Responses of stream zooplankton diversity metrics to eutrophication and temporal environmental variability in agricultural catchments

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Abstract Eutrophication of rivers and streams in agricultural lands is one of the main threats for biodiversity and ecosystem functions. This study was focused on seven subtropical streams where agriculture is the predominant land use. We tested the hypothesis that (i) eutrophication causes a decrease in taxonomic and functional diversity of zooplankton, leading to potential consequences for the ecosystem integrity. Furthermore, given that the temporal variability in the environmental conditions of each stream may influence the species sorting mechanisms, we also hypothesized that (ii) streams with higher temporal environmental variability have greater taxonomic and functional alpha (α) and temporal beta (β_t) diversity measures regardless of the trophic state. Thus, we characterized the streams according to their trophic state and analyzed the zooplankton composition, α and β_t by using taxonomic and functional perspectives. We found differences in the zooplankton composition between mesotrophic and eutrophic streams. However, eutrophic streams supported similar taxonomic and functional α diversity and similar taxonomic β_t diversity to mesotrophic ones. These results were mainly explained by the occurrence of rare species occupying different temporal niches in eutrophic systems. On the contrary, functional β_t diversity was lower in the eutrophic streams, being nestedness the ecological mechanisms underlying the variability in the zooplankton functional groups. Streams with higher temporal environmental variability supported greater α taxonomic diversity. However, the β_t diversity metrics showed no correlation with the environmental variability, suggesting that the environmental filters of the studied systems were the overriding determinants of species turnover. Our study suggests that both taxonomic and functional perspectives should be considered to improve our knowledge on the biotic responses to environmental changes. Also, among all metrics analyzed on the zooplankton community, functional β_t diversity was the most sensitive indicator of the eutrophication impact.

Keywords Freshwater · Functional traits · Land use · Microcrustacean · Rotifers · Species richness

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Introduction

Rivers and streams are among the most threatened ecosystems in the world, as they extensively undergo

diverse anthropogenic interventions that intensify the eutrophication process (Schäfer et al. 2016). Eutrophication is one of the most important disturbances that cause environmental, economic, and social damages (Jeppesen et al. 2010). In agricultural lands, eutrophication of rivers and streams can occur because of soil erosion and subsequent runoff of fine sediments, nutrients, fertilizers, and agrochemicals such as pesticides, as well as high densities of livestock (Tilman et al. 2001; Mesa et al. 2015; Harrison et al. 2019).

The impacts of eutrophication on biodiversity may lead to either direct effects such as loss of species, or indirect effects such as alterations in biological interactions, trophic structure, and primary productivity, with consequences for ecosystem function and services provision (Wang et al. 2016; Cook et al. 2018; Bhagowati and Ahamad 2019). These biodiversity loss–related changes can be complementarily measured via taxonomic and functional approaches. In this regard, different biodiversity metrics can provide a valuable approach to the system's biological complexity and integrity (Simões et al. 2020). Therefore, they could be used as monitoring and management tools to establish priority areas for protection or mitigation of environmental impacts.

Previous studies have shown that freshwater eutrophication in agricultural areas is associated with a decline in local (alpha) and regional (gamma) diversity in several aquatic ecosystems (Wang et al. 2016), with eutrophication also modifying spatial beta diversity (β_{spat}) (Bini et al. 2014). However, the relationship between the trophic states of aquatic systems and β_{spat} seems to be more complex than expected considering recent contrasting findings. Some works have found a decline in β_{spat} associated with the homogenization of communities at a regional scale (Hawkins et al. 2015; Siqueira et al. 2015; Socolar et al. 2016) while others have found that eutrophication increases β_{spat} because of rare but tolerant taxa and contributes to the decline of some relatively common but sensitive species (Hawkins et al. 2015; Simões et al. 2020). Unlike spatial beta diversity, the variation of community composition in time (i.e., temporal beta diversity, β_t) has received comparatively less attention. Cook et al. (2018) found a strong relationship between eutrophication and β_t of invertebrate communities, suggesting that eutrophication causes an expansion of the temporal niche of exploitative taxa, thereby homogenizing the communities. However, further studies are required to understand how eutrophication affects the temporal variability of other communities such as zooplankton.

In addition to taxonomic diversity, functional diversity has been suggested as an important metric because it is based on the functional traits of species present in a community. Functional traits define species in terms of their ecological roles (i.e., how they interact with the environment and with other species) (Diaz and Cabildo 2001; Cadotte et al. 2011). Thus, a measure of diversity based on these functional traits may provide a better understanding of the relationship between biodiversity and ecosystem function (Mouchet et al. 2010; Vaughn 2010; Hooper et al. 2012). Studies demonstrated that agricultural intensification could reduce the functional diversity of different animal communities through the selection of species characterized by a standard set of functional traits (e.g., broader habitat use and diet breadth) (Flynn et al. 2009; Ding et al. 2017; Nevalainen and Luoto 2017). This functional homogenization can generate instability in the trophic structure and severe consequences for the whole ecosystem.

The impacts of eutrophication on the taxonomic and functional diversity of stream species may also be influenced by other factors such as each specific system's environmental variability, described by climatic (e.g., temperature, precipitations) and limnological conditions (e.g., dissolved oxygen, nutrients, pollutant concentrations). For example, it has been proved that the temporal variability of environmental conditions causes an increase in diversity metrics by favoring the presence of specialist species occupying particular temporal niches (Simões et al. 2013; Lopes et al. 2019). Therefore, this variation can be a confounding factor in highly variable systems when their diversity metrics are analyzed. Moreover, some studies have been conducted in the Pampean region regarding the influence of agricultural land use on the streams' water quality (Di Marzio et al. 2010; Mugni et al. 2013; De Geronimo et al. 2014; Frau et al. 2019) and on the inhabiting organisms (Rodrigues Capítulo et al. 2001; Cochero et al. 2013; Paracampo et al. 2020). However, scarce information currently exists regarding the relationship between temporal variations in the environmental conditions and biodiversity of aquatic communities. The variation in agricultural calendars, crop type, agrochemical application, and cattle rotation associated with climatic events (e.g., heavy rains) can promote extensive changes in the temporal dynamics of natural communities linked to these agroecosystems. Nonetheless, this premise has not been accurately tested especially for zooplankton. Knowing the impact of agricultural stream eutrophication on

taxonomic and functional diversity, considering environmental variability, may allow us a better understanding of the system's ecological integrity and to establish risk categories for its management.

Within lotic aquatic systems, zooplankton is a key community because it links predators and primary producers and participates in nutrient recycling. Zooplankton can respond rapidly to anthropogenic environmental variations because of its small size, short generational time, and broad functional traits (Vieira and Bio 2011; Mano and Tanaka 2016). Thus, this community is largely appropriate for the evaluation of eutrophication effects and may be used as a tool in biomonitoring programs (Simões et al. 2015; Jeppesen et al. 2011).

This study focused on seven streams located in the northern area of the Pampean region of Argentina, an area where agriculture is the predominant land use. We characterized these streams according to their trophic status and analyzed their zooplankton composition, alpha diversity (α), and temporal beta diversity (β_t) from a taxonomic and functional perspective.

