Acta Limnologica Brasiliensia

Publication of the
Brazilian Association of
Limnology

Original Article
*Acta Limnologica Brasiliensia*, 2024, vol. 36, e6
https://doi.org/10.1590/S2179-975X5623
ISSN 2179-975X on-line version

# Flood did not cause the taxonomic and functional homogenization of Chironomidae (Diptera) community in a Neotropical floodplain

## A cheia não causou homogeneização taxonômica e funcional da comunidade de Chironomidae (Diptera) em uma planície de inundação neotropical

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**Cite as:** Silva, J.P.S. and Petsch, D.K. Flood did not cause the taxonomic and functional homogenization of Chironomidae (Diptera) community in a Neotropical floodplain. *Acta Limnologica Brasiliensia*, 2024, vol. 36, e6. https://doi.org/10.1590/S2179-975X5623

**Abstract: Aim:** We investigated the hypothesis that flood decreases the taxonomic and functional beta diversity of Chironomidae (Diptera) larvae among floodplain lakes, causing biotic homogenization. **Methods:** We collected benthic samples using a modified Petersen grab in 18 lakes in a flood period (March 2011) and a drought period (September 2011) in the Upper Paraná River floodplain. We compared the taxonomic and functional beta diversity of Chironomidae among lakes in flood and drought periods using a multivariate dispersion analysis (PERMDISP). **Results:** We found similar taxonomic and functional beta diversity of the Chironomidae between hydrological periods. **Conclusions:** We did not find evidence of biotic homogenization due to flood pulse. Our findings suggest other mechanisms besides increasing connectivity and environmental similarity due to flood pulse that may structure the benthic community, such as variation in the identity of flood-tolerant morphospecies across lakes.

**Keywords:** biotic homogenization; beta diversity; Upper Paraná River floodplain; zoobenthos.

**Resumo: Objetivo:** Nós investigamos a hipótese que a cheia reduz a diversidade beta taxonômica e funcional de larvas de Chironomidae (Diptera) em lagoas de inundação causando homogeneização biótica. **Métodos:** Coletamos amostras bentônicas usando uma draga do tipo Petersen modificado em 18 lagoas em um período de cheia (março de 2011) e um período de seca (setembro de 2011) na planície de inundação do alto rio Paraná. Nós comparamos a diversidade beta taxonômica e funcional nos períodos de cheia e de seca usando uma análise de dispersão multivariada (PERMDISP). **Resultados:** Nós encontramos que a diversidade beta de Chironomidae foi similar entre os períodos hidrológicos. **Conclusões:** Nós não encontramos evidência de homogeneização biótica devido à cheia. Nossos resultados sugerem outros mecanismos além do aumento da conectividade e da similaridade ambiental devido ao pulso de inundação estruturam a comunidade bentônica, tais como a variação na identidade das espécies tolerantes à cheia entre as lagoas.

**Palavras-chave:** homogeneização biótica; diversidade beta; planície de inundação do alto rio Paraná; zoobentos.

## 1. Introduction

Floodplains are areas periodically flooded by the lateral overflow of rivers (Junk et al., 1989). Usually, during the flood, aquatic environments tend to be biologically less distinct since flood pulse tends to increase connectivity among habitats and homogenize the environmental characteristics (Thomaz et al., 2004, 2007). On the other hand, during the drought, many lakes are isolated again and become more distinct from each other due to chemical and physical changes in their habitats (Thomaz et al., 2004; Bozelli et al., 2015).

The flood pulse can not only promote higher environmental similarity (i.e., related to limnological features such as nutrients, pH, dissolved oxygen and turbidity) but also contribute to an increase in biological similarity, resulting in a decrease in beta diversity (Thomaz et al., 2007; Petsch, 2016). Beta diversity can also be defined as the variability in species composition between sampling units (Anderson et al., 2006), generated both by species differences and replacement (Baselga, 2010). A reduction in beta diversity may indicate processes related to taxonomic biotic homogenization, characterized by increasing species similarity between space or time (McKinney & Lockwood, 1999; Olden et al., 2004).

