



# The zooplankton of tropical streams: is it determinism or stochasticity that drives the spatial and temporal patterns in community structure?

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## Abstract

The comprehension of the ecological structure and the functioning of natural and/or impacted lotic ecosystems is the purpose of most studies concerning rivers and streams. This study aimed to investigate the main factors influencing the zooplankton community organization in nine impacted tropical streams of three different sub-basins of the Cinzas River basin, Paraná state, Brazil. We tested the hypothesis that macro-factors such as productivity, current velocity, habitat structure, and stream order and stretches (headwater, middle and mouth), are the main factors structuring the zooplankton community in tropical streams. Zooplankton was represented by 101 taxa, mainly testate amoebae, followed by rotifers, cladocerans and copepods. Results showed that the greatest differences in physical and chemical characteristics and those related to zooplankton community structure were observed among the three sub-basins studied. However, we found that these differences were not related to the environmental heterogeneity, but were rather influenced mainly by spatial factors related to stochasticity in the structuring of planktonic communities. Thus, our results suggest that connectivity between environments within the same sub-basin, associated with random processes driven by dispersal, may determine the existence or not of spatial patterns, among stream order or stretches, and temporal patterns, between seasons, in the community attributes here analyzed.

**Keywords** Plankton · Lotic environments · Spatial scale · Environmental heterogeneity · Longitudinal gradient

## Introduction

Lotic environments function as open hydrological systems, where there is a constant flow from the source to the mouth, promoting alteration in the physical structure over time and space, besides carrying out exchanges with the terrestrial environment in an intense manner (Gomes, Gomes, et al., 2020; Thorp et al., 2006). In such systems, connectivity along the drainage basin is an important parameter if we consider the stretch (source, middle, and mouth) and the order of the streams (1st, 2nd, and 3rd order). Stretch and order influence aspects such as water flows, sediment discharge, organic matter, solutes, and also the biotic communities, which are more susceptible to changes (e.g., movements of organisms) from upstream to downstream of the river network (Wohl, 2017). Some of these parameters are responsible for habitat structuring and can interfere with current velocity and even ecosystem productivity.

Stream ecosystems vary considerably in their structure, due to channel-specific characteristics, and how they can structure communities, aspects that have been tested by

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some models. For example, the Stream Zonation Concept (SZC) proposed by Illies and Botosaneanu (1963), defines a series of discontinuous communities along rivers, separated by larger fauna transition zones, caused by changes in the river slope and its flow velocity. In addition to this, the River Continuum Concept (RCC) proposed by Vanotte et al. (1980), defines changes in biotic communities, both in composition and distribution levels, as important bases for studies of longitudinal zonation of aquatic communities in lotic environments, where the environmental characteristics of a given section of a river depend on environmental conditions and geographical positioning (Vanotte et al., 1980; Statzner & Higler, 1985; Ferreira, et al., 2010).

Such models address several features that influence aquatic communities in lotic environments. Among them, especially the temperature, substrate discharge and structure, light, and nutrients affect primary productivity and the input of organic matter (Czerniawski, 2013), which directly influence the structuring of aquatic biota (Gutierrez et al., 2020). In addition to these, macrofactors such as productivity, current velocity, habitat structure (environmental heterogeneity) and stream order and stretch (source, middle and mouth) can be important in structuring these communities in tropical streams (Blatterer, 2002). Moreover, lotic environments differ fundamentally in connectivity when compared to lentic ones. One can envisage that dispersal rates among localities are higher in streams and rivers than among lakes and ponds without stream connections (Gomes, Gomes, et al., 2020). Because of this, high connectivity among habitats may lead to higher homogeneity of assemblages inhabiting lotic environments (Heino et al., 2015a). The zooplankton community is an important link in the trophic chain in aquatic environments because it connects predators and primary producers (Gutierrez et al., 2020). They have short reproductive cycles (generally from one week to months) (Lampert & Sommer, 2007) and studies on lotic systems are still scarce and deserve further research efforts (Picapedra et al., 2019).

Given that the reproductive rate of plankton is often lower than its drift downstream, zooplankton-typical organisms cannot develop large populations in environments with high current velocity (Czerniawski & Domagała, 2014). Lotic environments can be unfavorable to zooplankton development due to rapid temperature oscillations, the strength of water currents, which depend on the heterogeneity of the river bed, and other physical and biological factors, such as turbulence (influence on zooplankton filtration, predation, and reproduction) and the concentration of suspended solids, which can limit feeding efficiency, and the erosive effect of the water current (Lair, 2006; Golec-Fialek et al., 2021). Interestingly, these features of lotic systems determine that the zooplankton community in rivers and streams is influenced by a strong input of fauna from other compartments such as benthic and littoral, structuring a community known

as riverine zooplankton or potamoplankton (Lansac-Tôha et al., 2009).

