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Original Research

Hydrodynamic and trophic variations reshape macroinvertebrate food webs in urban ecosystems

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ABSTRACT

Urbanization is modifying aquatic ecosystems, with hydrodynamic and trophic variations altering biotic assemblages in rapidly expanding cities worldwide. Despite the fundamental bioenergetic role of food webs within these assemblages, their responding mechanism to the hydrodynamic and trophic variations remains largely unknown. Here we show that hydrodynamic and trophic loss, coupled with the weakening of cascade controls by key trophic guilds, leads to a significant decline in the structure, function and stability of macroinvertebrate food webs. Utilizing the allometric diet breadth model and biomass balance model, we established representative food webs for macroinvertebrate groups under varying hydrodynamic and trophic stresses. We found that such losses have reduced ~75% trophic guild richness, ~85% biomass flux, and ~80% biomass storage. These reductions promote trophic guild specialization, further destabilizing food web, eroding interactive strength asymmetry, and diminishing the control of trophic guilds. Furthermore, macroinvertebrate food webs show divergent stability responses under similar stress levels, mainly driven by differences in the cascade controls exerted by key trophic guilds. Our results underscore the critical role of hydrodynamic and trophic variations in shaping urban aquatic ecosystems and highlight the significance of both external environmental revitalization and internal food web dynamics enhancement in restoring the ecological stability in urban settings.

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1. Introduction

Over half of the global population now lives in cities, and this percentage will increase to two-thirds by 2050 [1,2]. Today, unprecedented urbanization rates are occurring in the developing world, mainly in Asia and Africa [3], where many smaller cities have rapidly transformed into megacities [2]. A growing number of cities and the formation of a large urban agglomeration have further intensified resource use and biodiversity and, consequently, ecosystem degradation [4]. The ecosystems of many urbanized environments worldwide are also exposed to warmer climates [5] and modified land use [6], thus having become increasingly

homogeneous [7] and fragmented [8]. This phenomenon, known as the “urban syndrome”, often results in urban ecosystems acting as unstable systems with reduced resistance and resilience against disturbances [9] and markedly deteriorated ecosystem goods and services [10].

For instance, in freshwater ecosystems such as rivers, streams, lakes, and reservoirs, less permeable land cover resulting from urban growth can alter the hydrological process, leading to larger, more frequent flood events [11]. Urban channel regulation substantially modifies flow dynamics, sediment transport, nutrient cycling, and pollutant dispersion, thus degrading the aquatic environment [8,12,13]. Hydrodynamic and trophic conditions are crucial factors that influence biotic assemblages in these altered urban aquatic systems [14,15]. Specifically, trophic conditions, or the availability of allochthonous and autochthonous food sources, provide the necessary material and energy to initiate, develop, and

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maintain biotic assemblages in the urban environment [16]. Through interactions with substrates, hydrodynamic conditions play a direct role in determining the heterogeneity [17], suitability [18], and stability [19] of aquatic habitats. Hydrodynamics can also indirectly affect biotic assemblages by influencing trophic dynamics. Specifically, flow velocity impacts the distribution and retention of food sources [15], while water depth, associated with temperature and oxygen stratification and light availability, influences primary productivity [20] and energy transfer efficiency [21].

As one of the most important biotic components of the aquatic system, macroinvertebrates act as critical links between basal food sources (e.g., primary production and detritus) and higher trophic levels (e.g., fish) in the food web [22]. Due to their limited mobility, higher sensitivity to disturbances, and predictable responses to the environment, as revealed by their compositional changes [23], these biota are qualified indicators of the dynamics of aquatic ecosystems and are, therefore, widely used for rapid biomonitoring and bioassessment programs for the ecological health of rivers, streams, lakes, and reservoirs [24–26].

The diversity and composition of macroinvertebrates in response to hydrodynamic and trophic variations in urban aquatic systems have been investigated worldwide [27–30]. Macroinvertebrates achieve optimal diversity when hydrodynamic and trophic conditions are moderately favorable [31]. However, extreme environmental variations can disrupt this equilibrium, leading to dominance by fugitive species or superior competitors for available niches and declining diversity [18]. In particular, shifts in macroinvertebrates occur in response to extreme urban eutrophication and oxygen depletion, characterized by a range of adaptation strategies to change, such as smaller body size, multiple reproductive cycles per year (multivoltinism), burrowing capabilities, and a modified predation approach [32,33]. With increased river trophy, primary macroinvertebrate taxa, such as amphipods, decapods, dipterans, ephemeropterans, and odonates, exhibit a subsidy-stress (unimodal) response to system disturbance. In contrast, a few groups, including coleopterans and hemipterans, often show a monotonic increase, whereas trichopterans consistently show a decrease in the assemblage at a time of increased river and lake trophy [34,35].

Hydrodynamic conditions also differentiate macroinvertebrate preferences. For instance, approximately 30% (e.g., oligochaetes and gammarids), over 60% (e.g., baetids, hydropterygids, and nemourids), and less than 10% (e.g., simuliids) of taxa favor weak, moderate, and strong hydrodynamic conditions, respectively [36]. Hydrodynamic losses and increased sedimentation create conditions only favorable for species, such as chironomid midges, oligochaetes, and gastropods, which are tolerant of disturbances, causing them to dominate the habitat [24,37,38]. Conversely, intense hydrodynamic conditions often dislodge most macroinvertebrates from their respective habitats. Studies have indicated that aquatic macroinvertebrates with morphological or behavioral adaptations can withstand disturbances, thus increasing their chances of survival [36].

Despite extensive research on the diversity and composition of macroinvertebrates, a comprehensive understanding of the interactive networks involved in the response of biota to urbanized and disturbed aquatic systems and associated environmental factors is lacking [39,40]. Specifically, the macroinvertebrate food web, consisting of trophic interactions, such as predation and competition, illustrates the intricate relationships in the biological assemblages of a given aquatic ecosystem [22,41]. Thus, one should recognize that macroinvertebrates form a collection of individual species and an extensively interconnected biotic system through a web of species interactions and dynamics [42,43]. The arrangement and

strength of these interactions are crucial for determining the composition and diversity of macroinvertebrates and maintaining the entire aquatic ecosystem's stability [44]. Therefore, this issue is vital for understanding urban aquatic ecosystems' functioning.

Based on previous observations of the terrestrial food web [45,46] and trophic extensions of island biogeography theory [47], we have made a preliminary prediction of how hydrodynamic and trophic variations influence the macroinvertebrate food web in urban ecosystems. Increased hydrodynamic condition losses and limited trophic sources can alter the macroinvertebrate food web. Such food webs are often simplified in structure, function, and stability due to the heightened vulnerability of higher trophic-level organisms and the extinction of specialists facing stressed conditions [48,49]. Consequently, the influence of hydrodynamic and trophic variations on the macroinvertebrate food web in urban aquatic ecosystems is predictable because such variations often lead to a more truncated trophic network.

Quantifying changes in the structure, function, and stability of the macroinvertebrate food web in megacities such as Beijing significantly contributes to understanding the urban ecosystem, thus leading to improved urban management. To this end, we conducted extensive field investigations across Beijing in 2019 and 2020 for ecological and food web analyses of the city's different water bodies, including rivers, streams, lakes, and reservoirs. We aimed to achieve the following: (1) identify the representative biological groups across a gradient of hydrodynamic and trophic stresses in Beijing and characterize these groups' macroinvertebrate diversity and composition, (2) establish representative food webs to characterize the trophic structure and estimate the biomass flux of each biological group, (3) determine the food web stability and identify the key trophic guilds for individual biological groups, and (4) analyze how macroinvertebrate food web structure, function, and stability is impacted by stresses related to hydrodynamic and trophic variations in the rapidly urbanized areas of Beijing.