One of the community responses to hydrological cycles is related to species traits once a functional approach can improve our understanding of how communities are shaped by ecological processes such as flooding (e.g., attributes of higher dispersion or tolerance to low dissolved oxygen conditions). Functional attributes represent any measurable morphological, physiological or phenological characteristic at the individual level that indirectly affects biological efficacy through detected effects on its growth, reproduction or survival (Violle et al., 2007). Also, communities can be more similar regarding their response functional traits due to some anthropogenic or natural cause, driving functional homogenization (e.g., Gentilin-Avanci et al., 2021; Feng et al., 2023; Rivera et al., 2023). One of the main anthropogenic actions that decrease functional diversity in freshwater ecosystems are deforestation and agriculture (Colares et al., 2022). These interferences promote habitat loss and chemical changes in freshwater ecosystems, causing some rare species to disappear, thus promoting the functional redundancy of the remaining species (Violle et al., 2017) and functional homogenization (Petsch, 2016). On the other hand, the flood pulse is the main example of a natural cause of biotic homogenization in freshwater ecosystems (Thomaz et al., 2007; Petsch, 2016).

Among the aquatic communities of the Upper Paraná River floodplain, Chironomidae larvae (Diptera) correspond to the most frequent, abundant, and diverse benthic invertebrates (Takeda et al., 2004; Petsch et al., 2015, 2017; Bertoncin et al., 2019). Chironomidae is divided into 11 subfamilies and 22 tribes (Ferrington Junior, 2008). The composition and distribution of Chironomidae larvae in the Upper Paraná River floodplain are strongly related to environmental filters, such as the high heterogeneity of habitats, which are influenced by the environmental changes promoted by the hydrological regime (Takeda et al., 2004).

We investigated the effect of flooding on the taxonomic and functional beta diversity of Chironomidae larvae in 18 lakes in the Upper Paraná River floodplain (Brazil). We investigated the hypothesis that the flood promotes taxonomic and functional biotic homogenization of Chironomidae among floodplain lakes. If this hypothesis is confirmed, we expect to find a lower taxonomic and functional beta diversity of Chironomidae among lakes during the flood than during the drought period.

## 2. Materials and Methods

### *2.1. Study area*

Our study was part of the Long-Term Ecological Research program (PELD/CNPq). The sampled area comprises the last dams free stretch on the Paraná River in Brazil (Agostinho et al., 2008). We sampled 18 lakes in two periods (Figure 1): flood (March 2011) and drought (September 2011).

### *2.2. Sampling period*

In 2011, large fluctuations were observed in the hydrometric level of the Paraná River. In March 2011, during the first sampling, the water level was higher than 6m, when all lakes were connected by the flood (Souza Filho, 2009). In September 2011, during the second sampling, the water level was below 3m, characterizing a drought period (Figure 2).

### *2.3. Data collection*

We sampled five bottom samples in each lake with a modified Petersen grab (0.0345 $m^{-2}$). The sedimentological content was fractioned with the aid of a set of 2mm, 1mm and 0.2mm sieves. The biological material retained on the last sieve was fixed in commercial alcohol (92.6°) for subsequent screening under a stereoscopic microscope in the laboratory.