Although lower diversity is found in lotic environments, especially in streams, when compared with lentic ones, many species can find suitable conditions for the development of dense populations (Ejmont-Karabin & Kruk, 1998). The dominance of different groups in zooplankton generally provides a good idea of the hydrodynamic conditions prevailing in the sampled areas, with the dominance of microcrustaceans in areas with longer water residence time, while the dominance of rotifers is an indication of shorter residence times (Lansac-Tôha et al., 2009; Sampaio et al., 2002). On the other hand, an expressive participation of testate amoebae in plankton samples characterizes environments with a greater influence of lotic conditions (Gomes, Gomes, et al., 2020).

In tropical regions, especially in Brazil, studies on the ecology of the zooplankton community in lotic environments have increased in recent decades, contributing to a better understanding of the main mechanisms involved in the regulation of abundance, diversity and spatio-temporal patterns (Gomes, Barbosa, et al., 2020; Gomes, Barbosa, et al., 2020; Gomes, Gomes, et al., 2020; Perbiche-Neves et al., 2012; Picapedra et al., 2017; Silva et al., 2021). However, most of the studies have focused on the influence of abiotic conditions or parameters on communities, leaving the understanding of biotic interactions between communities restricted to few studies. For example, Perbiche-Neves et al. (2012) found a negative relationship between water velocity and increased turbidity in zooplankton abundance and richness; on the other hand, the authors demonstrate that tributaries are important for increasing zooplankton richness in the main channel. Also, according to Gomes, Barbosa, et al. (2020), environmental and spatial variables may not have significant effects on the structure of zooplanktonic communities in streams, which may indicate a strong influence of stochastic factors. The aquatic environments in the tropical region can be considered as less unstable than those located in the temperate region environments. In the tropics, atypical and extreme conditions, such as edaphic and climatic conditions, are only rarely observed (Kwok et al., 2007).

Thus, the aim of this study was to investigate the main factors intervening in the organization of the zooplankton community in tropical streams of different sub-basins of the Cinzas River watershed, situated in southern Brazil. Based on RCC, we tested the hypothesis that macrofactors (productivity, current velocity, habitat structure and stream order and stretch (source, middle and mouth) are the main structuring factors of the zooplankton community in tropical streams. More specifically, the following predictions were tested: (i) the abundance of zooplankton organisms responds to the longitudinal gradient and stream order, with higher density at the mouth of streams where the lowest current

velocity is recorded, while richness will be more influenced by environmental heterogeneity (i.e., site-by-site environmental variation) in different sections and streams; (ii) These patterns will be more pronounced in the dry season, as a function of greater channel stability and uniqueness of each compartment.

## Material and methods

### Study area

The study was conducted in three watersheds (Água das Araras, Eucalipto and Água da Divisa streams) belonging to the lower stretch of the Cinzas River basin, in the State of Paraná, Brazil ( $23^{\circ} 10' 51''$  S,  $50^{\circ} 38' 49''$  W and  $23^{\circ} 9' 3''$  S,  $50^{\circ} 31' 8''$  W). The Cinzas River originates in the center and its mouth is in the northern region of Paraná State. Its basin covers an area of 9658 km<sup>2</sup>. The three watersheds are located in the geographical region of the third plateau of Paraná, which is characterized by its rugged terrain, with altitude varying between 600 and 700 m. All the environments are within an agricultural area, with a predominance of soybean, corn and wheat crops (Água das Araras stream

