



Influence of spatial and environmental factors on the structure of a zooplankton metacommunity in an intermittent river

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Abstract Hydrological disconnection in intermittent rivers is known to increase β -diversity by limiting the dispersal of species and decreasing environmental similarity between sites. Knowledge of the mechanisms driving variation within and between local communities helps elucidate the role of environmental and spatial processes responsible for community composition at multiple scales in intermittent rivers. In this study, we investigated the spatial and environmental patterns of zooplankton β -diversity in an

intermittent river in a semiarid region in Brazil. We hypothesized that (1) the zooplankton metacommunity is determined primarily by turnover, and (2) the structure of the zooplankton metacommunity is more heavily influenced by environmental than spatial factors. Our samples yielded 46 taxa of rotifers and cladocerans. β -taxonomic diversity was high, with a predominance of turnover compared with nestedness. The partitioning analysis showed that environmental and spatial processes had a significant influence on the distribution of zooplankton species, but the former had the greatest explanatory power. In the redundancy analysis, high values of temperature, oxygen and submersed macrophytes were significantly correlated with species variation. The observed β -diversity

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values closely reflected the turnover pattern, whereas Cladocera and Rotifera diverged between predictive processes. Our results highlight the importance of adopting appropriate conservation measures for intermittent river networks as a whole.

Keyword Lotic ecosystem · Stream · β -diversity · Semiarid · Caatinga

Introduction

Understanding the factors affecting the distribution of species and the mechanisms regulating community structure has long been a primary concern among ecologists. When the mechanisms responsible for variations within and between communities are identified, such observations shed light on the role of environmental and spatial processes, which act at multiple levels to determine the composition of the local community (Beisner et al. 2006; Nogueira et al. 2010; Grönroos et al. 2013; Palheta et al. 2021). A set of local communities connected by means of dispersal is called a metacommunity, in which some communities are shaped mostly by environmental processes, while others are most strongly influenced by spatial processes (Leibold et al. 2004; Holyoak et al. 2005). Variations in assemblage between habitats may result from a combination of abiotic factors, biotic interactions and dispersal processes.

The hydrological regime, or more precisely, hydrological connectivity, is probably the most important environmental factor structuring biological communities in hydrographic basins (Bunn & Arthington, 2002). Connectivity is highly variable in intermittent aquatic systems, making them excellent models for testing the premises of metacommunity theory (Heino et al. 2015a). Intermittent rivers are characterized by seasonal flow interruptions or completely dry periods (Datry et al. 2014). Flow intermittency is associated with complex climate determinants, which cause irregular rainfall in semiarid regions and directly impact the hydrological regime (Liu and Negrón Juárez 2001; Medeiros et al. 2008). Intense water flow variation is known to play a crucial role in the community structuring of such ecosystems (Ward and Stanford, 1995; Datry et al. 2014; Rodrigues-Filho et al. 2020).

Due to seasonal patterns of rain and drought, intermittent systems display great variations in water flow and numerous disconnectivity events. Intermittence dynamics may generate differences in species composition among local sites (β -diversity). For example, according to Heino et al. (2015a), high spatial connectivity favors the exchange of zooplanktonic organisms by passive dispersal, homogenizing community composition across the stream. Greater β -diversity is synonymous with greater dissimilarity between local richness (α -diversity) and regional richness (γ -diversity) (Koleff et al. 2003). The increase in variability may be explained by dispersal limitations associated with species-specific traits, the spatial configuration of communities, local history, and environmental heterogeneity, which create niches favoring some species over others (Chase, 2010; Al-Shami et al. 2013; Padiál et al. 2014; Bozelli et al. 2015; Anas et al. 2017). β -diversity is impacted by two species displays, nestedness and turnover. The first comprises the occurrence of spatially separated subsets of species within a larger and richer system, while the second explains β -diversity as the result of species substitution along space and/or time (Baselga, 2010; 2012). Between both processes, the turnover component contributes most to β -diversity in stream communities (Vitorino-Júnior et al. 2016; Epele et al. 2019; Rodrigues-Filho et al. 2020; Silva et al. 2020). Thus, β -diversity is often the result of substitution along a sufficiently long ecological gradient, whether by historical environmental characteristics, as well as its selection by species and spatial restrictions or species-species interactions (Whittaker, 1952; Baselga, 2010). In addition to the turnover component, other factors, such as environmental and spatial factors, are important processes that may influence metacommunity structure (Cottenie, 2005). For zooplankton assemblages, especially in lotic habitats, environmental factors have been suggested to be more important driving mechanisms than spatial factors (Padiál et al. 2014; Zhao et al. 2017).

