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***Research Article***

# Changes in fish assemblages caused by different Neotropical biomes

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**ABSTRACT.** We studied the leading causes of the spatial distribution pattern of fish species assemblage in the transition region between Cerrado-Caatinga biomes, in the São Francisco River (Brazil). Biotic and abiotic variables were collected at 17 sampling sites located in three sub-basins, in two periods during 2015. Some 1689 individual fish were sampled, distributed in 69 species, 51 genera, 22 families and seven orders. There was a low overlap of species, with only seven species in common among the three sub-basins. The most substantial degree of sharing occurred between sub-basins from the Cerrado biome, with 22 restricted species. *Crenicichla lepidota*, *Psellogrammus kennedyi*, and *Hoplosternum littorale* were associated with the sub-basin from Caatinga, and *Astyanax* aff. *eigenmanniorum* and *Bryconops* aff. *affinis* with Cerrado sub-basins. The fish assemblage showed significant spatial variation between biomes, and the distribution was determined by an interaction of regional altitude variable with local variables such as river width, substrate and water velocity (environmental factors), but geographical factors were also important. Fish assemblage difference along a large river course has significant implications for conservation strategies, management or evaluation of biodiversity, needing several strategies for their preservation considering small geographic areas.

**Keywords:** ichthyofauna, spatial pattern, variation partition, São Francisco River, Brazil.

## INTRODUCTION

Richness and abundance of species may differ in space and time, and it is conditioned by the capacity of colonization in a specific place or region, finding favorable conditions and resources, and acting also in biological interactions such as competition, predation, and parasitism (Begon *et al*., 2009). The communities ecology uses a series of physical and ecological attributes to explain the distribution of fish species (Súarez & Junior, 2007). However, the importance of several factors influencing the structure of communities depends on the scale at which the study is performed (Jackson *et al*., 2001).

Habitat characteristics act as species filters because they decrease the choices for one species to colonize a specific environment (Poff, 1997). Factors of large-scale variables such as altitude, declivity, and position of the stream in the basin can be reflected in differences in the composition and diversity of fishes. Local factors can also be added, which can act on the ecological structure, physiological parameters (Gerhard *et al*., 2004) and modifications caused by humans (Peressin & Cetra, 2014). The hydrological regime, width and depth of the river (Súarez & Lima-Junior, 2009), velocity (Allan & Flecker, 1995; Valério *et al*., 2007) and variation of the water flow (Silvano *et al*., 2000) are other important variables which can apply pressure to fish assemblages. Thus, the species are not distributed randomly and uniformly in the aquatic ecosystems, and the patterns of distribution is a result of historical and present processes (Oberdorff *et al*., 2001; Wiens & Donoghue, 2004).

Although deterministic and stochastic processes are both important influences on the organization of fish assemblages, studies were made to identify which of these are responsible for the main control of communities. Grossman *et al*. (1982, 1985) maintain that fish species assemblages are organized naturally on stochastic type, but other researchers have concluded that deterministic factors act in the regulation of fish communities (Yant *et al*., 1984; Gorman, 1986; Morán-López *et al*., 2006; Súarez *et al*., 2007; Súarez & Junior,

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2008). However, the most likely is an interaction between random and deterministic elements, and this combination acts in the definition of fish assemblages (May, 1986; Strange *et al*., 1992; Súarez & Junior, 2005).

Describing and quantifying the spatial pattern of fish species assemblage can help in a better comprehension of the processes responsible for the observed patterns. The São Francisco River hydrographic basin (592,794 km²) is one of the most important biogeographical units for Neotropical fishes (Reis *et al*., 2003; Albert & Reis, 2011). This basin has regions with distinct environmental and geographic characteristics, which can determine the presence of different patterns of species distribution.

