



Small hydropower dam alters the functional structure of macroinvertebrate assemblages in a Neotropical savanna river

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Abstract Hydropower dams and their reservoirs are major disturbances affecting riverine ecosystems worldwide. However, most existing knowledge comes from large hydropower systems. We evaluated the upstream and downstream effects of a small run-of-river hydropower dam on the functional structure of benthic macroinvertebrate assemblages in a Neotropical savanna river. We found that functional originality and divergence were significantly higher near the dam site. In contrast, functional dispersion was higher at free-flowing sites upstream and downstream of

the dam. Sites near the dam had greater proportions of univoltine organisms with spherical and low-flexibility bodies. On the other hand, free-flowing sites had increased proportions of multivoltine organisms with flattened bodies and flexible. The macroinvertebrate assemblages at all sites were mainly homogeneous and composed functionally generalist taxa. This study enhances our understanding of the environmental effects of small run-of-river dams on benthic macroinvertebrates, emphasizing the usefulness of functional characteristics for those assessments.

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Introduction

The environmental effects of hydropower dams and reservoirs are well-documented worldwide (Ruhi et al., 2018; Arantes et al., 2019; Flecker et al., 2022). However, most of the existing knowledge comes from large hydropower systems (> 30 MW, ANEEL, 2020), with high flow regulation and extended water residence times (Zhang et al., 2010; Chaudhari & Pokhrel, 2022; Ruhi et al., 2022). On the other hand, small hydropower dams (≤ 30 MW, ANEEL, 2020) represent approximately 90% of the global hydropower facilities (Couto & Olden, 2018). In most cases, those facilities are run-of-river systems, considered less environmentally harmful (Anderson et al., 2015; Singh et al., 2015).

Brazilian environmental law defines small hydropower dams as having generating capacities of up to 30,000 MW and reservoir areas of up to 13 km² (ANEEL, 2017). Because most sites suitable for the construction of large hydroelectric dams are already occupied by existing dams, and small hydropower dams have lower construction costs and are easier to license, small dams have been the focus of construction projects in recent decades (Almeida et al., 2009; Fearnside, 2014). Identifying the traits that respond to the environmental impacts caused by the presence of small hydropower dams is essential because traits are less constrained by biogeographic and evolutionary patterns and thus can be more widely and consistently applied and compared to other rivers similarly affected (Martins et al., 2021a). This is especially important for neotropical rivers, because most data on the subject derived from temperate ecosystems (Cortés-Guzmán et al., 2021).

Hydropower dams, even small ones, change the natural flows of water, sediments, wood, and nutrients (Thomson et al., 2005; Ticiani et al., 2022) and cause substantial changes in the structure and dynamics of aquatic habitats, both upstream and downstream of the dams (Xiaocheng et al., 2008; Wang et al., 2022). These changes negatively affect the taxonomic and functional diversity of benthic macroinvertebrates (Petrin et al., 2013; Wang et al., 2023). Furthermore,

dam-altered habitats often favor the establishment of non-native species (Karatayev et al., 2010; Linares et al., 2018; Jovem-Azevêdo et al., 2021), resulting in local functional changes (Wang et al., 2023). Thus, changes in the natural characteristics of a river impose new environmental restrictions, filtering out taxa not adapted to the new conditions and facilitating colonization by invasive species (Ruhi et al., 2018).

Different environmental factors act as filters, selecting functional traits that enable species to survive under specific local conditions (Statzner et al., 2004; Wong et al., 2019). Calapez et al. (2018) found that the respiratory mode responded to low flow and reduced dissolved oxygen, resulting in an increase in the drift of gill breathers, whereas active dispersal (e.g., flying) was affected by the combination of both stressors. The homogenization of the aquatic habitat resulting from land use (e.g., agriculture, pasture, and urbanization) resulted in the loss of macroinvertebrate characteristics with low body flexibility and a univoltine reproductive cycle (Castro et al., 2018). Thus, to characterize the functional composition of benthic assemblages, analyses based on multiple functional traits have recently been used widely (Dedieu et al., 2015; Liu et al., 2021; Roux & Clinton, 2023). Key traits include feeding mode, respiration, voltinism, locomotion, and body flexibility and shape (Luiza-Andrade et al., 2017; Erasmus et al., 2021; Paz et al., 2022).

Although studies have characterized the effects of small hydropower systems on the taxonomic structure of benthic macroinvertebrate assemblages (e.g., Linares et al., 2019; Ferreira et al., 2022; Couto et al., 2023), there is still a knowledge gap on how the functional structure and composition are affected. As part of a large, joint, scientific assessment of the ecological effects of a run-of-river dam in the Pandeiros River basin in Brazil, we aimed to develop methodologies to support decision-making regarding a possible decommissioning of the Pandeiros dam, which, if realized, will be the first in South America. Previous studies in this effort have found significant correlation between the presence of the small hydropower dam and changes in taxonomic structure (Linares et al., 2019), as well as facilitating the establishment of invasive species (Linares et al., 2018, 2022).

This multiyear river study can add to studies by providing temporal data for the planned dam decommissioning. Because benthic macroinvertebrate

assemblages have high turnover rates (Datry et al., 2016; Libório & Tanaka, 2016), multiyear studies can give important insights on how small hydropower dams affect the structure and functioning of benthic macroinvertebrate assemblages. Thus, our data will play a crucial role in assessing the biological effects of dam removal. Therefore, our objective was to understand how a small hydropower dam changed the functional structure of benthic macroinvertebrate assemblages in a Neotropical savanna river. To achieve our objective, we tested two hypotheses. (1) The macroinvertebrate functional traits in sites near the dam differ from those in free-flowing sites. (2) Sites near the dam support a distinct functional diversity and have assemblages with lower specialization compared to free-flowing sites. We predicted that the functional diversity indices (functional richness, functional evenness, functional divergence, functional dispersion, and functional originality) would have lower values, and the assemblages would be more generalist in sites close to the dam (Fig. 1).