2. Materials and methods

2.1. Study area and sampling design

Beijing (115.7–117.4° E, 39.4–41.6° N; 16,410 km²), China's capital city, is one of the largest megacities in the world, supporting a population as high as 22 million. The local gross domestic product of Beijing is CNY 4026.9 billion (around USD 554.5 billion), ranking seventh highest among global cities in 2022. Located in the median latitudes, Beijing has a monsoon climate with a temperature ranging from –5 to 35 °C (12 °C, on average) and a mean annual precipitation of around 600 mm. From 2019 to 2020, we surveyed a range of environmental conditions and sampled benthic macroinvertebrates in the five main river systems in Beijing, including the Yongding, Chaobai, Beiyun, Jiyun, and Daqing. We conducted field investigations from late summer to early autumn 2019 and 2020 to avoid the disturbances of mid-summer flood events.

Based on the Beijing Water Authority's technological regulations, 61 investigation sites were preliminarily classified into four types of water bodies based on broad landscape-scale features: suburban rivers (14 sites), urban rivers (16 sites), artificial lakes (ten sites), and water supplying reservoirs (21 sites) [50]. For each site, we conducted 3–12 sampling events across different periods, cumulatively yielding 219 samples (patch scale, equivalent sampling area of 1 m²; Fig. 1). Detailed conditions of the four types of water bodies are shown in [Supplementary Material Fig. S1](#). The methodological specifics for the collection of macroinvertebrate samples, the gathering of coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM), and the measurements

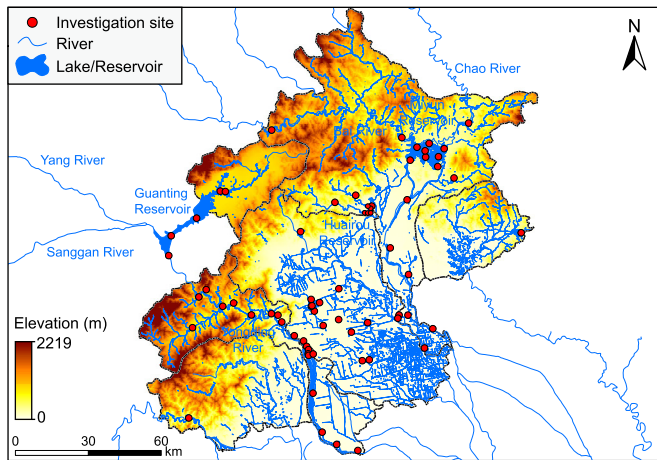


Fig. 1. Distribution of the investigation sites for the dynamics and structure of the freshwater food webs in Beijing.

of hydrodynamic conditions (including the mean flow velocity [v] and water depth [h]) and trophic conditions (including the chemical oxygen demand [COD_{Mn}], the concentration of chlorophyll- a [Chl_a], total nitrogen [TN], and total phosphorus [TP]) are elucidated in [Supplementary Material Text S1](#).

2.2. Hydrodynamic and trophic stresses quantification

How the hydrodynamic and trophic variations associated with urbanization would cause stress on the water body in Beijing was quantified using a data-driven scoring method, hereafter referred to as the hydrodynamic and trophic stress score (HTSS). In addition to the 219 samples, ten other sites were selected and sampled as “reference sites” following Moss et al. [51], who described the site characteristics as natural and primitive. The statistical means of values of environmental variables (noted as X_{ref}) for these reference sites represented ideal natural conditions for water bodies in Beijing. Given the varying degrees of hydrodynamic and trophic stresses in Beijing, the environmental variable values for the 219 samples ranged from minimum (X_{min}) to maximum (X_{max}) conditions, which also encompassed the reference condition, X_{ref} ([Supplementary Material Fig. S2](#)). Therefore, we derived the gradient lengths of environmental variables for the 219 samples that were lower ($L = X_{ref} - X_{min}$) and higher than the reference sites ($H = X_{max} - X_{ref}$).

For values that fell in the interval [$X_{ref} - 10\%L$, $X_{ref} + 10\%H$], we evaluated this environmental condition as “near-reference” and assigned a score of 0 to the samples. For the values that fell in the intervals [$X_{ref} - 40\%L$, $X_{ref} - 10\%L$] or [$X_{ref} + 10\%H$, $X_{ref} + 40\%H$], we determined that these environmental conditions were “slightly stressed” and assigned scores of -2 and 2 , respectively. The conditions of “stressed” samples were assigned a score of -4 ($[X_{ref} - 70\%L$, $X_{ref} - 40\%L]$) or 4 ($[X_{ref} + 40\%H$, $X_{ref} + 70\%H]$), and the conditions of “heavily stressed” samples were assigned a score of -6 ($[X_{min}$, $X_{ref} - 70\%L]$) or 6 ($[X_{ref} + 70\%H$, $X_{max}]$). Thus, the two hydrodynamic and four trophic stresses of each sample were scored using the HTSS, as shown in [Supplementary Material Table S1](#). Integrated stress for a sample was then quantified by the sum of the absolute values for the HTSS of different hydrodynamic and trophic variables, with a higher value representing heavier stress. Notably, the positivity or negativity of the score for a specific environmental variable indicated only a higher or lower value than the reference site.

2.3. Biological group classification

Based on the preliminary classification of water bodies in Beijing (suburban and urban rivers, artificial lakes, and reservoirs), hierarchical clustering (R package “stats”, function “hclust” [52]) was applied to the 219 samples to determine the types of biological groups. Pairwise distances between sites were measured using macroinvertebrate dissimilarities calculated by the Bray–Curtis formula (R package “vegan”, function “vegdist” [53]). To assess whether assemblages in the classified biological groups correlated with hydrodynamic and trophic conditions, a canonical correspondence analysis (R package “vegan”, function “cca”) was then applied to the macroinvertebrate data for the sample’s distribution over the gradients of these two environmental factors. Due to the normality and variance homogeneity of data, the overall difference in stress scores and biotic indices among biological groups was tested using Kruskal–Wallis analysis, and post-hoc analysis was performed using the Bonferroni-corrected method (R package “agricolae”, function “kruskal” [54]). Moreover, an analysis of similarities was applied to compare the compositions of macroinvertebrates among groups measured by the Bray–Curtis distance, with post-hoc significance detected by the Bonferroni-corrected method (R package “vegan”, function “anosim”).

2.4. Food web analysis

A food web analysis of macroinvertebrates was performed using the allometric diet breadth model (ADBM) [55] and the biomass balance model [56]. The ADBM predicts the foraging behavior of the biological community and food web structure and dynamics, thus helping to provide a mechanistic, structural model of the food web in the river system [57]. To obtain the complete food web structure and dynamics as a predation preference matrix, 29 trophic guilds (see [Supplementary Material Table S2](#)) were assigned to macroinvertebrates based on their taxonomic positions and feeding traits [58]. Herbivores and detritivores mainly fed on primary producers and particulate organic matters, respectively. The predation preferences for (facultative) carnivores were thought to be largely determined by foraging profitability, which was quantified using ADBM. Given the food web (i.e., the predation preference matrix), the biomass flux along the web was estimated using the biomass balance model. This model would yield a predation flux matrix for the food web, which could be further calculated for stability estimation and key trophic guild identification [59]. This methodology for food web analysis has been successfully applied to both terrestrial and aquatic ecosystems worldwide (e.g., African rivers [21], North American lakes [57], European farmlands [56], Arctic tundra [60], and Arctic streams [61]). Details outlining the methodology used for food web analyses are provided in [Supplementary Material Text S2](#).