This study determines the spatial distribution pattern of fish species assemblages in the transition zone of the Cerrado-Caatinga biomes, in the middle portion of the São Francisco River basin. We aimed to answer the following questions: i) how fish species are spatially distributed? ii) which environmental variables are more strongly related to its distribution? iii) which factors (environmental and geographic) most closely explain the variation of species composition? We tested the hypothesis that fish species composition varies among the sub-basins even when these are connected by a large river (São Francisco River), due to differences in the environmental features within the Cerrado and Caatinga biomes.

## MATERIALS AND METHODS

### Study area

The São Francisco River is one of the largest rivers in South America (about 2,700 km length), is also one of the most important for electricity supply, drinking water, and fishing for 20 million people (Brito & Magalhães, 2017). Face to its dimension; this hydrographic basin is separated into four areas: High, Middle, Sub-middle and Low São Francisco (CBHSF, 2014). The river's watershed reaches 521 cities across six states Minas Gerais, Bahia, Goiás, Sergipe, Pernambuco, Alagoas and three biomes (Atlantic Forest, Cerrado and Caatinga). The final stretch of the São Francisco River in the semi-arid region of Brazil, an area comprising savanna-like vegetation where severe periodic drought brings difficulties to survival along certain areas within river valley.

The Middle portion of the São Francisco River comprises the stretch between the municipality of Pirapora (MG) and Remanso (BA), representing 53% of the the total area of the São Francisco basin. The sampled area comprised the Grande, Corrente and Rãs rivers sub-basins, between the cities of Barreiras and Guanambi, in Middle São Francisco, Bahia State.

The Grande River sub-basin has an area of 76,630 km², although the Corrente River sub-basin comprises an area of 34,875 km². Both sub-basins have a tropical climate with a dry winter ("Aw"), according to Köppen (Alvares *et al*., 2013). The most of the Grande and Corrente rivers sub-basins have their sources in the occidental highlands of the São Francisco River, where the Cerrado biome is dominant (INEMA, 2017). The Rãs River sub-basin is located in a region with low rainfall (Silva & Clarke, 2004), with predominance of the Caatinga biome, where the most tributaries are intermittent, and waters are turbid (INEMA, 2017). This sub-basin has a dry semi-arid climate at low latitude and altitude ("BSh"), according to Köppen's classification (Alvares *et al*., 2013).

### Data sampling

Samplings were carried out in February and August 2015 at 17 sites (Fig. 1): four sites in the Grande River sub-basin (Cerrado); nine sites in the Corrente River sub-basin (Cerrado); and four sites in the Rãs River sub-basin (Caatinga).

The samples were collected in 50 m stretches. At each stretch, data were collected along three cross-sections at 5, 25 and 45 m. In each of these sections, the following variables were measured: width (m), depth (m), substrate type, water velocity (m $s^{-1}$, using a floating object).

The substrate type was classified in the following categories: i) leaves, ii) branches and trunks; iii) silt (<0,6 mm), iv) sand (0,6-2 mm), v) gravel (>2-16 mm), vi) pebbles (>16-64 mm), vii) boulders (>64-265 mm) and viii) blocks (>265 mm). A value between 1 to 4 was attributed for the proportion of each category to classify the composition of the substrate, being 1 until 24%, 2 between 25-49%, 3 between 50-74%, and 4 up to 75%. These categories were grouped into two groups, and the values were calculated from a weighted mean of each substrate. The categories i, iii and iv were grouped as small substrates, and the categories ii, v, vi, vii and viii as large substrates.