β -diversity in intermittent ecosystems is influenced by the relationship between biotic and environmental filters and by limitations in the dispersal of strictly aquatic species (Datry et al. 2016). The disconnected nature of intermittent rivers provides highly diversified habitats, favoring species with different ecological demands, including limnetic zooplankton (Astorga et al. 2014; Leigh and Datry, 2017). These

animals respond very quickly to environmental changes, as observed in intermittent systems, with many zooplankton species benefiting from the ability to produce resting eggs that can remain in diapause for extended periods under unfavorable conditions (Cáceres and Soluk 2002; Palazzo et al. 2008). Similarly, other features, such as a short life cycle, small body size and passive dispersal, are also important elements in the spatial and environmental processes structuring zooplankton communities in intermittent systems (Rolls et al. 2016; Zhao et al. 2017).

Knowledge of the peculiarities of metacommunities in intermittent river networks is necessary to design biodiversity conservation strategies different from those used in perennial systems (Maltchik, 2006; Barbosa et al. 2012; Winemiller et al. 2016). Intermittent streams compose half of the global river network and may be growing proportionally in response to climate change (Datry et al. 2014). These systems not only have local interacting communities but also provide habitats that can be studied to appreciate the spatial and environmental processes determining metacommunity structure in water-courses. The analysis of spatial and environmental processes in this study contributes to current knowledge of nestedness and turnover patterns in zooplankton metacommunities in semiarid regions. High levels of nestedness suggest prioritizing the conservation of species-rich systems, while high levels of turnover indicate the need for protecting disconnected waterbodies against the injurious effects of substitution.

In this study, we investigated the spatial and environmental patterns of zooplankton β -diversity in an intermittent river and evaluated the composition at different sampling sites to determine the contribution of turnover and nestedness to β -diversity. In addition, we quantified the effects of spatial and environmental factors on the two components of β -diversity. The results were used to test the following two study hypotheses: (1) the zooplankton metacommunity is determined primarily by turnover, and (2) the structure of the zooplankton metacommunity is more heavily influenced by environmental than spatial factors.

Methods

Study site and sampling procedures

At a length of 633 km with a drainage area of 75,669 km², the Jaguaribe River (4°39'30"–5°40'00" S; 37°35'30"–38°27'00" W) is the largest intermittent river system in northeastern Brazil. It is located in a semiarid tropical region with an evapotranspiration rate higher than 2000 mm/year, from which it flows out into the Atlantic Ocean (Krol et al. 2006; Alvares et al. 2013). The hydrological regime is determined by the interplay between the rainy season (December–May; average rainfall: 1270 mm) and dry season (June–November; average rainfall: 320 mm), but during the study period (2014–2015), the region was stricken by drought, with an annual rainfall of, approximately 350 mm (FUNCEME, 2017; Fig. 1). The combination of low rainfall indices and elevated evapotranspiration rates favors intermittency and the disconnection of tributaries from the main stem.

Sampling rounds occurred in the rainy seasons in April and May of 2014 and 2015, respectively. Information on the physical and chemical variables of water as well as zooplankton samples was collected along the riverbank (Fig. 2). The sampling points were previously defined following the protocol developed