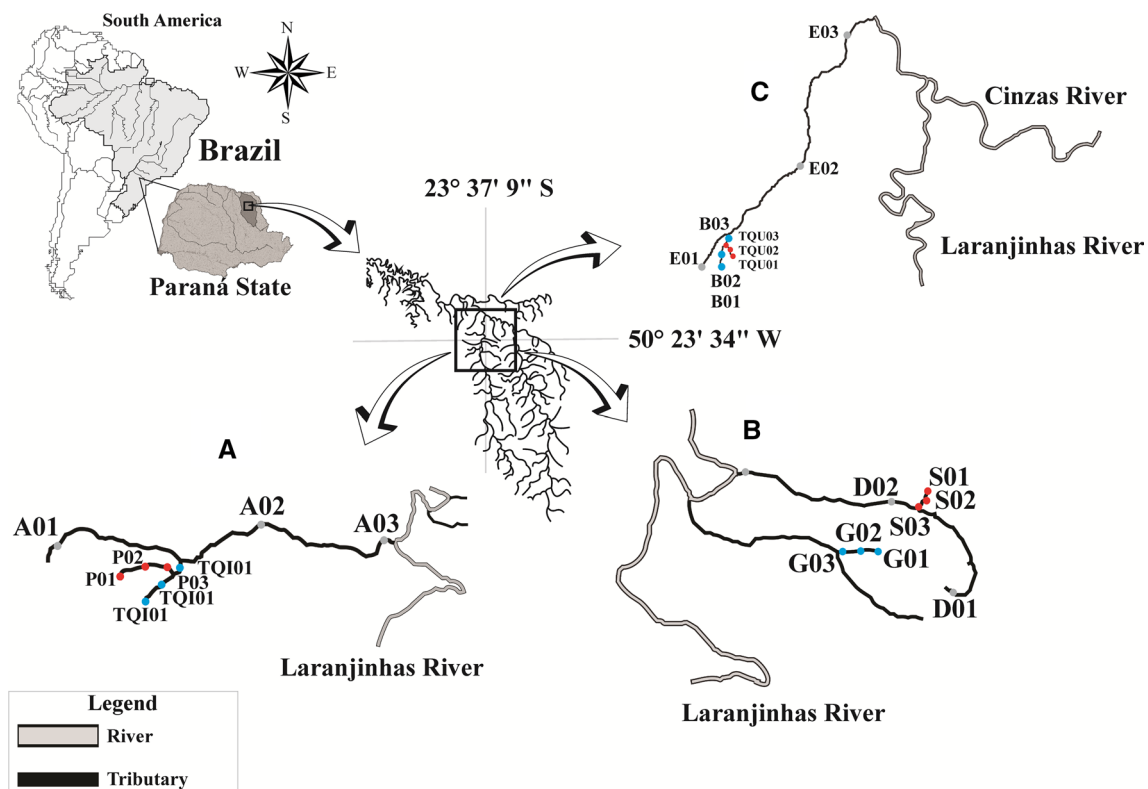
and Eucalipto) and grapes, vegetables, legumes, citrus and corn (Água da Divisa stream) (Fig. 1).

One stream from the first, second, and third order according to Strahler (1957), was selected for each watershed (SM1), and three sampling points were located along each stream (source, middle course, and lower course or mouth). In this way, sampling was carried out at 27 points through the rainy (March) and dry (September) seasons, during the year 2014, totaling 54 samples. For this purpose, it was assumed that each sampling point, from streams of the same magnitude, would act as a replicate. All streams are located in rural areas, and some stretches have been heavily modified by anthropic activity, such as removal of riparian vegetation, flow control, and channelization.

### Sampling

#### Zooplankton community

The zooplankton community was sampled by filtering the water collected from the subsurface of the environments, using a conical net with 68  $\mu$ m mesh, with the aid of a 20L graduated bucket. Between 50 and 300L of water were filtered according to the characteristics of each sampling site. The collected material was put in 250 ml plastic bottles



**Fig. 1** Map of the location of the different watershed studied and their sampling points (a=Água das Araras stream watershed; b=Água da Divisa stream watershed; c=Eucalipto stream watershed)— red filled circle 1st order; blue filled circle 2nd order; grey filled circle 3rd order

and preserved in 4% formaldehyde solution buffered with calcium borate ( $\text{CaCO}_3$ ). In the laboratory, the samples were processed according to Wetzel and Likens (2001) and Bicudo and Bicudo (2006), where each sample was concentrated to a volume of 50 ml. After homogenization and with the aid of a common optical microscope (Bioptika) and Sedgewick-Rafter chamber, 5 ml of each sample was analyzed. Identification of zooplankton organisms was performed, whenever possible, at the species level, based on morphological characteristics and with the help of specialized bibliography (Koste, 1978; Reid, 1985; Elmoor-Loureiro, 1997; Souza, 2008; Paggi, 1995; Siemensma, 2021).

### Environmental Variables

For each sampling point, water was collected from the sub-surface through a 5L plastic jug, for the determination of the physical and chemical variables: Ammoniacal Nitrogen, Nitrite, Total Dissolved Phosphorus, Reactive Phosphate (P-ortho) and chlorophyll-a, following the protocols described in APHA (2017). With the help of a Hanna HI 9828 multiparameter probe, environmental variables such as pH, electrical conductivity, dissolved oxygen, oxygen saturation (%), total dissolved solids and water temperature were measured. Water transparency was measured using a Secchi disk. The width and depth of each sampled site were also measured. Current velocity was estimated using a General Oceanics flow meter. We also gathered data from substrate type and macro-structures such as percentage of leaves, branches, trunks, and rocks, using a visual inspection of a square of  $0.25 \text{ m}^2$  in triplicates. All environmental variables used have been shown to influence zooplankton richness, abundance and composition (Lansac-Tôha et al., 2009).

### Data analysis

We calculated the specific richness, through the total sum of species, and the abundance of organisms, expressed in individuals per cubic meter (ind.m<sup>-3</sup>), by the formula:

$$(N * V_{Co}) / (V_{Ct} * V_F)$$

where  $N = n^\circ$  organisms counted in the sample;  $V_{Co}$  = concentrated volume;  $V_{Ct}$  = volume counted;  $V_F$  = filtered volume in m<sup>3</sup>.

