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Environmental variables as predictors of fish community composition in semiarid aquatic systems

Variáveis ambientais como preditoras da assembleia de peixes em sistemas aquáticos semiáridos

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Abstract: Aim: To understand the distribution of fish species and their use of habitat, a range of environmental variables were evaluated as predictors of fish assemblage composition and richness in tropical semiarid aquatic systems. Methods: We surveyed the species composition of fish assemblages in semiarid aquatic systems and established their degree of association with the structure of the aquatic habitat. Sites consisted of stream reaches with surface water flow, isolated temporary pools, and manmade reservoirs. Fish sampling was conducted on four occasions during the wet (April and June 2006) and dry seasons (September and December 2006). The correlation between richness and abundance with the habitat structure was evaluated using stepwise multiple regression. Patterns of variation in fish assemblage composition across sites were evaluated using Nonmetric Multidimensional Scaling, and the Indicator Species Analysis was used to determine which species were significant indicators of sites. To establish multivariate correlations and test the hypothesis of local fish composition being associated with the environmental variables we used a Canonical Correspondence Analysis. Results: Morphometric variables, stream reach width, stream length and elevation explained 75.6% of the variation in fish richness. Macrophyte cover and overhanging vegetation added to the predictive power of the model equation, where the final model explained 86.9% of the variation in fish richness. Canonical Correspondence Analysis showed a significant relationship between fish composition data and site morphology (altitude, bank slope and littoral depth). Among the water quality, habitat composition and substrate variables, temperature, sand, and gravel showed higher correlation with the CCA axes. Conclusions: These results indicated that fish communities assume different structures and compositions across different habitat types following the environmental heterogeneity in dryland aquatic systems.

Keywords: intermittent streams; reservoirs; conservation; substrate composition.



Resumo: Objetivo: Para entender a distribuição das espécies de peixes e seu uso do habitat, uma série de variáveis ambientais foi avaliada como preditoras da composição e riqueza de assembleias de peixes em sistemas aquáticos semiáridos tropicais. Métodos: Nós avaliamos a composição de espécies de peixes em sistemas aquáticos semiáridos e estabelecemos seu grau de associação com a estrutura do habitat aquático. Os locais amostrados consistiram em trechos de riachos temporários com fluxo de água superficial, poças temporárias isoladas e reservatórios artificiais. A amostragem de peixes foi realizada em quatro ocasiões durante as estações úmida (abril e junho de 2006) e seca (setembro e dezembro de 2006). A correlação entre riqueza e abundância com a estrutura do habitat foi avaliada utilizando regressão múltipla. Os padrões de variação na composição da comunidade de peixes entre os locais foram avaliados utilizando Escalonamento Multidimensional Não-Métrico, e a Análise de Espécies Indicadoras foi utilizada para determinar quais espécies eram indicadoras significativas dos locais. Para estabelecer correlações multivariadas e testar a hipótese de que a composição local de peixes está associada às variáveis ambientais, utilizamos uma Análise de Correspondência Canônica. Resultados: A regressão múltipla mostrou que as variáveis morfométricas, largura do trecho do riacho, comprimento do riacho e elevação explicaram 75,6% da variação na riqueza de peixes. A cobertura de macrófitas e a vegetação marginal adicionaram ao poder preditivo do modelo da equação, onde o modelo final explicou 86,9% da variação na riqueza de peixes. A Análise de Correspondência Canônica mostrou uma relação significativa entre os dados de composição de peixes e a morfologia dos locais amostrados (altitude, inclinação da margem e profundidade litorânea). Dentre as variáveis de qualidade da água, composição do habitat e substrato, a temperatura, areia e cascalho apresentaram maior correlação com os eixos da CCA. Conclusões: Esses resultados indicaram que as comunidades de peixes assumiram diferentes estruturas e composições nos diferentes tipos de habitat de acordo com a heterogeneidade ambiental em sistemas aquáticos de regiões secas.

Palavras-chave: rios intermitentes; estrutura do habitat; conservação; composição do substrato.

1. Introduction

Patterns of distribution of fish species within ecosystems are frequently attributed to the underlying structure of the available habitat (Junqueira et al., 2016). This habitat is typically described as physical underwater structures, such as rocks, submerged wood, macrophyte and algae, along with shelter or overhead protection provided by littoral features, including shoreline overhanging vegetation or logs lying across the stream margins (Stewart-Koster et al., 2007). Arguably, the quality and quantity of the habitat affect the structure and composition of fish communities (Vono & Barbosa, 2001), by changes in water depths, velocity, influencing substratum type, littoral features (such as overhanging vegetation), and underwater structures (Medeiros & Arthington, 2011; Stewart-Koster et al., 2007).