We tested the hypotheses that (i) eutrophication causes a decrease in zooplankton biodiversity (composition, taxonomic diversity, and ecological functions) and that (ii) temporal variability in environmental conditions exerts a positive effect by favoring the presence of specialist species occupying particular temporal niches. Thus, we predict that (a) eutrophic streams support less α diversity than mesotrophic ones because that condition favors fewer functional traits of eutrophication-tolerant species; (b) eutrophic streams support less β_t than mesotrophic ones, leading to more temporally homogenous communities; **(c)** among different β_t diversity components, nestedness is the underlying ecological mechanism in eutrophic streams because environmental filters are stronger than mesotrophic ones, and the assemblages of each sampling period are represented by tolerant subsets of species/functional groups. Finally, we predict that (d) streams with higher environmental variability have greater taxonomic and functional α and β_t diversity.

Material and methods

Study area and environmental characterization

We conducted our study in the Pampean ecoregion (Santa Fe, Argentina). The area has a temperate climate, with temperature ranging from 9 °C during the winter to 27 °C during the summer, and precipitation ranging between 900 mm and 1000 mm, yearly. In this area, traditionally farmers employed a mixed agriculture (e.g., wheat, corn, sunflowers, and sorghum) but in recent decades, it has been replaced by intensive soybean monocultivation (Mugni et al. 2013). A total of seven streams located in three sub-basins of the Paraná Medio River were sampled in the same site during four sampling dates. The selection of the sampling times was carried out considering the agricultural calendar of the Santa Fe province recommended by the National Institute of Agricultural Technology (INTA). Two samplings were carried out in the pre-sowing phase (November 2016 and November 2017) and two samplings in the low activity phase (April and August 2018). The pre-sowing phase is characterized by a high pesticide and fertilizer application because the fields are prepared to control the emergence of weeds and begin the sowing. During the low activity phase, it is expected that no chemical substances will be added to the soil because it is a harvest period or because there are no crops present in the fields.

The selected streams presented similar morphological and hydraulic characteristics. They are of similar limnological hierarchy (second-third order), running through the center-south in a west-east direction along a longitudinal transect of 132 km. The soil type is Molisol (large Argiudol group, typical and aquic subgroup), with a silty loam surface texture and a silty clay subsurface texture (GeoINTA 2014), and they are characterized by absence of floating macrophytes in the riverine bank. All of them are influenced by agricultural activities because it is the predominant land use in their catchment area (Fig. 1).

Samplings and laboratory procedures

At each sampling point, three replicas were considered for physicochemical sampling in four campaigns in the seven streams ($N = 84$ for each variable). The limnological variables measured in situ were temperature (°C), pH, dissolved oxygen (ppm), percentage of O_2 saturation (%OD), and conductivity (mS cm^{-1}), and water flow (cm s^{-1}) was estimated with a current meter (A.OTT Kempten) and photosynthetic active radiation (PAR) used to estimate the light extinction coefficient (K_d, m^{-1}). The first four variables were measured with HANNA multiparameter sensors. PAR was estimated with a radiometer LI-COR model LI-192 and light

extinction coefficient (K_d, m^{-1}) was calculated by using the formula proposed by Wetzel (1983). Finally, the depth in sampling sites was estimated with a bathymetric lantern (m).

In each sampling date, water samples were also taken to estimate inorganic dissolved nutrients concentration and chlorophyll-*a* (Chl-*a*) by triplicate. The nitrates plus nitrites ($NO_3^- + NO_2^-$) were analyzed by reducing nitrate with hydrazine sulfate and subsequent determination of nitrite by diazotization with sulfanilamide, ammonium (NH_4^+) was determined by using the indophenol blue method, while soluble reactive phosphorus (SRP) was estimated by the ascorbic acid method following the recommendations of APHA (2005), expressing the concentrations obtained as μg L^{-1}. $NO_3^- + NO_2^- + NH_4^+$ were considered as dissolved inorganic nitrogen (DIN) for the rest of this study. Chl-*a* was processed by using GF/F filters with 90% acetone through maceration in a glass grinder and subsequent dark storage at 4 °C for 24 h. Subsequently, the extracts were clarified and measured with a spectrophotometer at 664 nm and 750 nm and at 665 nm and 750 nm after acidification with 0.1 N HCL (APHA, 2005). The results obtained were expressed in μg L^{-1}. Additional samples were also collected for the biochemical oxygen demand (BOD_5) and chemical oxygen demand (COD) estimation. The BOD_5 was measured by an LDO BOD probe, model LBOD 10101, HACH brand, and the oxygen consumption during the incubation was calculated by differences between the initial and final value, considering dilutions when it was necessary. BOD_5 was expressed in mg L^{-1}. For the COD estimation, water samples were digested for 2 h at 150 °C with $K_2Cr_2O_7$ in acidic medium. The colorimetric determination was carried out at 420 ηm and expressing the result in mg L^{-1}.

Three zooplankton samples were taken in each stream at each sampling date, using a Schindler-Patalas plankton trap (20 L) fitted with a 50-μm mesh net. The filtered material was fixed in situ with formaldehyde 10% and stained with erythrosine. The counts of microzooplankton (Rotifera and Copepoda nauplii) were carried out with an optical microscope using Sedgwick Rafter chambers. The counts of the macrozooplankton (Cladocera and Copepoda) were done in a Bogorov chamber (5 mL). A minimum of 100 individuals were counted in each sample, at 200× of magnification. All organisms were identified to the lowest possible taxonomic level (e.g., Copepoda were classified at the order level, because most individuals found

in the samplings were larval stages). The taxonomical classification was done based on Ringuelet (1958), Koste (1978), Paggi (1979), Paggi (1995), and Korinek (2002), among others.

The functional classification was based on the combination of seven functional traits of the species found in each stream at each sampling date. The functional traits were mean body length, feeding type, food source, habitat, reproduction type, life cycle, and escape ability (Appendix I). Body length was measured in at least ten specimens found in samples when it was possible. Feeding type was characterized according to Krztoń et al. (2019), and based on available literature (Barnett et al. 2007; Obertegger and Manca 2011). The food source was described considering three categories established by Krztoń et al. (2019): bacterivorous and/or detritivores (B), algaevorous (A), and predator (P). Habitat was characterized considering the typical preference of each taxon as follows: limnetic (Lm), littoral (Lt), and benthonic (Be). Reproduction type was classified as sexual or asexual, life cycle as short or long (mainly for copepods), and escape ability as low and rapid, according to zooplankton species morphological characteristics and behavioral abilities.

Statistical analyses

The streams were first classified in two trophic categories (mesotrophic and eutrophic) on the basis of their Chl-*a* concentration (Fig. 2) suggested by Dodds and Oakes (2006; 2016). Also, we performed a hierarchical cluster analysis (UPGMA method) based on Euclidean distance of the nutrients (SRP and DIN), Chl-*a*, DBO_5, and COD mean values by streams standardized. Significant differences between the resulting groups were tested by using a non-parametric multiple variance analysis (NPMANOVA) based on the same independent variables.

We used principal component analysis (PCA) to evaluate the main patterns of variation of each stream within the major environmental gradients by considering all sampling dates. Data were previously log-transformed, centered, and standardized, and the dispersion of the correlation matrix was used. Axes were selected according to the Kaiser-Guttman criterion (Legendre and Legendre 1998).

A permutational multivariate dispersion test (PERMDISP; Anderson et al. 2006) was performed to test and compare the environmental variability of each

stream. We calculated Euclidean distance standardize matrices between sampling dates according to the environmental variables set. Finally, we tested differences in multivariate dispersion among streams through the Tukey's honestly significant difference test.