To evaluate prediction i), an analysis of variance (two-way ANOVA) was performed for zooplankton richness and abundance values in the different stream sections (source, middle, and mouth) and among stream orders (1st, 2nd, and 3rd order). In addition, a Pearson correlation analysis was performed to verify whether habitat heterogeneity would be the main regulating factor for zooplankton species richness.

The values of habitat heterogeneity were obtained using the Shannon diversity index (Shannon & Weaver, 1949), calculated for the different habitat descriptor variables (substrate type and macro-structures such as: percentage of leaves, branches, trunks, rocks). Before running these analyses we checked for homogeneity and normality assumptions, and no data transformation was needed.

To evaluate the prediction (ii), an analysis of variance (one-way ANOVA) between the two periods (dry and rainy) of the study was performed to verify if the observed patterns would be more pronounced in the dry period.

A Redundancy Analysis (RDA) was performed using the site-by-site abundance matrix of zooplankton species and the site-by-site matrix of environmental variables, including flow, temperature, pH, electrical conductivity, dissolved oxygen, dissolved phosphorus, ammonia, total dissolved solids (TDS), and chlorophyll-a. We checked the multicollinearity with Variance Inflation Factor (VIF) and variables with VIF values higher than 10 were excluded from the analysis. In this case, conductivity and TDS showed collinearity and the latter was excluded.

We also performed a partial redundancy analysis to verify the unique contribution of environmental, spatial and stretch of the river components and their interactions. The spatial component was computed using distance-based Moran's eigenvector maps (dbMEM<sub>s</sub>) from a geographic distance matrix. In order to minimize discrepant effects between variables, we used Hellinger transformation for biologic data, while abiotic data were previously standardized. All analyses were performed in the R program version 4.1 (2021), using the “stats” package to calculate the ANOVAs, “vegan” package for performing the RDA and partial RDA, “adespatial” to compute the MEMs and “ggplot2” for visualization. All results were tested at a significance level of  $p < 0.05$ .

## Results

### Taxonomic composition, species richness and abundance of zooplankton

A total of 101 taxa belonging to four taxonomic groups were recorded, with testaceous protozoa (51) standing out, followed by Rotifera (31), Cladocera (12) and Copepoda (7) (SM 2). Testate amoebae were represented by 7 families, the most species-rich being Arcellinidae, Centropyxidae and Diffflugidae, while for rotifers the Brachionidae, with 10 species, and Lecanidae, with 8 species, stood out. The cladocerans were best represented by Daphnidae and Chydoridae, and the copepods by Cyclopidae, especially their young forms (SM 2).

Regarding the species recorded, *Centropyxis aculeata*, *Centropyxis ecornis*, *Arcella vulgaris*, *Diffflugia cylindrus*

(2.96%) and *Diffugia tuberculata* (2.87%) stood out among the testaceans. Among rotifers, the highest frequencies of occurrence were recorded for *Lecane bulla*, Bdelloidea, *Platyonus patulus* and *Kellicottia bostoniensis*. The cladocerans were best represented by *Moina minuta*, *Daphnia gessneri*, *Ceriodaphnia silvestri*, *Alona glabra* and *Coronatella popei*. For copepods, the larval forms (nauplii) of Calanoida and Cyclopoida were the most frequent.

The results obtained for species richness showed values between 1 and 25 species, with a mean of 9 species for the rainy season, and between 0 and 24 species, with a mean of 10 species for the dry season. These values were quite variable for the different orders and stream sections. Thus, the results of ANOVAs for total richness and for each zooplankton group did not show significant differences among orders, stretches or seasons, nor for interactions terms (Fig. 2; SM3; SM4). Moreover, Pearson's correlation analysis ( $p < 0.05$ ), which tested the relationship between species richness and habitat heterogeneity, showed no significant influence of this variable on the zooplankton community in these streams.

For zooplankton abundance, the recorded values ranged from 30 to 8500 ind.m<sup>-3</sup>, averaging 1746 ind.m<sup>-3</sup> for the rainy season, and from 0 to 3870 ind.m<sup>-3</sup>, averaging 1112 ind.m<sup>-3</sup> for the dry season. When considering the different groups, testate amoebae were the ones that presented the highest mean density (about 60%), followed by rotifers (19%), while copepods represented 17% and cladocerans 4% of the zooplankton abundance. Temporally, a decreasing trend in the number of organisms was observed in the rainy season (Fig. 3b). Despite the observed trends, the results of the ANOVAs, which evaluated the effects of orders, stream stretches (source, middle and mouth) and sampling period on the abundance of the zooplankton

community and its individual groups, did not show significant results, as was also observed for the interactions terms (Fig. 3; SM5; SM6).