3. Results

3.1. Environmental and biotic characteristics of biological groups

A total of 32,063 macroinvertebrates belonging to 52 families and 124 genera were collected from Beijing water bodies. Arthropoda was the most predominant group (104 genera), followed by Mollusca (19 genera) and Annelida (12 genera). Hierarchical clustering ([Fig. 2a](#)) identified five types of biological groups for 219 samples, comprising G1 (52 samples), G2 (35 samples), B3 (66 samples), B4 (17 samples), and B5 (49 samples). The compositions of individual biological groups in water body type and the river drainage system in the Beijing megacity indicated that the samples in G1, G2, and G3 came from multiple sources ([Fig. 2b and c](#)),

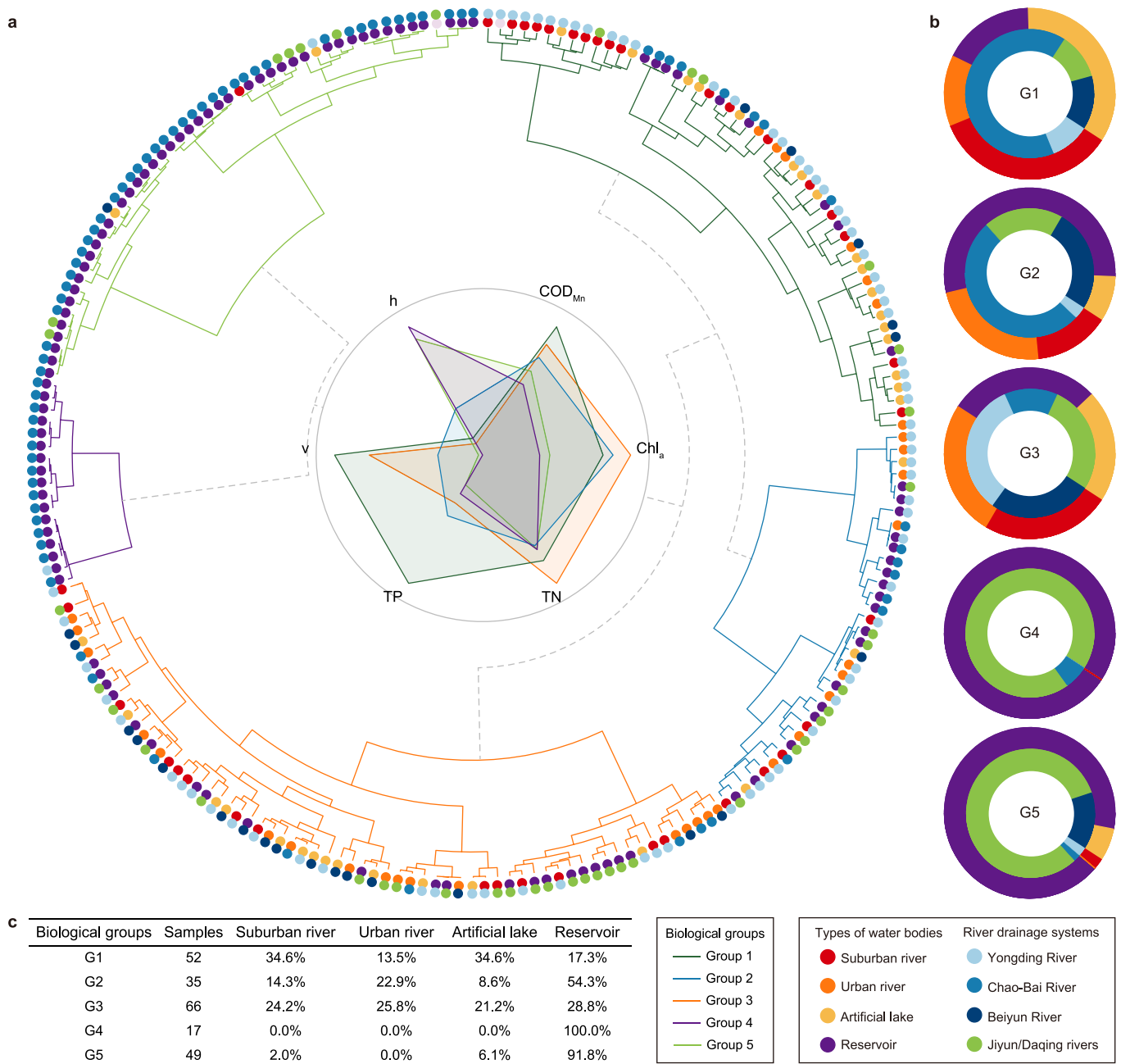


Fig. 2. a, Classification of five biological groups (G1–G5) for 219 samples from water bodies in Beijing based on hierarchical clustering. Pairwise dissimilarity among samples was measured by the Bray–Curtis distance. Relative values for hydrodynamic (*v* and *h*) and trophic (COD_{Mn} , Chl_a , *TN*, and *TP*) conditions among groups were normalized and compared in the central radar plot. b, Sample composition for the G1–G5 regarding the water body type and river drainage system. c, Proportional composition for the G1–G5 in different water body types samples.

suggesting that these patch-scale groups did not strictly correspond to the type of water body or drainage system at a landscape scale. In contrast, G4 and G5 were mostly composed of samples from reservoirs in the Jiyun and Daqing rivers (Fig. 2b and c). A detailed summary of HTSSs on water bodies is provided in Supplementary Material Table S3.

Significant differences among the five biological groups were observed via eight HTSS environmental variables (except *TN*) and 17 biotic indices (Table 1). Integrated stress, calculated as the sum of the absolute value of the HTSS of each environmental variable, was significantly lower for G1–G3 (17.6 ± 5.2 , hereinafter mean \pm s.d.)

than it was for G4–G5 (21.9 ± 4.0). Trophic conditions, calculated as the average of the HTSSs of trophic variables, were higher for G1–G3 (-0.33 ± 1.85) compared to G4–G5 (-1.66 ± 1.71), as indicated by increased concentrations of COD_{Mn} , Chl_a , and *TP*. G1–G3 exhibited relatively less hydrodynamic stress (4.13 ± 1.72), calculated as the average of the absolute values of the HTSSs of *v* and *h*, than G4–G5 (5.75 ± 0.68), as indicated by a higher flow velocity and a lesser water depth. Meanwhile, although not statistically significant, the samples from G1 were more trophically enriched and less hydrodynamically stressed than those from G2 and G3.

Table 1

Values (mean ± s.d.) of hydrodynamic and trophic stress score (HTSS) and biotic indices for five biological groups (G1–G5) in water bodies in the city of Beijing. Regular superscript represents significant ($p < 0.05$) in Kruskal-Wallis and post hoc test results, and italic superscript represents significant ($p < 0.05$) in ANOSIM and post hoc test results. Abbreviations: RA = relative abundance, EPT = Ephemeroptera, Plecoptera, and Trichoptera, RB = relative biomass. Groups in brackets indicate the number of the sample data.