The taxonomic differences in the zooplankton composition among the streams were analyzed through a similarity percentage procedure (SIMPER) with 9999 permutations performed on the Bray–Curtis triangular matrix. Abundance data were square root transformed for the analysis. A posteriori permutational multivariate analysis of variance (NPMANOVA) was performed to analyze whether those differences were statistically significant.

To identify the dominant, occasional, rare, and common species of all streams and those of each trophic category, we constructed three Olmstead–Tukey diagrams by plotting the (log) frequency of occurrence and (log) mean abundance of each species (Sokal et al. 1979). An average of these variables (frequency of occurrence and mean abundance of each species) was calculated and included in each axis. Therefore, the plot resulted in four quadrants that defined the type of taxa according to their appearance in (a) dominant (frequent and abundant taxa); (b) occasional (abundant and non-

frequent taxa); (c) rare (non-frequent and non-abundant taxa); and common (frequent and non-abundant taxa) (Claps et al. 2009).

The taxonomic α diversity was considered as the species richness registered in each stream at each sampling date (Magurran 2013). Accordingly, the functional α diversity was measured as functional richness (FRic) and calculated based on the combination of the seven selected functional traits as mentioned above. Higher FRic values indicate larger differences in the combination of functional traits for the community (Villéger et al. 2008). The taxonomic β_t was considered as the variability of the zooplankton species among the sampling dates. The functional β_t was considered as the variability of the zooplankton functional diversity among the sampling dates. We used the PERMDISP test to assess the variability of the zooplankton among the sampling dates (β_t diversity) from both taxonomic and functional perspective. A centroid was computed for each group, and the distances between each sampling date and the centroid were considered as β_t diversity. The significance ($P < 0.05$) of the differences in β_t between each sampling date was tested using a permutation test with 999 permutations.

We also partitioned total beta diversity into its two components: the spatial turnover and the nestedness
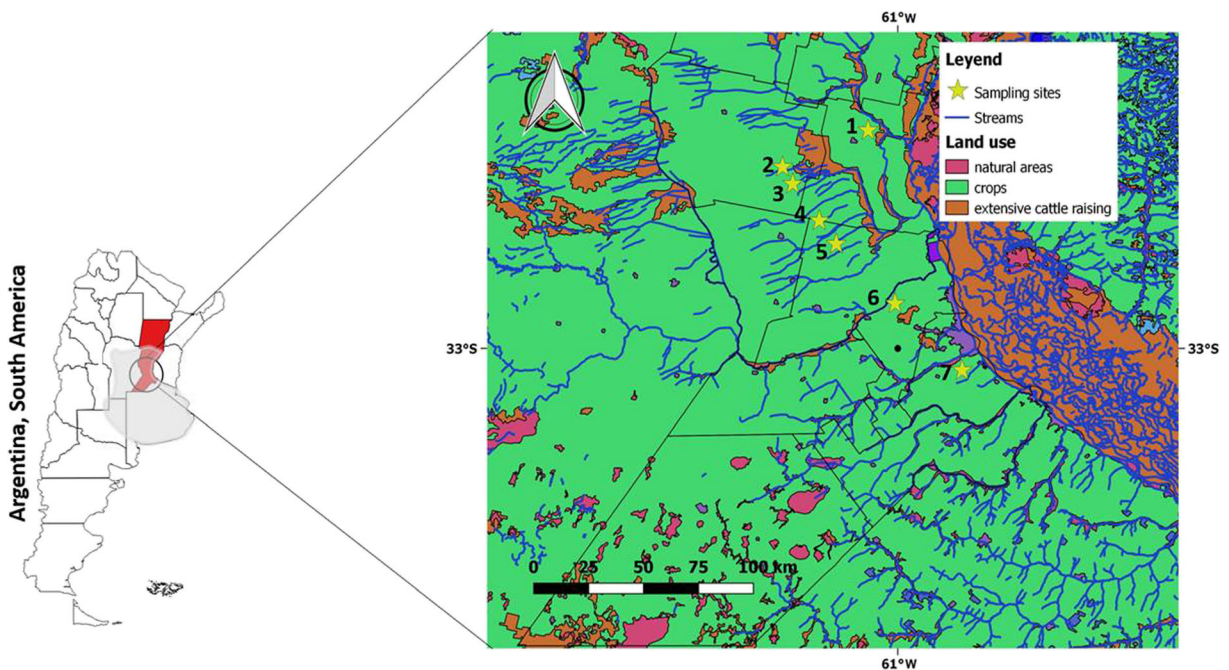

Fig. 1 Study area and sampling sites of the seven subtropical Pampean streams (S1–S7), Santa Fe (in red), Argentina (modified of Frau et al. 2020). The gray area shows the whole Pampean region in Argentina

(Baselga 2010). Species nestedness occurs when the biotas of sites with smaller numbers of species are subsets of the biotas at richer site, while spatial turnover implies the replacement of some species by others (Baselga 2010). Here, turnover and nestedness were measured temporally.

We used an analysis of covariance (ANCOVA) to test the difference in the values of taxonomic and functional α and β_t diversity metrics among streams and between the trophic categories at a significance level of $p < 0.05$. For these analyses, the environmental variability (according to the PERMDISP test) was used as co-
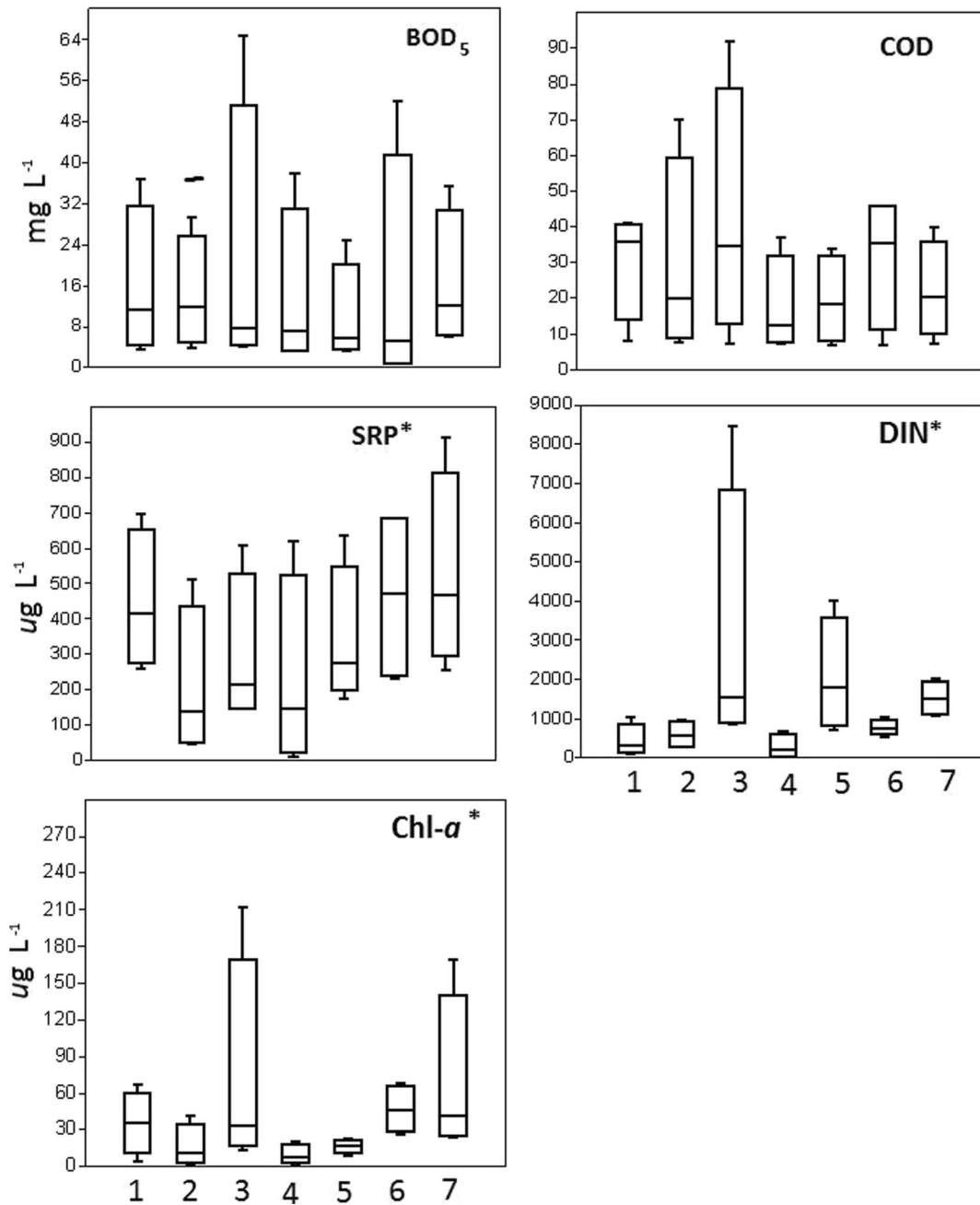

