	Air (Plastron or spiracle)	Res3
Trophic groups	Collector-gatherer	Tro1
	Collector-filterer	Tro2
	Herbivore (includes scrapers)	Tro3
	Predator	Tro4
	Shredder	Tro5

it has frequently been applied to estimate macroinvertebrate phylogenetic diversity (Heino and Tolonen, 2017; Rocha et al., 2018). The taxonomic information used contained six categories (i.e., species, genus, family, order, class, and phylum) by referring to relevant taxonomic keys and an online database (http://www.sp2000.org.cn/browse/browse_taxa).

2.4. Environmental variables

We separately constructed two independent environmental data matrices (i.e., local and land-use variables). The measurement of local and land-use variables was described in our previous studies (Liu et al., 2021; Liu et al., 2022) and was also depicted in supplementary S1. Briefly, we measured a total of 24 local variables, including water depth (WD), velocity (Vel), river width (RW), turbidity (Tur), transparency (Trans), sand and silt, gravel, pebble, cobble and boulder, substrate diversity (Sub_simpson), conductivity (Cond), pH, dissolved oxygen (DO), salinity, water temperature (WT), ammonium nitrogen (NH_4^+N), chemical oxygen demand (COD_{Cr}), total nitrogen (TN), biochemical oxygen demand after 5 days (BOD_5), total phosphorus (TP), fecal Coliform Unit (FCU), fluoride (FLU) and suspended solids (SS).

Seven buffer-scale land-use variables (i.e., agriculture, grass, water, bare land, urban land, forest and others) were considered, representing the main land-cover elements across our study region (Liu et al., 2022). To do this, we first delineated three rectangle buffer zones (i.e., length \times width: 2 km \times 0.5 km; 2 km \times 1 km; 2 km \times 2 km) at the upstream of each site based on the digital elevation model (DEM: 30-m spatial resolution; <https://www.gscloud.cn/>) using the software ArcGIS 10.5 (Esri, Inc.). Then, we interpreted the optical image with 16-m spatial resolution provided by GF-6WFV camera (Shot at the 2019–09–30; <https://www.cnsageo.com/>) within each buffer zone. Then, the proportion of each land-use category within the buffer zone was used in the subsequent analyses. Notably, we here used the land-use data of 2 km \times 2 km buffer zone in the data analysis, because there was a higher correlation between land-use distance and dissimilarity matrices of all beta diversity measures (Supplementary Table S2).

2.5. Spatial factors

Spatial factors were used as proxies for dispersal-related processes (Borcard et al., 2004). To do this, Moran's eigenvector maps were employed to generate spatial factors modeling the spatial structures of sampling sites based on overland Euclidean distances among sites (Borcard and Legendre, 2002; Borcard et al., 2004). While watercourse distances could be assumed to be influential for river macroinvertebrates (Tonkin et al., 2018), we had to use overland distances because different rivers were not connected via watercourses (Liu et al., 2022). The generated MEMs eigenvalues showing positive autocorrelation were retained and used as spatial predictors in further analysis (Borcard et al., 2004). Usually, the first larger MEMs eigenvalues represent broad-scale spatial patterns, whereas those with smaller MEMs eigenvalues represent fine-scale spatial patterns (Borcard and Legendre, 2002; Heino et al., 2015). In the current study, a total of 21 MEMs eigenvalues describing positive autocorrelation were obtained and used as spatial factors in community modeling. The above analysis was conducted using the R package *adespatial* (function: "create.MEM.Model") (Dray et al., 2021).

2.6. Data analysis

2.6.1. Beta diversity

First, a sampling unit-based rarefaction-extrapolation curve was used to evaluate the completeness of sampling. Here, we used the incidence-based rarefaction based on Hill numbers of order $q = 0$. Confidence intervals (95%) were estimated using 1000 bootstrap replications. The sampling completeness curves were obtained in the R package *iNEXT* (function: "iNEXT") (Hsieh et al., 2016).

Furthermore, we followed the approach proposed by Podani and Schmera (2011) and Carvalho et al. (2012), to calculate and decompose total taxonomic, functional and phylogenetic beta diversity. In this scheme, total beta diversity was decomposed into replacement and richness difference components. Total beta diversity (B_{total}) (in our case based on Sørensen dissimilarity) reflects the total differences among communities. Replacement is related to turnover of taxa identities alone, while richness difference describes the absolute difference of taxonomic richness of each community (Cardoso et al., 2014). Under the abundance-weighted beta diversity partitioning scheme, B_{repl} shows that the individuals of some taxa at one location are substituted by the equal number of individuals from different taxa at another place, while B_{rich} refers that differences in the amount of individuals among the two focal communities (Podani et al., 2013). Both incidence-weighted (i.e., $\text{abund} = \text{FALSE}$) and abundance-weighted beta diversity measures (i.e., $\text{abund} = \text{TRUE}$) were calculated in the R package *BAT* (Cardoso et al., 2015).