HTSS/Biotic index		G1 (52 samples)	G2 (35 samples)	G3 (66 samples)	G4 (17 samples)	G5 (49 samples)		
HTSS	Integrated stress	16.7 ± 5.4 ^{G4,G5}	17.7 ± 5.0 ^{G4,G5}	17.6 ± 5.2 ^{G4,G5}	21.8 ± 3.3 ^{G1,G2,G3}	21.9 ± 4.2 ^{G1,G2,G3}		
	Trophic	Trophic condition	0 ± 2.0 ^{G4,G5}	-0.6 ± 1.5	-0.2 ± 1.9 ^{G4,G5}	-1.7 ± 1.5 ^{G1,G3}	-1.6 ± 1.8 ^{G1,G3}	
		<i>COD_{Mn}</i>	2.2 ± 3.2 ^{G2,G4,G5}	-0.1 ± 2.6 ^{G1}	0.9 ± 2.8 ^{G4,G5}	-2.0 ± 3.1 ^{G1,G3}	-1.1 ± 3.2 ^{G1,G3}	
		<i>Chl_a</i>	-0.9 ± 3.0	-0.1 ± 2.3 ^{G5}	-0.6 ± 3.2 ^{G5}	-2.2 ± 2.0	-2.1 ± 2.5 ^{G2,G3}	
		<i>TP</i>	-0.4 ± 3.3 ^{G5}	-0.8 ± 3.3	-0.4 ± 3.1 ^{G5}	-2.0 ± 3.4	-2.6 ± 3.4 ^{G1,G3}	
	Hydrodynamic	Hydrodynamic stress	3.5 ± 1.7 ^{G2, (G4),G5}	4.7 ± 1.7 ^{G1,G3, (G4),G5}	3.9 ± 1.6 ^{G2, (G4),G5}	6.0 ± 0 ^{(G1), (G2), (G3)}	5.7 ± 0.7 ^{G1,G2,G3}	
		<i>v</i>	-4.7 ± 2.2 ^{G2, (G4),G5}	-5.6 ± 1.4 ^{G1}	-5.0 ± 1.8 ^{(G4),G5}	-6.0 ± 0 ^{(G1), (G3)}	-6.0 ± 0.3 ^{G1,G3}	
	Biotic indices	Biodiversity	<i>h</i>	2.4 ± 2.1 ^{G2, (G4),G5}	3.8 ± 2.7 ^{G1, (G4),G5}	2.9 ± 2.3 ^{(G4),G5}	6.0 ± 0 ^{(G1), (G2), (G3)}	5.5 ± 1.3 ^{G1,G2,G3}
			Taxa richness	10 ± 9 ^{G4,G5}	5 ± 4	5 ± 3 ^{G4,G5}	3 ± 1 ^{G1,G3}	3 ± 1 ^{G1,G3}
			Shannon-Wiener Index	1.3 ± 0.8 ^{G4,G5}	1.1 ± 0.7 ^{G4}	1.3 ± 0.5 ^{G4,G5}	0.5 ± 0.4 ^{G1,G2,G3}	0.9 ± 0.4 ^{G1,G3}
Compositional Structure		Arthropoda richness	5.2 ± 6.6 ^{G3,G5}	2.4 ± 2.8 ^{G3,G4,G5}	1.2 ± 1.9 ^{G1,G2}	0.9 ± 0.4 ^{G2}	1.1 ± 0.8 ^{G1,G2}	
		Abundance (ind. m ⁻²)	1067 ± 4986 ^{G3,G4}	129 ± 114 ^{G3,G4}	201 ± 180 ^{G1,G2,G4}	2048 ± 1271 ^{G1,G2,G3,G5}	144 ± 89 ^{G4}	
		RA of Arthropoda (%)	41 ± 36 ^{G2,G3,G4}	68 ± 27 ^{G1,G3,G4,G5}	15 ± 21 ^{G1,G2}	3 ± 3 ^{G1,G2}	21 ± 18 ^{G2}	
		RA of Mollusca (%)	46 ± 37 ^{G2,G3,G4,G5}	24 ± 26 ^{G1,G3,G4,G5}	82 ± 23 ^{G1,G2,G4,G5}	0 ± 1 ^{G1,G2,G3}	4 ± 8 ^{G1,G2,G3}	
		RA of Annelida (%)	13 ± 30 ^{G3,G4,G5}	8 ± 12 ^{G4,G5}	2 ± 6 ^{G1,G4,G5}	96 ± 3 ^{G1,G2,G3}	76 ± 19 ^{G1,G2,G3}	
		RA of Insecta (%)	24 ± 23 ^{G2,G3,G4}	66 ± 27 ^{G1,G3,G4,G5}	9 ± 13 ^{G1,G2,G5}	3 ± 3 ^{G1,G2}	21 ± 18 ^{G2,G3}	
		RA of EPT (%)	9 ± 17 ^{G2,G3, (G4), (G5)}	1 ± 5 ^{G1}	2 ± 8 ^{G1}	0 ± 0 ^(G1)	0 ± 0 ^(G1)	
Functional Structure	RA of Chironomidae (%)	6 ± 11 ^{G2,G5}	64 ± 27 ^{G1,G3,G4,G5}	6 ± 9 ^{G2,G5}	3 ± 3 ^{G2,G5}	21 ± 18 ^{G1,G2,G3,G4}		
	Dominance	0.43 ± 0.32 ^{G4,G5}	0.44 ± 0.28 ^{G4}	0.35 ± 0.18 ^{G4,G5}	0.74 ± 0.23 ^{G1,G2,G3}	0.51 ± 0.22 ^{G1,G3}		
	Biomass (g m ⁻²)	15.354 ± 26.698 ^{G5}	18.264 ± 30.631 ^{G5}	17.501 ± 17.567 ^{G5}	3.901 ± 1.951 ^{G5}	2.966 ± 1.214 ^{G1,G2,G3,G4}		
	RB of filtering collector (%)	14 ± 24 ^{(G4),G5}	6 ± 14 ^{(G4),G5}	10 ± 20 ^{(G4),G5}	0 ± 0 ^{(G1), (G2), (G3)}	0 ± 1 ^{G1,G2,G3}		
	RB of gathering collector (%)	15 ± 31 ^{G2,G3,G4,G5}	34 ± 38 ^{G1,G3,G4,G5}	1 ± 4 ^{G1,G2,G4,G5}	95 ± 18 ^{G1,G2,G3}	81 ± 30 ^{G1,G2,G3}		
Tolerance	RB of scrapper (%)	60 ± 38 ^{G3,G4,G5}	48 ± 43 ^{G3,G4,G5}	84 ± 23 ^{G1,G2,G4,G5}	4 ± 18 ^{G1,G2,G3}	15 ± 30 ^{G1,G2,G3}		
	Biological Index	5.6 ± 1.8 ^{G2,G4,G5}	6.7 ± 1.2 ^{G1,G3,G4,G5}	5.6 ± 0.7 ^{G2,G4,G5}	9.1 ± 0.3 ^{G1,G2,G3}	8.5 ± 0.6 ^{G1,G2,G3}		
Assemblage structure	G1 ^{G2, G3, G4, G5}	G2 ^{G1, G3, G4, G5}	G3 ^{G1, G2, G4, G5}	G4 ^{G1, G2, G3, G5}	G5 ^{G1, G2, G3, G4}			