Different techniques were applied to sample the fish. For sand river beaches, a Picard-type trawl-net (6×2.6 m) was cast five times, and when the site had vegetation, another net (1×0.6 m, of 1 mm mesh size) was cast ten times. Three kinds of gill nets (25×2.5 m, with a mesh size of 30, 50 and 100 mm between opposing nodes) were installed and left for 1h 30 min; and a jar net (3 m diameter, 40 mm mesh size) were cast 15 times at each sampling site. After sampling, fishes were anesthetized with benzocaine hydrochloride and fixed with formalin

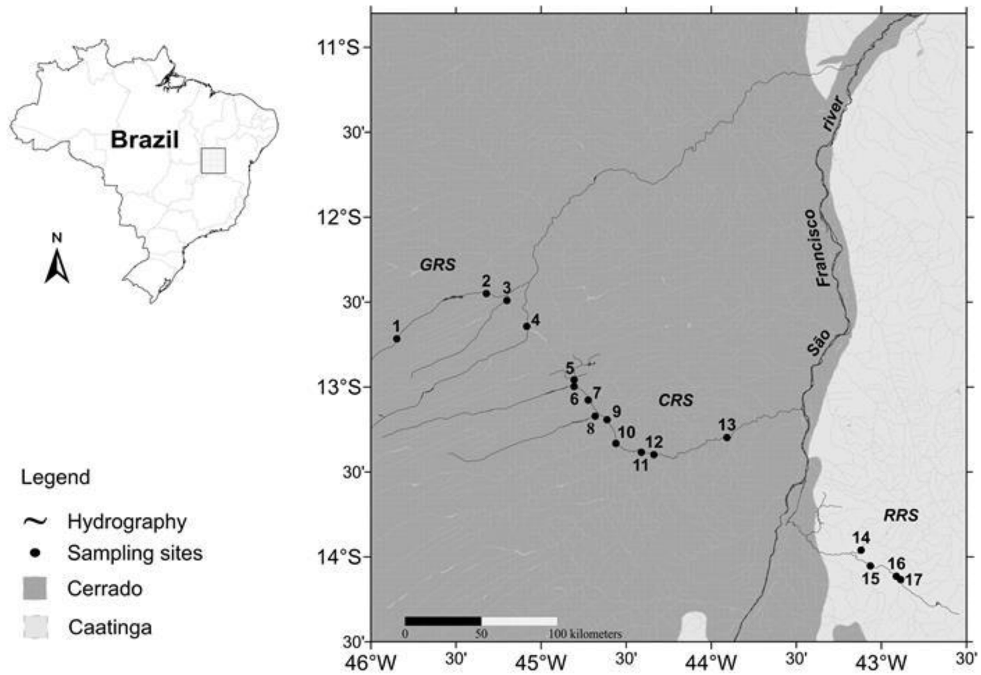


**Figure 1.** Sampling sites in Grande (GRS), Corrente (CRS) and Rãs (RRS) rivers sub-basins.

10% by 48 h, with subsequent conservation in ethanol (70%). All individuals were incorporated into the ichthyologic collection of the Instituto Nacional da Mata Atlântica (INMA), Laboratory of Zoology.

### Data analysis

Because of the differences of techniques and number of repetitions in each sub-basin, we used occurrence data and importance index (*IP*) calculated for each species $\left(IP_{ij} = N_{ij} \times B_{ij} / \sum\left(N_{ij} \times B_{ij}\right)\right)$. The variables $N_{ij}$ and $B_{ij}$ correspond to the number of individuals and biomass, respectively, of species $i$ in sample $j$. The index $IP$ is a modification of ponderable index proposed initially by Beaumord & Junior (1994) (Ferreira & Petrere, 2009), useful to measure the representativeness of each species as a relative contribution (values varying between 0-1).

Non-metric multidimensional scaling analysis (NMDS) was used to verify trends in the spatial distribution of fish, with the dissimilarity Jaccard coefficient. This analysis sorts the points in a bidimensional plot, where the relative distances reflect the dissimilarity between samples. The resolution distortion is expressed by Stress (S), and the closer to zero the better is the relationship between the original distance of the objects and the configuration obtained (Legendre & Legendre, 1998). A Permutation Multivariate Analysis of Variance procedure (PERMANOVA) with 9999 permutations was used to test the significance of patterns given by NMDS, also using the Jaccard coefficient. The relation of the importance of the species with the ordered points was verified with the function 'Envfit' to overlap the matrix of IP index of the species with the ordination by NMDS. Function Envfit finds directions in the space ordinate, for which the factors show maximum correlations with the configuration (Oksanen *et al*., 2016). After an adjusted correlation coefficient ($R^2$) for the *IP* of each species, a random test with 9999 permutations was used to verify the significance of importance of each species for all axes in conjunction.