Taxonomic beta diversity and its two components were calculated based on the site-by-taxon matrix (Cardoso et al., 2015) using the R package *BAT* (function: "beta"). For the partitioning of functional beta diversity, we produced the inter-species trait distances (i.e., taxon-by-taxon matrix) based on the scaled and centred functional trait values (i.e., taxon-by-trait matrix) using the Gower distance in the R package *BAT* (function: "gower") (Cardoso et al., 2015). The Gower distance was selected because it allows for both binary and continuous factors to be considered (Rocha et al., 2018). Then, we generated a trait-based tree using the unweighted pair group method with arithmetic means (i.e., UPGMA) based on the taxon-by-taxon matrix (Cardoso et al., 2014). Then, we calculated the functional beta diversity and their two components based on the site-by-taxon matrix and trait-based tree. As for phylogenetic beta diversity, taxonomic distance between species was first calculated using the R package *vegan* (function: "taxa2dist") (Oksanen et al., 2017). Further, a Linnean tree based on the taxonomic distance was built using the R package *BAT* (function: "Linnean") (Cardoso et al., 2015). Accordingly, phylogenetic beta diversity and its two components were calculated using the R package *BAT* (function:

“beta”) (Cardoso et al., 2015).

Furthermore, we calculated multiple-site overall beta diversity and its components of three facets (i.e., incidence-weighted and abundance-weighted) for all sampling sites ($n = 69$) in the R package BAT (function: “beta.multi”) (Cardoso et al., 2015). Besides, we calculated the ratio of Brich to Btotal (i.e., Beta ratio = Brich/Btotal) for taxonomic, functional and phylogenetic facets. The Beta ratio represents the relative roles of richness difference and replacement on total beta diversity. A value of Beta ratio < 0.5 implies that replacement component contributed more to total beta diversity, whereas a value of Beta ratio > 0.5 implies that total beta diversity is driven more by richness difference component (Qian et al., 2021).

We further examined the correlation of pairwise measures of beta diversity and its components against a variable that denotes the urbanization gradient (i.e., PIA) using Mantel tests with Spearman’s correlation with 9999 permutations. The statistic value of Mantel tests represents the relationship between both dissimilarity matrices, with a greater statistic metric indicating a stronger correlation. Mantel tests were performed using the R package vegan (function: “mantel”) (Oksanen et al., 2017).

2.6.2. Null-models

To examine whether the observed beta diversity patterns of functional and phylogenetic facets differed from communities assembled at random, we employed a “shuffling tip” null-model procedure (Swenson et al., 2011). For this purpose, the names of the species/traits on the tips of both functional and phylogenetic trees were firstly randomly shuffled 999 times but retained the structure of the two trees (Swenson et al., 2011). Next, standardized effect sizes (SES) of the total beta diversity and its components were calculated, as follows:

$$SES = \text{Obs} - \text{Meannull} / \text{SDnull}$$

where Obs is the observed values of total beta diversity and their components, and Meannull and SDnull represent the mean and standard deviation values from the null model. SES is a value of the randomness of community structure, with negative and positive values indicating functional and phylogenetic clustering and overdispersion, respectively (Swenson et al., 2011). Values of SES higher than -1.96 or < 1.96 imply significantly clustering or overdispersion, respectively ($\alpha = 0.05$). These analyses were performed in the R packages BAT (Cardoso et al., 2015) and picante (Kembel et al., 2010).

2.6.3. Distance-based RDA and variation partitioning

We determined the ecological drivers of the three facets of beta diversity using distance-based redundancy analysis (db-RDA) (Legendre and Anderson, 1999) and associated variation partitioning (Legendre et al., 2005). Prior to data analysis, certain percentage data (i.e., land-use and substrate composition variables) and remaining environmental variables (except pH) were transformed by square root and $\log(x + 1)$, respectively. Then, each transformed local and land-use data was scaled to meet the requirement of db-RDA (Liu et al., 2022). We also deleted one of the environmental variables from each dataset that were highly correlated (Spearman’s $> |0.75|$) (Liu et al., 2022).

Thereafter, a global db-RDA model was run considering all variables within each set of these predictors (i.e., local, land-use and spatial factors) separately. Forward selection procedures were run to select the key factors using the R package adespatial (function: “ordiR2step”) only if the full model was significant ($P < 0.05$) (Dray et al., 2021). Last, variation partitioning was used to reveal the pure and shared effects of three sets of predictors on each facet of beta diversity (Peres-Neto et al., 2006). Variation partitioning were conducted using the R package vegan (function: “varpart”) (Oksanen et al., 2017). Variation in beta diversity and its two components was expressed by adjusted R^2 values (Adj. R^2) of pure and shared contributions. The statistical significance of pure effects of each explanatory dataset was analyzed in the R package vegan

(function: “anova.cca”) (Oksanen et al., 2017).