Methods

Study area

Our sites were in the 145-km-long Pandeiros River, Minas Gerais State, southeastern Brazil (Fig. 2). The Pandeiros River drainage is a priority conservation area in the Neotropical savanna (Cerrado) (Drummond et al., 2005), being protected by State Law No. 11.901, which established the Environmental Preservation Area (EPA) Pandeiros (Minas Gerais, 1995). The Pandeiros River EPA is 380,000 ha and is formed by a mosaic of phytophysiognomies in the Cerrado biome. The region's semiarid climate is characterized by average temperatures between 26 °C and 29 °C (IGAM, 2014). During the dry and rainy periods studied, average precipitation varied from 14 to 270 mm, respectively (INMET, 2024).

The small hydropower plant (SHP Pandeiros), located in the middle course of the river, was installed in 1957, and its reservoir has an area of 280 ha, with a free crest dam height of 10.3 m (Fonseca et al., 2008). When operational, its turbines produced up to

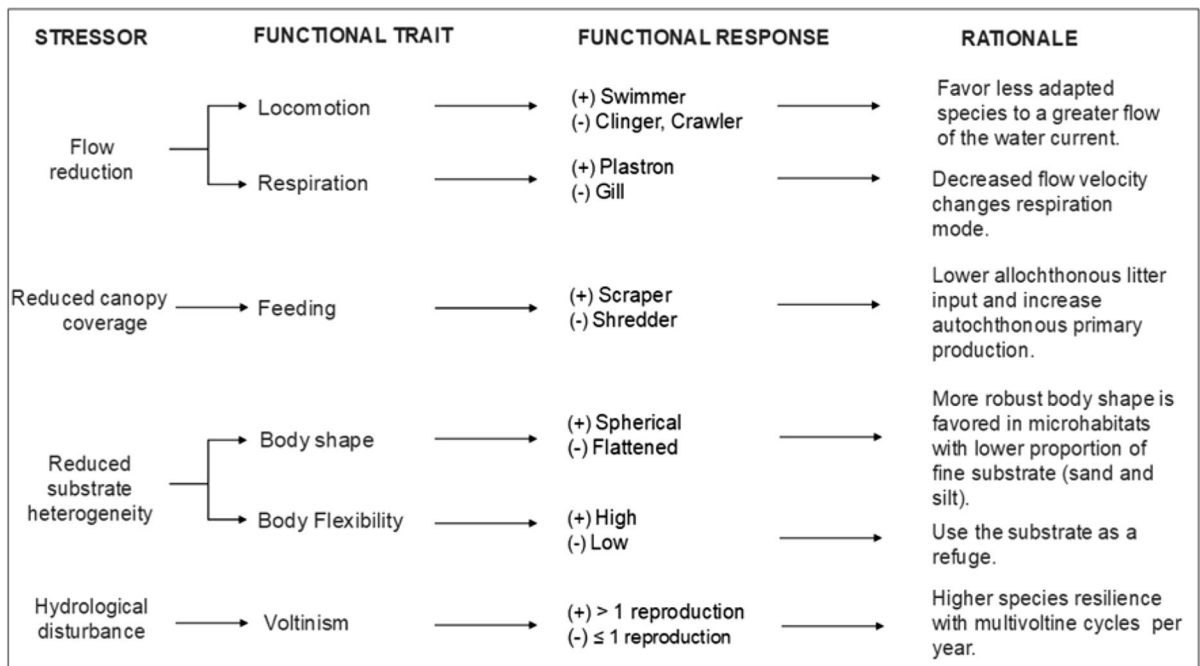


Fig. 1 Predictions for trait category responses to the hydroelectric system. Signs (+) and (–) indicate, respectively, a potential increase or potential decrease in the abundance of a

given trait category (Statzner & Bêche, 2010; Feio & Dolédec, 2012; Castro et al., 2018; Firmiano et al., 2021)

