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Characterization and predictors of the zooplankton community in the *Veredas* wetlands in Brazilian savanna

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Abstract Vereda is a wetland ecosystem typical of the Cerrado biome characterized by diverse vegetation with dynamic and transitional areas of riparian forests, gallery forests, flooded forests, and humid grassland. In general, they are associated with controlling the flow of the water table, carbon storage, and high biodiversity and are essential to the maintenance of most rivers in the Cerrado biome. Besides that, Vereda is poorly studied, especially zooplanktonic groups. To lessen this knowledge gap, we evaluated the effects of seasonality and environmental predictors on the zooplanktonic community of Vereda. For that, we sampled zooplanktonic assemblages in the Veredas in the dry and wet seasons. We found environmental influence but not for the zooplankton community. The characteristic low conductivity seems to be an important environmental filter for

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R. G. Strutz · C. Carnicer Programa de Pós-graduação em Ecologia e Conservação, Universidade do Estado de Mato Grosso - UNEMAT, Nova Xavantina, Brazil zooplankton species occurrence in these systems, since the *Veredas* that registered major levels of richness and density were those with high electrical conductivity. Highlighting that some zooplankton species with a more restricted distribution were detected in this study: *Acroperus tupinamba*, which occurs in Brazil and Ecuador; *Monospilus* sp., for which only two species of this genus were registered in Brazil, both with restricted distribution, found thus far in only two protected areas of the Cerrado biome.

Keywords Wetland · Small floodplain · Lotic environment · Littoral zooplankton · Brazilian savannah

Introduction

Wetlands are aquatic ecosystems that are essential worldwide because they are very productive and harbor high biodiversity. In parallel, these aquatic ecosystems provide various ecosystem services, such as water purification, nutrient cycling, and food resources (Mitsch et al. 2015). Recognizing their importance, the Ramsar Convention advocates for the protection and sustainable use of wetlands (https://www.ramsar.org/). Nonetheless, human activities are a significant threat to wetlands; according to Davidson (2014), more than 50% of the total area of wetlands was lost, making them the most vulnerable natural ecosystem (Wantzen and Junk 2000; Hu et al. 2017; Lynch et al. 2023). Despite their importance, wetlands are understudied (Junk 2013; Junk et al. 2014) worldwide. In Brazil, there has been emphasis on large wetlands, such as the Pantanal, Amazon, and Paraná, and little attention has been given to smaller wetlands, such as the *Veredas* of the Cerrado biome (Brazilian savannah) (Junk 2013; Junk et al. 2014).

Vereda is a typical ecosystem in the Cerrado, characterized by diverse vegetation, with transitional areas composed of riparian forests, gallery forests, flooded forests, and humid grassland (Da Cunha et al. 2015). The Veredas are formed adjacent to small watercourses (Lima and Silveira 1991; Ab'Sáber 2003), formed by hydromorphic soils and the presence of organic turfs associated with shallow water tables (Oliveira et al. 2009; Bijos et al. 2017). Wetlands of the Veredas type can be observed in flat terrain (i.e., lowlands) or steep areas (i.e., hills or plateau areas). In lowlands, the most common places to form, Veredas cover extensive areas and do not have well-defined watercourses. On the other hand, the Veredas found in valleys or steep areas are less extensive and have better-defined watercourses, in general, small streams (Silveira et al. 2022). In the Cerrado, Veredas play important roles in regulating the water table and maintaining rivers (Lima and Silveira 1991; Ab'Sáber 2003).

There have been few studies dedicated to characterizing the biodiversity in the Veredas (Gomes et al. 2020; Faquim et al. 2021), and even fewer focus on the zooplanktonic groups, resulting in knowledge gaps about local biodiversity. For example, among zooplanktonic groups, it is estimated that for rotifers, at least 30% of the species recorded in Brazil come from aquatic environments in the Cerrado, and approximately 4% are possibly endemic (Padovesi-Fonseca et al. 2015). Similar knowledge gaps are expected for other zooplanktonic groups, given their high endemism levels (Padovesi-Fonseca et al. 2015, 2021). Furthermore, only a small proportion of studies about zooplankton in the Cerrado addressed the different zooplankton groups together (Alarcão et al. 2014; Pinese et al. 2015; Gomes et al. 2020; Picapedra et al. 2022). Most studies have been limited to a single group of these organisms, as is the case for microcrustaceans (Sousa and Elmoor-Loureiro 2008, 2013; Sousa et al. 2013; Elmoor-Loureiro 2014; Fonseca et al. 2018).