Fig. 2 Box plot showing the chemical characteristics (BOD_5: biological oxygen demand, COD: chemical oxygen demand, SRP: soluble reactive phosphorous, DIN: dissolved inorganic nitrogenous and Chl-a: chlorophyll-a) for each stream. Asterisks indicate significant differences among streams. Post hoc Tukey tests are shown in Supplementary material II

variable (Sokal and Rohlf 1981). Also, the specific relation between environmental variability and taxonomic and functional α and βt diversity metrics were evaluated through a single non-parametric correlation tests on the averaged values (Spearman rank). The statistical analyses were performed in the FD (dbFD function), vegan (betadisper function), and betapart (functional.- beta.pair function) packages in the R software v 0.99.903 (R Development Core Team 2015), CANOCO 5 (ter Braak and Smilauer 2002) and PAST v 2.17 (Hammer et al. 2001).

Results

Environmental characterization

The mean limnological variables measured in situ are shown in Table 1. Monthly precipitations registered in November 2016, April 2017, August 2017, and November 2017 were 19, 58.9, 78.5 and 42 mm, respectively (Registros Publiométricos, Gobierno de Santa Fe). In general, water flow was low during the three first sampling dates (mean 3 ± 3.6 m^{3}s^{-1}) and increased in November 2017 in all the streams (mean 41 ± 15 m^{3}s^{-1}). The water temperature ranged between 13 °C and 32 °C; conductivity was always greater than 1 mS cm^{-1} (between 1 and 11.3 mS cm^{-1}), with significant differences among some streams (Appendix II); dissolved oxygen saturation (DO%) was in general higher than 100%, and also differed among some streams (Appendix II). The light extinction coefficient (K_d) showed the highest values for sites S1, S6, and S7 (> 10 m^{-1}), while the lowest values were recorded for site S4 (0.67 m^{-1}). Significant differences were found for this variable among S6 and S2, S3, S4, and S5 (Appendix II). The pH ranged between 6.47 and 9.05 (both in S2). The chemical variables (BOD$_5$, COD, SRP, DIN, and Chl-a) also varied among the streams (Fig. 2). According to the criteria established by Dodds (2006; 2016) based on Chl-a, we were able to characterize the streams in two main groups mesotrophic (S2, S4, and S5) and eutrophic (S1, S3, S6, and S7). The cluster dendrogram performed with the chemical variables showed a similar grouping pattern (Fig. 3). It is important to note that despite that S3 was separated of the other two groups in the cluster dendrogram, it was included in the eutrophic category because of its high values of BOD$_5$, COD, and DIN, and the mean Chl-a

that fits within the eutrophic category of Dodds (*op cit*) (Fig. 2). A significant difference was found between the two characterized groups based on the chemical variables above mentioned (NPMANOVA, $F = 5.07$, $p = 0.02$).

The PCA ordered all sampling sites according to seven environmental variables selected by a forward selection procedure (Fig. 4). The first axis was mainly defined by the combination of Chl-a, water flow, SRP, and conductivity (explaining 36% of the variability of the data), and the second axis by the combination of DO%, pH, and DIN (explaining 27% of data variability). The two axes accounted for 63% of the total variation. Overall, streams S1, S6, and S7 were positively related to Chl-a and SRP, while stream S3 was positively related to Chl-a, DIN, DO%, and conductivity values. Streams S2 and S4 were mainly characterized by low Chl-a and SRP values, while stream S5 was characterized by its lower DO% and conductivity values.

The PERMDISP showed differences in the environmental variability of the studied streams (pseudo-$F = 8.69$; p value < 0.001). The following gradient was found, from the lowest to the highest temporal variability: S5 < S4 < S6 < S1 < S2 < S7 < S3 (average distance to the centroid of each group was: 1.99; 2.16; 2.27; 2.32; 2.38; 3.38, and 3.96, respectively).

Community composition

A total of 95 taxa were recorded in all samples (80 for Rotifera, 12 for Cladocera and 3 for Copepoda) (Appendix III). The mean zooplankton density in all streams was 125 ind L^{-1} (min: 26 ind L^{-1} in S4; max: 249 ind L^{-1} in S7). The species composition differed among the eutrophic and mesotrophic streams (PERMANOVA, $p = 0.043$). Twenty-one taxa were responsible for 70% of this variation according to the SIMPER analysis, belonging to the genera *Brachionus*, *Keratella*, *Trichocerca*, *Filinia*, *Synchaeta*, Bdelloidea Rotifera, and to the Cladocera genus *Graptoleberis*.

From 95 taxa recorded in all samples, 10 taxa (10.5%) were present in all streams, 12 (12.6%) were found only in the mesotrophic streams, and 25 (26.3%) were found exclusively in the eutrophic ones (Fig. 5). The remaining 48 taxa were partially shared between some mesotrophic and some eutrophic streams, but not in all of them. Among the exclusive taxa of the mesotrophic streams, 58% were cladocerans and 42%

Table 1 Coordinates and mean (±SD between parentheses) values of limnological variables of the seven streams measured in situ at each sampling date. DO%: dissolved oxygen saturation, K_d: light extinction coefficient