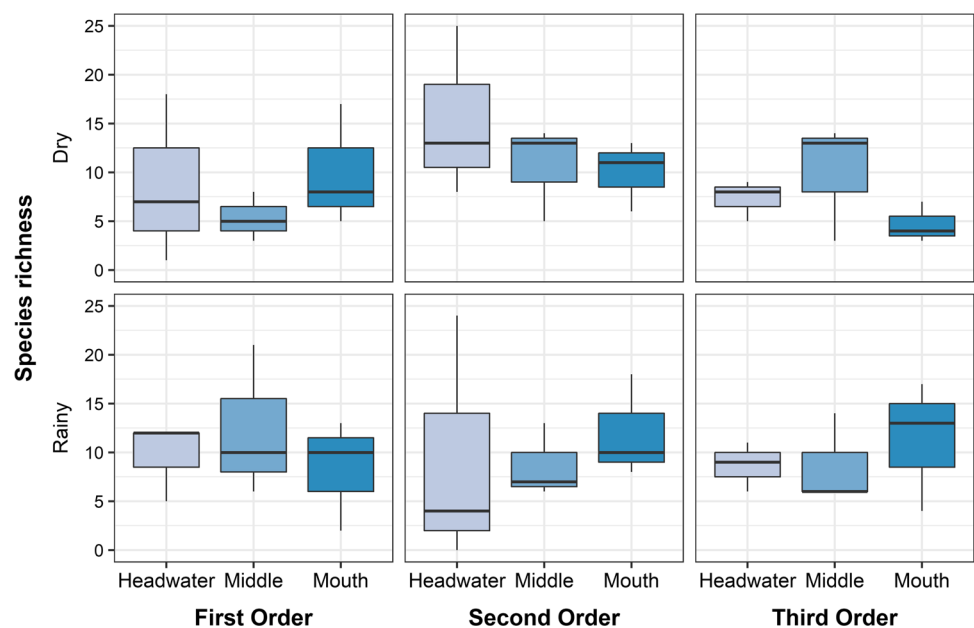
### Abiotic variables, zooplankton and the characterization of micro-basins

The results of the Redundancy Analysis (RDA) explained 31% of the total variability of the data. Furthermore, the percentage of explanation provided by the analysis was significant ( $p < 0.005$ ). The greatest differences in physical and chemical characteristics and those related to zooplankton community structure were observed among the three sub-basins studied (Fig. 4).

Thus, on axis 1, a differentiation is observed between the sub-basin of the Divisa River, characterized by the highest values for conductivity (Cond) total phosphorus (PT), and the sub-basin of the Araras River, where the highest values of chlorophyll-a and current velocity were recorded. On the other hand, axis 2 of this analysis discriminated the samples from these first two sub-basins from those taken from the Eucalipto River sub-basin, characterized by higher orthophosphate values (Fig. 4).

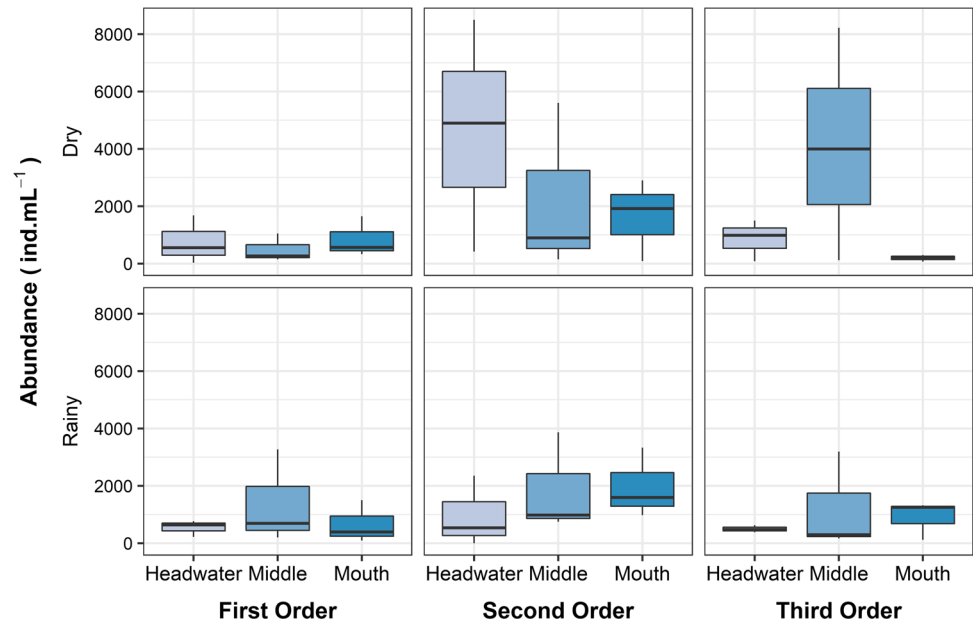
Regarding the species, most of the rotifers were more positively correlated to axis 1, characterizing, in general, the samples from the Divisa River sub-basin, while most of the cladocerans and copepods were negatively correlated to this axis and positively correlated to axis 2, showing their higher abundance in the Eucalipto River sub-basin. In relation to the testate amoebae, these were mostly negatively related to axis 2, thus characterizing most of the samples obtained from the sub-basin of the Araras River (Fig. 4).