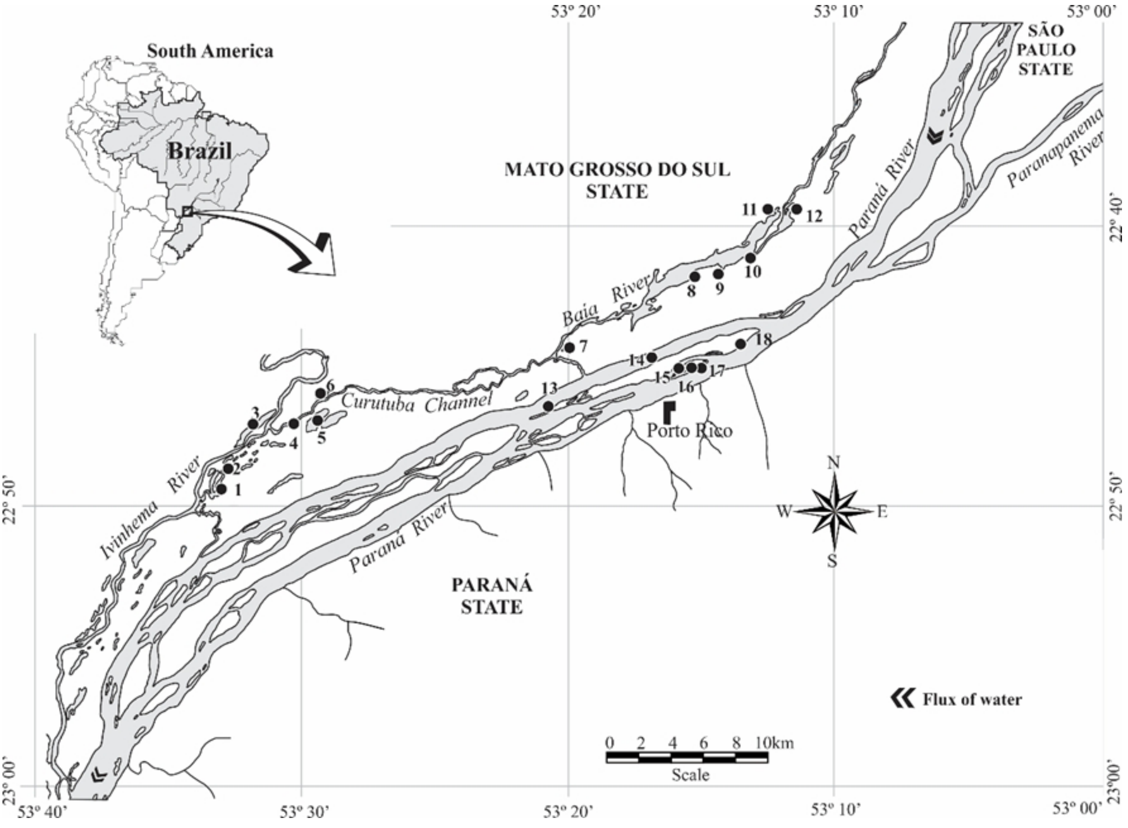

**Figure 1.** Location of lakes sampled in the upper Paraná River floodplain. (1) Boca do Ipoitã Lake; (2) Capivara Lake; (3) Finado Raimundo Lake; (4) Jacaré Lake; (5) Sumida Lake; (6) Cervo Lake; (7) Traíra Lake; (8) Pousada das Garças Lake; (9) Porcos Lake; (10) Aurélio Lake; (11) Maria Luiza Lake; (12) Onça Lake; (13) Ressaco do Manézinho; (14) Ressaco do Bilé; (15) Ressaco do Leopoldo; (16) Genipapo Lake; (17) Clara Lake; (18) Pousada Lake.

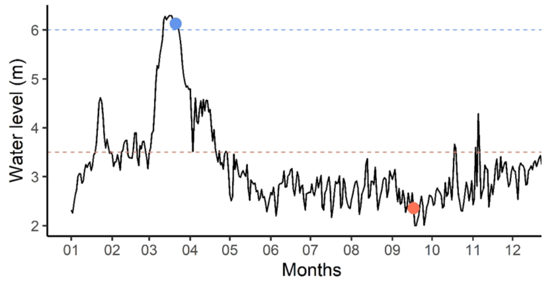

**Figure 2.** Fluviometric level of Paraná River in 2011. When the Paraná River level reaches 6m, a total flood occurs (March 2011, blue), while the Paraná River level below 3.5m indicates a drought period (September 2011, orange).

Chironomidae larvae were desiccated and mounted on slides with Hoyer solution according to the methodology proposed by Trivinho-Strixino & Strixino (1995) and later identified in an optical microscope using Epler (2001) and Trivinho-Strixino (2011) keys. The identified organisms are deposited in the Zoobenthos laboratory (NUPELIA/UEM).

We also measure environmental features during sampling, such as water temperature (°C) and dissolved oxygen (mg/L) near the bottom, electrical conductivity (µS/cm), depth (m), pH, turbidity (NTU), chlorophyll (µg/L), total suspended material (µg/L), total nitrogen (µg/L) and total phosphorus (µg/L). Fluviometric level data of the Paraná River were obtained through daily measurements with a ruler installed in Porto Rico city (Paraná, Brazil).

### *2.4. Chironomidae traits*

The traits were defined following to previously cited literature. We searched for traits related to trophic habit (collector-gatherer, collector-filter, predator, and wood miner), life habit (tubes in the sediment, associated with macrophytes, associated with sediment and swimmers), type of refuge (built with allochthonous material, fixed and retractable nets and without shelter) and the presence of adaptations to low conditions of dissolved oxygen (abdominal tubules and hemoglobin).