For zooplankton communities, it is well established that different habitats and local environmental conditions play a crucial role in the survival and reproduction of different species in ecosystems (i.e., ecological niche theory-Hutchinson 1957). Studies on zooplankton community ecology have emphasized the influence of local factors such as morphometric characteristics (Paquette et al. 2022), seasonal and climate (Stephan et al. 2017), and water quality on the spatial distribution of these organisms in ecosystems (Padovesi-Fonseca and Rezende 2017; Wan Maznah et al. 2018). On the other hand, other studies have highlighted the influence of spatial factors and dispersal ability as important contributors to establishing and structuring the community (i.e., Unified Neutral Theory of Biodiversity and Biogeography—Hubbell 2001). Previous studies have shown that seasonal, environmental, and spatial factors contribute to clarify the structuring of zooplanktonic communities in Cerrado streams (Gomes et al. 2020; Padovesi-Fonseca et al. 2021; Pedroso et al. 2021).

Here, it is evident that there is a need to lessen gaps in biodiversity knowledge of the mechanisms that determine the distribution and structure of zooplanktonic communities in the Veredas. For this to happen, we want to contribute to current knowledge by evaluating the influence of seasonal, environmental, and spatial factors on the structuring of zooplanktonic communities in the Veredas. For that, we outline the following specific hypotheses and premises: (i) Due to the little knowledge available about Veredas, it is expected to register new occurrences or new records of zooplanktonic species. (ii) As a complex and dynamic environment (Da Cunha 2015), we expect the environmental variables to reveal dissimilarities between the sampling seasons. (iii) Knowing that the zooplankton community responds quickly to environmental changes (Fernández-Aláez et al. 2018), we expect that the zooplankton community will respond seasonally, and (iv) we expect that environmental factors will influence the composition of zooplankton more than spatial factors.

Methods

Study area

Veredas are localized between the cities of Barra do Garças and Nova Xavantina, state of Mato Grosso (Cerrado Biome), and distributed in headwaters of the microbasins of the Araguaia and Rio das Mortes (Fig. 1). The climate is classified as Aw according to the Köppen classification and has two defined seasons: dry winter and rainy summer (Kottek et al. 2006; Alvares et al. 2013). The annual mean temperature ranges from 22 to 25 °C, and the annual mean

precipitation ranges from 1200 to 1800 mm (Alvares et al. 2013). The altitude above sea level ranges from 734 to 300 m. The *Veredas* streams sampled are waterways from first to third order according to the classification of Sthaller (Horton 1945; Strahler 1957). The streams associated with the *Veredas* are characterized by vegetation surrounded by grasses