To select the variables which best explain the pattern of species distribution, a redundancy analysis (RDA) was performed. An index matrix *IP* of species was used as the dependent variable and environmental data as the explanatory (independent) variable. The multicollinearity effect among environmental variables was verified using factors of inflation of variation (FIV). The selection of variables was performed by stepping forward through the permutations to select the best model to explain the data variation, and it was used as criteria for selection of the value of Akaike's Information Criterion (AIC). The significance of RDA was tested by using analysis of variance (ANOVA) with a permutation test (function 'permutest'; permutations = 9999).

Variation partition was employed to quantify the relative contribution of environmental factors (local variables) and geographical variables (sub-basins) on the distribution of fish species assemblages. We used the function 'varpart' for partition of the total explained variation from RDA (adjusted $R^2$) in isolated contributions ("pure") and combined of different predictors (Peres-Neto *et al.*, 2006). In contrast to common $R^2$, the adjusted $R^2$ is impartial, and its expected value is $R^2 = 0$ (Oksanen *et al.*, 2016). In our study the observed variation was partitioned into the following factors: i) pure environmental (variation explained exclusively by local variables), ii) pure geographic (variation explanation is related only with sub-basins), and iii) environmental and geographical shared (explanation shared by environmental and geographic factors). The remains are a percentage of variance not explained by these predictors (residuals of analysis) (Borcard *et al.*, 1992). ANOVA with a permutation test (function permutest; permutations = 9999) was used to verify the partitions significance.

We used $P = 0.05$ as the significance level for all analyzes. PERMANOVA was performed in PAST software (Hammer *et al.*, 2001), and other analyses were made using the 'Vegan' package (Oksanen *et al.*, 2016) for R 3.3.2 Cran project software (R Development Core Team, 2016).

## RESULTS

The Grande and Corrente rivers sub-basins had the higher values of altitude and superficial water velocity, and the predominance of block, boulder, pebble, and gravel. In contrast, the Rãs River sub-basin had sites at lower altitudes, more lentic or stagnant waters and a predominance of sand and silt. The rivers with major widths (sites 11, 12 and 13) were found in Corrente River sub-basin, as well as the deeper (site 13), followed by site 17 in Rãs River sub-basin (Table 1).

Some 1689 individual fish were sampled, comprising 69 species, in 51 genera, 22 families and seven orders (Table 2). Characiformes and Siluriformes composed 87% of species. The most species-rich family was the Characidae (21 species), followed by Loricariidae (9 species).

There was low species overlap, with only seven in common between the three sub-basins. The greatest sharing was between the Grande and Corrente rivers sub-basins, with 22 species in common. The highest species richness was found in the Corrente River sub-basin (58 species), where 22 species were exclusive, whereas the Rãs River sub-basin showed the lowest species richness (21 species) and six were exclusive.

The Grande River sub-basin was represented by 34 species, four being exclusive. *Acestrorhynchus lacustris* (*IP* = 53%) and *Metynnis maculatus* (*IP* = 19%) were the most representative species for the Grande River sub-basin, although for the Corrente River sub-basin were the species *Astyanax* aff. *eigenmanniorum* (*IP* = 66%) and *Bryconops* aff. *affinis* (*IP* = 10%). *Crenicichla* aff. *lepidota* represented 84% of total importance in the Rãs River sub-basin, followed by *A. lacustris* (*IP* = 9.5%).