### *2.5. Data analysis*

To test our hypothesis of biotic homogenization during the flood period, we investigated whether Chironomidae beta diversity among lakes is lower in flood than drought. Taxonomic beta diversity was based on a Jaccard dissimilarity calculated from Chironomidae incidence data. We also calculated Bray-Curtis dissimilarity based on abundance data, but the results were similar compared to Jaccard dissimilarity (mean distance to centroid in flood: 0.593; drought: 0.587; P = 0.862). In contrast, functional beta diversity was calculated from a dendrogram performed using Chironomidae traits, and then the Gower distance was applied. We calculated the taxonomic and functional beta diversity of Chironomidae separately for each hydrological period as the mean distance of each lake to the centroid in a multivariate space (PCoA) using a multivariate dispersion analysis (PERMDISP; Anderson et al., 2006). This way, higher average distances to centroids indicate higher beta diversity values, i.e., higher dissimilarity between species and traits. To test if beta diversity values differ between hydrological periods, we used permutational null models with 999 randomizations. We performed all analyses in the R program version 3.4 (R Core Team, 2022) using the *vegan* (Oksanen et al., 2017), *FD* (Laliberté et al., 2014) and *adespatial* (Dray et al., 2018) packages. We constructed the figures using the *ggplot2* package (Wickham et al., 2016).

## 3. Results

We found a total of 56 morphospecies of Chironomidae represented by three subfamilies: Chironominae (46 morphospecies), Tanypodinae (9 morphospecies) and Orthocladiinae (1 morphospecies). We found 51 morphospecies in the drought and 26 in the flood period (Table 1). The most abundant morphospecies in the flood period were those of the genus *Chironomus*, while in the drought period, they were those of the genera *Tanypus* and *Polypedilum*. We observed that 65% of the morphospecies found in the flood period had adaptations for oxygen uptake (e.g., abdominal tubules and/or hemoglobin), and 63% of the morphospecies found in the drought period had the same adaptations.

We observed the highest dissolved oxygen values, pH, turbidity, chlorophyll and nutrients in the drought period (September 2011). On the other hand, the highest temperature and conductivity values were recorded during the flood period (March 2011) (Table 2).

**Table 1.** Chironomidae morphospecies presence (1) absence (0) from 18 lakes of the upper Paraná River, floodplain in flood (March) and drought (September) periods of 2011.

| | FLOOD | DROUGHT |
|---|---|---|
| **CHIRONOMINAE** | | |
| ***Asheum*** | 1 | 1 |
| ***Beardius phytophilus*** | 0 | 1 |
| ***Caladomyia capaopreto*** | 0 | 1 |
| ***Caladomyia ortoni*** | 1 | 1 |
| ***Caladomyia* sp. A** | 0 | 1 |
| ***Caladomyia* type B** | 0 | 1 |
| ***Caladomyia* type H** | 1 | 0 |
| ***Chironomus antonioi*** | 0 | 1 |
| ***Chironomus fittkaui*** | 1 | 1 |
| ***Chironomus gigas*** | 1 | 1 |
| ***Chironomus* gr. *salinarius*** | 1 | 1 |
| ***Chironomus paragigas*** | 1 | 1 |
| ***Chironomus sancticaroli*** | 0 | 1 |
| ***Chironomus strenzkei*** | 1 | 1 |
| ***Chironomus* type F** | 0 | 1 |
| ***Chironomus* type H** | 1 | 0 |
| ***Cladopelma forcipis*** | 1 | 1 |
| ***Cryptochironomus reshchikov*** | 1 | 1 |
| ***Dicrotendipes* sp. 3** | 0 | 1 |
| ***Endotribelos ficus*** | 0 | 1 |
| ***Endotribelos* sp. 2** | 1 | 1 |
| ***Endotribelos* sp. 3** | 1 | 1 |
| ***Fissimentum desiccatum*** | 0 | 1 |
| ***Fissimentum* sp. 2** | 1 | 1 |
| ***Goeldichironomus neopictus*** | 1 | 1 |
| ***Goeldichironomus petiolicola*** | 1 | 1 |
| ***Goeldichironomus serratus*** | 0 | 1 |
| ***Goeldichironomus* type B** | 0 | 1 |
| ***Oukuriella jatai*** | 0 | 1 |
| ***Parachironomus cayapo*** | 0 | 1 |
| ***Parachironomus longistilus*** | 0 | 1 |
| ***Pelomus psamophilus*** | 0 | 1 |
| ***Polypedilum (Tripodura)* sp. 3** | 0 | 1 |
| ***Polypedilum (Tripodura)* sp. 4** | 1 | 1 |
| ***Polypedilum* sp. 3** | 0 | 1 |
| ***Polypedilum* sp. 4** | 1 | 0 |
| ***Pseudochironomus*** | 0 | 1 |
| ***Saetheria* sp. 1** | 0 | 1 |
| ***Stempellina*** | 0 | 1 |
| ***Stenochironomus*** | 1 | 1 |
| ***Tanytarsus fittkaui*** | 0 | 1 |
| ***Tanytarsus giovanni*** | 1 | 1 |
| ***Tanytarsus* type D** | 1 | 1 |
| ***Tanytarsus* type E** | 1 | 1 |
| ***Tanytarsus* type F** | 0 | 1 |
| ***Xestochironomus*** | 1 | 0 |
| **TANYPODINAE** | | |
| ***Ablabesmyia* gr. *annulata*** | 0 | 1 |
| ***Ablabesmyia Karelia* 1** | 1 | 1 |
| ***Coelotanypus* sp. 1** | 0 | 1 |
| ***Coelotanypus* sp. 2** | 1 | 1 |
| ***Labrundinia* sp. 12** | 0 | 1 |
| ***Procladius* type B** | 1 | 1 |
| ***Tanypus punctipennis*** | 0 | 1 |
| ***Tanypus* sp. 2** | 0 | 1 |
| ***Tanypus stellatus*** | 0 | 1 |
| **ORTHOCLADIINAE** | | |
| ***Paracladius*** | 0 | 1 |