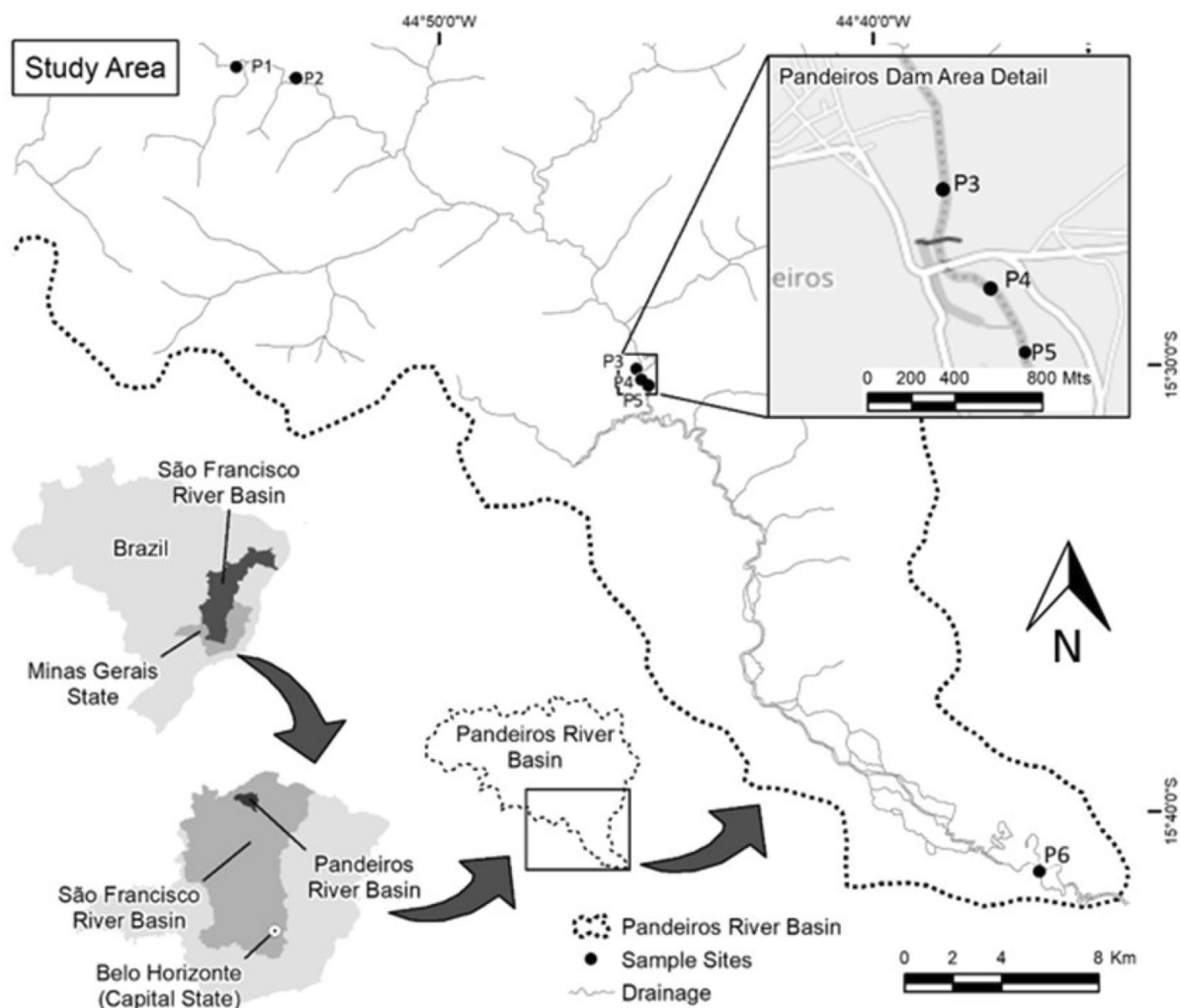


Fig. 2 Site and study area locations

4.2 MW (Fonseca et al., 2008), but its powerhouse was deactivated in 2007. Since then, the Pandeiros River and its tributaries have been studied (Santos et al., 2015; Martins et al., 2021b; Junqueira et al., 2022) to provide data for decommissioning (Linares et al., 2019)

Site selection

We selected six sites (Table 1) to represent the variation of environmental conditions related to the dam and reservoir (Fig. 2). At each site, we measured water temperature ($^{\circ}\text{C}$) and dissolved oxygen (mg/L) with a YSI model ProSolo meter, pH with a Digimed

DM-2P meter, turbidity (NTU) with a Digimed DM-TU meter, and conductivity ($\mu\text{S}/\text{cm}$) and total dissolved solids (TDS) with a Digimed DM-3P meter. In addition, we determined total alkalinity by the Gran method (Carmouze, 1994) with titration of 0.01 N sulfuric acid (Supplementary Material, S1).

Fauna collection and identification

We sampled macroinvertebrate assemblages ten times over five years at each site to assess seasonal and annual differences. Dry season samples were taken in September 2014, April and June 2015, May and August 2019. Rainy season sampling

Table 1 Site locations and descriptions

Site	Geographic coordinates	Dam Proximity	Site description
P1	15°23.364" S 44°54.662" W	Free-flow site upstream of the dam, about 20 km	Wide channel (> 5 m), shallow water depth (< 1 m), and has natural riparian vegetation and a sandy bottom substrate
P2	15°26.454" S 44°49.240" W	Free-flow site upstream of the dam, about 12 km	Wide channel (> 5 m), shallow water depth (< 1 m), and has natural riparian vegetation and a sandy bottom substrate
P3	15°29.921" S 44°45.465" W	Directly affected by the dam, 500 m upstream	Wide channel (> 10 m), low depth (< 2 m), sandy bottom substrate and alternation between areas with natural riparian vegetation and without vegetation along its banks
P4	15°30.289" S and 44°45.442" W	Directly affected by the dam, 50 m downstream	Narrow channel (< 5 m), a deeper water column (> 3 m), sandy sediment in a rocky matrix and natural riparian vegetation on its banks
P5	15°30.773" S 44°45.222" W	Located 500 m downstream from the dam	Wide channel (> 5 m), low water depth (< 1 m), sandy sediment and alternation of natural riparian vegetation with deforested areas
P6	15°41.669" S 44°35.390" W	Located 30 km downstream from the dam	Wide channel (> 5 m), a deeper water column (> 2 m), sandy sediment with a soft bottom and alternation of natural riparian vegetation and pasture on its banks

occurred in December and January 2014, February 2015, November 2019, and February 2020. We collected four substrate samples at each site using a kick-net sampler (30 cm aperture, 250 μm mesh, and 0.09 m² area) along a 15 m transect. The substrates were stored in plastic bags filled with 70% alcohol. We took the samples to the Laboratory of Benthos Ecology at the Universidade Federal de Minas Gerais, where we washed them through a 250- μm mesh sieve. All macroinvertebrates were identified under a stereoscopic microscope (32 \times) by using the taxonomic keys Merritt & Cummins (1996), Mugnai et al. (2010), Hamada et al. (2014). We identified Ephemeroptera, Plecoptera, and Trichoptera to genus (Olifiers et al., 2004; Pes et al., 2005; Salles, 2006), other macroinvertebrates to family, and Annelida to subclass because of limited taxonomic knowledge for the neotropical region. All macroinvertebrates were deposited in the Reference Collection of Benthic Macroinvertebrates, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais.

Functional trait characterization

We used a database of six traits distributed in 23 categories to characterize the functional structure of macroinvertebrate assemblages (Table 2). We chose traits to reflect the organisms' ability to deal with multiple environmental changes, for example, food resources, oxygen availability, and life cycle (Mondy & Usseglio-Polatera, 2014; Paz et al., 2022). In addition, we included morphological and mobility adaptations linked to flow restrictions, such as body flexibility, body shape, and locomotion. Although some studied macroinvertebrates, such as Oligochaeta and Corbiculidae, lack an aerial stage in their life cycle, most sampled taxa, including certain Coleoptera and Hemiptera, have a flying stage. Because flying dispersal ability can alter their resilience to disturbances (Ding et al., 2017; Oliveira et al., 2024), such as those caused by dams, we assigned significant weight to this trait in the fuzzy coding approach. Most data used to compile the functional traits were obtained from studies of neotropical organisms (Tomanova &