Usually, these factors are integrated and habitats tend to vary and segregate into discrete hierarchical patches (Frissell et al., 1986). Despite that, human activities have degraded or modified the physical habitat of aquatic freshwater fish throughout the world (Hall Junior et al., 2002), specially promoting the conversion of lotic systems into lentic ones, changing the habitat's dynamics and functioning (Bunn & Arthington, 2002). In the semiarid region of Brazil, the major interferences to the ecological integrity of natural systems are the construction of dams, levees, artificial channels, and inter-basin water transfers, which change natural patterns of aquatic habitat diversity, and, in turn, biological diversity (Maltchik & Medeiros, 2006).

In general, many studies showed that more complex habitat types provide favorable condition for fish, such as growth substrate, spawning sites as well as food and protection from predation (Cucherousset et al., 2007; Jeffres et al., 2008; Pusey & Arthington, 2003), contributing to biotic community structure (richness and abundance distribution). Different species of fish exhibit particular preferences for different habitat types, thus creating local patterns of composition of species assemblages (Junqueira et al., 2016) as predicted by the Niche Theory (Hutchinson, 1957). Therefore, a greater diversity of microhabitats associated with the littoral features (e.g., Vono & Barbosa, 2001) has been linked to an increase of species diversity (Casatti et al., 2012).

The wide spatial and temporal variations of environmental conditions in dryland streams leads to diverse physical habitat and distinctive patterns of local habitat structure (Hodges & Magoulick, 2011). Given that, limited dispersion may create discrete patches of communities. By integrating Niche and Neutral Theories to this rationale it is expected that fish richness and composition respond in proportionate manner to specific patterns in habitat changes (see, for instance, Corrêa et al., 2011; Lanés et al., 2018). From the perspective of the Neutral Theory, species diversity (consequently, its composition) is resulted from random processes in local scales and may not necessarily be the result of differences in the ecological niches of species. Nevertheless, the debate surrounding Niche Theory versus Neutral Theory and their respective applicability in describing natural systems remains an ongoing topic of discussion (Wennekes et al., 2012).

In the specific case of dryland streams, the physical habitat exhibits spatial and temporal dynamics due to the interplay between stream channel morphology and hydrological variability (Farias et al., 2012; Medeiros et al., 2008). The condition of the in-stream physical habitat may be influenced by factors operating at distinct scales (Boys & Thoms, 2006). At the catchment level, geomorphological and climate features influence hydrology, sediment deposition, nutrient inputs, and channel morphology (Davies et al., 2000; Mugodo et al., 2006). On local level, water's physical and chemical attributes, as well as land use and management practices, contribute to shaping stream habitat (Hodges & Magoulick, 2011). The influence of spatial processes on local communities, may not strictly adhere to either Niche or Neutral theories, but rather represents an intricate interplay between both, as suggested in some studies (Adler et al., 2007; Gravel et al., 2006), since "niche-like and neutral-like dynamics are opposite ends of a continuum" to be determined by "the degree to which species overlap in their abiotic niches" (Thompson et al., 2020).

Here, we investigated the relationship between physical habitat variables and fish species richness and distribution in the semiarid fish communities - a largely unknow community (see Lima et al., 2021). Specially, we measured fish richness and species composition across flowing intermittent streams, temporary pools and artificial reservoirs in intermittent drainages in semiarid Brazil in order to evaluate whether the species composition of fish assemblages is influenced by the structure of the aquatic habitat. We hypothesize that the fish abundance and local composition of the community will be predicted by environmental variables associated with local features of the catchment area.

2. Material and Methods

2.1. Study area

This study was conducted in the Brazilian semiarid region, specifically within river catchments that flow through a dry shrubby deciduous open forest (the "Caatinga"). Thermal amplitude is low in the study area, with averages ranging from approximately 25 to 30.0 °C, and the average annual precipitation varying between 600 and 1100 mm. Altitudes range between 100 and 1000 m (Silva et al., 2017).

To assess a wide range of environmental variables, six sites were selected to represent typical artificial and natural temporary environments (Figure 1).



Figure 1. Study area showing major river systems and sampling sites in the semi-arid region of Brazil. Seridó stream (SE), Cipó stream (CI) and Recanto reservoir (RE) (Piranhas-Açu catchment), Escama-Peixe stream (EP, Moxotó River), Mulungu reservoir (MU, Ipanema River) and Salobro reservoir (SA, Una River).

Sites consisted of stream reaches with surface water flow (during the rainy season) or isolated temporary pools (during the dry season) and artificial reservoirs created from stream impoundment. Sampling was conducted during the year of 2006 on four occasions during the rainy (April and June) and dry seasons (September and December).

