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ANIMAL SCIENCE

High taxonomic turnover and functional homogenization of rotifer communities in an amazonian river

EWERTTON S. GADELHA, BÁRBARA DUNCK, NADSON R. SIMÕES, EDUARDO T. PAES & ALBERTO AKAMA

Abstract: Patterns of beta diversity of plankton communities in rivers have been mainly determined by hydrological factors that alter the dispersion and composition of species and traits. Rotifers in the Guamá River (eastern Amazonian River) were sampled (monthly between October 2017 and June 2019) to analyze the temporal variation of taxonomic and functional beta diversity and its partitions (turnover and nestedness) as well as the effects of temporal, environmental, and seasonal dissimilarities. Taxonomic turnover and functional nestedness over time were observed as well as functional homogenization, which was arguably due to the hypereutrophic condition of the river. There were no seasonal differences in taxonomic and functional beta diversity probably due the low environmental dissimilarity. This study demonstrated that this Guamá River stretch presented low environmental dissimilarity and hypereutrophic waters, which benefited the establishment of a community of species with high taxonomic turnover over time, but with low functional dissimilarity and loss of some functions related to the functional traits evaluated in the ecosystem. It is important to point out that temporal studies should evaluate both taxonomic and functional aspects of communities, mainly because the effect of environmental changes may be more noticeable at the functional level of communities.

Key words: Environmental dissimilarity, functional traits, beta diversity, plankton, lotic environment.

INTRODUCTION

One of the main issues in ecology is understanding the determining factors and mechanisms of biodiversity (Villéger et al. 2013). It is recognized that the composition of species alone is not enough to understand the structure of assemblies (Swenson et al. 2012) and their effects on the functioning of the ecosystem without considering the functional facet of biodiversity (Díaz et al. 2007, Hillebrand & Matthiessen 2009). Function-based approaches and functional traits are increasingly being used as an alternative to traditional approaches to study biodiversity (Swenson et al. 2012).

Measures that assess biodiversity and that incorporate the functional traits of species help to understand the niche, its needs and its effects on the environment (Barnett et al. 2007, McGill et al. 2006, Rosado et al. 2015, Visconti et al. 2018). Functional traits are defined as any measurable individual-related morphological, physiological, or phenological characteristics from the cellular level to a complete organism (Violle et al. 2007). An important biodiversity assessment tool that incorporates functional aspects is functional beta diversity. Unlike taxonomic beta diversity, which allows changes in species composition between sites or over time (Anderson et al. 2011) to be evaluated, functional beta diversity estimates the differences between communities based on the functional traits of the species (Villéger et al. 2013).

Studies of beta diversity over time describe changes in taxonomic and functional composition between different periods (Korhonen et al. 2010), and may reflect two different phenomena known as beta diversity partitions, which result from nestedness and turnover (Whittaker 1960, Tuomisto 2010). Nestedness of community of species occurs when biotas of sites with fewer species are subsets of biotas in richer areas, reflecting a process of species loss as a consequence of any factor that promotes the ordered disaggregation of communities. In addition, functional aspects are related with the loss of functional traits or functional homogenization (Olden 2006). Turnover implies the substitution of some species by others as a consequence of environmental, spatial, and/or temporal restriction (Whittaker 1960, Baselga 2010), and for functional aspects it indicates a greater substitution of functional traits among communities (Villéger et al. 2013). Most studies have focused on evaluating beta diversity with taxonomic aspects. However, some studies have already demonstrated that a functional approach is more sensitive in capturing the effects of environmental changes, especially when changes in taxonomic beta are not evident (Braghin et al. 2018, Simões et al. 2020, Diniz et al. 2021).

Beta diversity patterns can be affected both by deterministic and stochastic processes (Tuomisto 2010). Deterministic processes are based on niche theory, which assumes that environmental filtering and biotic interactions play an important role in shaping the composition of local communities (Leibold et al. 2004, Cadotte & Tucker 2017). On the other hand, stochastic processes are related to the importance of colonization rates, speciation, random extinction, and disturbances (Chase & Myers 2011). Studies on river plankton have shown that beta diversity and its partitions are determined by both environmental and spatial factors, and that hydrological factors influence the dispersion and composition of functions and species (Lopes et al. 2014, Gianuca et al. 2017, Serafim-Júnior et al. 2019). Furthermore, anthropic action (e.g., dams and eutrophication) can alter environmental filters and cause disturbances in aquatic environments, leading to providing functional homogenization in the plankton (Braghin et al. 2018, Pineda et al. 2020, Simões et al. 2020).