The results of the canonical correspondence analysis (Fig. 3) also clearly discriminated the distributions of the 219 samples from five biological groups along the gradients of trophic conditions and hydrodynamic conditions and indicated consistent results in group-trophy and -hydrodynamics relationships with those presented in Table 1. In brief, the integrated stress on the five groups exhibited an increasing gradient from G1 to G2 + G4 to G4 + G5, with groups suffering from growing trophic deficiency and

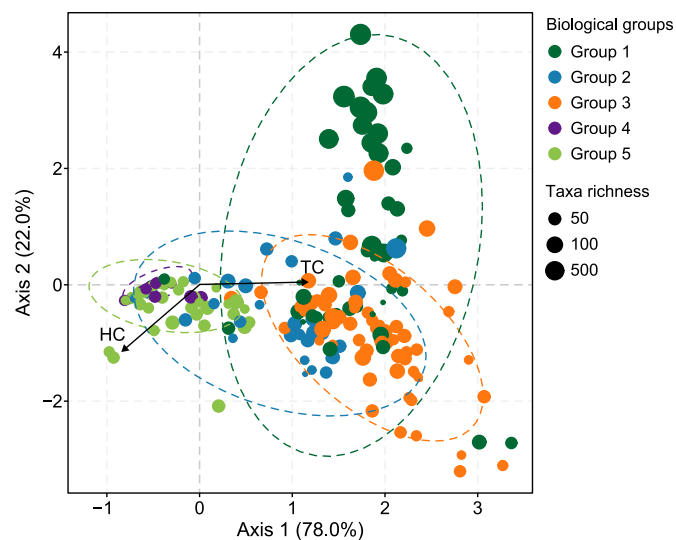


Fig. 3. Canonical correspondence analysis coordinates the 219 samples collected from the five biological groups (G1–G5), examining their distributions along gradients of hydrodynamic (HC) and trophic (TC) conditions.

hydrodynamic losses along this gradient. Macroinvertebrate characteristics, including biodiversity, morphological, and functional structures, and tolerance, were also found to differ among groups (Table 1). In contrast to increasing hydrodynamic and trophic stresses, a decreasing trend in macroinvertebrate richness was observed in G1 (10 ± 9), G2 + G3 (5 ± 3), and G4 + G5 (3 ± 1). G1 comprised a comparable number of arthropods (relative abundance [RA]: 41 ± 36%) and mollusks (RA: 46 ± 37%). Among aquatic insects, Ephemeroptera, Plecoptera, and Trichoptera (EPT) were found to be 1.5 times more abundant than chironomids. Despite the similar taxa richness in G2 and G3 and in G4 and G5, the taxa composition was found to differ to a great extent among groups. Specifically, arthropods (RA: 68 ± 27%; especially insects, RA: 66 ± 27%) dominated over mollusks (RA: 24 ± 26%) in G2, while mollusks (RA: 82 ± 23%) dominated over arthropods (RA: 15 ± 21%) in G3. Notably, aquatic insects in G2 were mainly composed of chironomids (RA: 64 ± 27%) rather than EPT taxa (RA: 1 ± 5%). As for G4 and G5, oligochaetes (RA: 96 ± 3%, G4; 76 ± 19%, G5) dominated both, leading to significantly higher dominances in G4 + G5 (0.57 ± 0.24) than those in G1 + G2 + G3 (0.40 ± 0.26). G5 was also composed of considerable individual chironomids (RA: 21 ± 18%).

As the trophic conditions decreased, the biomass of the biological groups significantly decreased from G1 + G2 + G3 (16.946 ± 23.659 g m⁻²) to G4 + G5 (3.207 ± 1.404 g m⁻²). However, more macroinvertebrate individuals were found in both eutrophic (G1: 1067 ± 4986 ind. m⁻²) and oligotrophic groups (G4: 2048 ± 1271 ind. m⁻²), which consequently resulted in the unpredictable response of average individuals of macroinvertebrates to the trophic change. Groups in different trophic conditions were also characterized by different compositions in functional feeding groups. Specifically, scappers feeding on periphyton dominated in

G1 + G2 + G3 (relative biomass [RB]: $68 \pm 37\%$), while gathering collectors feeding on benthic FPOM were mostly found in G4 + G5 (RB: $85 \pm 28\%$). Despite the presence of a small portion of functional feeding groups in all groups (RB: $7 \pm 18\%$), filtering collectors feeding on suspended FPOM in G1 + G2 + G3 (RB: $10 \pm 20\%$) were more abundant than those in G4 + G5 ($0 \pm 0\%$). Moreover, the Biological Index for G1 + G2 + G3 (5.8 ± 1.4) was significantly lower than that for G4 + G5 (8.6 ± 0.6). The lower Biological Index was also consistent with G1, G2, and G3, which mostly consisted of more sensitive taxa (e.g., EPT), and G4 and G5, which mostly comprised more tolerant taxa (e.g., oligochaetes).

3.2. Food web structure, biomass flux, and trophic stability of biological groups

The results of the macroinvertebrate predation preference derived from the ADBM are shown in Fig. 4. This model was not applied to G4 and G5, since the predators were absent in those environments. Of the 28 trophic guilds analyzed, ten (35.7%) were identified as (facultative) predators in G1, while seven out of 21 (33.3%) trophic guilds were identified as (facultative) predators in G2 and G3. One to five trophic guilds were identified as prey significantly preferred by predators in G1, G2, and G3 (Fig. 4, deep red points). Predators with a smaller body size (located in the top-left corner of the predation preference matrix) exhibited a more limited range of prey options in their diet, whereas larger predators (situated in the bottom-right corner of the matrix) consumed multiple prey species simultaneously. Highly preferred prey was also found to be primarily distributed near the matrix diagonal, indicating that preys slightly smaller than predators in body size were the most efficient food source. Due to the observed variances in body size, the same predators in different biological groups might have shown different prey preferences. For instance, the carnivorous beetles in G2 and G3 had much wider diet breadths than those in G1, possibly due to their larger body sizes in G2 and G3.

After predicting the food web structure with the ADBM, the connectance (C) and trophic guild richness (S) were determined for each biological group, as listed in Table 2. The observed response

patterns in G1, G2 + G3, and G4 + G5 under increasing hydrodynamic and trophic stresses showed a decrease in the S, consistent with the decline in taxa richness. This decrease in the S suggests a deterioration of potential trophic interactions or reduced trophic complexity due to trophic deficiency and hydrodynamic loss. In contrast, the C in G1 + G2 + G3 was lower than in G4 + G5, indicating a higher ratio of actual trophic interactions among all potential interactions as stresses increased.

The results of biomass fluxes along food webs derived from the biomass balance model are shown in Fig. 5. Trophic indices associated with food web functioning are listed in Table 2, including the annual biomass flux, biomass storage, energy transfer efficiency (calculated as the ratio of biomass storage to annual flux), the maximal trophic level (TL_{max} , an indicator of trophic complexity, which compensates for the S), the ratio of biomass flux between the green food web (GFW, the primary production-based food web) and the brown food web (BFW, the detritus-based food web), and a portion of primary biomass flux (directly originating from food sources) in the total biomass. With hydrodynamic and trophic stresses in G1 increasing to G2 + G3 and then to G4 + G5, the annual biomass flux decreased continuously, while the biomass storage experienced a minor increase before decreasing significantly. This contrasting response of biomass storage and flux to stresses is further highlighted by G1 exhibiting notably lower energy transfer efficiency than the other biological groups, thus

Table 2
Values of food web structure, function, and stability indices for the five biological groups G1–G5. GFW and BFW indicate the biomass fluxes along the primary production- and detritus-based food web, respectively.