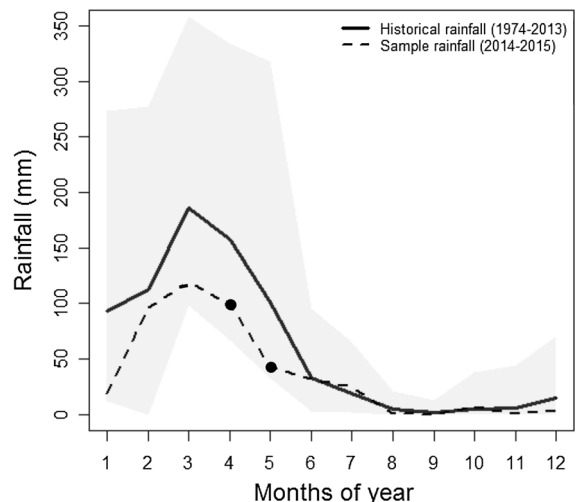


Fig. 1 Rainfall between 1974 and 2014 (shaded area), average monthly rainfall between 1974 and 2014 (continuous line) and rainfall during the sampling period (2014–2015) (dotted line). The black dots indicate the months of sampling. Source: Fundação Cearense de Meteorologia e Recursos Hídricos (Ceará State Foundation for Meteorology and Water Resources)

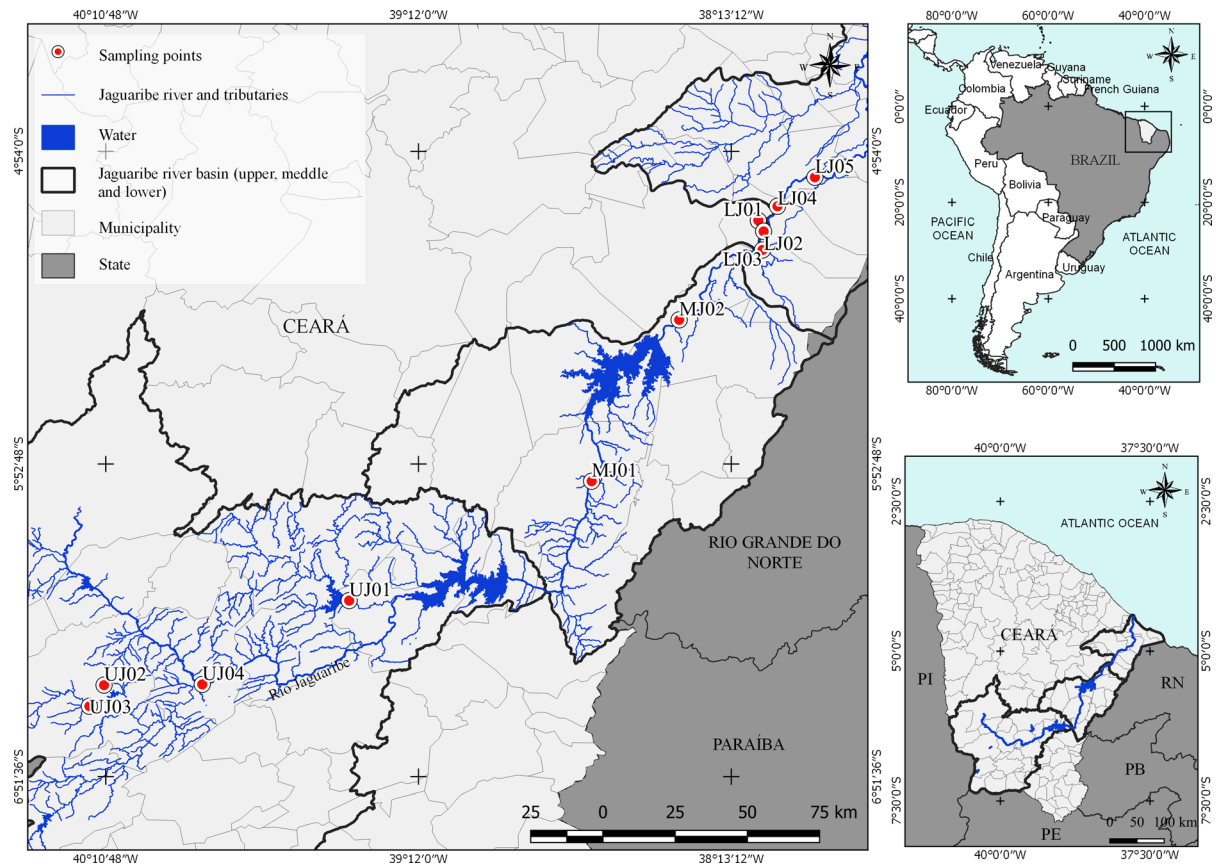


Fig. 2 **a** Geographic location of the State of Ceará, Brazil, **b** subbasins in the Jaguaribe River highlighted in bold: Upper, Middle and Lower Jaguaribe, and **c** sampling points along the