**Table 2.** Environmental variables (mean ± standard deviation) of 18 lakes in the Upper Paraná River floodplain during the flood (March 2011) and drought period (September 2011).

| | Temp. | D.O. | pH | Cond. | Turb. | TSM | Chl. | TN | TP |
|---|---|---|---|---|---|---|---|---|---|
| **Flood** | 27.8 (±0.8) | 5.05 (±2.8) | 6.3 (±0.5) | 50.0 (±5.4) | 2.72 (± 4.2) | 1.37 (±0.9) | 3.3 (±2.3) | 776.9 (±95.1) | 20.2 (±5.2) |
| **Drought** | 23.7 (±1.9) | 6.5 (±1.8) | 6.9 (±0.6) | 35.8 (±18.5) | 15.8 (±8.9) | 1.5 (±0.8) | 15.7 (±17.5) | 1251.8 (±436.8) | 60.5 (±59.5) |

Temp. = water temperature (ºC); D.O. = dissolved oxygen (mg/L); Cond. = conductivity (uS/cm); Turb. = turbidity (NTU); TSM = total suspended material (ug/L); Chl. = chlorophyll (ug/L); TN = total nitrogen (ug/L); TP = total phosphorus(ug/L).

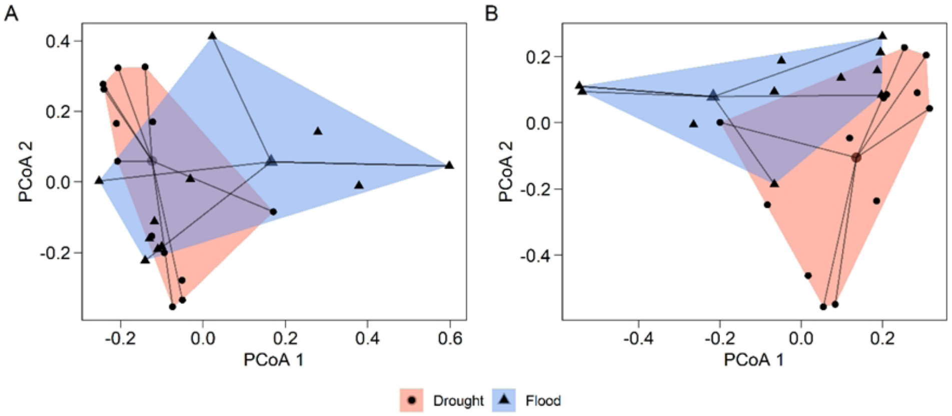

**Figure 3.** Taxonomic (A) and functional (B) beta diversity of Chironomidae among flood (blue) and drought (red) floodplain lakes in the upper Paraná River floodplain.

Despite the lower number of Chironomidae morphospecies in the flood period, the hypothesis that the flood reduced taxonomic beta diversity was not supported, as the mean distance to the centroid was similar between the flood (0.619) and the drought period (0.624) ($F_{(1,16)}$= 0.261; P = 0.878; Figure 3A) using Jaccard dissimilarity (based on incidence). We found similar results estimating taxonomic beta diversity with Bray-Curtis dissimilarity based on abundance (mean distance to the centroid in flood = 0.593; mean distance to the centroid in drought = 0.587; $F_{(1,16)}$= 0.031; P = 0.862). We also found a similar functional beta diversity of Chironomidae among lakes during the drought period (mean distance to the centroid = 0.583) and flood period (mean distance to the centroid = 0.543) ($F_{(1,16)}$= 1.313; P = 0.267; Figure 3B).