**Fig. 2** Variation in species richness of zooplankton among orders, stretches and periods of sampling, in tropical streams of southern Brazil. The central lines denote the median value, box denotes 25 and 75 percentiles, whiskers represent respectively the smallest and largest value within 1.5 times interquartile range below and above percentiles





**Fig. 3** Abundance of zooplankton among orders, stretches and periods of sampling, in tropical streams of southern Brazil. The central lines denote the median value, box denotes 25 and 75 percentiles, whiskers represent respectively the smallest and largest value within 1.5 times interquartile range below and above percentiles



### Influence of environmental and spatial variables on zooplankton structure

RDA results revealed that the contribution of environmental and spatial factors differed in explaining ciliates community structure between dry and rainy seasons (Fig. 5). According to the explanatory power (adjusted  $R^2$ ), the ciliate communities were more strongly determined by spatial (Spa) than environmental (Env) conditions in the dry season (4% and 1.5%, respectively), while in the rainy season environmental and spatial variables explained the same variation in the ciliates community (5.2% in both dry and rainy seasons). Meanwhile, the gradient of the river stretch component (Grad) showed low contribution in both seasons, especially during the rainy season. Besides, a great amount of variation remained unexplained.

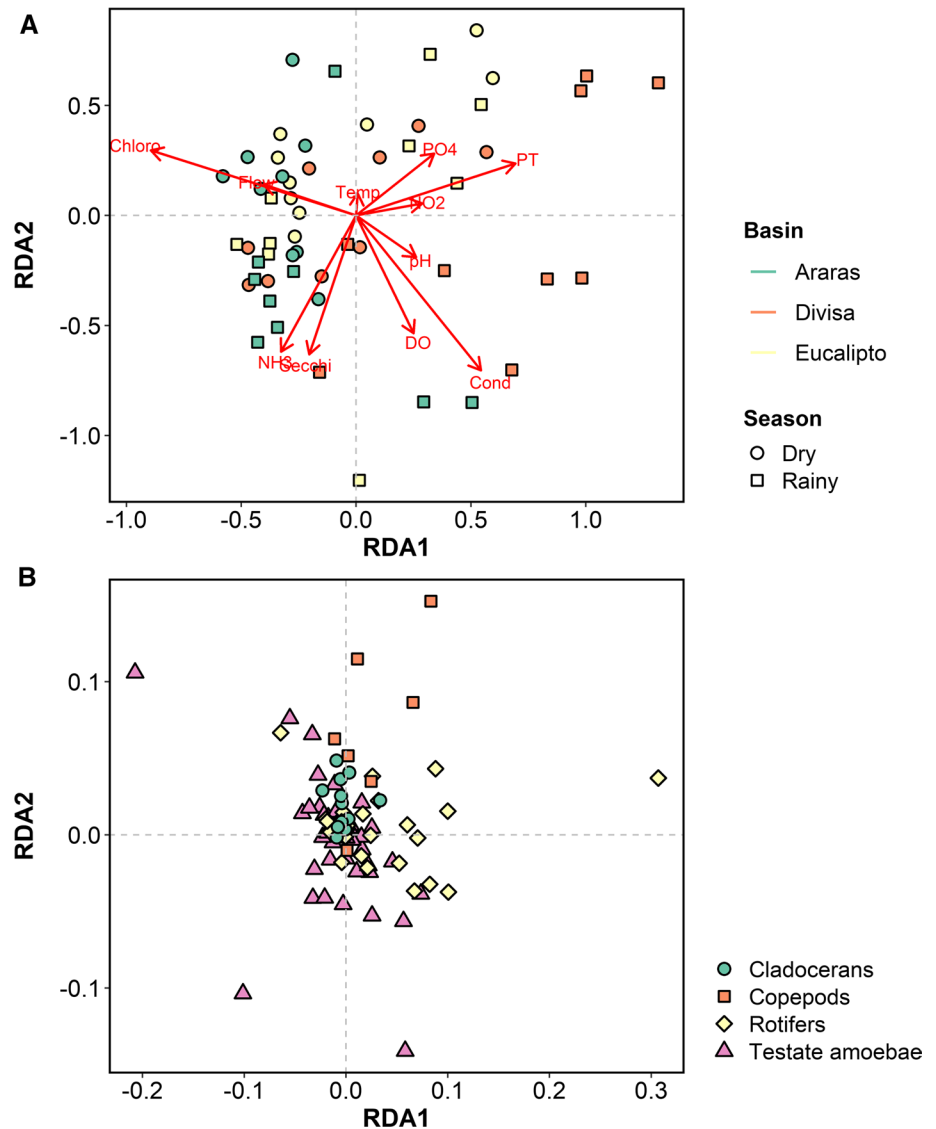
### Discussion

Studies indicate the importance of abiotic and biotic factors at the local level (Dodson & Frey, 2001; Williamson and Reid, 2001), as well as regional processes, for example, at the watershed level (Heino et al., 2015a, 2015b; Gomes, Gomes, et al., 2020; Padovesi-Fonseca, 2021). In this study, the predictions that zooplankton would respond directly to local environmental factors, related to macrofactors determined by the longitudinal gradient of each stream, as well as by stream order and hydrological period, were all refuted. On the other hand, the results of RDA and the Analysis of Partition of Variance suggest the influence of geographic distance on community organization when considering the studied micro-watersheds.