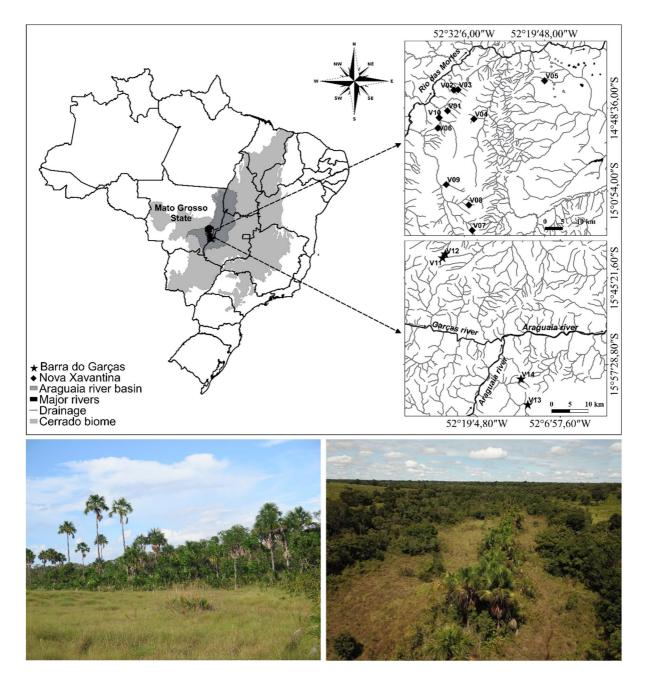


Fig. 1 Veredas sampled in the Upper Araguaia River Basin, Cerrado biome, Brazil

and herbs and in general with the presence of *Mauritia flexuosa* (Buriti) palms (Ribeiro and Walter 2008). The palms do not form a canopy, leaving vegetation coverage ranging from 5 to 10%.

Zooplanktonic community sampling

The zooplanktonic communities were sampled in the dry season (2016–2017) and rainy season (2020). We sampled 14 streams during the dry season, and out of those, 11 streams were resampled during the rainy season. To perform sampling, we chose a lentic stretch of stream and filtered 600 L of water through a mesh plankton net (68 µm) using a motor pump (Honda WX10T model). Then, we fixed the collected material in 4% formaldehyde buffered with sodium tetraborate (borax). The zooplankton was identified, and the density of each taxon was counted using a binocular optical microscope (Olympus CX23) and 1 mL Sedgewick-Rafter counting chambers. Then, the entire sample was analysed. The identification of the collected material was carried out using specialized bibliographic material (e.g., Koste 1978; Dussart and Defaye 1995; Segers 1995; Elmoor-Loureiro 1997; Suárez-Morales et al. 2020).

Environmental data

To measure environmental variables such as pH, turbidity, water conductivity, water temperature, dissolved oxygen, and total dissolved solids, we used a multiparameter limnological probe (Horiba, model U-50) at a single point of the stream. We measured depth and width at five points in the sample section. The surface water flow was measured by the time it takes a floating object (a rubber ball) to travel for one meter in the center of the stream channel.

Data analysis

To assess the environmental dissimilarity between the sampling seasons (hypothesis ii), we first performed a Principal Component Analysis (PCA) with the environmental variables. The aim PCA is to demonstrate the relationship of environmental variables with the sampled sites between seasons (Legendre and Legendre 1998). Additionally, we performed nonmetric multidimensional scaling (NMDS) using a Euclidean distance matrix to detect the environmental gradient

in each sampling season. The environmental variables were standardized (scale x to zero mean and unit variance) and checked for high correlations between them, but no high correlation (r > 6.0) was found. Then, we performed an ANOSIM to test the environmental dissimilarity between the dry and rainy seasons.

To characterize the zooplankton community (hypothesis iii), we first performed a T test using log-transformed total density data and total richness data (response variables) and dry and rainy seasons (independent variables). Both data sets were previously tested for normality (Shapiro–Wilk test). The zooplankton composition data were obtained by the Hellinger transformation of zooplankton density data. Later, we performed an ANOSIM accompanied by NMDS to compare the zooplankton composition in the dry and rainy seasons. For these analyses, we used the functions "anosim" and "metaMDS" in the *vegan* package (Oksanen et al. 2022).

To investigate the primary predictor for the zooplankton community (hypothesis iv), we performed a multiple regression on distance matrices (Zapala and Schork 2006; Lichstein 2007; Haynes et al. 2013). The response variable was a zooplanktonic community matrix (represented by the Bray-Curtis distance of Hellinger transformed density data) in the dry and rainy seasons separately. The independent variables were the spatial predictor (an Euclidean distance matrix of geographical coordinates) and the environmental predictor (the Euclidean distance of all standardized environmental variables). The Veredas that could not be sampled in the rainy season (V05, V06, V10) were also removed from the matrices of the dry season. Multiple regression on distance matrices (MRM) was carried out using the "MRM" function available on the ecodist package (Goslee and Urban 2007).