main stretch of the Jaguaribe River according to the respective basins (UJ—Upper Jaguaribe, MJ—Middle Jaguaribe and LJ—Lower Jaguaribe)

by Mendonça et al. (2005). Thus, a total of 11 streams were chosen along the river basin divided into three river stretches: Upper, Middle and Lower Jaguaribe (Supp. Table 2). In each one, a 50 m segment was specified and divided into four equidistant transects (0 m, 16 m, 34 m and 50 m) where the environmental parameters were recorded and then averaged to obtain a representative value for the sampling site. Environmental variables included dissolved oxygen (mg/L), pH, electrical conductivity (mS/cm), total dissolved solids (TDS) and turbidity (NTU), which were measured using a multiparameter water quality instrument (Horiba) at the most downstream extremity of each transect. We also measured flow velocity with a flow meter, starting 10 cm from the margin, as well as the presence or absence of submerged and emerged microphyte covers.

Following the environmental measurements, zooplankton were collected within each transect. A graded bucket was used to sample 50 L of surface water, which was subsequently filtered through a plankton net with a mesh size of 63 μm . Two water samples were collected at each sampling point, which included 11 samples. The filtered organisms were immediately placed in a solution of 4% formaldehyde (neutralized with sodium tetraborate) and sucrose. All organisms were counted using a Sedgwick-Rafter counting chamber under optical microscopy. The species were identified with the aid of identification keys (Koste, 1978; Segers, 1995; Elmoor-Loureiro, 1997) and with the assistance of specialists. Three major groups of zooplankton were observed: copepods, cladocerans and rotifers. However, copepods were excluded from analysis due to the predominance of nauplii and

juveniles, which could not be taxonomically identified.

Calculation of beta diversity and its components

The taxonomic diversity of zooplankton was based on site-to-site variation in species composition (beta diversity). The beta diversity and its components (i.e., turnover and nestedness) were calculated from the composition matrix after Hellinger transformation using Bray–Curtis dissimilarity (Baselga, 2010). This framework consists of decomposing the Bray–Curtis dissimilarity into two variations in the abundance of species (turnover) and the decrease or increase in abundances between local sites (nestedness). We decided to account for the abundance of species because quantitative data have been shown to be more informative in providing diversity patterns within and among local sites (Baselga, 2010). These calculations were made for all datasets and separately for rotifers and cladocerans, which were used as response variables in statistical analysis.

Predictor variables

We tested the collinearity between the seven environmental variables using the variation of inflation (VIF), excluding values > 3 from further analysis. The following variables were retained for the subsequent analyses: temperature, oxygen, turbidity, conductivity, TDS, water velocity, and submerged and emerged microphyte cover. We standardized these variables as the mean = 0 and standard deviation = 1. Data from measurements for these variables are available in Supp. Table 2.

A spatial predictor matrix was constructed using spatial analysis capable of describing the spatial structure at the sampling points and was derived by distance-based Moran's eigenvector map analysis (db-MEM; Borcard et al. 1992). db-MEM variables are linearly independent (orthogonal) and are obtained from the spectral decomposition of a truncated distance matrix resulting from the spatial relationship among water bodies (Borcard et al. 1992). By identifying different scales, db-MEM analysis allows investigation of complex patterns of spatial variation: the first eigenvectors capture broad-scale variation, while eigenvectors with smaller values capture fine-scale variation (Diniz-Filho and Bini 2005; Legendre,

2012). Additionally, the advantages of db-MEM are that Moran's I coefficients can be used to select eigenvectors with positive spatial autocorrelation ($p < 0.05$) (Blanchet et al. 2011). As a final result, only MEM-1 was retained for statistical analysis ($p < 0.05$).