Among aquatic organisms, rotifers constitute the plankton group with the highest species richness and population density in many freshwater ecosystems like rivers and lakes (Lansac-Tôha et al. 2009, Matsumura-Tundisi et al. 2015, Costa et al. 2016, Zhao et al. 2017, Branco et al. 2018, Picapedra et al. 2019). These organisms are crucial in continental food networks since they intermediate the flow of matter and energy transfer from producers to higher trophic levels (Almeida et al. 2009). Thus, studies on the functional structure of this community can help understand the ecosystem processes such as productivity and nutrient cycling, and serve as a proxy for the general condition of the environment (Díaz & Cabido 2001, Braghin et al. 2018).

According to Chaparro et al. (2019), hydrological conditions (e.g., river level) and environmental heterogeneity are important environmental filters for rotifers functional beta diversity because functional beta diversity has responded positively when these variables increase. The same pattern was observed for taxonomic beta diversity, which, according to Lopes et al. (2014) and Soares et al. (2015), is positively correlated with environmental heterogeneity and therefore represents a deterministic process of environmental filtration. Several studies indicate that taxonomic beta diversity may increase over time in river ecosystems (Bonecker et al. 2013, Soares et al. 2015, Lopes et al. 2017). This increase is explained by the variability of limnological conditions, which promotes a greater spatial heterogeneity that consequently makes the communities more spatial and heterogeneous over time (greater beta diversity) (Bonecker et al. 2013).

Based on the above considerations, this study aims to evaluate the dynamics of temporal variation of taxonomic and functional beta diversity and their respective partitions (turnover and nestedness) in the rotifer community in a lotic system in the eastern Amazonian region. The relationships between these biodiversity measures were also evaluated using temporal dissimilarity, environmental heterogeneity, and seasonality.

To achieve these objectives the following hypotheses were tested: (i) Taxonomic beta diversity is positively related to functional beta diversity and ii) taxonomic and functional beta diversity are higher in the rainy season. A positive relationship between functional and taxonomic beta diversity and higher values in the rainy season are expected due to the increase in the connection and flow of nutrients and organisms between aquatic systems (rivers, lakes, and floodplains), in productivity levels, and in richness of pelagic and coastal rotifer species (Bonecker et al. 2013, Serafim-Júnior et al. 2019) in this higher rainfall period. These characteristics would lead to higher values of taxonomic and functional beta diversity; (iii) the turnover component is responsible for changes in the beta diversity of the rotifer community. Turnover is expected to be the main component of variation in functional and taxonomic beta diversity due to the water flow in lotic environments, which favors the dispersion of planktonic species (Gianuca et al. 2017a, Braghin et al. 2018); (iv) functional and taxonomic beta diversity are positively correlated with environmental dissimilarity and/or temporal dissimilarity. A positive relationship between functional and taxonomic beta diversity and the environmental dissimilarity is also expected because environmental dissimilarity favors changes in species composition for several distinct communities due to the greater availability of niches (Leibold et al. 2004) and in species traits over time (Simões et al. 2020).

MATERIALS AND METHODS

Study location

Samples were carried out monthly from October 2017 to June 2019. The wettest months are considered to be from January to June, and the least rainy from July to November. The study was carried out in the Guamá River (1°28’36.8” S 48°29’32.1” W), located in the city of Belém, in the state of Pará, Brazil. This city was built on an estuarine sedimentary peninsula, and delimited by the Guamá River to the south, which is between 1360 and 2000 m wide and 700 km long (Ramos 2004). The mouth of the Guamá River receives a strong influence from ocean tides, and has constant sediment inputs from Guajará bay, which may become slightly brackish at the peak of the less rainy period (Monteiro et al. 2009). In this region, the rainy season corresponds to the months of December to June, and the least rainy season occurs between the months of July to November (Bastos et al. 2002).

Due to the great amount of suspended material, the Guamá River has high turbidity, muddy aspect, greenish-yellow color and little light penetration. Based on its physicochemical properties this area is classified as a freshwater environment (Santos et al. 2014). On the other hand, Lima & Santos (2001) consider this area an atypical estuarine due to the slight salinity increase recorded in periods of lower rainfall intensity when an unmistakable penetration of Atlantic Ocean waters occurs. For the purposes of this study, the area of study will be considered as a freshwater environment as proposed by Santos et al. (2014).