To achieve a multivariate response between environmental predictors and biological data, we performed a redundancy analysis (RDA). We then used forward variable selection to obtain an ordination constrained to the explanatory variable of interest (P < 0.05). For that, we used the "ordistep" function available on the vegan package (Oksanen et al. 2022). We checked the collinearity with the variance inflation factor (VIF) using the "vif" function available in the *car* package (Fox and Weisberg 2019). VIF values < 10 indicate variables that are independent of

each other (Graham 2003; Borcard et al. 2018). For the RDA in the rainy season, the variables conductivity and dissolved oxygen were removed to control for multicollinearity. Prior to analysis, the environmental data matrix was standardized, and the zooplankton density matrix was transformed using log(x+1). All analyses were performed in the R programming environment (R Core Team 2022).

Results

Environmental characterization

In both seasons, the *Veredas* streams sampled had very low electrical conductivity and total dissolved solids. The availability of dissolved oxygen varied widely in the dry season, while the mean value of dissolved oxygen was lower during the rainy season. The pH was always below seven, with the mean value being lower during the rainy season. On average, the depth of the *Veredas* streams increased considerably during the rainy season, along with the water temperature, while the water flow decreased slightly. The average stream width increased little during the rainy season, and the standard deviation of these values was lower at this time of the year, indicating that the *Veredas* had more similar widths in the rainy season (Table 1).

The PCA explained 60% of the environmental variability in both seasons in the first two axes (Axis 1 and 2, explained 36 and 24% of the variability, respectively). Furthermore, the ANOSIM (R=0.32; P=0.001) and the NMDS analysis (stress=0.105) showed differences between seasons. These results showed that the environmental characteristics of the streams were different between the dry and rainy seasons (Fig. 2a, b).

Zooplankton characterization

We recorded a total of 69 zooplankton taxa, including 41 rotifers, 16 cladocerans, and 12 copepods (9 adult copepods). Of these, 48 taxa were found in the dry season samples, and 43 were found in the rainy season (21 of which were not found in the dry season). The rotifers and cladocerans were mostly identified down to the species level. Whereas copepods, the adult forms were distributed into the family (for

Table 1 Mean values (mean) and standard deviation (STD) of environmental variables in *Veredas* streams (n = 14), comparing dry and rainy seasons, in the Araguaia River basin

Environmental variables	Dry		Rainy	
	Mean	STD	Mean	STD
Conductivity (µS cm ⁻¹)	0.01	0.01	0.01	0.02
Dissolved oxygen (mg L ⁻¹)	11.70	6.00	4.51	1.67
pH	4.94	0.84	3.93	0.87
Water temperature (°C)	25.18	1.86	28.03	2.76
Total dissolved solids (mg L^{-1})	0.02	0.06	0.01	0.01
Depth (cm)	28.84	15.87	46.84	13.76
Water flow (m s^{-1})	0.17	0.12	0.22	0.26
Stream width (m)	3.00	3.57	3.68	1.48

Harpacticoida) and genus (for Cyclopoida), and the other stages of development were counted as distinct taxa, due to their different ecological roles: nauplii (larval stage), Harpacticoida copepodites, and Cyclopoida copepodites (stage juvenile). We highlight the record of the genus *Monospilus* sp. (Cladocera) in Vereda V10 in the dry season as a new occurrence for this region (Table S1), and some zooplankton species with a more restricted distribution were detected in this study: *Acroperus* cf. *tupinamba*.

Veredas with higher richness also presented a higher density of organisms during both dry and rainy seasons. The zooplanktonic community was similar across all *Veredas*, with a greater proportion of rotifer group compared to other zooplanktonic groups as well as for the density of organisms. There were no significant differences in zooplankton richness (t = -0.8, df = 10, P=0.442), density (t = -0.54, df = 10, P=0.604) and composition (ANOSIM R=0.06; P=0.121) between seasons. The similarity in the zooplanktonic community between the two seasons was evident in the NMDS ordering analysis (stress=0.195, Fig. 3).