2.2. Fish sampling

Fish collection was carried out during daylight hours using four different types of sampling gear (Medeiros et al., 2010): a short beach seine net (4 m long, 1.5 m high and 5 mm mesh), a long beach seine net (20 m long, 2 m high and 12 mm mesh), one set of gill nets (30 m long and 1.5 m high, divided into three 10 m panels of 35, 45 and 55 mm mesh) and one cast net (2.4 m high and 12 mm mesh). The capture effort was standardized across sampling occasions and sites, (i) to passive methods the capture effort was measured in hours (representing the number of hours of the gill nets in the water), and (ii) to active methods the capture effort represented the number of hauls (for seine nets) or the number of throws (for the cast net). Hauls were similar across all sampling occasions and sites, being approx. 10 m long for the large seine net and 3 to 5 m long for the short seine net.

Fish caught were fixed in 10% formalin neutralized with sodium tetraborate and later transferred to 75% ethanol. Sorting and identification of specimens were carried out at the Fish Morphology and Taxonomy Laboratory at the Federal University of Paraíba, Brazil. Voucher specimens were deposited after identification in the Ichthyological Collection of the same institution. The specimens were treated according to Brazilian rules of scientific curation (Malabarba & Reis, 1987) and fish were collected under the Brazilian Institute for the Environment and Renewable Natural Resources license no. 032DIFAP/IBAMA from 23 March 2006.

2.3. Environmental data

The structure of the habitat was measured as (1) physical and chemical variables, (2) stream reach morphology, (3) substrate composition, and (4) habitat structure. Physical and chemical variables were measured using portable equipment for pH (TECNOPON MPA-210), conductivity (μ S*cm⁻¹) (TECNOPON MCS-150), dissolved oxygen (mg*L⁻¹) and temperature (°C) (Lutron DO-5510). Transparency (cm) was measured using a Secchi disk, and water velocity (m*s⁻¹) was estimated using

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the float method (Maitland, 1990). Stream reach or site morphology were evaluated by the average width (cm) and depth (cm) taken from three transects placed across the stream reach, pool or reservoir. Catchment scale variables (such as elevation and river length) were measured using handheld GPS and satellite imagery. Littoral depth was taken as the depth at one meter from the land/water interface. The substrate composition and habitat structure were estimated in 9 to 12 survey points of 1 m² measured in the margins (see Medeiros et al., 2008). In each survey point, the proportion (%) of sediment composition (classified as mud, sand, gravel, and cobbles) and littoral and underwater structures (e.g., macrophytes, grass, submerged vegetation, overhanging vegetation, leaf litter, algae, and woody debris) were visually estimated (Medeiros et al., 2008; Pusey et al., 2004).

2.4. Data analysis

Abundance of each species was standardized per unit of effort of capture, where the number of fish captured was divided by the number of hours or replicates of each sampling technique on each sampling occasion and site (henceforth termed CPUE abundance) (Medeiros et al., 2010). Fish richness was corrected using rarefied analyses for the average number of individuals from all sampling occasions using PRIMER-e 5.0 (Clarke & Gorley, 2001). The CPUE abundance and rarefied richness were compared among study sites using one-way ANOVA followed by post hoc multiple comparisons using Tukey's HSD test (α=0.05) (Zar, 1999). CPUE abundance was square root transformed, and the environmental variables were log_{10} (x+1) transformed to enhance normality and homogeneity of variances (Maltchik et al., 2010; Sokal & Rohlf, 1995).

To describe fish richness and species composition across flowing intermittent streams, temporary pools and artificial reservoirs, the correlation between rarefied richness and CPUE abundance (dependent variables) with the habitat structure (independent variables) for each habitat type was evaluated using stepwise multiple regression (SMR) with forward selection, where variables are entered in the model based on the significance (probability) of the F value (Maltchik et al., 2010; Sheridan & Lyndall, 2001).

To test the hypothesis that fish abundance and local community composition will be predicted by environmental variables associated with local characteristics of the catchment areas, a range of statistical analyses was performed, as follows.

Patterns of variation in fish assemblage composition across sites were evaluated using Nonmetric Multidimensional Scaling (NMDS), based on the relativized Bray-Curtis distance of the arcsine square root transformed data matrix. The Multiresponse Permutation Procedure (MRPP) (Biondini et al., 1985; McCune & Grace, 2002) was used to test for significance of differences in fish composition across sites/sampling occasions. The value of "A" is presented as a measure of the degree of homogeneity between groups compared to random expectation. The Indicator Species Analysis (ISA) was used to determine which species were significant indicators of sites. An indicator value (IV) for each species for every site was calculated using the method of Dufrene & Legendre (1997). This value is tested for significance using the Monte Carlo test (999 permutations).

To establish multivariate correlations and test the hypothesis of local fish composition being associated with the environmental variables, a Canonical Correspondence Analysis (CCA) was performed (McCune & Grace, 2002). The data matrix was centered and normalized, and the correlations tested by the Monte Carlo test with 999 permutations. The environmental variables were $\log_{10}(x+1)$ transformed (Maltchik et al., 2010). Statistical analyses (α =0.05) were performed on PC-ORD 7.0 (McCune & Mefford, 1999).