Table 2 Functional traits and categories for freshwater macroinvertebrates

Type	Trait	Categories	Code
Life history	Voltinism	≤ 1 reproduction/y	Univoltine
		> 1 reproduction/y	Multivoltine
Mobility	Locomotion/Habitat	Burrower	Burrower
		Crawler	Crawler
		Clinger	Clinger
		Swimmer	Swimmer
		Flyer	Flyer
Morphology	Respiration	Integument	Integument
		Gill	Gill
		Plastron	Plastron
		Spiracle	Spiracle
	Body flexibility	< 10°	Low
		> 10–45°	Average
		> 45°	High
	Body shape	Streamlined	Streamlined
		Flattened	Flattened
		Cylindrical	Cylindrical
Spherical		Spherical	
Foraging	Feeding mode	Gathering-collector	Gatherer
		Shredder	Shredder
		Scraper	Scraper
		Filtering-collector	Filterer
		Predator	Predator

Usseglio-Polatera, 2007; Castro et al., 2017; Jovem-Azevêdo et al., ; Amaral et al., 2021; Firmiano et al., 2021; Martins et al., 2021a; Linares et al., 2022). When information from neotropical taxa was unavailable, we compiled research from North America (Pilière et al., 2016; Poff et al., 2006).

We determined the affinity of each taxon for each trait category by using a fuzzy coding approach (Chevenet et al., 1994). We assigned a score to each taxon describing its affinity to each trait category, ranging from 0 (no affinity) to 3 (maximum affinity) (Chevenet et al., 1994; Tomanova & Usseglio-Polatera, 2007). For each ‘taxon × trait’, the affinity scores were then transformed into a relative usage frequency distribution by dividing the taxon affinity scores by the categories of a fuzzy coding trait by their sum. Affinity scores were standardized so that their sums were equal to 1, ensuring the same weight for each taxon and each trait in subsequent analyses. Assemblage trait profiles were obtained by multiplying the frequency of each trait category by the abundance of each species (Gayraud & Philippe, 2001). A

trait-by-site matrix was created, containing the frequency of each trait at each location, for subsequent analysis

Functional diversity

We calculated five complementary functional diversity indices: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) (Villéger et al., 2008), functional dispersion (FDis) (Laliberté & Legendre, 2010), and functional originality (FOri) (Mouillot et al., 2013). These components of functional diversity reflect different aspects of species in functional space (Mason et al., 2005; Rojas et al., 2021). FRic is defined as the volume of the functional space (volume of the convex hull) occupied by the species of an assemblage, regardless of their abundance (Villéger et al., 2008). FEve measures the regularity with which the functional space is occupied by the abundance of species in an assemblage (Villéger et al., 2008). FDiv quantifies the total proportion of abundance supported by

the species of an assemblage within the functional trait space (Villéger et al., 2008). FDis represents the mean distance of species from the centroid in the resulting multivariate space, weighted by the relative abundance of the corresponding species (Laliberté & Legendre, 2010). Finally, FOr is the weighted average distance between a species and the closest species in the functional space (Mouillot et al., 2013).

To obtain the five functional diversity indices, we used the *alpha.fd.multidim* function of the mFD package (Magneville et al., 2022) in R (R Development Core Team, 2016). We used Gower's dissimilarity (Gower, 1966) to create a distance matrix with the functional traits table, from which we extracted independent axes via Principal Coordinate Analysis (PCoA). We used those axes and the taxa abundance matrix to calculate functional diversity indices (Schleuter et al., 2010). We maintained the first six PCoA axes after testing the functional space quality (Magneville et al., 2022; Supplementary Material, S2).

Functional specialization

We evaluated the functional specialization of the assemblages by using indices proposed by Mondy & Usseglio-Polatera (2014). A Taxon Specialization Index (TSI) was calculated for each taxon and each trait. A maximum TSI value (i.e., 1.00) corresponds to a truly specialist taxon (i.e., using only one trait category), whereas a true generalist taxon (i.e., using all trait categories uniformly) exhibits a lower TSI value. The community specialization index (CSI), which estimates the functional homogenization associated with each feature and each site, was calculated by averaging the individual staggered TSIs of all taxa weighted by their respective log-transformed abundances. Finally, we calculated each site's global specialization index by averaging each feature's CSI. Lower CSI values mean more generalist communities. Thus, for a given characteristic, such as feeding habits, a taxon that is 100% predator is categorized as a specialist, whereas a taxon that is 50% gathering collector and 50% filtering collector is considered a generalist. Scripts for TSI and CSI indices are available in Mondy & Usseglio-Polatera (2014).