By analysing the data for each climate season, we found that environmental conditions among *Veredas* were an important predictor for zooplanktonic community variability during the rainy season but not in the dry season (Table 2). The forward selection in RDA revealed two significant environmental variables (water temperature and total dissolved solids) as the most important predictors for rainy season data ($R^2_{adj} = 0.44$, F=4.94, P=0.001). For dry season data, dissolved oxygen

Fig. 2 a Principal component analysis (PCA) with all environmental variables of *Veredas* streams in the Araguaia River basin in the dry (D) and rainy (R) seasons; **b** nonmetric multidimensional scaling (NMDS) of *Veredas* streams in the Araguaia River basin in the dry and rainy seasons using the environmental variables

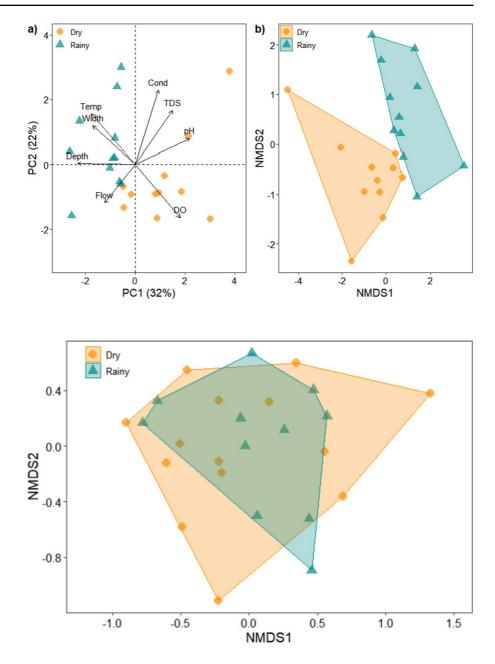


Fig. 3 Nonmetric multidimensional scaling (NMDS) based on zooplankton community density in *Veredas* streams in the Araguaia River basin in the dry and rainy seasons

was identified as the most important predictor of zooplankton density data ($R^2_{adj} = 0.10$, F=2.46, P=0.037). For the entire data set, we identified conductivity as the most important environmental variable for explaining zooplankton density data ($R^2_{adj} = 0.12$, F=3.92, P=0.008).

 R^2_{adj} adjusted regression coefficient, P p value

Table 2 Results of multiple regression of distance matrices(MRM) between matrices of biological distance (density ofzooplankton) and environmental (Env) and spatial (Spa) dis-tances. (Standardized coefficients)

Predictors		Coef.	Р	R^2_{adj}	Р
Dry	Env.	0.17	0.419	0.05	0.402
	Spa.	0.07	0.675		
Rainy	Env.	0.49	0.015	0.37	0.004
	Spa.	0.18	0.276		

significant relationships are indicated in bold

 R^2_{adj} adjusted regression coefficient, P p value

Discussion

There is still limited knowledge about the biodiversity of the Veredas ecosystems, especially regarding microscopic groups such as zooplankton (Junk et al. 2006; Fonseca et al. 2018; Pedroso et al. 2021). The zooplankton taxa listed in this study (Table S1) are primarily cosmopolitan and neotropical (Smirnov 1996; Segers 2007). Among those, Acroperus cf. tupinamba has a more restricted distribution, with records in the Neotropical region registered thus far in Brazil and Ecuador (Sinev and Elmoor-Loureiro 2010). Notably, the genus Monospilus sp. was registered only in the dry season of the Veredas stream V10. In Brazil, only two protected areas of the Cerrado biome reported the occurrence of two species of this genus, Monospilus brachyspinus and Monospilus macroerosus (Sousa et al. 2017, 2018). As predicted in our hypothesis (i), our study could increase knowledge about the species that can be found in Veredas streams. Therefore, encouraging studies about biodiversity in understudied regions such as Veredas is necessary to lessen these knowledge gaps.