Environmental parameters

For the sampling of chlorophyll-a, the methodology of CETESB (2014) was followed. We collected water from the subsurface with a 200 ml polyethylene bottle for further analysis of chlorophyll-a in a spectrophotometer, and the sample was filtered in the laboratory. Based on chlorophyll-a values, the trophic state index (TSI) was estimated as proposed by Cunha et al. (2013). Precipitation data were obtained and compiled in the National Institute of Meteorology database (http://www.inmet.gov.br/portal/index.php?r=bdmep/bdmep), while water height data were obtained through the National Institute for Space Research (http://ondas.cptec.inpe.br/).

Community sampling

Sampling was performed at a single point with two subsamples by horizontal drag, for 2 minutes, in a subsurface with a flow meter coupled in a conical plankton net (mesh size= 64 µm, diameter= 60 cm) totaling 36 samples. The samples were filtered and stored in a 200 mL polyethylene container properly labeled and fixed in 4% formaldehyde neutralized with Sodium Tetraborate (Brandão et al. 2011). The subsamples were summed and the density of the organisms were expressed in individuals per liter (ind. L^{-1}). For the quantitative analysis of the rotifer community, 10% of the water volume in samples (20 ml) were filtered, and the specimens were extracted with a Hansen-Stempel pipette as proposed by Bottrell et al. (1976). The rotifers were viewed under a binocular optical microscope (Nikon model OPTIPHOT 2) with a 200x magnification and identified at the lowest possible taxonomic level through the works of Koste & Shiel (1986), Sharma & Sharma (1999) and Fontaneto et al. (2008).

Functional traits

According to Barnett et al. (2007), Litchman et al. (2013) and Hébert et al. (2016), functional traits incorporate ecological aspects of the community and describe the response of organisms to environmental conditions. Traits can predict the dominance among species based on their competitive resource skills. Thus, a continuous quantitative characteristic (body size) and four categorical characteristics (feeding mode, feeding habits, predator escape strategies and habitat) were selected (Table I). To measure the functional traits of average body size (µm), the mean size per species was calculated, and a maximum of 10 photos (10 individuals) were captured of each species using Software Image Tool 3.0. For the species that could not be photographed, the average size provided by Bonecker et al. (1998) was used for organisms captured in the floodplain of the upper Paraná River. The categorical characteristics feeding mode, feeding habit, predator escape strategies and habitat were obtained from Bonecker et al. (1998), Hampton & Starkweather (1998) and the Japanese National Institute of Environmental Studies (http://www.nies.go.jp/chiiki1/protoz/index.html).

Data analysis

The difference in environmental variables (water level, rainfall, trophic status index and chlorophyll-a) between the periods evaluated for seasonality (rainy and less rainy) were tested using a t-test.

For beta diversity analysis, a presence-absence matrix from a quantitative matrix with 30 identified rotifer species and 18 months of sampling (11 rainy months and 7 less rainy months) was used. The Sorensen index (βsor) was used to calculate the paired dissimilarity of species composition among all samples (Baselga & Orme 2012).

Previously to the calculation of functional beta diversity, the distance matrix between the functional traits of the species was calculated using the Gower distance coefficient (Gower 1966), which was later transformed into a dendrogram. To calculate functional dissimilarity (functional beta diversity), the Sorensen index was adapted to functional traits (Melo 2013) by using the functional dendrogram and the presence-absence matrix of species. Taxonomic and functional βsor were decomposed into two components that represent results from nestedness (βnes) and turnover (βsim), taxonomic according to Baselga & Orme (2012) and the latter according to Melo (2013). Although the Baselgas's method overestimates the turnover component and underestimates species richness (Podani & Schmera 2011, Carvalho et al. 2012), it is widely used, which allows comparisons with other studies. The "ade4" (Chessel et al. 2004) and "vegan" (Oksanen et al. 2017) packages were used to construct the functional distance matrix and the dendrogram. "Beta.pair" function (Baselga 2010) was used to estimate taxonomic beta diversity while "functional.beta.pair" diversity was used to analyse functional beta diversity.

To test the hypothesis (i) of a positive correlation between functional and taxonomic beta diversity, the Mantel test (1000 permutations, function "mantel", package "ecodist") was applied. We applied a permutational analysis of variance to test the hypothesis (ii) that the taxonomic and functional beta diversity is

Table I. Description of the used functional traits of rotifers species.