Trophic index	G1	G2	G3	G4	G5
Connectance C	0.26	0.30	0.25	0.47	0.43
Trophic guild richness S	28	21	21	6	7
Annual biomass flux ($g\ m^{-2}$)	51.71	47.32	46.20	9.75	7.41
Biomass storage ($g\ m^{-2}$)	15.35	18.26	17.50	3.90	2.97
Storage/annual flux	0.30	0.39	0.39	0.40	0.40
Maximal trophic level TL_{max}	3.97	3.12	3.20	2.00	2.00
GFW/BFW	0.26	0.41	0.45	0.01	0.29
Primary flux/total flux (%)	93.1	99.0	98.5	100.0	100.0
Average $ \lambda_{min} $	0.380	0.097	0.471	0.001	0.008

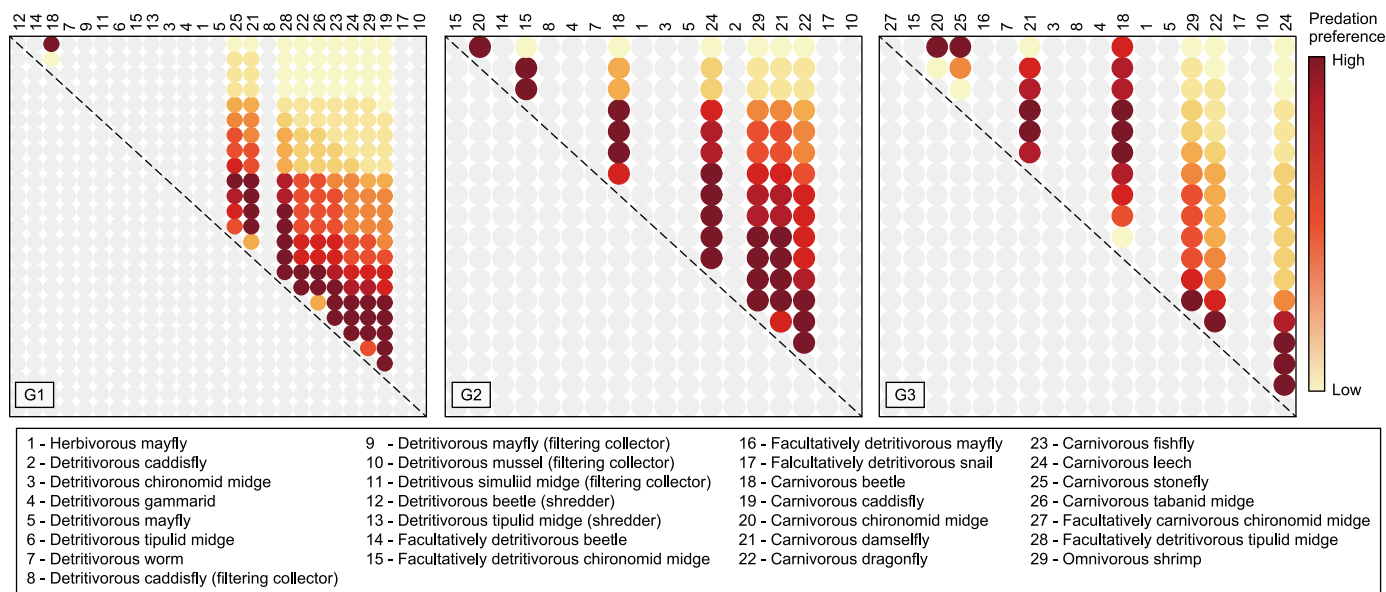


Fig. 4. Macroinvertebrate predation preference matrices are derived using the allometric diet breadth model (ADBM) for the three biological groups (G1–G3). Predators are absent in groups G4 and G5, making the prediction models inapplicable for those environments.

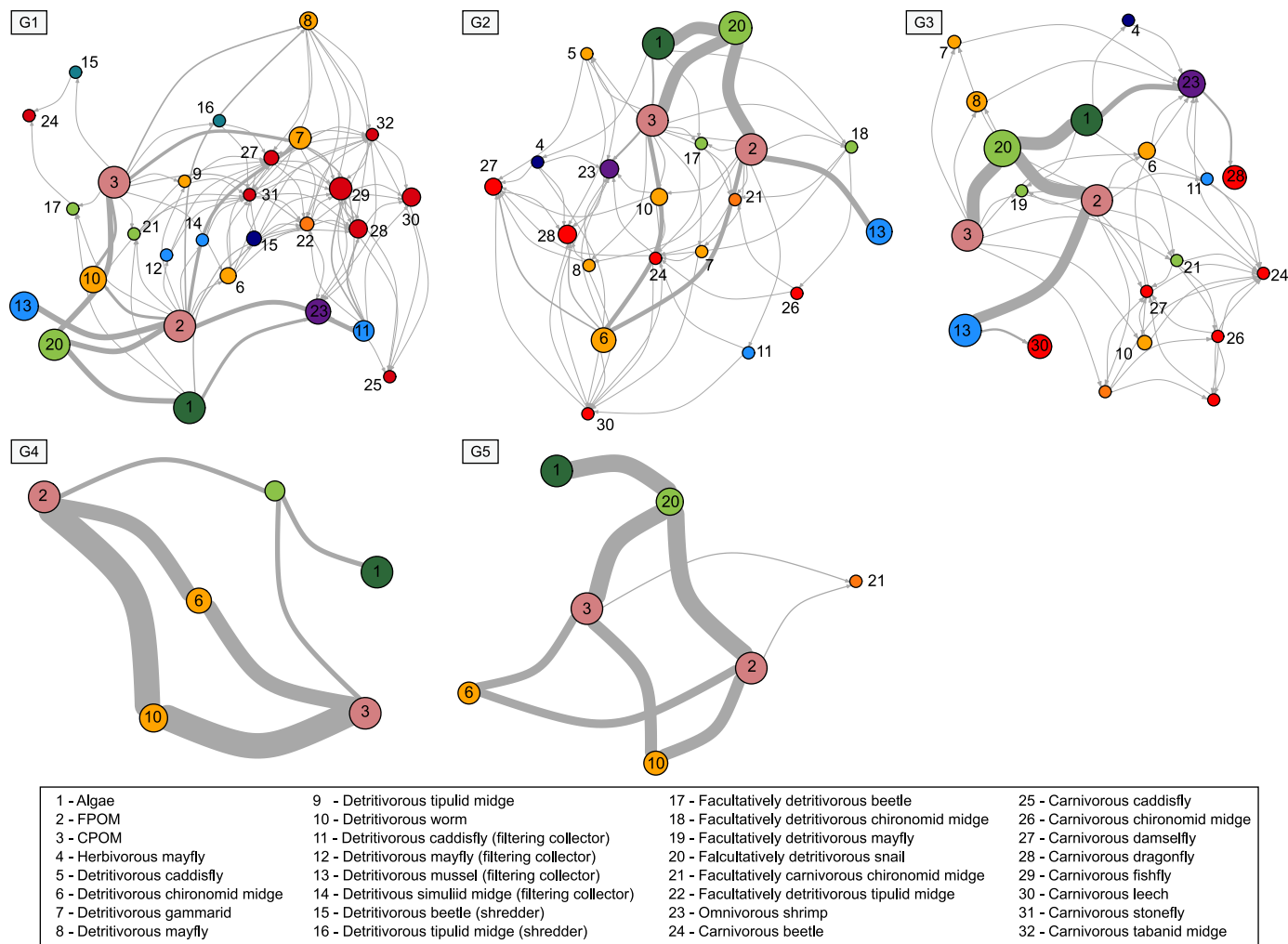


Fig. 5. Biomass fluxes along food webs are estimated using the biomass balance model for the five biological groups (G1–G5). The node size indicates the amount of biomass storage for each trophic guild. The width of the linking vector indicates the amount of annual biomass flux between the trophic guilds.