3. Results

3.1. Taxonomic composition and multiple-site beta diversity

A total of 133 taxa were captured, belonging to 4 phyla, 8 classes, 20 orders, 68 families, and 119 genera. Taxonomic composition varied considerably among different urbanization-level rivers (Supplementary Fig. S2). The sample coverage was 0.94 (ChaoRichness = 178) in all sampling sites (Supplementary Fig. S3), indicating adequate macro-invertebrate sampling in this study region. Taxonomic richness varied considerably among sites, ranging from 3 to 29 (average value = 10.6). *Limnodrilus* sp. (relative abundance: 20.2%), *Limnodrilus hoffmeisteri* (14.4%), *Chironomus* sp. (9.7%), *Biomphalaria straminea* (7.9%) and *Polypedilum* sp. (5.5%) were the dominant taxa across the study region.

Across the whole river system, three facets of abundance-weighted beta diversity were higher than incidence-weighted measures (Fig. 2). Both incidence-weighted and abundance-weighted taxonomic beta diversities were higher than those of functional and phylogenetic facets (Fig. 2). Moreover, multiple-site incidence-weighted taxonomic and phylogenetic beta diversities were primarily driven by the replacement component (Beta ratio: 0.34, and 0.41; Fig. 2), compared to functional facets (Beta ratio: 0.53; Fig. 2). In contrast, richness difference contributed more to all facets of multiple-site abundance-weighted beta diversity (Beta ratio: 0.51, 0.61, and 0.57; Fig. 2).

3.2. Responses of incidence-weighted and abundance-weighted beta diversities to the urbanization gradient

There was a significant negative relationship between the urbanization gradient and three facets of incidence-weighted and abundance-weighted beta diversities, but the rate of decline with the urbanization gradient varied among the facets (Fig. 3, Table 2, Supplementary Table S3). Overall, incidence-weighted beta diversity declined more sharply than abundance-weighted measures. Furthermore, abundance-weighted taxonomic beta diversity declined more strongly than functional and phylogenetic measures, compared to a similar decrease of incidence-based beta diversity. As for the two components, richness

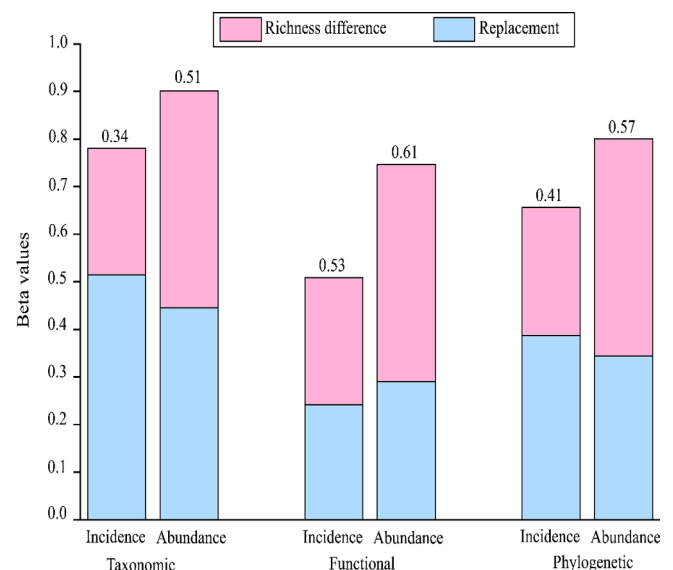


Fig. 2. The relative contributions of replacement and richness difference components (i.e., Brepl and Brich) to incidence-weighted or abundance-weighted beta diversity of taxonomic, functional and phylogenetic facets (i.e., Btotal). The values above the bars represent the ratio between the richness difference and multiple-site overall beta diversity.