3. Results

Regarding the hydrological variation (water velocity) across sites and sampling occasions (Table 1), the Seridó stream displayed velocities fluctuating between $0.12 \text{ m}^*\text{s}^{-1}$ and $0.16 \text{ m}^*\text{s}^{-1}$, except for dry conditions noted in September and December. Similarly, the Cipó stream showed a velocity of $0.16 \text{ m}^*\text{s}^{-1}$ in April, which declined to zero in subsequent months. The Recanto reservoir began with a velocity of $0.10 \text{ m}^*\text{s}^{-1}$ in April but had no flow in later months, indicating initial water flow over the spillway. In contrast, the Salobro reservoir, Mulungu reservoir, and Escama-Peixe stream consistently registered zero water velocity

Table 1. Environmental variables averaged for the sampling occasions (± SD) for the study sites in the semi-arid region of Brazil. Seridó stream (SE), Cipó stream (CI) and Recanto reservoir (RE) (Piranhas-Açu catchment), Escama-Peixe stream (EP, Moxotó River), Mulungu reservoir (MU, Ipanema River) and Salobro reservoir (SA, Una River).

	SE	CI	RE	EP	MU	SA
Morphology						
River length (km)	163.2	83.1	110.2	196.8	214.0	212.7
Elevation (m)	226.0	169.0	270.0	402.0	725.0	713.0
Water velocity (m*s-1)	0.1 (±0.1)	0.04 (±0.1)	0.03 (±0.1)	0.0	0.0	0.0
Maximum bank slope	30.0	60.0	60.0	90.0	30.0	30.0
Maximum depth (cm)	98.8 (±16.6)	67.8 (±8.2)	117.0 (±27.9)	95.0 (±15.0)	124.0 (±18.8)	65.0 (±4.2)
Littoral depth (cm)	53.3 (±24.9)	33.3 (±9.3)	36.3 (±13.8)	50.7 (±1.9)	30.4 (±8.5)	6.7 (±1.5)
Stream width (m)	11.8 (±7.1)	15.4 (±3.4)	90.5 (±13.7)	25.6 (±5.0)	247.8 (±15.8)	313.7 (±17.4)
Water quality						
Water temperature (°C)	31.4 (±2.1)	30.4 (±3.3)	31.6 (±2.7)	29.0 (±0.1)	27.7 (±2.0)	26.7 (±2.8)
Dissolved oxygen (mg*L-1)	6.0 (±0.5)	4.9 (±1.6)	7.1 (±2.5)	5.2 (±0.3)	5.1 (±2.3)	6.1 (±3.3)
Transparency (cm)	30.8 (±16.4)	42.3 (±15.6)	67.4 (±16.3)	37.4 (±10.9)	60.8 (±20.7)	42.1 (±13.7)
Habitat composition (%)						
Macrophyte cover	2.1 (±4.2)	0.0	35.7 (±21.1)	0.0	0.0	12.8 (±22.6)
Littoral grass	11.1 (±10.4)	5.8 (±11.7)	2.1 (±4.0)	0.7 (±1.2)	34.5 (±22.3)	5.2 (±6.5)
Submerged vegetation	2.5 (±5.0)	0.8 (±1.5)	4.2 (±8.3)	0.0	11.2 (±17.4)	7.3 (±12.5)
Overhanging vegetation	0.0	17.1 (±15.5)	10.4 (±15.8)	0.0	0.0	0.9 (±1.6)
Leaf litter	0.4 (±0.4)	1.5 (±0.6)	6.5 (±11.5)	0.4 (±0.1)	1.9 (±2.1)	0.0
Algae	5.1 (±3.6)	21.4 (±2.9)	17.7 (±11.3)	0.1 (±0.1)	7.8 (±5.5)	17.3 (±3.1)
Root masses	0.0	2.3 (±2.3)	0.0	0.0	0.0	0.0
Woody debris	2.6 (±1.3)	4.7 (±1.3)	7.2 (±2.1)	1.1 (±0.8)	15.5 (±0.4)	0.9 (±0.7)
Substrate composition (%	b)					
Mud	66.4 (±22.5)	17.8 (±21.7)	48.1 (±32.2)	40.5 (±7.7)	52.7 (±32.1)	94.4 (±4.6)
Sand	23.7 (±16.2)	60.0 (±27.5)	45.5 (±36.1)	55.6 (±7.6)	45.1 (±33.0)	3.9 (±2.0)
Gravel	0.0	9.2 (±0.0)	4.3 (±0.7)	2.7 (±1.9)	0.0	1.7 (±0.4)
Cobbles	6.3 (±9.2)	10.5 (±9.9)	0.0	0.4 (±0.5)	1.0 (±1.2)	0.0
Rocks	2.8 (±3.9)	2.5 (±5.0)	0.0 (±0.0)	0.8 (±0.7)	1.3 (±2.5)	0.0
Bedrock	0.8 (±1.7)	0.0	2.1 (±4.2)	0.0	0.0	0.0

throughout the year, indicating a lack of water flow, but the Escama-Peixe stream flooded between sampling occasions. This data collectively suggests minimal to no water flow in these locations during the observed period.