Among the sampled species, 40% are endemic to the São Francisco River basin (28 species), and 6% are introduced (four species): *Coptodon rendalli* (tilapia), *Hyphessobrycon eques* (tetra-serpae), *Metynnis lippincottianus*, and *M. maculatus* (pacus) (Eschmeyer *et al.,* 2017). The species *Pachyurus francisci* and *Harttia* cf. *garavelloi* are classified as 'Near Threatened' (NT), and *Eigenmannia microstoma*, *Harttia longipinna*, and *Characidium bahiense* are in the category of Deficient Data (DD) (Portaria MMA Nº444, 2014).

The NMDS analysis ordinated the sampling sites into two groups. The sampling sites located in the Grande and Corrente river sub-basins were ordinated in the left side of Figure 2, although the Rãs River sub-basin sampling sites were grouped towards the right side of the biplot.

This pattern of ordination was confirmed by PERMANOVA (Pseudo-$F = 2.82$; $P = 0.0001$), which paired test showed that the fish composition of the Grande and Corrente rivers sub-basins were significantly different from the Rãs River sub-basin (Table 3).

It was possible to observe that the distribution of sampling sites is related to the biome in which the rivers run, suggesting a robust spatial variation.

The IP index values of five species showed significant association with the ordination by NMDS ($P < 0.05$) (Fig. 3). The species *Crenicichla lepidota, P. kennedyi* and *H. littorale* were associated with the Rãs River sub-basin, considering that the last two are restricted to the sites of the Caatinga biome. *Astyanax* aff. *eigenmanniorum* and *Bryconops* aff. *affinis* were restricted to the Grande and Corrente rivers sub-basins and showed a significant association with the area sampled in the Cerrado biome.

Among the variables used in RDA, altitude, width, water superficial velocity and the substrates of larger size were significantly related to the variation obtained. The RDA concentrated 31.7% of fish assemblage variation (Pseudo-$F = 1.39$; $P = 0.01$), being both first axis of analysis and represented 21.7% of data variability (11.7% for first axis and 10% for second axis) (Fig. 4).

Axis 1 was characterized by the species variation, *Hyphessobrycon diastatos*, *Hisonotus vespuccii,* and *Hemigrammus gracilis*, which were related to higher

**Table 1.** Sampling sites in Grande (GRS), Corrente (CRS) and Rãs (RRS) rivers sub-basins in Middle São Francisco, with locations, altitudes (m.a.s.l), mean ± standard deviation of width (m), depth (m) and water superficial velocity (m $s^{-1}$), predominant substrates and fishing techniques. G: gill net; T: trawl-net; J: jar net; O: other nets.