indicating that trophic guilds in G1 require more biomass input and output (a condition of dynamic biomass exchange) to sustain a unit of biomass storage than they do in other groups. In all groups, the biomass flux from BFW constituted over 69% of the total biomass flux. In contrast, contributions from GFW varied from 1% (G4) to 31% (G3). Biomass flux primarily occurred directly from the food source to the primary consumer, which accounted for over 93% of the total biomass and contributed to all fluxes in G4 and G5 due to the absence of predators.

The $|\lambda_{\min}|$ values yielded by 1000 stability analysis iterations for each biological group are shown in [Supplementary Material Fig. S3](#). Skewed unimodal distributions of the $|\lambda_{\min}|$ were obtained and established as the average $|\lambda_{\min}|$ ([Table 2](#)). The average $|\lambda_{\min}|$ showed the following decreasing order: G3 > G1 > G2 > G5 > G4. This finding indicated that food web stability (defined as the potential to return to its original status after disturbance) in G1 + G2 + G3 was markedly higher than in G4 + G5. Interestingly, G3 exhibited the highest stability of all the groups, even though it had greater hydrodynamic and trophic stresses than G1.

3.3. Key trophic guilds in biological groups

Changes in average $|\lambda_{\min}|$ values in response to proportional variations in trophic guild biomasses are shown in [Fig. 6a–f](#). As the

hydrodynamic and trophic stresses increased from G1 to G2 + G3 + G4 + G5, the number of key trophic guilds dominating food web stability declined. Seven trophic guilds were identified as key groups for G1, including four detritivores (chironomids, gammarids, mayflies, and caddisflies), two carnivores (damselflies and fishflies), and facultatively detritivorous tipulids. Among these seven trophic guilds, fishflies, tipulids, and caddisflies dominated G1's food web stability. G1's stability continuously increased as the fishflies rose from 0 to 2 times the original biomass but decreased as the tipulid and caddisfly biomass increased. Chironomids, gammarids, and mayflies also negatively impacted G1's stability, but mainly within the absence range to approximately half of the original biomass. Damselflies positively affected G1's stability, but mainly within the range of less than the original biomass ([Fig. 6a](#)).

In G2–G5, facultatively detritivorous snails markedly dominated the food web stability of biological groups and were the only key trophic guild except for G2, where the detritivorous chironomids also played a significant role. The food web stability in G2–G4 increased as the snail biomass increased from 0 to 2 times the original biomass ([Fig. 6b–e](#)). However, chironomids negatively impacted G2's food web stability but mostly within a range of less than that of the original biomass ([Fig. 6b](#)).

suggesting that urban waters support relatively less diverse macroinvertebrate assemblages compared to suburban waters [68,81]. The biodiversity metrics we used for assessing variations in hydrodynamic and trophic conditions in Beijing have become some of the most effective indicators for distinguishing stress levels among biological groups [68]. In contrast, macroinvertebrate abundance was found to be high in slightly and heavily stressed groups, indicating that the number of macroinvertebrate individuals in a small patch can vary; thus, it may not be a reliable measure for assessment.

This result contrasts previous findings that large-scale terrestrial assemblages consistently decline toward city centers as urbanization stress increases [82]. We attribute the unpredictability of macroinvertebrate abundance to the sensitivity of small-bodied benthos to patch-scale factors, especially local hydrodynamic and trophic conditions [18]. This sensitivity could lead to increased abundance under either slightly stressed conditions (trophic enrichment and higher biodiversity) or heavily stressed conditions (trophic deficiency, lesser biodiversity, and fewer fugitive taxa monopolizing the biological group) [31]. We also observed a markedly negative response from the relative abundance of EPT taxa to increased hydrodynamic and trophic stresses (Table 1). This finding is consistent with the general understanding that most taxa belonging to EPT are particularly sensitive to anthropogenic disturbances and are ideal indicators of habitat primitiveness [18,68].

With an increase in the hydrodynamic and trophic stresses associated with urbanization, we observed marked, predictable changes in the macroinvertebrate food web structure and functioning in Beijing, implying that these metrics can effectively quantify the impacts of environmental variations on aquatic ecosystems concerning bioenergetic processes [83]. As hydrodynamic and trophic stresses intensified, it was argued that trophic guild richness and the maximal trophic level would notably decrease, suggesting that these stresses could promote a structurally and functionally simpler trophic network in urban aquatic systems [59]. Comparable findings have also been documented in terrestrial ecosystems in urban settings [82].

Interestingly, connectance, another measure for describing trophic complexity, exhibited a positive response to urbanization stress in our study. We believe this outcome arose from connectance influenced by the food web structure and the generalist trophic guilds in the food web [82]. Despite an overall decline in macroinvertebrate assemblages due to hydrodynamic and trophic variations, different taxa in our study displayed varying tolerances to stress, with rarer taxa that were more sensitive to change having fewer trophic interactions than the other common taxa. It has been argued that specialist taxa dependent on limited food sources often disappear more quickly than generalists, resulting in a stressed food web more trophically connected by adaptable generalists feeding multiple food sources [82]. Consequently, survivors in the stressed food web were often common in biological groups found in various environments, as illustrated by the Venn diagram in Supplementary Material Fig. S5.

The ratio of biomass flux between GFW and BFW indicates the proportional contributions of various food sources in the ecosystem [84]. Our study found the highest biomass ratios in G2 and G3 (Table 1). Although the BFW, which relied on detritus as a food source, dominated all food webs, the biomass sourced from primary production also played a significant role in G2 and G3, in which algae were relatively abundant (as evidenced by the high Chl_a in Table 1). Conversely, G1 had fewer algae, likely due to increased hydrodynamic conditions, especially speedy water flow [85], resulting in a limited contribution from primary production to this biological group. Despite the increased primary flux (from food source to primary consumer) dominating all groups, we observed a

slight increase in the proportion relative to the total flux as urbanization stress increased. This finding suggests that trophic status (e.g., predators versus preys) can partially predict changes in the food web structure and function under hydrodynamic and trophic variations associated with urbanization [82]. We argue that predators would become more sensitive to these stresses than other lower trophic-level taxa, such as preys [61]. In summary, our findings indicate that the impact of hydrodynamic and trophic variations on food web structure and function is, to an extent, predictable in urban aquatic systems and has significant implications for understanding diverse ecological patterns in anthropogenic disturbances [43].