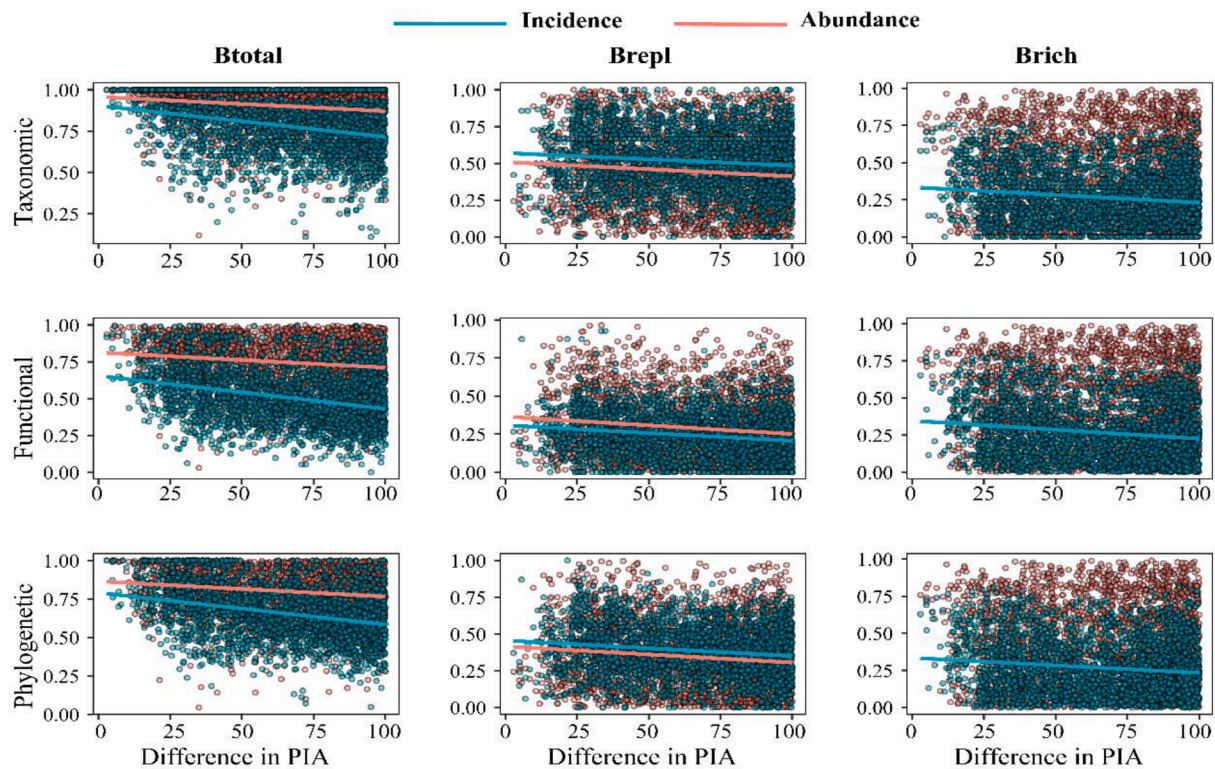


Fig. 3. The relationships between incidence-weighted or abundance-weighted beta diversity of taxonomic, functional and phylogenetic facets (i.e., Btotal, Brepl and Brich) and the urbanization gradient (i.e., difference in PIA between sites). Lines indicate significant relationship based on Mantel tests ($P < 0.05$). Green and red lines denote incidence-weighted and abundance-weighted beta diversities, respectively.

Table 2

Summary of the Mantel tests results between incidence-weighted or abundance-weighted beta diversity of taxonomic, functional and phylogenetic facets (i.e., Btotal, Brepl and Brich) and the urbanization gradient (i.e., PIA distances). The values are bold imply statistical significance ($P < 0.05$).

	Dissimilarity matrix	Taxonomic	Functional	Phylogenetic
Incidence	Btotal	-0.28	-0.28	-0.29
	Brepl	-0.11	-0.18	-0.14
	Brich	-0.12	-0.14	-0.11
Abundance	Btotal	-0.25	-0.15	-0.16
	Brepl	-0.08	-0.13	-0.11
	Brich	0.01	0.01	0.01

difference and replacement contributed nearly equally to the decrease of incidence-based beta diversity, while the decrease of abundance-weighted beta diversity was only contributed by replacement component (Fig. 3, Table 2, Supplementary Table S3).

3.3. Null-models

Overall, the SES values of incidence-weighted and abundance-weighted beta diversities of functional and phylogenetic facets and its replacement and richness difference components were not significant higher or lower than expected by chance (Fig. 4). By contrast, SES values of abundance-weighted functional and phylogenetic beta diversities (i.e., 0.37 and 0.42) and their replacement (i.e., -0.07 and -0.05) and richness difference components (i.e., 0.28 and 0.28) were closer to zero than the incidence-based measures (i.e., Btotal: -0.19 and -0.84, Brepl: -0.87 and -1.22, Brich: 1.12 and 0.83), indicating that when based on abundance data, functional and phylogenetic beta diversities showed randomness (Fig. 4).

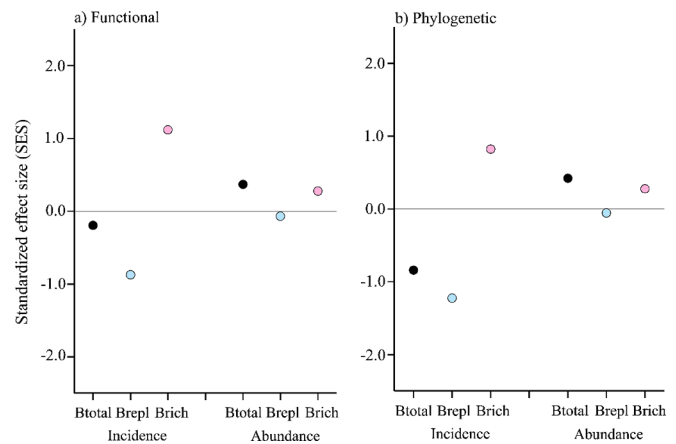


Fig. 4. Standardized effect size (SES) for incidence-weighted or abundance-weighted beta diversity of functional and phylogenetic facets (i.e., Btotal, Brepl and Brich). Negative/positive SES values represent clustering/overdispersion of functional and phylogenetic structure compared with the null model, respectively.