Functional traits	Feature type	Data type	Importance
Average body size	Morphologic	Continuous	It can reflect secondary productivity, larger size species. In general, presentes higher productivity in the position of the trophic web species (primary consumer) and in energy transference (larger organism have higher biomass to transfer to higher trophic levels) (Litchman et al. 2013).
Feeding mode	Feeding	Categorical	Represents the morphofunctional variability for food acquisition, reflecting the diversity of trophic niche, and can be related to secondary productivity and nutrient cycling (sucking, predator, filter and scraper).
Feeding habits			
Predator escaping	Behavior	Categorical	Describes different morphological and/or behavioral adaptations (vertical and horizontal migration, presence of spines, among others).
Habitat	Behavior	Categorical	The habitat type defines where the species are most easily found. It represents the participation of the species in the trophic chain of different compartments, affecting the processes of energy transfer and nutrient cycling.

greater in the rainy season than in the less rainy season (PERMANOVA, function “adonis”; package “vegan”; Anderson et al. 2008, Oksanen et al. 2018). To test the hypothesis (iii) that the turnover component is greater than the nesting pattern, we apply paired t-tests (function “t-test”) for each dissimilarity type (species and functional).

Environmental dissimilarity was estimated using a Euclidean distance matrix from logarithmic environmental variables (water level, precipitation and chlorophyll-a) and standardized by the Scale function between the months of sampling. We estimated the temporal dissimilarity between the sampling months also using a Euclidean distance matrix, and it was used as a temporal variation of the dataset (Dunck et al. 2015, Lopes et al. 2017). We use the partial Mantel test (1000 permutations, function “mantel.partial”, package “vegan”) to evaluate the hypothesis (iv) of positive correlation between taxonomic and functional beta diversities with the environmental dissimilarity matrix (water level, precipitation) and chlorophyll-a) controlling the effect of the temporal matrix, and with the temporal dissimilarity controlling the effect of the environmental matrix between the seasonal periods (wet and less rainy).

In addition to the partial Mantel test, multiple regressions were applied on distance matrices (“MRM function”, “ecodist” package, Legendre et al. 1994, Dunck et al. 2019) to test the hypothesis (iv) that functional and taxonomic beta diversity are explained by environmental dissimilarity and temporal dissimilarity. MRM involves a multiple regression of a response matrix on any number of explanatory matrices (Lichstein 2007). Here, environmental dissimilarity and temporal dissimilarity were explanatory variables for the taxonomic or functional beta diversity (response variables). The significance of the regression coefficients and determination coefficients were evaluated with 10,000 permutations. Since these parameters are tested by permutations, it is not necessary to test the assumptions (Legendre & Legendre 1998). The R platform was used to perform all analyses (R Core Team 2014).

RESULTS

Environmental variables

During the year of study, rainfall was significantly higher in the rainy season (t= 5.36, df= 11.97, p= 0.0002) and while other environmental variables, namely chlorophyll-a (t= 2.16, df= 11.58, p= 0.052), water height (t= -1.81, df= 12.14, p= 0.094) and TSI (t= 0.978, df= 12.19, p= 0.346) did not differ seasonally (Table II, Supplementary Material - Figure S1).

Rotifers

A total of 693 organisms were identified and distributed in 30 species belonging to 13 families. *Keratella cochlearis* (Gosse, 1851) and *Keratella americana* Carlin, 1943 were the most representative taxa throughout the study period. The density of organisms reached a minimum of 67 ind. L^{-1} (August/2019) and maximum 209016 ind. L^{-1} (September/2019). The individuals with highest average annual densities were *K. cochlearis* 10596 ind. L^{-1} (± 32765 SD), *Ascomorpha* sp. 14253 ind. L^{-1} (± 15679 SD) and *K. americana* 638 ind. L^{-1} (± 1284 SD). The most prevalent functional attributes during the months of study were herbivorous, pelagic, filter feeder, presence of spine and freshwater species, which accumulated an annual frequency of 86%, 92%, 91%, 80% and 96%, respectively (Figure 1).