	S 1	S 2	S 3	S 4	S 5	S 6	S 7
Coordinates	31°54′ 28.34″	32° 4′52.74″	32° 9′37.29″	32°19′ 55.24″	32°26′ 27.65″	32°43′ 4.16″	33° 1′46.18″
	61° 8′ 39.98″	61°34′ 11.37″	61°31′ 9.35″	61°23′ 18.16″	61°18′ 14.37″	61° 0′44.58″	60°40′ 54.29″
Water flow ($m^3 s^{-1}$)	7.55 (5.2)	9.66 (18.2)	13.59 (26.1)	11.77 (15.6)	20.47 (35.6)	14.18 (25.4)	14.55 (17.3)
Water temp (°C)	21.6 (7.4)	24.68 (6.1)	24.65 (5.2)	24.55 (4.2)	22.64 (3.9)	20.95 (3.2)	20.38 (6.3)
Conductiviy ($mS\ m^{-1}$)	3.46 (1.1)	2.4 (0.9)	8.60 (3.5)	3.70 (1.2)	3.01 (1.8)	5.84 (2.1)	3.41 (1.3)
DO%	72.46 (29.7)	175.77 (86.5)	177.05 (60.6)	177.96 (63.4)	105.24 (19.1)	84.71 (15.9)	112.69 (39.9)
K_d (m^{-1})	5.90 (5.2)	2.53 (1.8)	4.27 (2.3)	2.43 (1.6)	4.00 (2.6)	12.96 (4.1)	7.15 (5.3)
pH	7.59 (0.7)	7.80 (1.1)	7.78 (0.7)	7.75 (0.8)	7.49 (0.8)	7.36 (0.7)	8.21 (0.6)

rotifers; while in the eutrophic streams, only 4% were cladocerans and 96% were rotifers.

Within the taxa present in the seven streams, the most frequent and abundant taxa were suspension feeders rotifers (Bdelloidea, *Brachionus angularis*, *B. caudatus*, and *Keratella tropica*) and the scrapers cladoceran *Graptoleberis sp.* (Fig. 5a).

Among the exclusive taxa of mesotrophic streams, the dominant ones were the rotifers *Lecane cornuta*, *Harrigia eupoda*, and *Notholca squamula*, being all of them suspension feeders. Among cladocerans, the scrapers *Iliocryptus spinifer*, *Coronatella popei*, *Alona glabra*, and the free-living filters *Moina micrura* were the dominant species (Fig. 5b).

Among the exclusive taxa of eutrophic streams, the dominance was shared by suspension feeders (e.g., *Lecane inopinata*, *L. subtilis*, *Proales* sp., *Trichotria tetractis*) and piercer rotifers, such as *Trichocerca* and *Gastropus* sp. Likewise, several species with variable abundances, but very infrequent were recorded such as *Brachionus leydigii*, *B. havanaensis*, *Epiphanes* sp. *Trichocerca stylata*, and *Hexarthra* sp. Among

cladocerans, *Ceriodaphnia cornuta* (free-living filter) was the only one present in eutrophic streams being very abundant (Fig. 5c).

Taxonomic and functional α diversity metrics

The mean taxonomic and functional α-diversity differed among the streams (one-way ANCOVA, $F = 19.6$, $p < 0.01$ for the taxonomic and $F = 8.5$, $P < 0.01$ for the functional α-diversity), being both α diversities also significantly correlated between them (Spearman Rho = 0.62, $p < 0.001$). In general, sites with high taxonomic diversity also had high functional diversity and vice versa (Fig. 6). However, two contrasting patterns were observed in two streams in particular: in the stream S4 (mesotrophic), functional diversity was comparatively higher in relation to taxonomic diversity; and in stream 7 (eutrophic), functional diversity was comparatively lower in relation to taxonomic diversity (Fig. 6).

A significant positive correlation was found between the mean taxonomic α-diversity and the environmental variability (Spearman $r = 0.88$; $p = 0.016$); this was not

Fig. 3 Cluster dendrogram of sampling sites (Euclidean distance) based on nutrients (SRP and DIN), Chl-*a*, DOB₅, and COD values
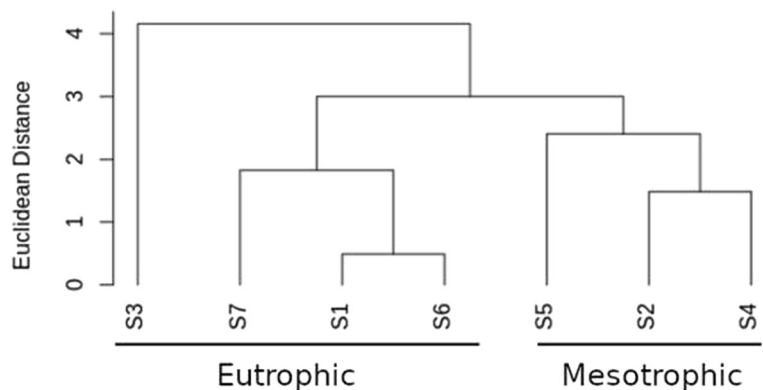
the case for the functional α-diversity and environmental variability (Spearman $r = 0.37$; $p = 0.42$). When the streams were grouped in eutrophic and mesotrophic categories, we did not find significant differences in the mean taxonomic and functional α-diversity (ANCOVA $F = 2.76$, $p = 0.19$ for taxonomic and $F = 1.09$, $p = 0.37$ for functional α-diversity) (Fig. 7a, b).

Taxonomic and functional β_t diversity metrics

No significant correlations were found between the environmental gradient and both β_t diversity metrics (Spearman $r = -0.31$, $p = 0.56$ for the taxonomic and $r = -0.54$, $p = 0.24$ for the functional β_t diversity). When the streams were grouped in eutrophic and mesotrophic categories, we found no significant differences in the mean taxonomic β_t diversity (ANCOVA $F = 1.26$, $p = 0.34$) (Fig. 7c). However, we found that the functional β_t diversity was significantly lower in the eutrophic than in the mesotrophic streams (ANCOVA $F = 9.26$, $p = 0.038$) (Fig. 7d).

Finally, the partitioning of the taxonomic β_t diversity showed that the turnover component was higher than

nestedness in all streams (Fig. 8a). On the contrary, the partition of the functional β_t diversity showed that the nestedness was higher than the turnover component (Fig. 8b). Moreover, we found that within the functional β_t diversity, the nestedness component of the eutrophic streams (S1, S3, S6, and S7) was even higher than those of the mesotrophic ones (ANOVA, $F = 36.75$, $p < 0.01$) (Fig. 8b).
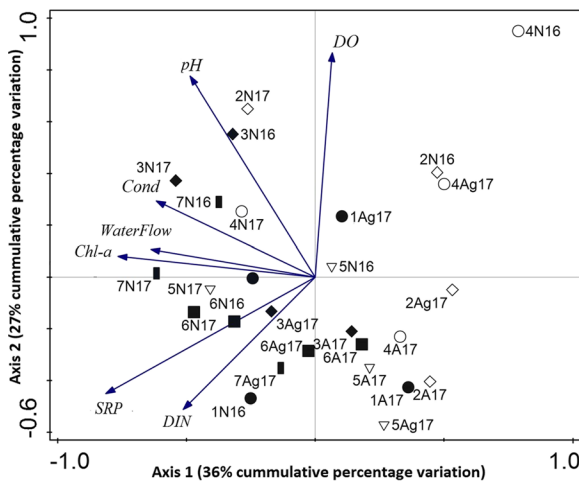