Data analyses

Temporal analyses

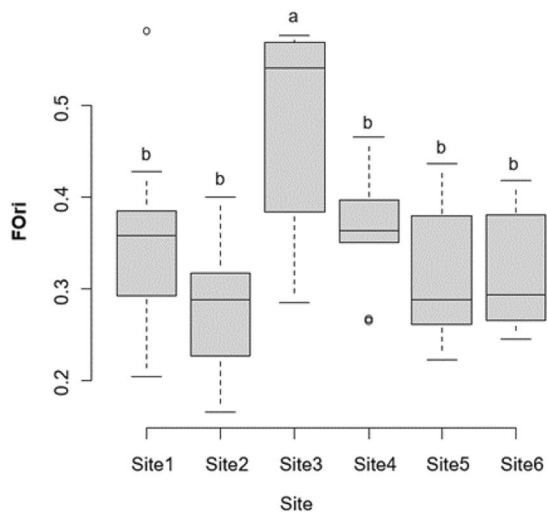
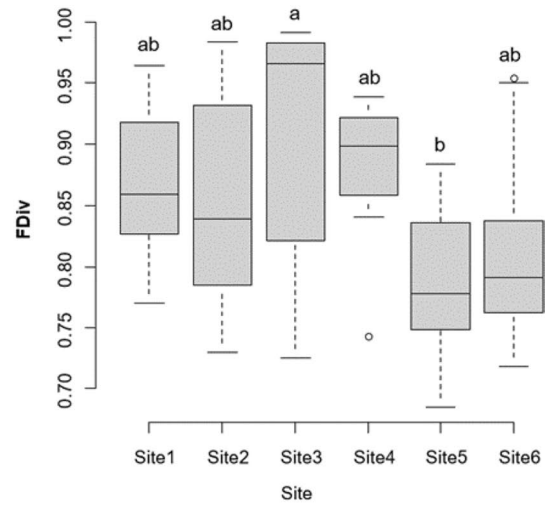
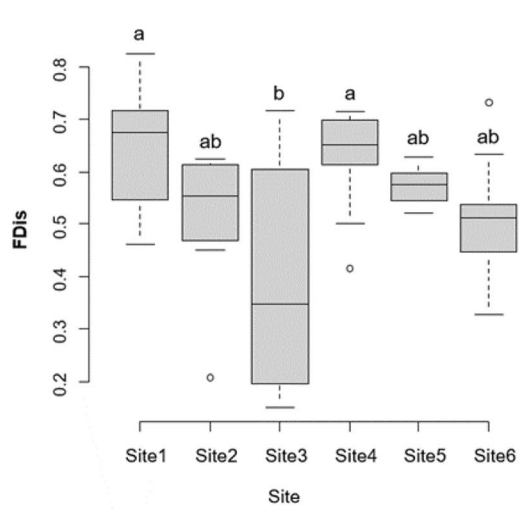
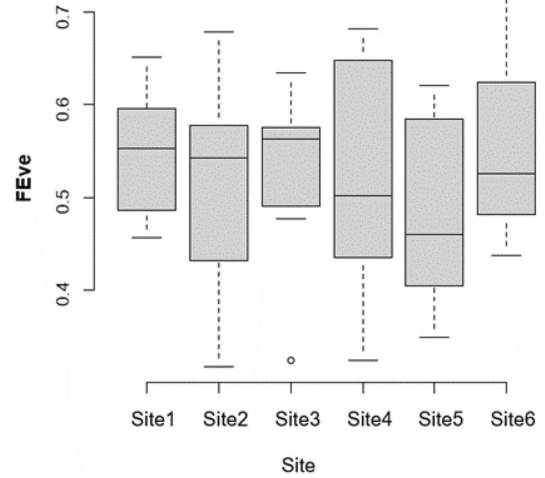
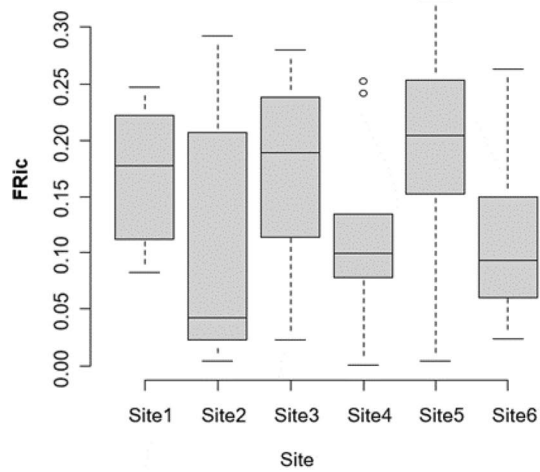
To verify possible seasonal differences, we ran a generalized linear model (GLM) with a Gaussian error structure for each functional diversity index (FRic, FEve, FDiv, FDis, and FOr). The assumptions of linearity, independence, and homoscedasticity were met. Then, we tested model significances using a variance analysis (*F* test). We did not observe significant differences between the dry and rainy seasons, nor between the different sampling years, and, therefore, grouped all six campaigns as replicas for each location.

Functional diversity and assemblage specialization

To test whether the functional diversity indices of macroinvertebrate assemblages in dam-affected sites showed a different profile from those in free-flowing sites, we performed a one-way analysis of variance (ANOVA). We then performed a post hoc Tukey HSD (Honest Significant Difference) test to identify significant differences ($P < 0.05$) between sites. Data normality and homoscedasticity were analyzed and confirmed by running Shapiro–Wilk and Bartlett tests, respectively.

Trait responses to environmental variables

To identify the bivariate association between traits and environmental variables, we performed both RLQ and fourth-corner methods (Dray et al., 2014; Dray & Legendre, 2008). RLQ analysis maximizes the covariance between traits and environmental variables mediated by species abundance (Dolédec et al., 1996). In contrast, the fourth-corner method facilitates quantifying and testing all positive and negative bivariate correlations between each trait category and each environmental variable (Dray et al., 2014). The Monte Carlo permutation test (9999 unrestricted permutations, $P < 0.05$) was used to test the global significance of model 2 (H1: assumes no relationship between R and L) and model 4 (H2: assumes no relationship between L and Q) (Dolédec et al., 1996). Fourth-corner analysis was then used to identify the relationship between trait categories and environmental variables based on the outcome of RLQ ordination



◀**Fig. 3** Differences in functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis), and functional originality (FOri) of macroinvertebrates. Horizontal lines are medians, and the ends of boxes are quartiles. Vertical lines are confidence intervals, and circles represent outliers from six site visits. Different letters indicate significant differences ($P < 0.05$) between disturbance categories. Post hoc Tukey HSD (Honest Significant Difference) tests were used for pairwise comparisons

(Pallottini et al., 2017). The false discovery rate method adjusted the P -values for the fourth-corner analysis (Dray et al., 2014).

A community-weighted means of trait values (CWM) analysis determined individual trait category differences among the sites. CWM is a mean trait value weighted by the relative abundance (Díaz et al., 2007) and represents the expected functional value of a random assemblage sample. We explored the differences in the weighted averages of the assemblage of trait category values (CWM) that contributed to the differences ($P < 0.05$) between the sample sites using the Kruskal–Wallis test. Trait categories showing significant differences between sampling sites were further tested using a pairwise post hoc Dunn's test, where the multiple comparisons were adjusted by Bonferroni correction.

All statistical and graphical analyses were performed with R software (R Development Core Team, 2016), using the *vegan* (Oksanen et al., 2017), *ade4* (Chessel et al., 2004), and *FD* (Laliberté & Legendre, 2010) packages.