| Site | Water body | Sub basin | Coordinates | Altitude (m) | Width (m) | Depth (cm) | Water velocity (m $s^{-1}$) | Predominant substrates | Fishing method |
|---|---|---|---|---|---|---|---|---|---|
| 1 | Roda Velha River | GRS | 45W50'46" 12S 42' 27" | 733 | 12.3 ± 5.2 | 103,2 ± 57.3 | 0.6 ± 0.15 | Pebble, boulder, and block | G, J e O |
| 2 | Fêmeas River | GRS | 45W19'16" 12S27'00" | 680 | 15.7 ± 2.6 | 128.1 ± 17.2 | 0.8 ± 0.05 | Pebble, boulder, and block | G, J e O |
| 3 | Galheirão River | GRS | 45W12'03" 12S 29' 26" | 654 | 15.0 ± 1.3 | 95.9 ± 25.8 | 1.2 ± 0.23 | Pebble, boulder, and block | G, J e O |
| 4 | Grande River Tributary | GRS | 45W05'01" 12S38'34" | 655 | 11.0 ± 3.9 | 139,9 ± 67.8 | 0.1 ± 0.1 | Silt, sand, and leaves | G, J e O |
| 5 | Guará River Tributary | CRS | 44W48'21" 12S57'29" | 648 | 3.8 ± 0.8 | 62.2 ± 9.7 | 0.3 ± 0.04 | Silt and branches | J e O |
| 6 | Guará River | CRS | 44W48'20" 12S59'48" | 634 | 15.0 ± 7 | 135.2 ± 20.4 | 0.2 ± 0.09 | Sand, gravel, and pebble | G, T, J, and O |
| 7 | Meio River | CRS | 44W43'21" 13S04'38" | 617 | 17.3 ± 2.9 | 128.8 ± 32.3 | 0.8 ± 0.4 | Sand, pebble and Boulder | G, T, J and O |
| 8 | Santo Antônio River | CRS | 44W40'56" 13S10'19" | 600 | 8.7 ± 0.03 | 79.5 ± 0.2 | 0.3 ± 0.18 | Silt, gravel and pebble | J and O |
| 9 | Meio River | CRS | 44W36'42" 13S11'33" | 547 | 10.9 ± 5.0 | 108.9 ± 39.3 | 0.2 ± 0.2 | Silt, pebble and boulder | G, J and O |
| 10 | Correntina River | CRS | 44W33'37" 13S19'54" | 488 | 18.6 ± 3 | 142.2 ± 8.46 | .15 ± 0.4 | Silt, pebble and Boulder | G and J |
| 11 | Correntina River | CRS | 44W24'39" 13S23'03" | 455 | 45.45 ± 5.2 | 116.2 ± 15.4 | 0.5 ± 0.1 | Silt, gravel and pebble | G, J and O |
| 12 | Correntina River | CRS | 44W20'12" 13S23'53" | 451 | 45.8 ± 2.0 | 122.7 ± 27.3 | 0.5 ± 0.05 | Silt, gravel and pebble | G, J and O |
| 13 | Correntina River | CRS | 43W54'29" 13S17'37" | 432 | 56.8 ± 6.7 | 586 ± 17.2 | 0.4 ± 0.04 | Silt, sand and block | G, J and O |
| 14 | Rãs River | RRS | 43W07'10" 13S57'38" | 463 | 6.4 ± 1.8 | 81.0 ± 31.7 | 0 | Silt and branches | G, J and O |
| 15 | Carnaíba de Dentro River | RRS | 43W03'52" 14S03'12" | 466 | 14.22 ± 6.8 | 91.5 ± 18.5 | 0 | Sand and leaves | J and O |
| 16 | Carnaíba de Dentro River | RRS | 42W54'45" 14S06'51" | 485 | 13.9 ± 1.4 | 119.7 ± 5.9 | 0 | Silt, leaves and block | J and O |
| 17 | Carnaíba de Dentro River | RRS | 42W53'11" 14S08'02" | 486 | 8.1 ± 1.55 | 154.3 ± 13.7 | 0 | Silt and leaves | G, J and O |

altitudes, greater water superficial velocity and large substrates. Rivers with these characteristics were associated with the Grande and Corrente rivers sub-basins. *Crenicichla* aff. *lepidota* and *Hoplias* gr. *malabaricus* have a stronger relationship with rivers at lower altitudes, lower water velocity and minor substrates (Axis 1), characteristics which are positively correlated with the Rãs River sub-basin. The species *Hemigrammus marginatus* and *Piabarchus stramineus* were associated with wider rivers (Axis 2), which was more closely correlated with the Corrente River sub-basin.

RDA with variance partition reveals that spatial distribution of fish species assemblages was explained in part by environmental factors (6%) and in part by geographic factors (7%), and a combination of these two factors explained 3%. The two factors analyzed explained 16% of variance found ($R^2$ adjusted = 0.16) (Pseudo-$F$ = 1.5; $P$ = 0.04). A large percentage of variance was not explained by any of the predictors analyzed (residue = 84%) (Table 4). The nMDS (Fig. 2) and RDA (Fig. 4) corroborate for a strong difference in the distribution of fish assemblages between sub-basins located in Cerrado (Grande and Corrente rivers sub-basins) and the Caatinga (Rãs River sub-basin) biomes. RDA shows that environmental and geographic factors explain in approximate proportions the distribution pattern found.