The taxonomic beta diversity presented an average of 0.56 (± 0.13 SD), and did not differ between rainy periods (mean of 0.47 ± 0.01 SD) and less rainy (mean of 0.55 ± 0.01 SD) (PERMANOVA total df = 17, residual df = 16, pseudo-F = 1.42, p = 0.14) (Figure S2a). The functional beta diversity presented an average of 0.63 (±0.35 SD), and did not differ between rainy periods (mean of 0.35 ± 0.1 SD) and less rainy (mean of 0.45 ± 0.15 SD) (PERMANOVA total df= 15, residual df = 14, pseudo-F = 4.71, p = 0.053) (Figure S2a). The average of taxonomic turnover component was 0.35 (±0.21 SD), significantly higher than those resulting from taxonomic nestedness (average of 0.21±0.18 SD) (t= -4.35, df= 152, p<0.001). The inverse was found for functional beta diversity, for which the resulting nestedness (average of 0.41 ± 0.38 SD) was higher than the turnover component (average of 0.20 ± 0.25 SD) (t= 4.47, df=135, p< 0.001) (Figure S3). Functional and taxonomic beta diversity were negatively related (Mantel test, R= -0.26, p= 0.014). No significant relationship between taxonomic beta diversity and environmental dissimilarity and temporal dissimilarity was found based on partial mantel tests and MRM (MRM, Less rainy period R2= 0.094, Rainy period R2= 0.033, Table III). However, a relationship between functional beta diversity and temporal dissimilarity during the less rainy period (MRM, Less rainy period R2= 0.77, p= 0.03, Temporal dissimilarity, Rainy period R2= 0.02, p= 0.60, Table III) was found based on MRM.

DISCUSSION

Our study did not find a seasonal difference in environmental variables. We demonstrated a negative relationship between taxonomic and functional beta diversity, which refuted the initial hypothesis of a positive correlation between them. These results indicate that the variation in species composition increased over time, but there was a decrease in the variation of functional traits of rotifers over time in this ecosystem. These results of taxonomic beta diversity was promoted by turnover, indicating species replacement over time, while a nestedness pattern of functional beta diversity occurred over time. These results indicate that despite the species replacement increased over time, there was a decrease in the variation of functional traits and increase in the functional similarity of rotifers over time in this ecosystem. There were also no seasonal differences in taxonomic and functional beta, which refuted our initial hypothesis of higher values of both in the rainy season. The absence of a seasonal effect on beta diversity in our study probably is due the low environmental dissimilarity and the absence of seasonality in the environmental variables, which did not show any seasonal differences.

Our results showed a low environmental dissimilarity and the environmental variables did not show a seasonal effect. The studied environment was predominantly characterized as hypereutrophic (Cunha et al. 2013), and the eutrophication observed can be considered a disturbance, which can generate biotic homogeneity (Olden 2006, Gianuca et al. 2017a, Liu et al. 2020). In addition, the Guamá River has a long extension, strong water flow, a bay connection and access to other secondary rivers, which contribute to the low temporal and seasonal environmental variability. The dissimilarity of limnological variables decreases with increasing water levels and river flow (Bozelli et al. 2015) because it connects aquatic habitats. Horizontal flows are produced from the river course (Thomaz et al. 2007, Bozelli et al. 2015), and this may explain the low environmental dissimilarity.

The negative relationship between taxonomic and functional beta diversity, taxonomic turnover and functional nestedness patterns indicates that the substitutions of species that occurred over time is mainly among functionally redundant taxa. And also that functional nestedness resulted from the loss of extreme combinations of functional

Table II. **Values average, maximum, minimum, and standard deviation of the environmental variables used in this study. Tide = height of water (m), Clha = chlorophyll-a, TSI = trophic state index, Rai = rainfall (mm), dC_Env = environmental dissimilarity, JAN- january, FEB- february, MAR- march, APR- april, JUN- june, JUL- july, AUG- august, SEP- september, OCT- october and NOV- november.**

	Samples	**Rai**	**Clha**	**TSI**	**Tide**	**dC_Env**
Less rainy	OCT17	223	0.76	21.57	2.80	1.07
	NOV17	103	1.09	22.95	0.65	1.14
Rainy	JAN18	363	2.65	26.33	0.65	1.3
	FEB18	672	1.46	24.17	3.1	1.47
	MAR18	507	1.75	24.83	0.70	1.05
	APR18	406	2.68	26.24	1.90	0.91
	JUN18	133	1.24	23.59	0.50	1.19
Less rainy	JUL18	135	0.81	22.02	1.90	1.10
	AUG18	193	1.39	23.98	3.15	0.98
	SEP18	171	1.41	24.05	2.40	0.84
	OCT18	135	1.41	24.05	2.50	0.88
	NOV18	246	1.30	23.77	3.10	0.79
Rainy	JAN19	414	3.43	27.28	2.90	1.1
	FEB19	453	1.88	25.10	0.20	1.23
	MAR19	625	1.54	24.37	0.10	1.38
	APR19	494	1.69	24.7	2.10	0.96
	MAY19	394	0.58	18.4	0.70	1.08
	JUN19	333	1.59	23.97	1.73	0.77
	Mean	333	1.59	23.97	1.73	1.07
	Minimum Maximum	103-672	0.58-3	18-27	0.10-3	0.78-1.00
	Standard deviation	175.58	0.72	1.97	1.10	0.20