Results

Functional diversity and assemblage specialization

We found a total of 46,711 individuals comprised of 86 different taxa. Functional richness ($F_{5,54} = 2.22$, $P = 0.06$) and functional evenness ($F_{5,54} = 0.62$, $P = 0.68$) did not differ significantly among the sampling sites (Fig. 3). On the other hand, functional divergence ($F_{5,54} = 3.58$, $P = 0.01$), functional dispersion ($F_{5,54} = 4.60$, $P = 0.001$), and functional originality ($F_{5,54} = 7.16$, $P \leq 0.001$), differed significantly among the sites (Fig. 3) (Table S1, Supplementary Material). Site 3 had the highest functional originality (0.47 ± 0.03) which differed significantly from all the other sites, as well as a significantly higher functional

divergence than site 5, but did not differ significantly from the other sites at a $P < 0.05$. Site 3 also had a significantly lower functional dispersion in relation to sites 1 and 4 (Fig. 3). Furthermore, the community specialization index (CSI) was not different between sampling locations ($F_{5,54} = 1.85$, $P = 0.12$, Fig. 4). The low CSI values, indicated generalist macroinvertebrate assemblages at all sites.

Trait responses to environmental variables

The RLQ and fourth-corner analyses revealed no significant relationship between the abundance of taxa and environmental variables (model 2, $P = 0.91$), nor the abundance of taxa and functional traits (model 4, $P = 0.10$) (Table 3). However, the composition of individual traits varied among sampling sites. We found significant differences ($P < 0.05$) among sample sites for 18 CWM trait categories (Table 4). Voltinism, body shape, and flexibility were the most affected functional traits, showing significant differences at a $P < 0.05$ for all trait categories (Table 4). Univoltinism, spherical shape, and low body flexibility were found more often in the dam sites 3 and 4 (Fig. 5). However, multivoltinism, flat body shape, and high body flexibility were associated with sites more distant from the dam (Fig. 5).

Discussion

Trait responses to water quality variables

No water quality variable influenced the trait composition of macroinvertebrate assemblages among the sampling sites. However, the first RLQ axis was responsible for the largest fraction of the explained variation. Previous studies have shown a relationship between environmental parameters and the functional structure of macroinvertebrates affected by small hydropower systems (Mueller et al., 2011; Tupinambás et al., 2014), whereas others have not (e.g., Principe, 2010; Scotti et al., 2022). Land use degrades water quality and assemblage composition (Moya et al., 2011; Castro et al., 2017), but the Pandeiros River drains an Environmental Preservation Area (Minas Gerais, 1995). Its basin lacks intensive economic activities and has low population density (IGAM, 2014) to maintain its water

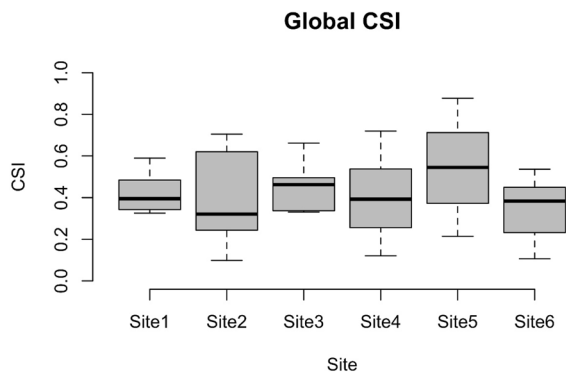


Fig. 4 General Community Specialization Index (CSI) for macroinvertebrate assemblages at each sampling site. Horizontal lines are medians, and the ends of boxes are quartiles. The vertical lines are confidence intervals the six site visits

Table 3 Multivariate analysis with (A) separate analysis showing eigenvalues and percentages of variance that represent the first axis of each analysis, and (B) RLQ analysis showing eigenvalues and percentage of total variance that accounted for the first RLQ axis

	Axis 1	
	Eigenvalue	% of variance
<i>(A) Separate analysis</i>		
Environment (PCA)	3.61	51.6
Abundance (COA)	0.23	26.9
Trait (FCA)	0.23	33.9
<i>(B) RLQ analysis</i>		
Eigenvalue	0.002	48.5
Covariance	0.043	
Correlation	0.096	
R/RLQ	2.225	61.5
L/RLQ	0.096	20
Q/RLQ	0.091	39.4

quality. However, assemblage traits may have been associated with measurements of physical habitat structure (Moya et al., 2011; Martins et al., 2021b; Kaufmann et al., 2022). Dams form reservoirs, which alter flow regimes, accumulate sediments, and increase widths and depths (Xiaocheng et al., 2008). Although the SHP Pandeiros is a small dam with short water residence time (Fonseca et al., 2008), the differences in trait composition probably resulted from physical changes in the sites influenced by the dam and reservoir.

Table 4 Kruskal–Wallis results concerning the differences among sampling sites for each trait category. Significant P -values ($P < 0.05$) are in bold

Trait	Category	Chi-Square	P
Respiration	Integument	21.776	< 0.001
	Gill	16.273	< 0.001
	Plastron	19.166	< 0.001
	Spiracle	10.806	0.055
Voltinism	Univoltine	26.448	< 0.001
	Multivoltine	26.448	< 0.001
Locomotion	Burrower	9.795	0.081
	Crawler	20.923	< 0.001
	Clinger	8.086	0.151
	Swimmer	15.071	0.010
	Flyer	16.97	0.004
Body flexibility	Low	28.942	< 0.001
	Average	13.187	0.021
	High	22.642	< 0.001
Body shape	Streamlined	14.403	0.013
	Flattened	21.684	< 0.001
	Cylindrical	23.028	< 0.001
	Spherical	27.719	< 0.001
Feeding mode	Gatherer	18.361	0.002
	Shredder	12.727	0.026
	Scraper	4.437	0.488
	Filterer	25.704	< 0.001
	Predator	5.943	0.311