## DISCUSSION

The high degree of endemism with a low overlap of species highlights the faunistic importance of the study area. The knowledge of the spatial pattern of these assemblages allows the analysis of the relative importance of several factors to explain the distribution trends found (Matthews & Robison, 1998).

The fish species distribution in the studied region was related to the Cerrado and Caatinga biomes. Rosa *et al*. (2003) analyzed the fish species distribution pattern in Caatinga and concluded that although the fish fauna of this biome distributed within four ecoregions, probably vicariate isolations initiated by geotectonic events in the past had generated a differential ichthyofauna in Caatinga domains. The studied areas are from the same hydrographic basin but are located in environments with different characteristics, which provide conditions for assemblages with different compositions. Mugodo *et al*. (2006) highlight that the fish species distribution can be influenced by environmental factors at different spatial scales. These factors act as species filters (Poff, 1997) because they determine the conjunct of species that will colonize and persist in a specific place.

**Table 2.** List of fish species sampled in Grande (GRS), Corrente (CRS) and Rãs (RRS) rivers sub-basins in Middle São Francisco River. Number of individuals (N); biomass (B, in grams); importance index (*IP*, in %); abbreviation for species (AS); richness (S). Species: endemic of the São Francisco River basin (*); introduced (**); Near Threatened (NT) and Deficient Data (DD) (Portaria MMA Nº444, 2014).