Gomes, Gomes, et al. (2020) observed in a study on stream zooplankton of central Brazil that only the spatial variables were able to influence the composition of the zooplankton community, corroborating other studies that also found space to be the main factor in structuring of zooplanktonic communities (Soininen et al., 2018; Bie et al., 2012; Dejenie et al., 2012). They suggested that absence of connectivity between sampled sites can be a factor for the significant explanation of the spatial component. In this context, our study seems to corroborate this idea because we recorded a greater dissimilarity in community structure when space is analyzed among the micro basins. However, at basin level, the freeflow watercourse allows species to disperse passively, following the direction of the flow, which may increase community similarity due to the mass effects mechanism.

Dispersal allows the colonization of species in environments to which they are best adapted. Fragment dynamics assumes that the physical environment is spatially homogeneous and can be occupied and unoccupied over time according to the rates of colonization and extinction, and by interactions between species and dispersal (Rocha et al., 2020). However, according to Lansac-Tôha et al. (2019) neither species sorting nor dispersal mechanisms may shape aquatic communities. Rather, community structure may display a high degree of stochasticity caused by random colonization and extinction events (Hubbell, 2011). This is likely to be the case of phytoplankton inhabiting lotic systems, where the recurrent instability of the water column, continuous downstream flow and high turbulence may impose limits on their colonization, establishment and development (Bovo-Scomparin et al., 2013; Jati et al., 2017). This may, in turn, lead to unexpected absences at sites that are otherwise

**Fig. 4** Ordination diagram for the first two axes of the Redundancy Analysis (RDA), according to **A** the abiotic variables (temperature = Temp; electrical conductivity = Cond; dissolved oxygen = DO; pH; flux; secchi; chlorophyll = Chlora; ammonia = NH<sub>3</sub> and total phosphorus = PT) and **B** the zooplankton species categorized by group (testate amoebae, rotifers, cladocerans and copepods)



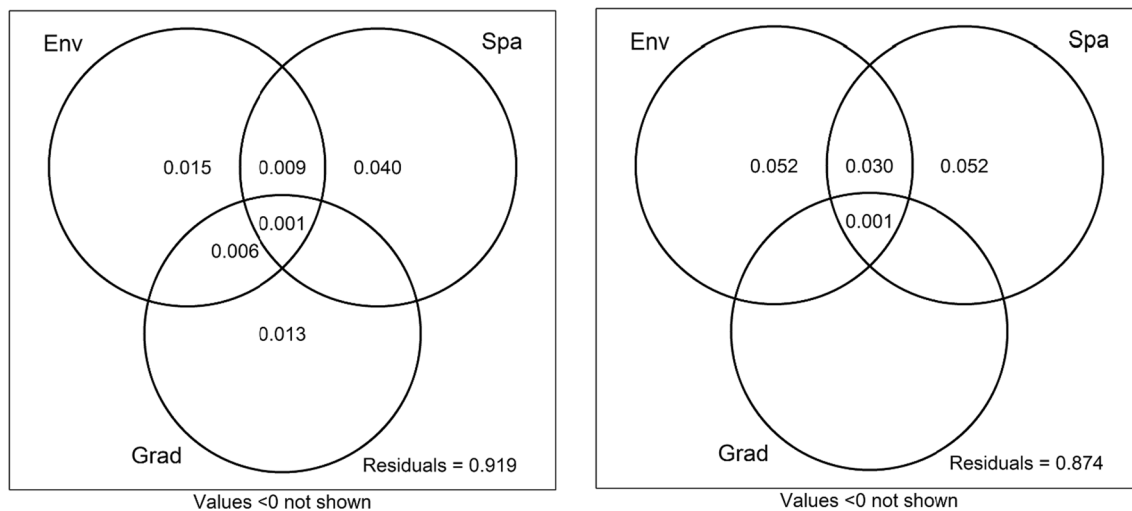
environmentally suitable, consequently weakening the action of environmental filtering (Heino et al., 2015a).