Site morphology varied considerably and was related to the nature of the study site (flowing stream, isolated pool or reservoir) (Table 1), with reservoirs being wider than stream sites. Marginal depths ranged from 6.7 (\pm 1.5) cm in Salobro reservoir to 53.3 (\pm 24.9) cm in Seridó stream. These indicate (along with bank slope values) how steep is the shore of the study sites, whereas the maximum depth and width indicate the overall size of the study site. With greater values of depth and width observed for the Mulungu reservoir (124.0 \pm 18.8 cm deep and 247.8 \pm 15.8 m wide), as opposed to 98.8 (\pm 16.6) cm in depth and 11.8 (\pm 7.1) m in width of the Seridó stream.

Among the water quality variables, average temperatures ranged from 26.7 to 31.6°C and dissolved oxygen between 4.9 and 7.1 mg*L⁻¹. Transparency reached a maximum average of $67.4 (\pm 16.3)$ cm. The habitat composition was rich in underwater and marginal structures, consisting generally of littoral grass, submerged terrestrial vegetation, algae (attached to the substrate and filamentous) and woody debris. Aquatic macrophytes were present mostly in the smaller reservoir (Recanto reservoir) and included floating plants (Salvinia sp., Pistia sp. and Azolla sp.), emergent plants (Nymphaea sp.) and submerged plants (Ceratophyllum sp. and Egeria sp.). Overhanging riparian vegetation, leaf litter and root masses were also present in the study sites. All sites studied had mostly mud and, to a lesser extent, sand as substrate composition (Table 2).

A total of 8737 fish distributed among 35 species, 12 families and 5 orders were collected. The richest family was Characidae with 12 species, followed by Cichlidae (6 species) and Curimatidae (4 species) (Table 2). Considering abundance, again Characidae was the family with the highest abundance (36.6%), followed by Cichlidae (30.4%) and Poecilidae (15.2%). Overall, Astyanax bimaculatus was the most abundant species (comprising 26.1% of the individuals collected) and the most frequently recorded, being present in 87% of the sampling occasions. Other abundant species were Geophagus brasiliensis (11.7%), Oreochromis niloticus (9.6%) and Characidium bimaculatum (8.1%), but these species had their distribution more concentrated in fewer sampling occasions (Table 2). Rare species,

represented by single and double individuals, were relatively common, namely *Psectrogaster rhomboides*, *Leporinus taeniatus, Compsura heterura, Moenkhausia costae, Serrasalmus rhombeus, Pseudancistrus papariae, Synbranchus marmoratus, Colossoma macropomum* and *Hemigrammus marginatus*. These species represented 25.7% of the species recorded. Common species, where considered as those present in more than 50% of all combined sampling occasions and sites. These were Astyanax *bimaculatus, Oreochromis niloticus, Geophagus brasiliensis* and *Hoplias malabaricus*.

To fish richness, the stepwise multiple regression showed that the model incorporating the morphological variables: stream reach width (R²-Change=33.2% and significance of F-Change=0.004), river length (R²-Change=32.3% and significance of F-Change<0.001) and elevation (R²-Change=10.1% and significance of F-Change=0.011) explained 75.6% of the variation (R²=0.756, F_{3.19}=19.5, p<0.001). Meanwhile, the habitat composition variables: macrophyte cover (R²-Change=5.7% and significance of F-Change<0.031) and overhanging vegetation (R²-Change=5.6% and significance of F-Change <0.015) also added to the predictive power of the model, where the final model explained 86.9% of the variation in fish rarefied richness (R²=0.869, F₅₁₇=22.5, p<0.001).

None of the substrate composition and water quality variables were important predictors of fish richness, failing to meet the selection criteria (significance for F-values greater than 0.05). Variation of CPUE abundance was explained only by the habitat composition variable overhanging vegetation (R²-Change=31.9% and significance of F-Change=0.005) and the water quality variable dissolved oxygen (R²-Change=13.5% and significance of F-Change=0.038) (Table 3). The model incorporating these variables explained 45.4% of the variation in CPUE abundance $(R^2=0.454, F_{2,20}=8.3, p<0.002)$. None of the morphological and substrate composition variables were important predictors of fish abundance, failing to meet the selection criteria (significance for F-values greater than 0.05). Fish rarefied richness (ANOVA, d.f.=5,17; F=11.4; p<0.001) was significantly different between study sites, with Seridó (SE) and Escama-Peixe (EP) stream sites showing significantly higher average richness. Average CPUE abundance was not significantly different across sites (ANOVA, d.f.=5,17; F=2.8; p=0.05).