4.3. Roles of trophic characteristics and key trophic guilds in stabilizing the urban aquatic food web

Our study revealed that trophic characteristics (particularly food web complexity and asymmetric interaction effects) and the main trophic guilds could be the primary factors influencing the stability of urban water bodies in Beijing. Food web complexity, as measured by trophic guild richness S and maximal trophic level $T_{L_{max}}$, indicates the ability of the ecological network system to resist oscillation [86]. Previous studies have suggested that urbanization often leads to habitat homogenization, reducing the strength of ecological niches for different trophic guilds consequently allowing a few trophic guilds to utilize available resources in the system [31]. This condition further simplifies food web complexity, weakening ecological stability [82]. Fewer trophic guilds cannot resist imposing disturbances in the ecosystem when acting as buffers against sudden biomass changes [87]. Our study also observed that as the magnitude of hydrodynamic and trophic stresses increased from G1 to G2 + G3 and then to G4 + G5, trophic complexity became further simplified, and stability generally declined (Table 2).

In addition to changes in trophic complexity, we found that the role of asymmetric interaction strength in stabilizing the food web in biological groups was essential. According to Vázquez et al. [88], asymmetric interactions often have a “degree” and a “strength” in quantitative mutualistic and antagonistic networks. In such networks (e.g., the food web), if a predator affects prey, the prey may not necessarily have a reciprocal effect on the predator. It can have profound implications for ecological dynamics. For instance, we commonly observed exploitative competition modules among macroinvertebrates in food webs in G1–G3 (e.g., algae, FPOM, and CPOM in Fig. 5a–c). Multiple trophic guilds consumed the same food source in these instances, showing different interaction strengths. While strong interactions are generally viewed as unstable, they are offset by weaker interactions that stabilize oscillations by jointly utilizing the growth of the food source [89]. Comparatively, food sources in G4–G5 (e.g., FPOM and CPOM in Fig. 5d and e) were connected with consumers via relatively stronger interactions. A similar asymmetric effect was observed in apparent competition modules, where consumers interacted with multiple food sources with varying strengths in G1–G3 (Fig. 5a–c) but equal strengths in G4–G5 (Fig. 5d and e).

We believe that hydrodynamic and trophic variations associated with urbanization significantly impact the reduction or weakening of the asymmetric effect in Beijing's aquatic food web system. Specifically, hydrodynamic loss and oligotrophication reduce nutrient input into the food web, decreasing carbon energy and food sources. This condition encourages consumers to become more efficient, as evidenced by the increased storage and annual flux ratios (Table 2). It would eliminate low-efficiency consumers, weaken asymmetric interactions, strengthen top–down control, and eventually induce oscillations in the food web [90].

Although food web stability decreased as the stresses in G1 increased to G2 + G3 and then to G4 + G5, G3 had significantly higher stability than G2. Even though G2 and G3 had similar stress levels and were dominated by detritivorous freshwater snails, G3 still had the highest food web stability (Fig. 6b and c). Snails in both biological groups had similar interaction strengths with their food sources, which could have resulted in an unstable module in the food web, as we previously noted when discussing apparent competition. However, we found that G3's instability was considerably reduced by the trophic cascade effect, in which leeches may have acted as weak interaction predators of snails. Studies have indicated that weak predators in the ecosystem often help regulate snail biomass growth and mitigate potential food web oscillations between snails and their food sources [91].

Based on the factors and mechanisms presented in this study, which contribute to a stable food web, we offer several suggestions for the further improvement of urban aquatic ecology in Beijing, specifically stabilizing trophic systems. We have recognized the importance of a safe drinking water supply source for Beijing's residents; therefore, we have approved the city's maintenance of stagnant and oligotrophic reservoir samples (primarily G4 and G5). Despite the negative impact on the macroinvertebrate food web in G4 and G5, we acknowledge the city's efforts to improve water quality. However, for samples in G2 and G3, which mostly consisted of suburban rivers and artificial lakes, we recommend implementing strategies designed to restore increased hydrodynamic and trophic states (Fig. 2b). We propose the following three strategies.

- (1) Increase the volume of ecological replenishment to reduce the time river water remains trapped in fragmented channels. This will effectively enhance the biological group inhabiting hydrodynamic conditions, improve the food web structure and dynamics and nutrient cycling in the system, boost longitudinal connectivity, and meet the natural needs of aquatic biota to complete their lifecycles.
- (2) Carefully plan, monitor, and evaluate engineering strategies that alter the trophic complexity of the food web in biological groups. We oppose channelization and hydrophyte removal because they homogenize substrate conditions, which can harm the diversity of benthic trophic guilds. Instead, small-scale improvements in riverbed structures, such as constructing artificial step-pools or riffle-pools, should be considered. These structures can significantly increase regional habitat heterogeneity and provide additional niches to support the diversity of trophic guilds.
- (3) Implement measures to enhance asymmetric trophic interactions, such as exploitative competition, apparent competition, and trophic cascade. For instance, to amplify the cascade effect, endemic predators could be introduced that feed on snails in food webs in which snails act as the key trophic guild responsible for stability, especially in cases in which modular stabilization from apparent competition is limited [92]. Following these recommendations, Beijing's urban aquatic food web can be improved, leading to a healthier, more stable aquatic ecosystem.

5. Conclusion

Our research provides important insight into the increasing influence of variations in hydrodynamic (reduced flow velocity and increased water depth) and trophic conditions (reduced concentrations of nitrogen, phosphorus, and chlorophyll-a) on the ecosystems of rivers, streams, lakes, and reservoirs across Beijing. A quantitative assessment of macroinvertebrate food web structure

and dynamics is crucial for megacities, such as Beijing, to determine how to invest their resources to improve the conservation and management of urban ecosystems. It should be noted that Beijing experiences persistent hydrodynamic and trophic stresses associated with urbanization, which negatively impacts the city's aquatic food webs and ecosystems. When these stresses become more severe, macroinvertebrate assemblages, the food web structure, and its dynamics will continuously deteriorate, triggering conservation actions from local authorities.

Increased hydrodynamic and trophic stresses in Beijing's urban water bodies would lead to a decrease and a possible shift in taxa richness in which the predominantly EPT community switched into the MCO community. The condition would lead to a simplified food web, usually weaker trophic interactions or lesser complexity, as indicated by trophic guild richness and maximal trophic level change, and trophic guild specialization, as indicated by a connectance change and a reduction in the biomass flux. Our study suggests that the stability of the food web in urban water bodies would decrease in response to hydrodynamic and trophic stresses due to several factors, including reduced trophic complexity, a loss of interaction strength asymmetry (weakening in exploitive and apparent competitions), and control by certain key trophic guilds. However, biological groups may have different food web stability despite uniform hydrodynamic and trophic stresses. This indicates that restabilization of aquatic food webs in megacities such as Beijing requires not only external improvements in environmental conditions but also internal modifications to the structure and dynamic of the food web themselves. Thus, to stabilize the aquatic food web structure and dynamics in megacities, we recommend implementing effective lake and river restoration measures. These measures include revitalizing hydrodynamic conditions (such as flow regimes) and enhancing trophic complexity by increasing trophic guild richness and reinforcing the effects of trophic processes, for instance, strengthening exploitative and apparent competition and controlling cascade.

Data availability

Data will be made available on request.

CRediT authorship contribution statement

Xiondong Zhou: Data Curation, Formal Analysis, Methodology, Visualization, Writing - Original Draft. **Congcong Wang:** Data Curation, Formal Analysis, Investigation. **Giri Kattel:** Conceptualization, Validation, Writing - Review & Editing. **Jiahao Zhang:** Data Curation, Investigation, Methodology, Resources, Validation. **Mengzhen Xu:** Conceptualization, Funding Acquisition, Investigation, Methodology, Project Administration, Resources, Supervision, Validation, 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.

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Appendix A. Supplementary data

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