Fig. 4 Principal component analysis (PCA) biplot showing the major patterns of temporal heterogeneity of the seven streams according to the selected environmental variables (the two axes accounted for 63% of the total variation). Each symbol represents one stream. Black symbols represent eutrophic streams and white symbols represent mesotrophic streams. The code for each symbol is constructed by the number of stream (1–7), the sampling month (A: April, Au: August, N: November), and the sampling year (16: 2016, 17: 2017). DO: dissolved oxygen saturation (%), Cond: conductivity, Chl-*a*: chlorophyll-*a*, SRP: soluble reactive phosphorous
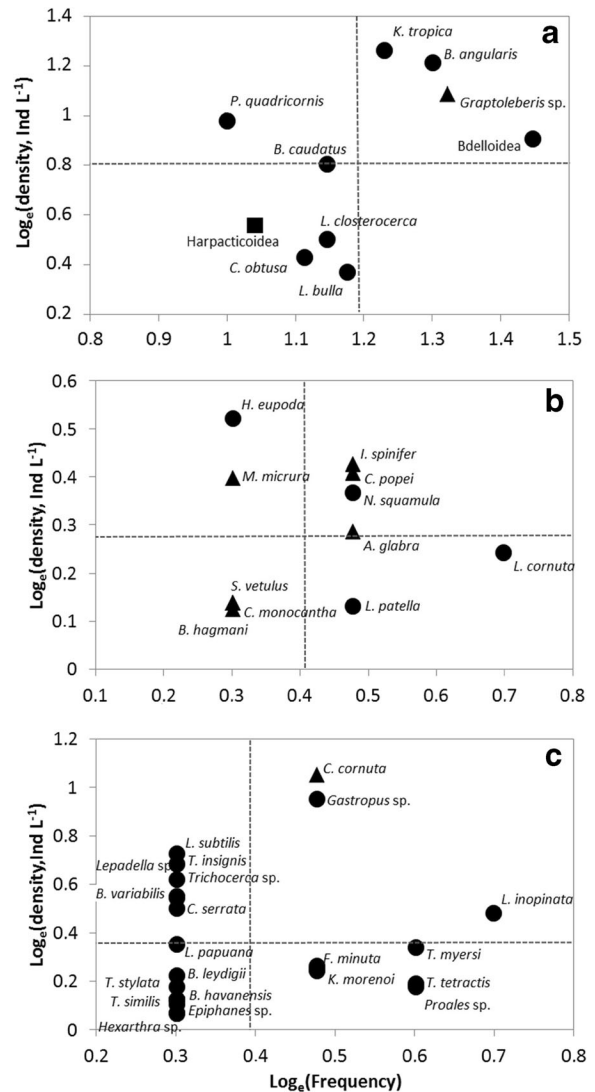

Fig. 5 Olmstead-Tukey diagram of shared taxa in all the streams (**a**), the exclusive taxa of mesotrophic streams (**b**), and exclusive taxa of eutrophic streams (**c**). Rotifers are represented by circles; cladocerans are represented by triangles and copepods by squares. Each quadrant represents the dominant species (upper right); the occasional (upper left); the rare (lower left); and common species (lower right)

Discussion

Environmental characterization

In this study, the results showed that the sampled streams were mainly characterized by high nutrient concentrations. This is typical of streams in areas worldwide where agriculture is the predominant land use (Alexander et al. 2000; Rabalais et al. 2002) and may be explained mainly by the high doses of fertilizers applied at each planting time along with the use of pesticides (Strayer et al. 2003; Freeman et al. 2007; Etchegoyen et al. 2017). Also, the high organic content in most sampling dates (measured as oxygen demands) may be due to the sporadic presence of cattle in the surrounding areas for drinking water and refreshment (Mesa et al., 2016). In addition, sporadic rain events during the sampling months may have influenced the
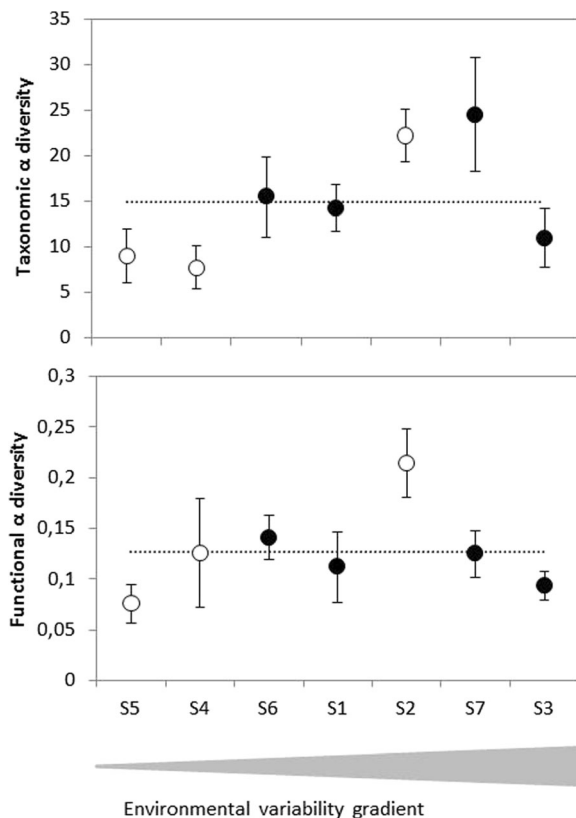
streams' water quality, as runoff water incorporates nutrients and other compounds from surrounding areas (Mugni et al. 2013).

Future climate-change scenarios proposed for the Pampean region expect an increment in rainfall events, which may enhance soil erosion and generate flooding, increasing the transport of sediments, nutrients, and contaminants (Rodríguez Capítulo et al. 2010). Under this scenario of land use modifications, it is possible that autotrophy of rivers will increase and that species adapted to turbidity and high nutrients load could become dominant.

Concentrations of dissolved inorganic nitrogen (DIN) and soluble reactive phosphorous (SRP) in the studied streams are similar to those found in other streams within the northern (Regaldo et al. 2017; Frau et al. 2019) and southern Pampean region (Rodríguez Capítulo et al. 2010; Mugni et al. 2013) in Argentina with high agricultural impact. All these studies suggest that the persistence of current agricultural trends will pose a risk to environmental sustainability because nutrient enrichment might trigger higher eutrophication with consequences for water quality and natural communities.

Overall zooplankton composition

Small organism size is a general pattern of zooplankton assemblages in highly productive systems (Jeppesen et al. 2011). Accordingly, we found that the cladoceran assemblage was mostly characterized by small genera, such as *Bosmina*, *Ceriodaphnia*, and *Graptoleberis* while larger taxa such as *Daphnia* and *Simocephalus* were absent. Regarding copepods, in eutrophic systems, cyclopoids tend to assume greater importance relative to calanoids (Conde-Porcuna et al. 2004; Jeppesen et al. 2007). In this study, we only found calanoid nauplii and an extremely low density of cyclopoids mainly in larval stages (copepodites). Other authors also reported that early stages of copepods were predominant in lotic systems with limited production, high predation risk, and lower adaptability to environmental variations (García-Chicote et al. 2019).