Veredas streams are mainly lotic water. In general, lotic ecosystems are unfavourable for the development of zooplanktonic organisms, due to rapid temperature fluctuations, water fast flows, and other factors (see more at Aggio et al. 2022). Zooplankton prefer backwater areas (Padovesi-Fonseca et al. 2021), but some taxa tolerate these conditions well (Matsumura-Tundisi et al. 2015), such as those adapted to living in the littoral zone of aquatic ecosystems. For example, Rotifera was the most abundant group in the sampled locations. This dominance pattern can be explained by the morphological and adaptive characteristics of this group, such as relatively small bodies, short life cycles, high reproductive rates, and predominantly parthenogenetic reproduction and resistance eggs (Allan 1976; Wallace et al. 2006). Among the organisms identified in the samples, the majority were representatives of littoral habit zooplankton, including rotifers of the genus Lecane (Segers 1996) and cladocerans of the family Chydoridae (Elmoor-Loureiro 1997). Copepods of the Cyclopoida and Harpacticoida orders also represent organisms with littoral and benthic habits (Esteves 1998).

The hydrological dynamics of drought and rain influenced the environmental conditions of the *Vere- das* streams. Our study showed significant differences

between the climatic seasons regarding the environmental gradient, in line with what was predicted by hypothesis (ii). Veredas are complex and heterogeneous systems with environmental characteristics that vary depending on location. The environmental structures of these locations can be determined by geological characteristics and historical factors associated with changes in relief (Gordon et al. 1997). For example, the type of bedrock in which the stream is located can influence the amount of solids dispersed in the water, while soil conditions can influence vegetation composition on the streambanks (Lewis 2008). The shape of the relief and its slope can also determine the flow of water, with steeper environments tending to have greater water velocity and narrower and deeper streams compared to less steep environments (Gordon et al. 1997; Lewis 2008).

Although it was not possible to find statistical differences in the zooplankton community in relation to seasonality, which refutes our hypothesis (iii), environmental variables are often important predictors of biological communities (e.g., Pinel-Alloul 1995; Bini et al. 2008; Declerck et al. 2011; Lopes et al. 2018; Pedroso et al. 2021). To Veredas streams was to recognize that conductivity, dissolved oxygen, water temperature, and total dissolved solids were the most important variable to organize the zooplanktonic community. These variables may act as an environmental filter for the development of the zooplanktonic community in the Veredas, as predicted by hypothesis (iv). Previous studies have already reported the importance of water temperature on zooplanktonic communities. In turn, the high temperature of water reduces the dissolved oxygen (Pinese et al. 2015), especially in shallow environments such as Veredas streams. Furthermore, Cerrado aquatic ecosystems are characterized by low electrical conductivity (Wantzen 2003, 2006; Gonçalves et al. Jr 2006), which may restrict the occurrence and/or establishment of certain species. Therefore, the Veredas streams with slightly higher conductivity values than expected may provide suitable conditions for more taxa to coexist, increasing local richness and abundance (Tundisi and Matsumura-Tundisi 2011).

Wetlands play an important role in water purification, nutrient cycling, and other ecosystem services (Convention on Wetlands 2021; Lynch et al. 2023). In particular, the *Veredas* are important for the maintenance of water resources once they are in the headwaters of the drainage basins. However, habitat fragmentation, land use conversion to agriculture, and siltation pose significant threats to the conservation of these Cerrado environments (Carvalho et al. 2009; De Marco et al. 2014), including the Veredas (Gonçalves et al. 2022). In recent decades, the rapid loss of wetland integrity has been reported worldwide (Hu et al. 2017). As underscored by a recent overview, "Biodiversity conservation is especially critical for freshwater biodiversity" (Lynch et al. 2023). Thus, the indepth understanding gained from our study regarding the Veredas can lead to better conservation efforts for these small wetlands. Specifically, to maintain the water depth required for local zooplanktonic communities, it is crucial to prevent the loss of zooplankton communities and a whole resulting food web.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interest The authors declare no competing interests.

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