Table 2. Abundance, percentage and frequency of occurrence (E.O.) of species collected in the study sites in the semi-arid region of Brazil. Seridó stream (SE), Cipó stream (CI) and Recanto reservoir (RE) (Piranhas-Açu catchment), Escama-Peixe stream (EP, Moxotó River), Mulungu reservoir (MU, Ipanema River) and Salobro reservoir (SA, Una River).

	SE	CI	RE	EP	MU	SA	%	F.O.
Characiformes								
Curimatidae							4.1	
Curimatella lepidura (Eigenmann & Eigenmann, 1889)	0	0	0	21	0	0	0.2	4.3
Psectrogaster rhomboides Eigenmann & Eigenmann, 1889	1	0	0	0	0	0	0.01	4.3
Steindachnerina notonota (Miranda-Ribeiro, 1937)	205	0	0	0	0	0	2.3	17.4
Cyphocharax gilbert (Quoy & Gaimard, 1824)	50	0	0	81	0	0	1.5	8.7
Parodontidae							0.3	
<i>Apareiodon hasemani</i> Eigenmann, 1916	0	0	0	27	0	0	0.3	8.7
Prochilodontidae							3.1	
Prochilodus brevis Steindachner, 1874	243	5	6	15	1	0	3.1	47.8
Anostomidae							0.2	
<i>Leporinus piau</i> Fowler, 1941	6	6	2	1	0	0	0.2	34.8
Leporinus melanopleura Günther, 1864	0	0	0	2	0	0	0.02	4.3
<i>Leporinus taeniatus</i> Lütken, 1875	0	0	0	1	0	0	0.01	4.3
Crenuchidae							8.1	
Characidium bimaculatum Fowler, 1941	3	0	702	0	0	0	8.1	21.7
Characidae							36.6	
Astyanax bimaculatus (Linnaeus, 1758)	542	40	697	126	857	21	26.1	87.0
Astyanax fasciatus (Cuvier, 1819)	123	1	8	24	0	2	1.8	43.5
Colossoma macropomum (Cuvier 1816) *	0	0	2	0	0	0	0.02	4.3
<i>Compsura heterura</i> Eigenmann, 1915	1	0	0	0	0	0	0.01	4.3
Hemigrammus marginatus Ellis, 1911	2	0	0	0	0	0	0.02	8.7
Moenkhausia costae (Steindachner, 1907)	0	0	0	1	0	0	0.01	4.3
Moenkhausia sp.	40	0	0	0	0	0	0.5	8.7
<i>Serrapinnus heterodon</i> (Eigenmann, 1915)	141	17	4	134	0	0	3.4	43.5
Serrapinnus piaba (Lütken, 1875)	68	0	0	0	0	0	0.8	4.3
Serrasalmus rhombeus (Linnaeus, 1766)	1	0	0	0	0	0	0.01	4.3
Tetragonopterus chalceus Spix & Agassiz, 1829	0	0	0	134	0	0	1.5	8.7
Triportheus signatus (Garman, 1890)	181	0	0	27	0	0	2.4	26.1
Erythrinidae		Ū	•		Ũ	Ũ	1.2	2011
Hoplias malabaricus (Bloch, 1794)	53	21	31	3	1	0	1.2	60.9
Siluriformes	00	21	51	0	'	0	1.2	00.0
Loricariidae							0.8	
Hypostomus pusarum (Starks, 1913)	66	4	0	1	0	0	0.8	30.4
Pseudancistrus papariae Fowler 1941	1	- 0	0	0	0	0	0.01	4.3
Heptapteridae	1	0	0	0	0	0	0.0 1	4.5
Pimelodella enochi Fowler, 1941	6	0	0	0	0	0	0.1	4.3
	0	0	0	0	0	0	0.1	4.5
Cyprinodontiformes							45.0	
Poecilidae	05	0	0	0	200	0	15.2	04.7
Poecilia reticulata Peters, 1860 *	25	0	0	0	322	0	4.0	21.7
Poecilia vivipara Bloch & Schneider, 1801	622	137	0	0	219	0	11.2	47.8
Synbranchiformes								
Synbranchidae				-			0.01	
Synbranchus marmoratus Bloch,1785	0	1	0	0	0	0	0.01	4.3
Perciformes								
Cichlidae							30.4	
Cichla ocellaris Bloch & Schneider, 1801 *	0	64	0	6	0	0	0.8	21.7
Cichlasoma orientale Kullander, 1983	104	39	0	0	0	0	1.6	30.4
Crenicichla menezesi Ploeg, 1991	27	0	1	0	0	0	0.3	21.7
Geophagus brasiliensis (Quoy & Gaimard, 1824)	7	0	1	29	911	72	11.7	65.2
Oreochromis niloticus (Linnaeus, 1758) *	324	0	1	79	19	415	9.6	69.6
Parachromis managuensis (Günther, 1867) *	0	0	0	0	0	553	6.3	17.4
Total	2842	335	1455	712	2330	1063		

* = Non-native species.