In addition, it has been demonstrated that large cladocerans and calanoid copepods are generally more sensitive to pesticide toxicity than microzooplankton, such as Chydoridae, rotifers, and cyclopoid copepods (Hanazato 2001). Therefore, it is possible that the high amount of pesticide applications in this region (Regaldo

Fig. 6 Mean (±SD) taxonomic and functional α-diversity of each stream, ordered according to the environmental variability gradient (established by the PERMDISP analysis), and classified according to their trophic condition. Black circles are eutrophic (S1, S3, S6, S7), and white circles are the mesotrophic ones (S2, S4, S5). The dotted line represents the mean α-diversity value of all streams

et al. 2018), along with predation pressure by small fish, may have determined zooplankton composition and size structure with a dominance of rotifers and small cladocerans and an absence of adult copepods (José de Paggi and Paggi 2008, Simões et al. 2013; Goździejewska et al. 2016; Braz et al. 2020; Gutierrez et al. 2020). In fact, at least five zooplanktivorous-insectivorous fish species were found in the streams (*Aphyocharax anisitsi*, *Bryconamericus iheringii*, *Cheirodon interruptus*, *Cnesterodon decemmaculatus*, and *Serrapinnus microdon*) with an average standard length of 30 (± 10) mm (Scarabotti et al. unpublished). Thus, although we did not study their stomach contents, it is likely that, as visual predators, they impose size-selective pressure on the zooplankton community by consuming large organisms such as microcrustaceans.

Meanwhile, rotifers accounted for 80% of the total zooplankton taxa recorded in all the streams. The most frequent and abundant taxa were Bdelloidea, *Brachionus angularis*, *B. caudatus*, and *Keratella tropica*. These taxa have also been recorded in similar systems with high nutrient and Chl-*a* concentrations and have also been associated with agricultural land use (Claps et al. 2009; De Paggi and Devercelli 2011; Illyová and Pastuchová 2012). Particularly,

B. angularis and *K. tropica* have been suggested as indicators of eutrophic conditions (De Paggi and Devercelli 2011; García-Chicote et al. 2019).

Differences in zooplankton composition between the two trophic categories

According to the characterization based on Chl-*a* concentration suggested by Dodds and Oakes (2006; 2016) for temperate streams, we classified the streams in mesotrophic (mean values between 10 and 30 $\mu g\ L^{-1}$) and eutrophic ones (mean values higher than 30 $\mu g\ L^{-1}$). The cluster analysis based on dissolved nutrients (SRP and DIN), Chl-*a*, BOD_5, and COD grouped the streams similarly, highlighting that eutrophication and enrichment with organic matter are closely related processes in these aquatic systems. Considering this categorization, we observed important differences in the zooplankton community.

We found that in the mesotrophic streams, 58% of zooplankton taxa were represented by cladocerans and 42% by rotifers while in the eutrophic streams, these proportions were unbalanced in favor of rotifers, as only 4% were cladocerans and 96% rotifers. This is consistent with previous works where increasing
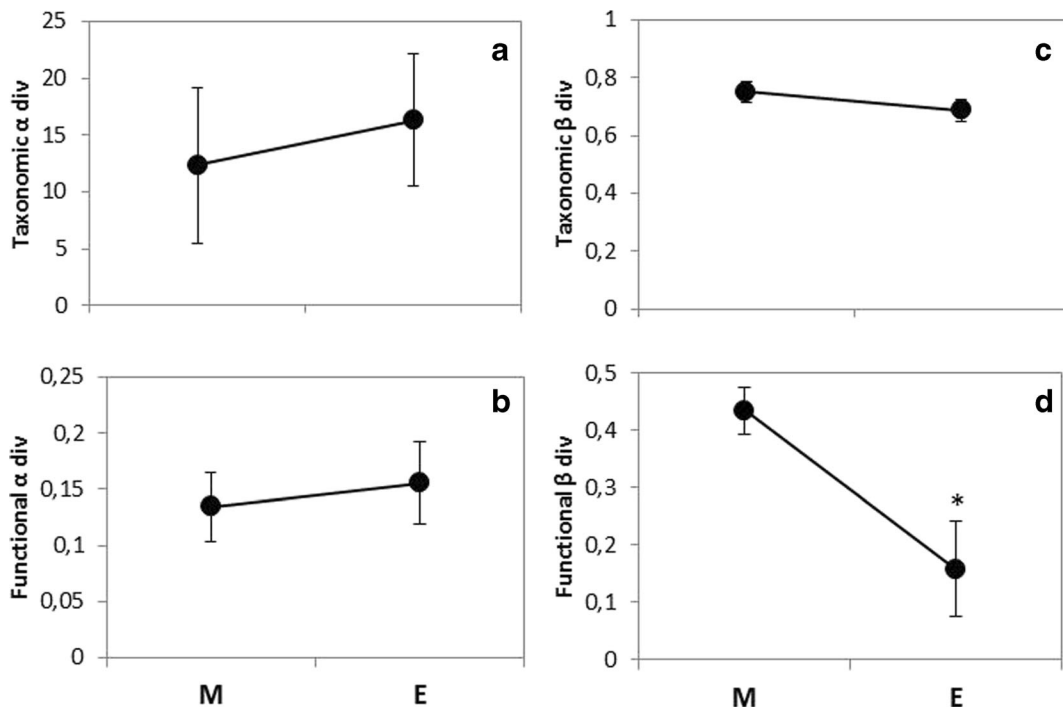

Fig. 7 Mean and ± SD of diversity metrics according to the trophic status (M: mesotrophic and E: eutrophic). Asterisk indicates significant differences (ANOVA, $P < 0.05$). Taxonomic α (**a**) and β_t diversity (**c**) and functional α (**b**) and β_t diversity (**d**)

eutrophication caused species replacement and a higher importance of rotifers and ciliated protozoans instead of cladocerans (García-García et al. 2012). The increase in rotifers in response to environmental disturbances has been suggested to be a consequence of their fast responses to fluctuating physical-chemical variables, wide trophic plasticity, short generational times, and high population turnover rates (Fontaneto et al. 2005; Parmar et al. 2016).

In the eutrophic streams, we found 24 exclusive rotifer taxa of which *Trichocerca* (5 spp.), *Lecane* (3 spp.), *Brachionus* (3 spp.), and *Filinia* (2 spp.) were the most representative genera. This is consistent with the report by De Paggi and Devercelli (2011) in other highly anthropically affected semilotic ecosystems. On the other hand, *Ceriodaphnia cornuta* was the only exclusive cladoceran. This genus has been documented as one of the most constant indicators of eutrophic degree in many aquatic systems (García-García et al. 2012).
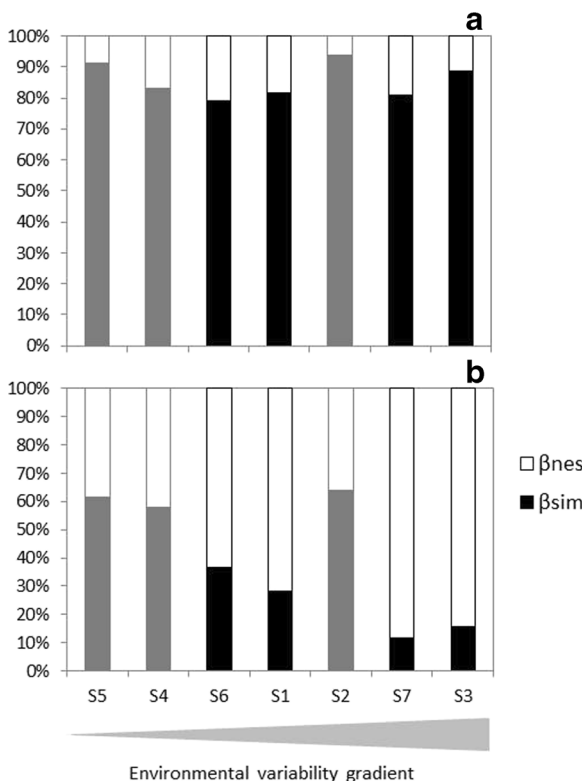
Fig. 8 Partitioned total beta diversity into its two components: spatial turnover (βsim) and nestedness (βnes), ordered according to the environmental variability gradient (established by the PERMDISP analysis), and highlighted according to trophic status (S1, S3, S6, S7: eutrophic; S2, S4, S5: mesotrophic). (**a**) taxonomic β_t diversity; (**b**) functional β_t diversity

The difference between mesotrophic and eutrophic systems also resulted in functional differences. Namely, suspension feeder rotifers, scrapers, and free-living filter cladocerans were the dominant trophic groups in mesotrophic streams, suggesting that the environmental conditions favored the growth and availability of palatable algae for a wide group of organisms (Sarma et al. 2005). Eutrophic streams were characterized by the shared dominance of suspension feeders and piercer rotifers. The dominance of the former trophic group may be associated with the increased importance of ciliated protozoans in the water column, a characteristic of eutrophic and hypertrophic systems (Debastiani et al. 2016).