space characteristics, similar results found by Braghin et al. (2018) for zooplankton in dammed rivers, and by Villéger et al. (2013) in fish assemblages in European rivers. The increase in the functional similarity of rotifers over time due to the substitution of species that have unique functional "roles" can lead to the establishing of species with similar "roles" in the ecosystem (i.e., species with various functional equivalents) (Olden 2006). For Soininen et al. (2017) the negative correlation between turnover and nestedness can be a result that the two diversities respond independently to environmental variables, pattern that may be seen in our study.

Functional redundancy promotes the maintenance of ecosystem processes in case disturbances extinguish species, which would be compensated by the presence of functionally similar taxa with different responses to changes in environmental factors or disturbances (Elmqvist et al. 2003). This long-term maintenance is a type of stability defined as resilience, that is, the ability of a community to return from its effects on ecosystem processes to an earlier state, after change due to a disturbance (Pillar et al. 2013). Thus, the Guamá River rotifer community has a high functional redundancy between seasonal periods. Redundancy indicate that the ecosystem functions performed by the species are robust and can be maintained when there

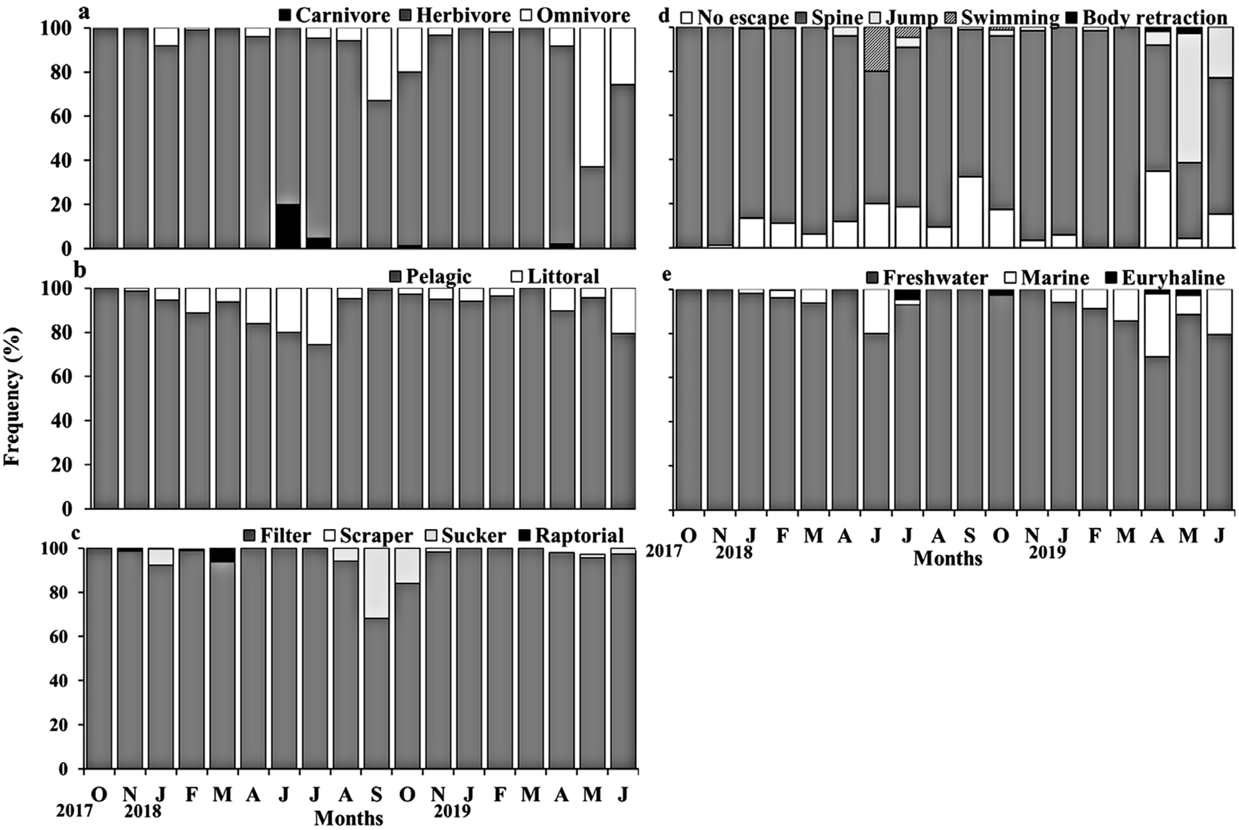

Figure 1. Relative frequency (%) of the functional traits of the rotifer community over the period of October/2017 to June/2019. Where, a- feeding habits: carnivore, herbivore and omnivore, b- habitat: pelagic and littoral, c- feeding mode: filter, Scraper, Sucker and raptor, d- predator escape: no escape, Spine, jump swimming and body retraction, e- freshwater, marine and euraline.

is a change in the diversity and composition of species, so that the community has a great resilience to disturbances in the functions performed by existing species (Micheli & Halpern 2005). According to the functional traits evaluated, functional traits are maintained over time, and species perform similar functions in communities and ecosystems despite the temporal variation in the composition of the rotifer community in the Guamá River. Furthermore, their replacement would have little impact on ecosystem processes developed by these communities.