Functional diversity and assemblage specialization

Our first hypothesis, that sites near the dam would support a distinct functional diversity and have less-specialized assemblages than free-flowing sites, was partially corroborated. Sites close to the dam supported a distinct functional diversity. Specifically, site 3 (reservoir), directly upriver from the dam, exhibited higher functional originality (FOri) compared to the other sites and had significantly higher functional divergence (FDiv) than site 5. The increase in FOri and FDiv is an indicator of niche differentiation, suggesting that the reservoir is composed of taxa sharing few functional characteristics with nearby taxa (Mouillot et al., 2013; Rojas et al., 2021). This result is related to the lower FDis observed at site 3 compared to the free-flowing sites 1 and 4, revealing a prevalence of taxa with uniform functional attributes in the reservoir. An increased functional dispersion

indicates that taxa exhibited higher functional dissimilarity (Cooke et al., 2019), suggesting that functional traits are better distributed in free-flowing sites along the Pandeiros River. However, out of the five functional diversity metrics, the dam and reservoir affected three (FOri, FDiv, and FDis). Furthermore, the dam and reservoir did not change the specialization of macroinvertebrate assemblages. When a community has a low CSI (Community Specialization Index), the specialization of taxa within that community is reduced. This may indicate that the taxa present in the assemblages had a wide range of ecological preferences, being able to adapt to different environmental conditions. In other words, a low CSI suggests that the community is composed of generalist species, which are not strongly specialized in resource or habitat use (Mondy & Usseglio-Polatera, 2014).

Linares et al. (2019) studied macroinvertebrate assemblages in the Pandeiros River. They pointed out a change in the functional feeding groups, with an increased abundance of filterer taxa at the dam site compared to free-flowing sites. In addition, they found that the reservoir favored an increase in non-native invasive taxa. The persistence of non-native species overlaps with native species in the functional space, resulting in an increase in FDiv and FOri (Rojas et al., 2021). These increases resulting from the presence of non-native species may be related to negative effects on the ecosystem, such as niche displacement and loss of native species (Carboni et al., 2021; Haubrock et al., 2021).

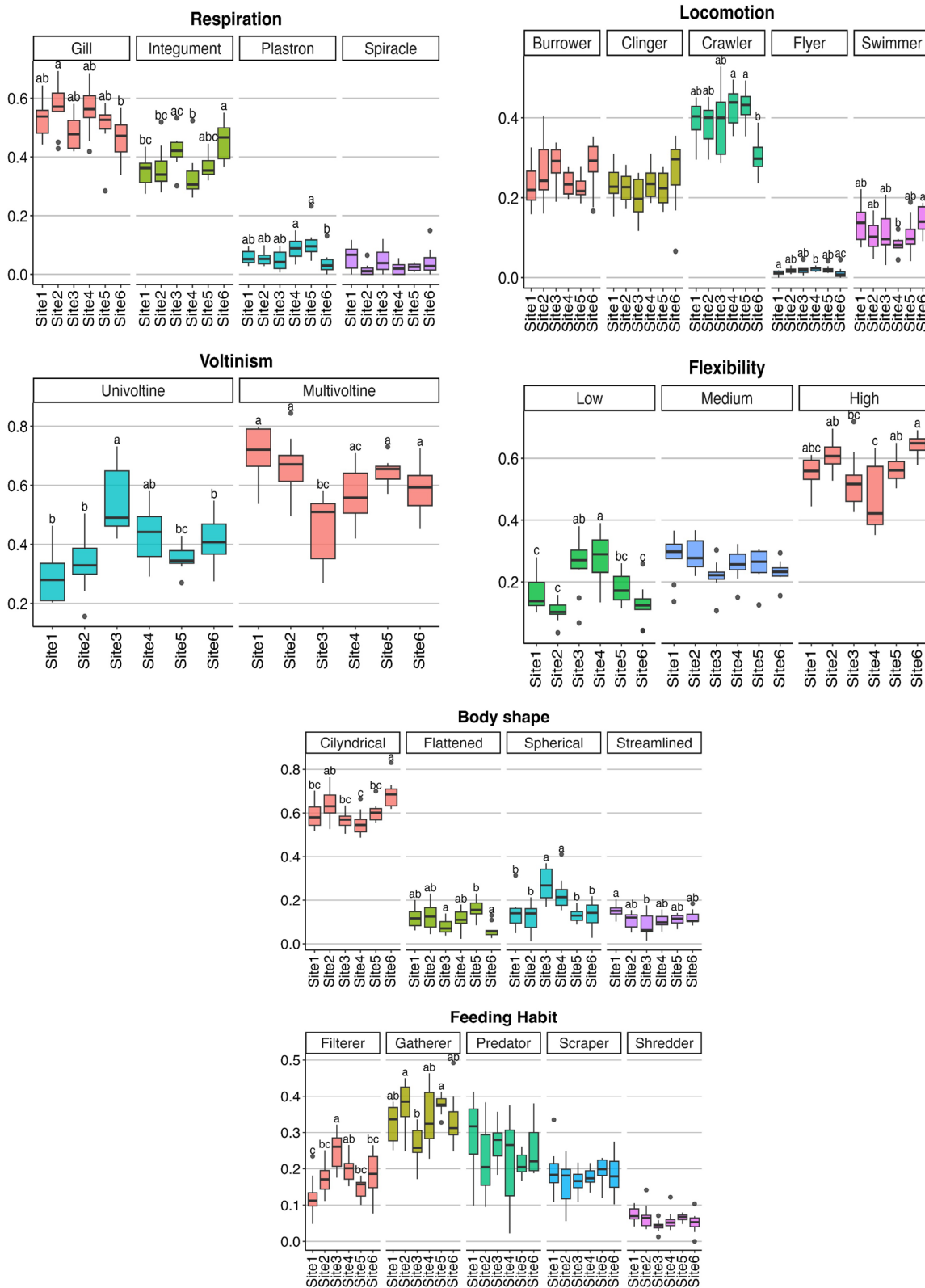
The hypothesis that the dam and reservoir would result in reduced functional complexity of local benthic macroinvertebrate assemblages was not corroborated. The macroinvertebrate assemblages at our sites were primarily composed of generalist taxa, suggesting the sampling sites were functionally more homogeneous, although the reservoir caused significant changes in functional diversity indices. The Pandeiros River substrate is predominantly sand and homogeneous throughout its course (Linares et al., 2018; Martins et al., 2021b) and this low substrate heterogeneity reduces habitat complexity, directly affecting the functional specialization of benthic macrofauna (Castro et al., 2018; Firmiano et al., 2021). This is because specialized taxa occupy restricted and highly suitable habitats, whereas generalists can occupy many habitats (Clavel et al., 2011; Mazzucco et al., 2015).