3.4. Distance-based RDA and variation partitioning

Local, land-use, and spatial variables were all influential in affecting incidence-weighted and abundance-weighted beta diversities. In general, local variables (explained variation ranging from 7.0% to 33.0%) accounted for the largest fractions of variation in all facets, especially for incidence-weighted beta diversity. The most influential local variables were mainly related to water quality (e.g., TN, TP, salinity, DO, and COD) and instream substrate conditions (e.g., %Sand and silt, %Pebble, and %Boulder) (Fig. 5). In terms of land-use, %Urban land and %Farmland were typically selected as significant factors (Fig. 5). Besides,

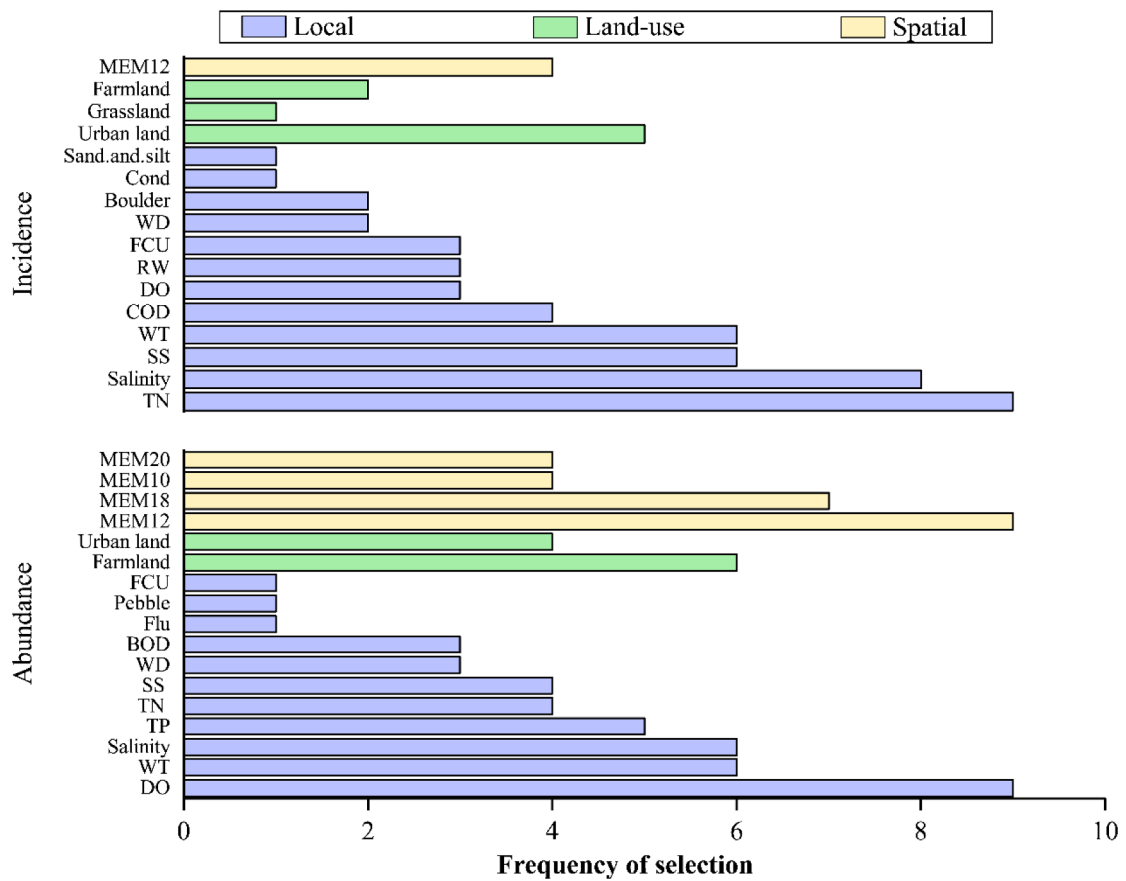


Fig. 5. Frequencies of the key factors selected from the local, land-use, and spatial dataset. Variables in each variable group are arranged in an ascending order.

the shared fractions (i.e., 1.0%–21.0%) of local variables and land-use explained a larger fraction of variation in beta diversity (Fig. 5, Fig. 6). Specifically, spatial factors (i.e., MEM12, MEM18, MEM 10, and

MEM20) explained more variation in abundance-weighted beta diversity (2.0%–10.0%) than incidence-based measures (0.0%–4.0%) (Fig. 5, Fig. 6; Supplementary Table S4; Fig. S4, S5, S6).