In lotic environments, the high flow of rivers provides greater dispersion of species, which together with eutrophication gradients can boost species substitution, and changes their tolerances to eutrophication (Declerck et al. 2007). Therefore, river flow, dispersion and eutrophication are responsible for the selection of organisms with characteristics that best suit environmental conditions. Gianuca et al. (2017a) hypothesized that functional redundancy may be a dominant pattern in homogeneous landscapes, which means that different species with similar characteristics are replaced (turnover) among

Table III. **Multiple regression on distance matrices (MRM) and partial Mantel test between matrices of environmental dissimilarity (dC_Env) and temporal dissimilarity (Time) and distance matrices of beta taxonomic and functional diversity between seasonality. Correlation (*r*) and statistical significance (*p*) after 10000 randomizations. *bold significative values p< 0.05.**

Beta	**Predictor**	**Mantel Partial**		**MRM**
diversity	**variable**	**Seasonality**		
		r	p	p
Taxonomic	dC_Env	0.01	0.45	0.97
		Less rainy		
	Time	0.27	0.12	0.23
	dC_Env	-0.15	0.79	0.42
		Rainy		
	Time	0.07	0.22	0.55
Functional	dC_Env	-0.42	0.90	0.08
		Less rainy		
	Time	0.85	0.08	**0.03***
	dC_Env	0.12	0.29	0.60
		Rainy		
	Time	-0.07	0.67	0.60

local communities. The studied environment did not present limnological differences between seasonal periods, and remained hypereutrophic over time, and therefore can be considered a limnological homogeneous environment. Functional redundancy is likely to happen because homogeneous landscape species need to be able to survive similar environmental filters (Gianuca et al. 2014). It is possible that the landscape's environmental homogenization, which may or may not result from a common environmental change, selects functionally redundant species. This leads to a rapid convergence of functional traits in the metacommunities (Gianuca et al. 2017a). Thus, homogeneity did not favor functional beta diversity in the study, since the low environmental variability allows only similar species to occur (Gerisch et al. 2012, Braghin et al. 2018).

In the studied environment the species that prevailed were rotifers with biomass between 0.1 and 0.5 µg.DW.m^{-3}, filter feeders, omnivores-herbivores, pelagics and those with spines or without predator escape strategies (Brachionidae, Euchlanidae, Lecanidae, Lepadellidae, Philodinidae and Proalidae) (Table SI). *Euchlanis* sp. Ehrenberg, 1832, captured in August 2018, was replaced by *Brachionus quadridentatus* Hermann, 1783 in the subsequent month, both have the same functional traits mentioned, except that the first species was littoral and the second pelagic. Organisms with these characteristics are probably more resilient to hypereutrophic environments and low environmental heterogeneity.