Relationships between zooplankton diversity metrics, trophic categories, and environmental variability

In relation to diversity metrics, we found a positive correlation between taxonomic and functional α diversity. This pattern was also found in other studies including different groups of organisms (Heino 2008; Villéger et al. 2008; Gallego et al. 2012; Abonyi et al. 2018), and supports the idea that functional diversity is partially a reflection of taxonomic diversity (Flynn et al. 2009). However, it is important to note that in this study, two streams showed no matching patterns between these two metrics, demonstrating that the relationship between functional and taxonomic diversity is complex and context-dependent in the sense that different functional traits can show individual responses to different environmental gradients (Cadotte, 2011). Namely, S4 had a high functional but a low taxonomic diversity (i.e., low functional redundancy) while S7 had a high taxonomic but a low functional diversity (i.e., high functional redundancy). This relation between the two approaches reflects the environmental fragility of the systems under eventual alterations because it encompasses both functional diversity (including traits and niches filled by species) as well as the stability of all that functions (i.e., the diversity of species that carry them out). In this respect, high functional redundancy may diminish the probability of a loss of ecosystem functioning by species loss while low functional redundancy can negatively affect ecosystem functioning through the loss of even a few species (Lopes et al. 2019).

Another relevant finding of our study was that α diversity (taxonomic and functional) showed no variations between the two trophic states (mesotrophic and

eutrophic), as opposed to our expectation (prediction a). The appearance of many rare species (mainly rotifers) in eutrophic environments may explain this result. Other studies also found that the increase in rotifers richness dampens the loss of species in the whole community and equates it with that of other less affected systems (Hawkins et al. 2015; Xiong et al. 2019). Thus, both metrics—despite being correlated—are important predictors of the state of aquatic systems because they reflect different aspects of the community and reveal environmental integrity and vulnerability to environmental changes (Gallego et al. 2012).

We found that β_t diversity was more reactive to the eutrophication process than α diversity. Taxonomic β_t diversity was largely driven by the turnover component while the nestedness component contributed more to functional beta diversity than the turnover. Similar results were found by Perez Rocha et al. (2019) and Braghin et al. (2018), who suggested that the environmental filters in these systems operate more strongly on functional groups than on species. In our study, this means traits were more sensitive to the increase in the trophic state of the streams than species. In this line, studies have also demonstrated that a functional approach is more sensitive in capturing the effect of environmental alterations, mainly when changes in taxonomic diversity are not evident (Braghin et al. 2018; Simões et al. 2020).

Contrary to our expectation, no differences in mean taxonomic β_t diversity were found between the two trophic groups, suggesting that no temporal taxonomic simplification occurred in the eutrophic streams compared with the mesotrophic ones. This result can also be explained by the high number of rare species (located in the lower-left quadrant of the Olmstead–Tukey diagram), particularly r-strategic rotifers, that appeared in the eutrophic streams, occupying specific temporal niches (Hawkins et al. 2015).

We found that functional β_t diversity was significantly lower in the eutrophic than in the mesotrophic streams, confirming our prediction (prediction b). However, we observed no differences in mean taxonomic β_t diversity between the two trophic groups. This means that although eutrophic streams accounted for high species turnover, as mentioned above, ecological functions remained similar throughout the studied period. This functional redundancy, where changing species resemble the same functions over time, denotes

a functional homogenization of the systems (Díaz and Cabido 2001) and has been considered an environmental disturbance indicator (Simões et al. 2020). The consequences of functional homogenization could imply the systems' reduced resistance and resilience against environmental impacts and an impoverishment of ecosystem services (Simões et al. 2020).

Moreover, within functional β_t diversity, we found that the nestedness component of the eutrophic streams (S1, S3, S6, and S7) was even higher than that of the mesotrophic ones (as in prediction c). This confirms that eutrophic streams have the strongest environmental filters that increase the importance of trait-sorting mechanisms (Cook et al. 2018).

Finally, we found a positive relationship between mean taxonomic α diversity and temporal environmental variability, confirming our last prediction (prediction d). The increasing number of taxa with temporal variability may be explained by the high occurrence of specialist r-strategic species occupying particular temporal niches (Lopes et al. 2019). However, higher taxonomic diversity with temporal variability increased functional diversity, suggesting that temporal variability did not change the species' ecological functions. This agrees with the assumption that highly variable habitats may contain only species with traits enabling them to overcome disturbances while more stable habitats may contain species with a wide variety of traits, which also include characteristics of disturbed habitats (Hildrew and Towsend 2007).

We did not detect a significant relationship between temporal environmental variability and β_t diversity metrics. This is in line with Lopes et al. (2019), who also found that zooplankton β_t diversity was uncorrelated with temporal variability in limnological factors in some isolated areas of a tropical reservoir. However, Lopes et al. (op. cit.) found higher β_t diversity in other areas associated with a fluvial pulse, suggesting that this last factor may play an important role in overall turnover mechanisms. The same conclusion was achieved by Simões et al. (2020) in an interconnected subtropical system influenced by hydrological pulses. These streams, where the influence of flooding pulses is absent, seem to have different mechanisms operating on taxonomic and functional β_t diversity. Moreover, the environmental filters proved to be stronger determinants of β_t diversity than their temporal variations per se. Unfortunately, only a few studies have analyzed the

diversity of streams associated with agricultural land use in relation to temporal environmental variability. This aspect needs further examination to achieve a more complete image of its ecological situation and devise appropriate protection measures.

Conclusions

In this study, we found different zooplankton compositions among mesotrophic and eutrophic systems. As regards diversity metrics, eutrophic streams supported equal taxonomic and functional α diversity and equal taxonomic β_t diversity compared with mesotrophic ones, which was opposite to our expectation. This equity was attributed to the appearance of rare, possibly highly tolerant species occupying different temporal niches in eutrophic systems. However, we found that functional β_t diversity was lower in the eutrophic streams, with nestedness being the underlying ecological mechanism of temporal variability in the zooplankton functional groups.

Temporal environmental variability was positively related to taxonomic α diversity, which was explained by the higher presence of specialist r-strategic species occupying particular temporal niches. β_t diversity metrics show no correlation with environmental variability, suggesting that the studied systems' environmental filters were more robust determinants of overall turnover mechanisms. In sum, both taxonomic and functional approaches should be considered to improve the assessment of organisms' responses to environmental changes, and beta diversity would likely be an appropriate indicator of environmental effects on biological communities.

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