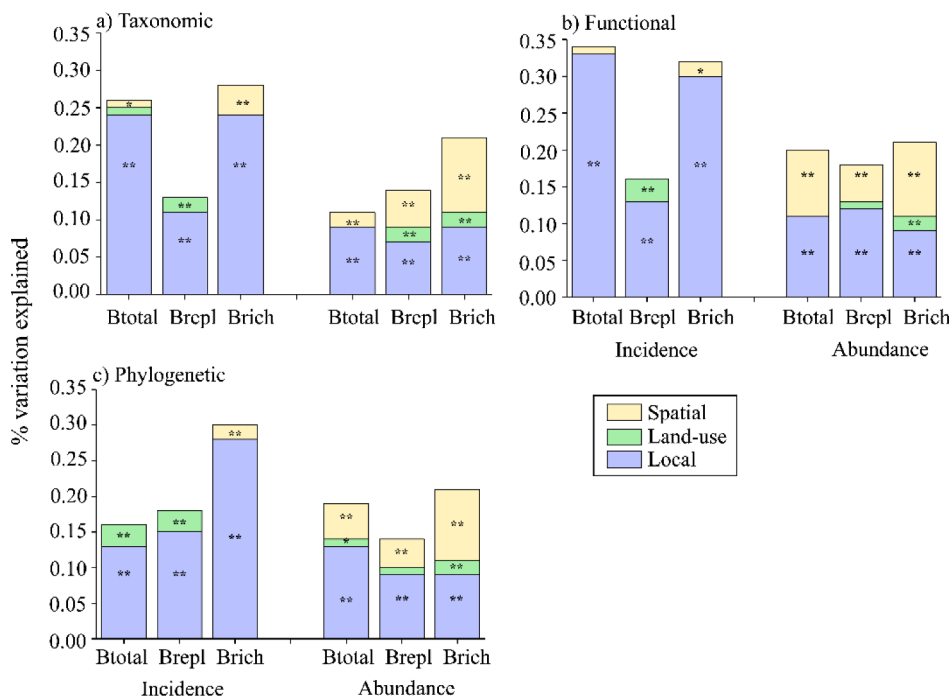


Fig. 6. Variation partitioning for incidence-weighted or abundance-weighted beta diversity of taxonomic, functional and phylogenetic facets (i.e., Btotal, Brepl and Brich) explained by pure effects of local, land-use and spatial factors. Values represent the adjusted R² values. *($P < 0.05$), **($P < 0.01$).

4. Discussion

To our knowledge, this is the first study that demonstrated the divergent responses of incidence-weighted and abundance-weighted beta diversities of river organisms to the urbanization gradient. We here reported several major findings, which mostly corroborated our three hypotheses. Across the entire study system, taxonomic and phylogenetic beta diversities based on incidence data were primarily driven by replacement component, whereas richness difference component contributed more to beta diversity based on abundance data (H_1). Along the urbanization gradient examined, both incidence-weighted and abundance-weighted measures showed increasing homogenization, with stronger patterns being based on incidence data. Such a pattern of homogenization was only determined by the replacement based on abundance data but was nearly equally contributed by replacement and richness difference when based on incidence data (H_2). Furthermore, we detected the deterministic processes (i.e., environmental filtering due to local and land-use factors) generally played a more important role in affecting incidence-weighted beta diversity, while stochastic mechanisms (e.g., dispersal-related processes) gained more relevance in controlling beta diversity weighted by abundance data (H_3). These findings could help to get better insight into the ecological mechanisms behind homogenization of river macroinvertebrate communities under rapid urbanization going on worldwide, the importance of which has been highlighted previously (Gál et al., 2019).

4.1. Divergent responses of incidence-weighted and abundance-weighted beta diversities to urbanization

Across the whole study system, there were similarities and differences in incidence-weighted and abundance-weighted beta diversities. On one hand, compared with the taxonomic facet, functional and phylogenetic beta diversities and associated replacement components were comparatively lower, suggesting functional and phylogenetic redundancy (Harrison et al., 2018; Liu et al., 2022; Swenson, 2011). Such a finding is in accordance with some previous macroinvertebrate studies (Heino and Tolonen, 2017; Jiang et al., 2021). On the other hand, we found that beta diversity was comparatively higher when based on abundance than incidence data. The higher abundance-weighted beta diversity was mainly due to abundance difference, indicating that a strong abundance gradient existed across sites (Baselga and Chao, 2016; Podani et al., 2013). For example, five dominant taxa (i.e., *Limnodrilus* sp., *Limnodrilus Hoffmeisteri*, *Chironomus* sp., *Biphalaria straminea* and *Polypedilum* sp.) accounted for nearly 60% of the total density of macroinvertebrate communities and occurred mainly in the urban river sites. In this case, a low abundance-assemblage is thus a subset of the assemblage with a higher abundance of organisms (Baselga and Chao, 2016). Alternatively, replacement component was dominant in beta diversity based on incidence data, which was consistent with the general pattern found in a variety of taxa and ecosystems (Soininen et al., 2018). One probable explanation for this result is that rare taxa (e.g., many EPT taxa) were not evenly distributed across the sites, and most were present only in a few sites (Supplementary Fig. S7) (Qian and Cuffney, 2014). This result also implies that the urban rivers harbored a species pool which is different from that in less urbanized rivers. Additionally, the different roles of replacement and richness difference to overall beta diversity may be attributable to spatial aggregation (McGlenn et al., 2018). More individuals of abundant taxa could thus be potentially sampled due to a strong spatial aggregation of these taxa in a given site (de Siqueira et al., 2021), thereby resulting in the predominance of richness difference patterns across sites.