Statistical analysis

The importance of environmental (E) and spatial (S) predictors for the β -diversity of zooplankton communities and for cladocerans and rotifers was determined by partitioning the variance in a partial distance-based redundancy analysis (db-RDA). The db-RDA was used because it allows the use of a dissimilarity matrix, such as Bray–Curtis beta diversity (Legendre and Gallagher 2001). Only variables with $p < 0.05$ (based on 999 Monte Carlo permutations) in a forward selection procedure were maintained in partial db-RDA. This procedure is fundamental to allow a more reliable interpretation of the importance of the predictor variables (Blanchet et al. 2008). Once the predictors were associated, the total variation in β -diversity was partitioned into four components: (E) pure environmental; (S) pure spatial; (ES) shared between space and environment; and (U) unexplained. Following the recommendations of Beisner et al. (2006), we estimated the adjusted coefficient of determination (R^2 adj). The significance of (E) and (S) components was tested using 1,000 permutations. Biplot ordination (only to environmental conditions) was constructed to visualize the relationships between species distributions and environmental conditions along the two axes of the db-RDA.

Results

We identified 45 taxa mostly dominated by rotifers (Supp. Table 1). This group displayed the greatest richness (37 taxa) and abundance of species. The most representative rotifer families were Lecanidae and Brachionidae (nine species each), while most cladocerans belonged to the family Chydoridae (four species). Rotifers also presented greater species density in all sampled river segments (Supp. Table 1).

β -diversity patterns

On average, the local zooplankton communities were 85% dissimilar. This variation was mostly explained by turnover of species distribution and abundance (76.3%; Table 1). The Cladocera and Rotifera groups did not strongly differ in regard to β -diversity. However, when the diversity was partitioned, Cladocera showed almost the same influence (51% for turnover and 49% for nestedness). In contrast, rotifers accounted for 71% of the variation explained by turnover and almost three times lower by nestedness (28.9%).

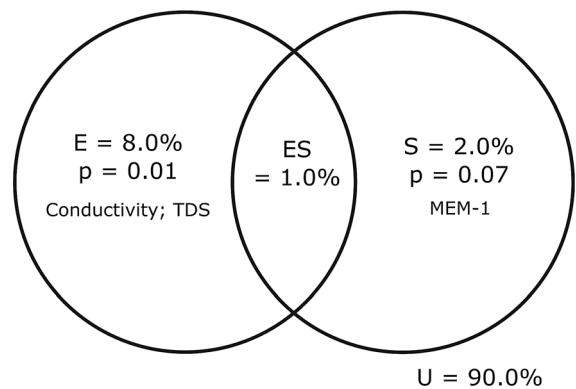
Predictors of β -diversity

Based on the forward selection procedure, one spatial eigenvector (MEM-1) and four environmental conditions (TDS, conductivity, water velocity and proportion of emerged macrophytes) were selected to explain the beta diversity of the zooplankton metacommunity (Fig. 3). Both the pure environmental and spatial factors were significant to the β -diversity of the entire zooplankton metacommunity but with different relative importances ($p < 0.05$; Fig. 3). However, while spatial factors were responsible for only 2%, environmental conditions explained 8% of the total metacommunity variation. Nevertheless, most community variation remained unexplained (90.0%; Fig. 3).

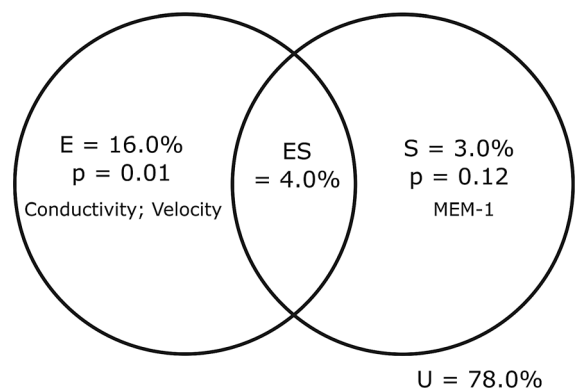
In contrast to all zooplankton metacommunities, the metacommunities of rotifers and cladocerans were explained by different factors (Fig. 3). For example, the composition difference of rotifers among local sites was strongly related to conductivity and water velocity ($E = 16\%$, $p = 0.01$) and to the joint effects between environment and space ($ES = 4\%$). On the other hand, the composition of cladocerans differed among spatially distant local sites ($S = 18.0\%$,