## 4. Discussion

Contrary to our hypothesis, we did not find taxonomic or functional homogenization of Chironomidae larvae due to flood pulse in the Upper Paraná River floodplain. Despite large variations in dissolved oxygen, pH, turbidity, chlorophyll, and nutrient levels between the flood and drought, the Chironomidae larvae variability among lakes was similar between hydrological periods. Our findings suggest that while Chironomidae morphospecies abundance and richness may decrease due to the flood effect (Petsch et al., 2015), taxonomic and functional beta diversity among lakes remained similar between different hydrological conditions. We added evidence for the controversy of flood homogenization effect because some studies found biotic homogenization due to flood pulse (e.g., Lopes et al., 2014 and Bozelli et al., 2015, investigating zooplankton in Brazilian floodplains) while other studies did not (e.g., Petsch et al., 2021a, investigating zooplankton and aquatic macrophytes in the Upper Paraná River floodplain).

The identity of tolerant species due to a disturbance as flood can vary among sites (such as found for land use disturbance; Johnson & Angeler, 2014; Petsch et al., 2021b). Chironomidae morphospecies tolerant to flood modifications may differ across lakes, creating some variability during the flood period. For example, changes in the substrate, influenced by the hydrological regime of the Paraná River, did not drastically change the composition of Chironomidae but decreased their density (Anjos et al., 2011). The oligotrophication promoted by dams upstream of the Upper Paraná River floodplain also changed the dominance of morphospecies persisting under such stressful conditions (Rosin et al., 2009).

The drought period is supposed to have higher beta diversity due to higher lakes isolation, which could lead these habitats to a heterogeneous state (Thomaz et al., 2007; Bozelli et al., 2015; but see Bertoncin et al., 2019 for extreme drought effects). However, flood conditions can also create some taxonomic and functional beta diversity of Chironomidae among lakes throught species replacement. For example, *Xestochironomus* is the unique morphospecies recorded with the wood mining trait and is favored by flooding because more branches and wood are carried to the pond due to flood pulse (Junk et al., 1989; Petsch et al., 2015). Indeed, *Xestochironomus* only occurred during the flood in a small pond with high riparian vegetation, contributing to generating beta diversity during the flood period.

Chironomidae larvae are among the most resistant macroinvertebrates in freshwater habitats (Molineri et al., 2020). They are widely distributed and functionally diverse (Martins et al., 2021; Arpellino et al., 2023). Many Chironomidae morphospecies show functional traits related to high resistance and resilience to flood effects (Serra et al., 2017). For example, we found a high proportion of Chironomidae larvae with adaptations for oxygen uptake in both periods, indicating their ability to support varying oxygen levels in the lakes. This finding corroborates the idea that oxygen availability is a crucial factor influencing the distribution and survival of many Chironomidae larvae (Rosin & Takeda, 2007) and pupae (Arpellino et al., 2023). During the flood, dissolved oxygen tends to be lower due to the accumulation of organic matter and greater decomposition (Anjos et al., 2011). When comparing adaptations for oxygen uptake of Chironomidae in drought and flood periods, we found no differences in the percentage of morphospecies with such adaptations, indicating the similarity of some response traits of Chironomidae between flood and drought periods.

We did not find evidence of biotic homogenization of Chironomidae due to flood pulse using taxonomic or functional facets. We highlight the complexity of river-floodplain systems because other mechanisms besides increasing connectivity and environmental similarity due to flood pulse may structure the Chironomidae community during the inundation period, such as variation in the identity of flood-tolerant morphospecies across habitats. Our findings contribute to understanding the ecological success of this family of aquatic insects in the Upper Paraná River floodplain and have implications for the conservation and management of river-floodplain ecosystems.

## Acknowledgements

We thank the Long-Term Ecological Research (LTER/CNPq) program for the opportunity to develop this study and the Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura from the Universidade Estadual de Maringá (Nupelia/UEM) for logistical support. We also thank Gisele D. Pinha for helping with the identification of Chironomidae larvae.

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**Received:** 23 June 2023
**Accepted:** 18 January 2024

**Associate Editor:** Victor Satoru Saito.