We found that both incidence-weighted and abundance-weighted beta diversities declined along the urbanization gradient, which was stronger for incidence data. Also, in line with the second hypothesis, we found that the decrease of beta diversity was differently driven by the

two components for incidence and abundance data. The decreased roles of richness difference based on incidence data suggested the loss of rare taxa with increasing urbanization, while the decreased importance of replacement implied that those taxa remaining in urban areas were mostly shared among sites (Liu et al., 2022; Soininen et al., 2018). In contrast, we found that the decrease of abundance-weighted beta diversity was only due to replacement, implying increasing dominance of a few abundant taxa across sites (Marcacci et al., 2021). As the degree of urbanization increases, these abundant taxa become more ubiquitously distributed in highly urbanized sites, which in turn increases the possibility of shared taxa among communities (Brice et al., 2017).

Our work demonstrated that urbanization also resulted in phylogenetic homogenization of macroinvertebrate communities, which was especially noticed for incidence data. Generally, such a decline of phylogenetic beta diversity could be attributed to at least two opposite processes: filtering of sensitive lineages in more evolutionary distinct clades, and favoring a few tolerant, closely related taxa (Harrison et al., 2018; Sol et al., 2017). We here found that some taxa from the same family (e.g., within the families Tubificidae and Chironomidae) became more frequent along the urbanization gradient. In contrast, many rare aquatic insects (e.g., within the orders Ephemeroptera, Plecoptera, Trichoptera, and Odonata) mainly occurred in the forest rivers (Supplementary Table S5). This means that urbanization could act as a strong environmental filter, shifting from more evolutionary distinct lineages to a subset of more generalist macroinvertebrate clades (Sol et al., 2017).

4.2. Ecological factors underlying beta diversity variations

Although both deterministic and stochastic processes were critical to incidence-weighted and abundance-weighted beta diversities, their relative importance differed considerably. Our results corroborated the third hypothesis that, compared with abundance data, beta diversity based on incidence data was more strongly influenced by deterministic processes. Moreover, negative values of SES indicated that the incidence-weighted assemblages were more phylogenetically and functionally clustered than abundance-weighted assemblages. This suggests that rare and abundant taxa differ in their responses to environmental gradients. Hence, the stronger environmental filtering for rare than abundant taxa may be attributed to their narrow habitat preferences (Leitao et al., 2016) and ecological strategies (Jousset et al., 2017; Pandit et al., 2009). Rare taxa often show a higher degree of environmental specialization (Heino and Grönroos, 2014), and their viability would largely depend on specific environmental factors (Mo et al., 2020). Furthermore, as specialization-disturbance hypothesis depicted (Vazquez and Simberloff, 2002), rare taxa with narrower ecological niches tend to be particularly sensitive to environmental stressors and are thus experiencing higher extinction risk when habitat conditions are altered (McKinney and Lockwood, 1999; Mouillot et al., 2013). Our sites sampled spanned a range of environmental conditions (Supplementary Table S1), where continuous environmental variations could act as strong deterministic filters selecting for specific rare taxa to occur at a site. On the other hand, as niche partitioning suggested, rare taxa typically utilize spatially limited and locally unusual resources, and could be more strongly influenced by local habitat conditions (Gaston et al., 1997). Alternatively, we found that stochastic mechanisms accounted for some variation in incidence-weighted beta diversity too. This result is reasonable because rare taxa may be constrained by demographic stochasticity due to their smaller population sizes (Chase et al., 2005; Orrock and Watling, 2010). In this vein, rare taxa with lower abundances and restricted distributions are prone to random births and deaths (Orrock and Watling, 2010; Siqueira et al., 2012).

Furthermore, we found that spatial factors explained more variation in abundance-weighted beta diversity than in incidence data. This result indicated that, once the abundant taxa are dominant in urban environments, stochastic processes could attain more relevance in shaping beta

diversity. Two plausible mechanisms could account for this pattern. First, the spatial signal on abundance-weighted beta diversity was probably generated by dispersal processes (e.g., drift, mass effects and dispersal limitation) (Heino et al., 2017). Some aquatic organisms, such as worms (e.g., Tubificidae and Naididae), are typically characterized to possess strong ability to drift (Cellot and Juget, 1998), or have higher relative abundances which would enhance their dispersal probability (Liu et al., 2015), thereby resulting in almost ubiquitous distributions. Additionally, strong spatial signals of abundance-weighted beta diversity may also be generated by dispersal limitation (Delettre et al., 1992; Liu et al., 2022). The dispersal of some dipterans (e.g., Chironomidae, Dulicidae, and Ceratopogonidae) was largely constrained by riparian land-use, which could prevent the adults of these aquatic organisms from tracking suitable locations (Delettre et al., 1992). Apart from the importance of dispersal-related aspects, it is possible that ecological drift may play essential roles in driving beta diversity patterns (Chase et al., 2005; Pandit et al., 2009). Most of the abundant taxa may utilize a broad array of resources and have similar environmental adaptations, thus being considered functionally equivalent. Therefore, random fluctuations in the abundances of functionally redundant taxa could also be responsible for relatively higher beta diversity in abundance than incidence data (Fig. 2) (Leitao et al., 2016; Zeni et al., 2020). Furthermore, deterministic processes also explained some variation of abundance-weighted beta diversity. These results may arise from the fact that abundant taxa occupy core ecological niches (Li et al., 2016; Umana et al., 2015). Thus, a much closer association with main habitat conditions can help these abundant taxa effectively exploit available resources (Umana et al., 2015). Specifically, we found that the total explained variations in beta diversity were relatively low. This result agrees with studies conducted elsewhere (Jiang et al., 2021; Rocha et al., 2018; Wu et al., 2022). It is plausible that other potential ecological mechanisms, such as biotic interactions (Vilmi et al., 2016) and unmeasured environmental variables (e.g., heavy metals) (Liao et al., 2019), may be responsible for observed patterns in our study.