	Axis 1	Axis 2	Axis 3
Eigenvalues	0.744	0.677	0.637
Monte Carlo test	0.005	0.001	0.002
Variance in species data			
% variance explained	13.6	12.4	11.6
Species-environment correlations	1.000	1.000	1.000
Monte Carlo test	0.001	0.001	0.001
Intra-set correlations			
Morphology			
River length	-0.380	-0.498	0.304
Elevation	-0.377	-0.772	-0.172
Water velocity	0.318	0.252	0.456
Bank slope	-0.712	0.266	-0.396
Littoral depth	-0.117	0.709	0.378
Width	-0.054	-0.674	-0.443
Water quality			
Temperature	0.238	0.586	-0.014
Habitat composition			
Macrophytes	0.383	0.138	-0.417
Debris	0.469	0.044	-0.022
Substrate composition			
Sand	-0.294	0.487	-0.179
Gravel	-0.347	0.083	-0.556

Table 3. Axes summary of CCA for the environmental variables and fish composition in the present study (only variables correlated 30% or more with a given axis are shown).

The NMDS explained 60.3% of the variation in the dataset, having a stress of 17.2. The first axis accounted for 30.2% of the variance explained. The study sites were segregated with regard to their fish composition (Figure 2) and significant differences in community composition were observed between all study sites (MRPP; A=0.72; p<0.001). Indicator Species Analysis showed that important species separating sites were Steindachnerina notonota (IV=100%; p=0.001), Crenicichla menezesi (IV=90%; p=0.001), Hypostomus pusarum (IV=78.3, p=0.001), Triportheus signatus (IV=73.6%; p=0.01), Prochilodus brevis (IV=63.8%; p=0.015), Cichlasoma orientale (IV=61.1%; p=0.017), Astyanax fasciatus (IV=55.1%; p=0.023) and Poecilia vivipara (IV=48.3%; p=0.019) for the Seridó stream reach (SE); Cichla ocellaris (IV=56.4%, p=0.021) for the Cipó stream site (CI); Characidium bimaculatum (IV=97.4%, p=0.001) for the Recanto reservoir site (RE), Geophagus brasiliensis (IV=64.3%, p=0.001) and Poecilia reticulata (IV=62.6%, p=0.018) for the Mulungu reservoir site (MU); Parachromis managuensis (IV=100%, p=0.002) for the Salobro reservoir site (SA); and Apareiodon hasemani (IV=66.7%, p=0.013), Tetragonopterus chalceus (IV=66.7, p=0.013) and Serrapinnus heterodon (IV=46.4%; p=0.042) for the Escama-Peixe stream site (EP).

37.6% of the variance in the data (the "inertia" was 5.4), and most of this variation was explained by the first axis (13.6%) (Table 3 and Figure 3). Nevertheless, axis 2 and 3 may not be disregarded as they also explained substantial portion of the variation in the data set (Table 3). Results of the analysis showed a significant relationship between fish composition data and the environmental variables, with the eigenvalues of the three axes too high to be expected by chance (see p values for eigenvalues and the species-environment correlations for the three axes in Table 3). The first and second axes of the CCA represented mostly the site morphology variables, since all morphology variables except maximum depth (water velocity was correlated with the third axis) were strongly correlated with the first and second axes. Among the water quality variables, only temperature was important descriptor for the fish community. Few of the habitat composition variables were correlated with the CCA axes and this correlation was generally low (below 46%). Across the substrate composition variables, none were correlated with the first axis and only sand and gravel showed higher correlation with the second and third axes, respectively (Table 3).

Canonical Correspondence Analysis explained

Environmental variables as predictors of fish community...



Figure 2. NMDS results for fish composition across the study reaches in the semi-arid region of Brazil. Vectors (inset box) show taxa correlated (r2 > 0.2) with samples in ordination space. Letters after site codes indicate sampling occasion (A=April, J=June, S=September and D=December).



Figure 3. Biplot of CCA showing the composition of fish assemblages in the sampling sites and occasions (\triangle Recanto reservoir, ∇ Cipó stream, \blacksquare Salobro reservoir, \blacktriangle Seridó stream, \blacksquare Escama-Peixe stream and \square Mulungu reservoir) and the explanatory environmental variables defined by CCA.

4. Discussion

Species richness and community composition of fish observed in this study align with findings from previous studies conducted in the semiarid region of Brazil (Medeiros & Maltchik, 2001a; Medeiros et al., 2010). The Characidae family being the most representative in terms of richness and abundance. For the most part, Characidae species sampled in this study are small-sized with relatively high fecundity and growth rates (Medeiros & Maltchik, 2000, 2001b) and generalist in feeding habits and in the use of habitat (Silva, 2012; Silva et al., 2010). Besides, the order Characiformes includes a large number of fish species from the Brazilian semiarid region (Rosa et al., 2003).