Table 1 Data from beta diversity (β_{Total}) for rotifers and cladocerans, besides its partitioning into Turnover and Nestedness components

	β_{Total}	β_{Turnover}	$\beta_{\text{Nestedness}}$
All groups	0.85	0.65 (76.3%)	0.20 (23.6%)
Rotifers	0.86	0.61 (71.0%)	0.24 (28.9%)
Cladocers	0.77	0.39 (51.0%)	0.37 (49.0%)



Rotifers metacommunity



Cladocerans metacommunity

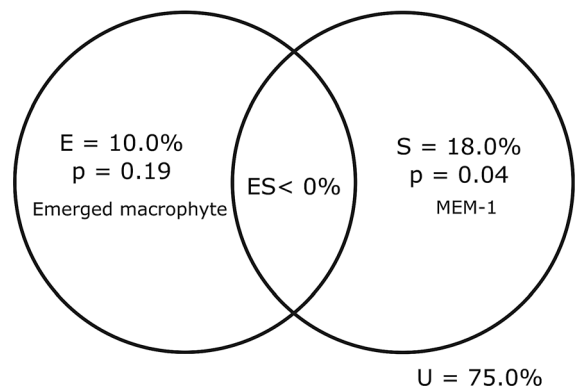


Fig. 3 Venn diagram showing partitioning analysis of hierarchical variance for all metacommunities (above) and rotifer (middle) and cladoceran (below) metacommunities. The p values are from ANOVA tests

$p = 0.04$), and although environmental conditions had considerable importance ($E = 10.0\%$), their relationship with the cladoceran metacommunity was not significant ($p = 0.19$).

density (Zhou et al. 2008). Extreme historical findings in flowless environments account for 100,000 rotifers/L (Iltis and Riou-Duvat 1971). Although the densities we found in the Jaguaribe River seemed too low, they were also found in other streams in the same semiarid region (Medeiros et al. 2011; Melo and Medeiros 2013). Therefore, it seems common in these semiarid conditions.

β -diversity values were explained by turnover rather than nestedness for all metacommunities and both rotifers and cladocerans (see Table 1), indicating a large difference in species composition among local communities. This pattern may be explained by the harsh environmental conditions and spatial disconnectivity of intermittent systems (Datry et al. 2014; Rodrigues-Filho et al. 2020). In fact, numerous disconnection events were observed throughout the Jaguaribe River, which generated different levels of isolation among sites, ranging from completely isolated to sporadically connected communities (E. Ramos, pers. obs.). This potential isolation of local communities promotes the spatial configuration of intermittent ecosystems that may directly affect β -diversity patterns by limiting or facilitating the occurrence among local communities (Datry et al. 2014). Once species are established, adverse environmental conditions, such as conductivity or TDS (Fig. 3), further shape the local assemblage (Larned et al. 2010). These combinations of factors (intermittent dynamics and environmental selection) tend to increase the complexity of spatial organization and thereby may explain the large importance of turnover on β -diversity in intermittent systems (Datry et al. 2016). For example, some species occurred only in certain environmental conditions, and *Keratella cochlearis* was more abundant when the TDS, conductivity, and emerging macrophyte values were high.

Spatial processes played a more prominent role in the Cladocera community, while Rotifera were mostly explained by environmental processes. This pattern is not consistent with that described by Zhao et al. (2017), who found the opposite. These authors noted that cladocerans are more mobile, thus being less influenced by spatial processes, while rotifers, due to their low mobility, are hardly influenced by spatial processes. However, we argue that the key point lies in the intermittence characteristic of the stream. Zhao et al. (2017) studied a perennial environment, which may favor a cladoceran swimming advantage

compared with rotifers. On the other hand, our study focused on an intermittent stream, and the discontinuous and disconnected spatial pattern may have had a strong influence on the Cladocera community. This channel characteristic may potentialize environmental filters, which are known to greatly impact the distribution patterns of microcrustaceans (Davidson et al. 1998). From the rotifer's perspective, they were most influenced by environmental processes because as spatial connection is lacking, their low swimming capacity is no longer an obstacle. Thus, when river regimes are perennial, crustaceans find environmental processes to be the main predictors of their diversity, while rotifers find spatial processes to be limiting to their diversity. However, along intermittent river regimes, the role changes and crustaceans become most influenced by space instead of environment, and the opposite occurs with rotifers.