These challenging conditions imposed by a high-velocity current strongly limit the establishment of typically planktonic populations, resulting in a specific species composition of such systems. In these environments, there is usually a greater exchange of fauna between the aquatic compartments, which leads to a greater contribution of typically benthic or littoral organisms (Lansac-Tôha et al., 2009). Thus, in well-structured lentic environments, zooplankton is normally dominated by rotifers and microcrustaceans (cladocera and copepods), while in lotic ones it is, testate amoebae that contribute remarkably to zooplanktonic composition (Picapedra et al., 2019).

In fact, testate amoebae formed the most representative group in our study, both in richness and abundance, related mainly to the hydrodynamic characteristics of the

environments. The streams analyzed are shallow and present a high-water flow, where interactions between the plankton compartment and the sediment, the preferred habitat of these organisms, are more pronounced, promoting a greater contribution of these organisms in the planktonic samples. Studying the occurrence of testate amoebae in the plankton samples, Velho et al. (2004) observed higher densities in compartments that presented hydrological characteristics similar to lotic environments (high current velocity, shallow and narrow). Other authors, such as Fulone et al. (2008), Portinho et al. (2016), Czerniawski and Kowalska-Górska (2018), and Sartori et al. (2021), emphasized the importance of current velocity as the main intervening factor in the relative contribution of zooplankton groups in lotic environments.

Of the 20 families belonging to the zooplankton groups studied, Diffugiidae, Arcellidae and Centropxyidae (testate



**Fig. 5** Venn diagrams of partial redundancy analysis (pRDA) results for the dry (left) and rainy (right) seasons. Relative contribution (adjusted  $R^2$ ) of the environmental component (Env), the spatial com-

ponent (Spa), stretch of river gradient (Grad), the shared components and residuals (R) that explain the variation in ciliates community structure

amoebae), and Brachionidae, Lecanidae and Euchlanidae (rotifers) were the most representative. The high contribution of testate amoebae, especially of the families Diffugiidae, Arcellidae and Centropyxidae, in continental aquatic environments is well documented (Arrieira et al., 2015; Lansac-Tôha et al., 2014; Picapedra et al., 2019). Regarding rotifers, Brachionidae and Lecanidae are commonly highlighted among the families with more species in several Brazilian aquatic environments (Lansac-Tôha et al., 2004). Among copepods, the predominance of the young state (nauplii and copepodids) has been commonly found in several aquatic environments, including lotic systems (Picapedra et al., 2019; Silva et al., 2021).

The importance of resources in structuring zooplankton communities in streams has generally been neglected, with more attention being paid to the relationships of organisms and physical and chemical water variables (Lair, 2006). Thus, one of the biotic factors that often act on the distribution and abundance of organisms within the aquatic environment is resource availability, especially algal primary productivity, expressed by chlorophyll-a concentration. However, due to the lotic characteristics of the streams studied, as well as their low nutrient concentration, no significant influence of chlorophyll-a on the abundance of the zooplankton community was observed, nor for the different groups of this community. In general, substrate structure affects the interactions between the aquatic environment and organisms, in addition to the availability of nutrients, reducing the primary production of the medium (Czerniawski, 2013).

On the other hand, high-order lotic environments (higher than third order) are more conducive to the development of the planktonic community, mainly due to the greater

distance between the banks. This allows greater incidence of light and thus greater primary productivity, which no longer occurs in environments lower than third order, which are narrow and therefore shaded by riparian vegetation (Segovia et al., 2017). Similarly, in the present study we did not observe a significant correlation between the abundance of zooplankton organisms and current velocity. As cited earlier, the presence of tecamebas in the plankton plot is attributed to hydrodynamic processes, such as resuspension from sediment and marginal vegetation (Alves et al., 2012).

The RDA results suggested that the major differences in physical and chemical characteristics, as well as those related to zooplankton community structure, respond to a larger spatial scale, that is, with the main differences observed among the three sub-basins studied.

In synthesis, the results obtained in the present research refute the hypotheses and predictions (i and ii) initially raised. Thus, neither order or stretch stream influenced richness and abundance of zooplankton assemblage, and this absence of influence did not differ between periods. Although zooplankton in lentic environments respond directly to factors such as hydrodynamics and productivity of the environment, in lotic ones, especially those of small size, like the ones analyzed here, it seems that spatial factors related to stochasticity in the structuring of planktonic communities are more important than environmental factors, and thus are the main drivers in the organization of such communities. Thus, our results suggest that connectivity between environments within the same sub-basin, associated with random processes driven by dispersal, determine the existence or not of spatial and temporal patterns in the community attributes analyzed here. However, further studies



are needed on the importance of macrofactors in structuring aquatic biotic communities and how they may affect the different metrics of zooplankton diversity.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s42974-022-00099-2>.

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## Declarations

**Conflict of interest** On behalf of all authors, the corresponding author states that there is no conflict of interest.

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