According to Gianuca et al. (2017b), eutrophication causes the loss of large zooplankton species and increases abundance of smaller species. Turbid waters inhibit the predation of these organisms and increase the survival rate of species without an escape strategy. Species that presented reduced escape capacity are responsible for maintaining trophic relationships, especially in lotic environments (Garcia et al. 2018). Therefore, this study corroborates the pattern found by Garcia et al. (2018) in a study that found a higher proportion of species with low escape strategy in a lotic environment.

The predominance of omnivorous-herbivorous filter feeder species in this study may have been favored by the hypereutrophic condition of the environment and consequently the increase in phytoplankton density. The temporal changes in rotifer diversity has been attributed to changes in phytoplankton trophic chains (Wagner & Adrian 2011), especially when changes occur in phytoplankton abundance and size (Obertegger & Manca 2011). The higher proportion of filter feeder rotifers reflects the ability of this group to survive in environments with reduced food quality. They are considered opportunistic and generalist in their diet since they obtain their food through water currents that drag algae and bacteria (Allan 1976).

A relationship between taxonomic beta diversity with environmental dissimilarity and environmental variables was expected as reported by previous studies (Leibold et al. 2004). Although environmental dissimilarity should intuitively influence beta diversity there are studies that have failed to show a significant relationship between these variables (Lopes et al. 2014, Soares et al. 2015). Thus, further studies are necessary to understand the role of environmental variables and environmental dissimilarity in the composition of rotifer species.

Finally, the temporal study of the taxonomic and functional beta diversity and their respective partitions of the rotifer community in the Guamá River was important to clarify the structure of this community in response to a hypereutrophic lotic environment with low environmental dissimilarity. This work motivates further studies in Amazonian environments, little known about the autecology of rotifer species. It is important to emphasize that temporal studies should assess both taxonomic and functional aspects of communities, mainly because the effect of environmental changes can be more noticeable at the functional level of communities.

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SUPPLEMENTARY MATERIAL

Figure S1. Environmental variable variation, environmental heterogeneity and beta diversity components from October/2017 to June/2019. Where, a- water height (m); b-chlorophyll-a (mg/m³); c- trophic state index - TSI; d- environmental heterogeneity; e-functional beta diversity; and f-taxonomic beta diversity.

Figure S2. Taxonomic (a) and functional (b) beta diversity boxplots of rotifers communities divided into two seasonal groups, rainy and less rainy. The strong line shows the median, the ends of the boxes show quartiles, and open circles show outliers.

Figure S3. Taxonomic (a) and functional (b) beta diversity boxplots of rotifers communities divided into their components resulting from nestedness and turnover on a time scale. The strong line shows the mean, the ends of the boxes show quartiles, and open circles show outliers.

Table SI. List of abundances of zooplankton species from the Rio Guamá over the study period.

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EWERTTON S. GADELHA[1]
https://orcid.org/0000-0002-5741-6547

BÁRBARA DUNCK[2,3]
https://orcid.org/0000-0003-0608-0614

NADSON R. SIMÕES[4]
https://orcid.org/0000-0002-4577-9033

EDUARDO T. PAES[3]
https://orcid.org/0000-0002-9429-2598

ALBERTO AKAMA[1]
https://orcid.org/0000-0003-0209-770X

[1]Museu Emilio Goeldi, Programa de Pós-Graduação em Biodiversidade e Evolução, Av. Perimetral, 1901, 66077-830 Belém, PA, Brazil

[2]Universidade Federal do Pará (UFPA), Programa de Pós-Graduação em Ecologia - PPGECO, Laboratório de Ecologia de Produtores Primários, Rua Augusto Corrêa, 1, 66075-110 Belém, PA, Brazil

[3]Universidade Federal Rural da Amazônia (UFRA), Instituto Socioambiental e de Recursos Hídricos, Av. Tancredo Neves, 2501, 66077-830 Belém, PA, Brazil

[4]Universidade Federal do Sul da Bahia, Programa de Pós-Graduação em Ciências e Tecnologias Ambientais, Rodovia Ilhéus, Km 22, 45604-811 Itabuna, BA, Brazil

Correspondence to: **Ewertton S. Gadelha**
E-mail: ewerttooo@yahoo.com.br

Author contributions

Ewertton Gadelha: led the study. Bárbara Dunck: conceptualization, methodology, formal analysis, writing - original draft, writing review and editing. Nadson R. Simões: conceptualization, methodology, writing - review and editing. Eduardo T. Paes: methodology, supervision, writing - review and editing. Alberto Akama: supervision, writing - review and editing. All authors discussed the results and contributed to the final manuscript.