Spatial and environmental factors explained 10% of the variation in zooplankton community composition, leaving a residual variation of 90%. This is expected in this type of study by the complex combination of biotic interactions, dispersal dynamics and nonmeasurable environmental variables (Padial et al. 2014; Rolls et al. 2016). For example, the spatial distribution of predators may act as a biotic filter selecting certain species (Rodrigues-Filho et al. 2020). In a regional context, these local effect predators could enhance the site-to-site difference in species composition and thereby increase the turnover importance to β -diversity. Spatial and environmental factors explain taxonomic composition more specifically since they reflect the peculiarities that determine metacommunity patterns (Beisner et al. 2006; Al-Shami et al. 2013).

The influence of spatial processes indicated that dispersal limitation combined with environmental variables produced an effect on the components of β -diversity. Geographic distance is a known potential cause of the limitation of zooplankton dispersal between local communities, although metacommunity structure is determined not only by distance but also by dispersal mode and ability (Grönroos et al. 2013; Padial et al. 2014; Santos et al. 2016; Tolonen et al. 2018; Rodrigues-Filho et al. 2018). Moreover, the dispersal of small organisms is associated with a good adaptive response to environmental change along a spatial gradient (De Bie et al. 2012; Padial et al. 2014; Soininen 2016; Tolonen et al. 2018). Thus, species-specific traits (e.g., body size, dispersal mode, and

dispersal strategy) have been correlated with dispersal success and, consequently, with community structure (Beisner et al. 2006; De Bie et al. 2012; Tolonen et al. 2018).

To better understand the relative impact of ecological processes at the metacommunity scale, we evaluated how spatial and environmental factors act on groups of organisms with different dispersal abilities: Cladocera and Rotifera (De Bie et al. 2012; Heino et al. 2015b; Santos et al. 2016). As in previous studies, environmental processes were found to have a significant influence on rotifers (Crispim and Freitas 2005; Melo Júnior et al. 2007; Medeiros et al. 2011). The turnover of rotifer species appears to have been primarily determined by environmental variables, as species are filtered by substantial changes in environmental conditions, increasing the β -diversity between segments on the same river.

Local biotic and abiotic factors provide an explanation for the observed turnover of cladocerans, as well as for nestedness along an environmental gradient. This finding suggests that spatial factors (e.g., dispersal barriers and limitations) may have a greater impact on the distribution of cladoceran species than environmental processes. Nevertheless, variables not evaluated in this study (e.g., the presence of macrophytes and local depth) may also have interacted with spatial and temporal factors, contributing to the observed patterns of cladoceran community structure.

The observed β -diversity resulted from turnover, while zooplankton metacommunity structure was primarily influenced by spatial and environmental processes, with the latter having the greatest explanatory power. The high level of turnover highlights the importance of conservation measures in all surveyed segments of the Jaguaribe River and is a reminder that spatial and environmental processes can have different impacts on ecologically similar groups of zooplankton.

Conclusion

Our evaluation of the spatial patterns of zooplankton β -diversity in an intermittent river system revealed high β -diversity was driven by turnover. Although spatial processes played some importance in structuring the metacommunity, environmental processes were most important to the metacommunity structure.

The Cladocera community was more strongly influenced by space, while rotifers were most influenced by environmental processes. Based on these findings, neither of the two study hypotheses (“the zooplankton metacommunity is determined primarily by turnover”, and “the structure of the zooplankton metacommunity is more heavily influenced by environmental than spatial factors”) could be rejected. In addition, spatial processes should be considered, as they indicate a dispersal limitation associated with the distance between water bodies and/or dispersal barriers. Our study also provides new insight into riverine zooplankton in intermittent river systems.

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