In comparison to other dryland river systems, the study sites showed well oxygenated, transparent and relatively warm water conditions throughout the study period (see, for instance, Medeiros & Arthington, 2011). The morphology of river reaches varied largely in correspondence with the nature of the study site, flowing stream, isolated pool or reservoir. The aquatic habitat exhibited a range of habitat elements available for colonization by the aquatic biota. Flowing stream and pool sites exhibited similar to greater array of marginal habitat elements and substrate composition when compared to the reservoirs. Previous studies in semiarid Brazil showed that the aquatic habitat complexity tends to be greater in streams compared to the reservoirs, contributing to the increased fish diversity (Medeiros et al., 2006; Medeiros et al., 2008).

The river reach morphology and habitat structure were the most important variables in explaining fish richness. The reach morphology, in particular its dimensions width, length, and elevation, is associated with different ranges of environmental variables that support various fish species. This relationship is corroborated by results of multivariate analyses which showed strong spatial segregation of the fish community into distinct assemblage patterns. The absence of water flow on most sites and the lack of longitudinal connectivity created distinct environmental conditions, leading to segregation of the fish community into localized patterns of species composition. Therefore, in the absence of water flow, the fish community would be expected to exhibit distinct compositions across different habitat types. This observation is further supported by the significantly different richness across sites, with regard to the Seridó (SE) and

Escama-Peixe (EP) stream sites, which showed higher average richness.

The findings regarding the fish abundance were less conclusive. There is no significant difference across sites, and only dissolved oxygen and overhanging vegetation were predictors of fish abundance. The abundance of fish in Brazilian semiarid aquatic systems exhibits a large spatial and temporal variation (Medeiros et al., 2010). Probably, this is associated with the movement of individuals within small stretches of river and between shallower and deeper areas in larger pools or reservoirs during flooding (Medeiros & Arthington, 2008). In addition, it may also be influenced by patterns of fish recruitment and spawning (Medeiros & Maltchik, 2000).

The importance of the riparian vegetation on the aquatic habitat is well-established (Gregory et al., 1991). Riparian vegetation provides shade and underwater structures that serve as refuge for fish, as well as spawning sites (Pusey & Arthington, 2003). In this study, variables associated with the presence of riparian vegetation were important predictors of fish richness (overhanging vegetation) and associated with assemblage composition (woody debris and water temperature). Probably, these variables contribute to adequate local environmental conditions, influencing the observed spatial segregation in fish community. The presence of aquatic macrophytes in reservoir and stream sites and their importance as predictors for richness and species composition, is also an indication of the role played by underwater habitat structures in creating local habitats spatially segregated available for fish use (Xie et al., 2001).

Habitat can be considered a framework through which environmental variables affect biological communities (Southwood, 1977). Nonetheless, in hydrologically variable systems, flow variability has been identified as a prominent factor affecting the habitat (Minshall, 1988; Poff & Ward, 1989). Dryland aquatic systems in Brazil are highly variable in terms of water flow and its magnitude (Maltchik & Florin, 2002). Even though results indicate that the structure of the habitat and site morphology are important predictors of fish fauna, the habitat template is multidimensional (Southwood, 1977), with the various environmental variables interacting among themselves. In semiarid systems of Brazil, the habitat structure is being driven by multiple components operating at different scales (Medeiros et al., 2008), with catchment characteristics and local morphology assuming predominance at their respective scales. This underscores the link between habitat structure and the biotic diversity at the local habitat level.

Alterations in natural water flow patterns due to reservoir and weir construction, is a frequent management policy for aquatic semiarid systems in Brazil, modifying the hydrological characteristics of the highly variable intermittent streams (Leal et al., 2005; Maltchik & Medeiros, 2006). This conversion of lotic to lentic systems changes the macrophyte assemblage structure, nutrient dynamics and longitudinal connectivity (Bunn & Arthington, 2002). This study showed that these modifications affected fish communities, since variables highly associated with water flow such as stream reach width, macrophyte cover, overhanging vegetation and dissolved oxygen were important predictors of fish assemblage. Therefore, the modification of natural patterns of water flow and promotion of lentic conditions has the potential to interfere with the fish fauna by favoring more opportunistic species better adapted to no flow conditions. This is corroborated by the fact the reservoir sites had fewer indicator species which were mostly introduced ones, such as Poecilia reticulata and Parachromis managuensis, or typically lentic ones such as Geophagus brasiliensis.

This study showed that fish communities exhibit distinct structures and compositions across various habitat types, reflecting the environmental heterogeneity inherent to each habitat. Richness and composition of fish were primarily influenced by two sets of environmental variables: site morphology and habitat characteristics. The first group of variables is related to the spatial hierarchy of the catchment, since river length and elevation are typically associated with the hierarchical organization of river systems. The second group of variables is more localized in nature, with underwater structures resulting from specific local processes, such as water flow within the river reaches and the influence of land use and riparian vegetation.

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