4.3. Caveats

There were two methodological aspects that may potentially influence our results. First, given that there is no universal method to categorize species as abundant or rare, we used incidence-weighted and abundance-weighted data as proxies on the relative roles of rare and abundant taxa in community assembly, respectively (Zhao et al., 2021). Generally, incidence-weighted and abundance-weighted measures weigh rare and abundant taxa in different ways in community analysis, thereby providing more comprehensive pictures into community structure (Koleff et al., 2003). Further studies should consider, how to categorize all taxa as rare or abundant (Rabinowitz, 1981), which is especially needed to better understand the roles of different taxa in the homogenization processes. Second, the phylogenetic beta diversity used in this study was calculated based on the Linnean taxonomic tree. Despite that this approach has been applied in previous macroinvertebrate studies (Heino and Tolonen, 2017; Hill et al., 2019; Rocha et al., 2018), a more nuanced approach based on true phylogenies would be worthwhile. Molecular-based phylogenetic beta diversity measures would help to elucidate the real responses of lineages with different evolutionary history to urbanization.

4.4. Implications for urban river management and biodiversity conservation

Our work showed that urbanization not only leads to taxonomic and functional homogenization, but it also resulted in more similar macroinvertebrate communities regarding their evolutionary relatedness. Overall, biodiversity facets and beta diversity components exhibited distinct patterns and responded differently to urbanization. Thus, exploration of different facets and components of beta diversity provides

a holistic understanding of how urbanization affects river macroinvertebrate communities, which have not been thoroughly explored in previous urban river homogenization studies (Gál et al., 2019; Olden et al., 2018). Importantly, our results showed the divergent responses of incidence-weighted and abundance-weighted beta diversities to urbanization. Beta diversity weighted by incidence data may have declined more sharply along the urbanization gradient compared with abundance data, implying that rare taxa are more sensitive to urbanization and may be more prone to local extinctions in highly urbanized environments (Chapman et al., 2018). Given the irreplaceable roles of rare taxa in maintaining key ecological functions and ecosystem stability in aquatic environments (Chapman et al., 2018; Mouillot et al., 2013), our results have clear implications for the conservation of rare taxa and mitigating the decline of river biodiversity in the face of rapid urbanization (Knop, 2016; Mouillot et al., 2013). On one hand, the dominance of replacement component for incidence-weighted beta diversity of taxonomic and phylogenetic facets indicated that a number of sites at the landscape scale should be protected to conserve communities with species sharing distinct phylogeny (Jiang et al., 2021). On the other hand, we found that incidence-weighted beta diversity was mainly driven by deterministic processes, with the local variables being the most important drivers of macroinvertebrate communities. Therefore, it would be feasible to improve local environmental conditions (e.g., habitat physical conditions, and water quality) via restoration to support higher overall biodiversity (Hill et al., 2019; Liu et al., 2022). Overall, by considering the roles of rare and abundant taxa and multiple facets and components of beta diversity, the current study provided a deeper understanding of how urbanization leads to biotic homogenization of river macroinvertebrate communities.

CRediT authorship contribution statement

Zhenyuan Liu: Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft. **Jani Heino:** Conceptualization, Methodology, Writing – review & editing. **Janne Soininen:** Conceptualization, Methodology, Writing – review & editing. **Tingting Zhou:** Conceptualization, Software, Data curation, Formal analysis. **Weimin Wang:** Conceptualization, Investigation, Writing – review & editing. **Yongde Cui:** Conceptualization, Writing – review & editing. **Yushun Chen:** Conceptualization, Writing – review & editing. **Zhengfei Li:** Conceptualization, Writing – review & editing. **Junqian Zhang:** Conceptualization, Formal analysis, Writing – review & editing. **Zhicai Xie:** Conceptualization, Formal analysis, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We acknowledge Mr. Shun Huang for drawing figures in original-draft writing. We acknowledge Mr. Lei Liang and Mrs. Fanghua Wang for their help in field sampling. We thank Mr. Xin Wang (Analytical & Testing Center, Institute of Hydrobiology, Chinese Academy of Sciences) for assistance in data analysis.

Funding

This work was supported by the program “Shenzhen City under the grant of Aquatic Ecological Monitoring and Assessment for Major rivers”

(No. 2019-07-233) and “Special Foundation for National Science and Technology Basic Research Program of China” (Grant No. 2019FY101903). JH was supported by Grant No. 331957 from the Academy of Finland.

Availability of data and materials

All data will be available in the data center of Institute of Hydrobiology, Chinese Academy of Sciences (<https://www.ihb.ac.cn>) after publication.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109357>.

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