Our second hypothesis, that the composition of macroinvertebrate functional traits in dam and reservoir sites would differ from free-flowing sites, was corroborated. We found that the composition of individual traits varied significantly among sampling sites despite finding no significant relationships between environmental metrics and functional traits. The trait composition responded to the dam and reservoir, locally favoring certain assemblage traits. Body shape is linked to resistance or resilience to substrate sedimentation (Dolédec et al., 2011). Organisms that live in areas with fine sediment accumulations generally have a cylindrical shape, capable of penetrating the fine sediment (Ding et al., 2017), which explains the predominance of this body shape in the reservoir site (site 3). In contrast, the streamlined body shape was predominant in the free-flowing site (site 1). The faster flows mean fewer fine sediments, which select organisms with more hydrodynamic bodies (Ding et al., 2017). Other studies have also reported that body shape confers adaptations to changes in flow and the relationship of the organism with the substrate (Edegbene et al., 2021; Silva et al., 2021). Thus, different traits are selected as the hydrological disturbance gradient changes (Feio & Dolédec, 2012).

For the site nearest the dam (site 4), the retention of fine sediments by the dam and the presence of rocky outcrops (Linares et al., 2019) favored taxa with low body flexibility (e.g., Naucoridae). Coarse substrates offer advantages to taxa with this characteristic, facilitating the occupation of the interstices of the rock as protection (Yao et al., 2017) and reducing the possibility of being carried away by the current. Therefore, we observed that under coarse substrate conditions, faster current can be a limiting factor for lotic taxa, resulting in a more hydrodynamic body shape and low body flexibility.

On the other hand, organisms with multivoltine reproductive cycles were associated with the reservoir site (site 3), contrary to our predictions. Changes in the number of reproductive cycles are consistently related to environmental disturbances, with a higher frequency of multivoltine individuals in the most disturbed locations, which facilitates rapid recolonization of disturbed aquatic environments (Díaz et al., 2007; Castro et al., 2018).

The observed functional structure in the macroinvertebrate assemblages indicated that the small hydropower dam and reservoir acted as a local



◀**Fig. 5** Box plots expressing relative abundance of traits among sampling sites (Kruskal–Wallis test). Significant differences ($P < 0.05$) given by the post hoc pairwise test (Dunn's test) among sampling sites. Different letters indicate significant differences between disturbance categories

environmental filter, selecting unique traits that allow some taxa to occupy those conditions. However, some traits did not differ significantly among the dam/reservoir sites and the free-flowing sites, which can be explained by the low environmental variability and the predominance of generalist individuals. Ceneviva-Bastos et al. (2017) reported that generalist aquatic insects showed trophic plasticity and opportunistic feeding habits, leading to greater niche overlap. Therefore, the use of multiple traits improves our ability to assess the functional response of macroinvertebrate assemblages to gradients of environmental disturbance (Feio & Dolédec, 2012; Castro et al., 2017).

The absence of significant differences in functional diversity indices between the dry and rainy seasons can be attributed to at least three environmental factors specific to the Pandeiros River. (1) The river location within a protected and relatively well-preserved area contributes to its overall environmental stability, which buffers the assemblages from the typical seasonal fluctuations observed in more disturbed or heterogeneous systems. This stability could result in a reduced impact of seasonal variations on the functional structure of the assemblages (Baker et al., 2023). (2) The relative homogeneity of habitats along the river's course, predominantly characterized by sandy substrates (Linares et al., 2019), plays a crucial role in maintaining functional stability across seasons. The lack of habitat heterogeneity may limit the range of ecological niches available, leading to a more uniform assemblage structure that does not vary significantly with seasonal changes in flow or resource availability (Frainer et al., 2018). (3) The Pandeiros River rarely experiences extreme seasonal flow fluctuations because of its low annual rainfall (INMET, 2024). The absence of pronounced flood pulses, often responsible for restructuring benthic communities (O'Leary & Wantzen, 2012), facilitates more continuous and stable assemblages throughout the year. These three reasons help explain the observed consistency in functional diversity indices between the dry and rainy seasons.

Summary and conclusions

This study expands the knowledge of small hydro-power system effects on selecting traits and functional diversity indices of macroinvertebrate assemblages at upstream and downstream sites. The FDis, FDiv, and FORi indices showed a strong relationship with the environmental pressures imposed by the dam, being sensitive to local hydrological conditions. Although the sampling sites showed functional homogenization, differences in reproductive cycles, body shape, and body flexibility indicate that certain traits were locally selected upstream and downstream of the dam. Additionally, the macroinvertebrate functional traits found in our study can be used for biomonitoring the decommissioning of other neotropical savanna river dams. Additional in situ studies of the functional structure of benthic macroinvertebrate assemblages should investigate the effects of riparian vegetation cover, riparian disturbance, channel morphology, habitat type, substrate quality, physical habitat complexity, and nutrient concentrations downstream and upstream of hydroelectric systems (Jimenez-Valencia et al., 2014; Silva et al., 2018; Herlihy et al., 2020; Martins et al., 2021b; Kaufmann et al., 2022).

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Author contributions PHMA, DMPC, MSL, and MC designed the study. PHMA and DMPC performed the statistical analyses. PHMA was involved in writing the original draft preparation. MC supervised the entire study. All authors contributed to reviewing the manuscript and approved the final version.

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Data availability Part of the analyzed data set is provided as supplementary material, and another part is available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval No approval of research ethics committees was required to accomplish the goal of this study because experimental work was conducted with an unregulated invertebrate species.

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