| Taxonomic list | GRS | | | CRS | | | RRS | | | AS |
|---|---|---|---|---|---|---|---|---|---|---|
| | N | B | *IP* | N | B | *IP* | N | B | *IP* | |
| **Order Clupeiformes** | | | | | | | | | | |
| **Family Engraulidae** | | | | | | | | | | |
| *Anchoviella vaillanti* (Steindachner, 1908)* | - | - | - | 2 | 1 | <0.01 | - | - | - | Avai |
| **Order Characiformes** | | | | | | | | | | |
| **Family Parodontidae** | | | | | | | | | | |
| *Apareiodon hasemani* Eigenmann, 1916* | - | - | - | 11 | 173.7 | 0.53 | - | - | - | Ahas |
| **Family Curimatidae** | | | | | | | | | | |
| *Curimatella lepidura* (Eigenmann & Eigenmann, 1889)* | - | - | - | 1 | 18.1 | 0.01 | 134 | 1017 | 84.03 | Clepi |
| *Steindachnerina elegans* (Steindachner, 1875) | 8 | 130.8 | 2.02 | 39 | 448.1 | 4.87 | - | - | - | Sele |
| **Family Prochilodontidae** | | | | | | | | | | |
| *Prochilodus costatus* Valenciennes, 1850* | - | - | - | 1 | 343 | 0.10 | 1 | 141.9 | 0.09 | Pcos |
| **Family Anostomidae** | | | | | | | | | | |
| *Leporellus vittatus* (Valenciennes, 1850) | - | - | - | 2 | 170.7 | 0.10 | - | - | - | Lvit |
| *Leporinus piau* Fowler, 1941 | 16 | 306.9 | 9.50 | 1 | 44.9 | 0.01 | 3 | 33.6 | 0.06 | Lpia |
| *Leporinus reinhardti* Lütken, 1875* | - | - | - | 1 | 29.3 | 0.01 | - | - | - | Lrei |
| *Leporinus taeniatus* Lütken, 1875* | - | - | - | 9 | 218.7 | 0.55 | - | - | - | Ltae |
| *Schizodon knerii* (Steindachner, 1875)* | - | - | - | 1 | 134.1 | 0.04 | 5 | 77.1 | 0.24 | Skne |
| **Family Erythrinidae** | | | | | | | | | | |
| *Hoplerythrinus unitaeniatus* (Spix & Agassiz, 1829) | 2 | 18.2 | 0.07 | - | - | - | - | - | - | Huni |
| *Hoplias* gr. *malabaricus* (Bloch, 1794) | 2 | 79.5 | 0.31 | 2 | 57.1 | 0.03 | 4 | 1002.5 | 2.47 | Hmal |
| **Family Acestrorhynchidae** | | | | | | | | | | |
| **Subfamily Acestrorhynchinae** | | | | | | | | | | |
| *Acestrorhynchus lacustris* (Lütken, 1875) | 65 | 422.9 | 53.19 | 46 | 162.5 | 2.08 | 72 | 213.2 | 9.47 | Acla |
| **Family Serrasalmidae** | | | | | | | | | | |
| *Metynnis lippincottianus* (Cope, 1870)** | 3 | 5.7 | 0.03 | - | - | - | - | - | - | Mlip |
| *Metynnis maculatus* (Kner, 1858)** | 33 | 290.2 | 18.53 | 2 | 24.7 | 0.01 | - | - | - | Mmac |
| *Myleus micans* (Lütken, 1875)* | 16 | 19.22 | 0.60 | 28 | 94.99 | 0.74 | - | - | - | Mmic |
| *Serrasalmus brandtii* Lütken, 1875* | - | - | - | 3 | 10.68 | 0.01 | 4 | 79.4 | 0.20 | Sbra |
| **Family Characidae** | | | | | | | | | | |
| *Psellogrammus kennedyi* (Eigenmann, 1903) | - | - | - | - | - | - | 6 | 4.1 | 0.02 | Pken |
| **Incertae sedis** | | | | | | | | | | |
| *Astyanax* aff. *eigenmanniorum* (Cope, 1894) | 3 | 17.4 | 0.10 | 182 | 1308.1 | 66.31 | - | - | - | Aeig |
| *Astyanax* aff. *fasciatus* (Cuvier, 1819) | 28 | 12.28 | 0.67 | 105 | 249.4 | 7.29 | - | - | - | Afas |
| *Astyanax lacustris* (Lütken, 1875) | 4 | 176.6 | 1.37 | 2 | 49 | 0.03 | 8 | 132 | 0.65 | Alac |
| *Astyanax rivularis* (Lütken, 1875)* | 5 | 16.2 | 0.16 | 11 | 24 | 0.07 | - | - | - | Ariv |
| *Astyanax* aff. *taeniatus* (Jenyns 1842) | 74 | 36.5 | 5.23 | 2 | 1.1 | <0.01 | - | - | - | Atae |
| **Subfamily Stethaprioninae** | | | | | | | | | | |
| *Orthospinus franciscensis* (Eigenmann, 1914)* | 15 | 28.3 | 0.82 | - | - | - | 15 | 31.2 | 0.29 | Ofra |
| **Subfamily Characinae** | | | | | | | | | | |
| *Phenacogaster franciscoensis* Eigenmann, 1911* | 13 | 7.5 | <1 | 68 | 43.07 | 0.01 | - | - | - | Pfran |
| *Roeboides xenodon* (Reinhardt, 1851)* | - | - | - | - | - | - | 3 | 22.1 | 0.04 | Rxen |
| **Subfamily Tetragonopterinae** | | | | | | | | | | |
| *Tetragonopterus chalceus* Spix & Agassiz, 1829 | - | - | - | 2 | 3 | <0.01 | 1 | 3 | <0.01 | Tcha |
| **Subfamily Cheirodontinae** | | | | | | | | | | |
| *Serrapinnus heterodon* (Eigenmann, 1915) | - | - | - | 10 | 2.96 | 0.01 | - | - | - | Shet |
| *Serrapinnus piaba* (Lütken, 1875) | 6 | 1.38 | 0.02 | 16 | 6.8 | 0.03 | 25 | 11 | 0.17 | Spia |
| **Subfamily Pristellinae** | | | | | | | | | | |
| *Hemigrammus brevis* Ellis, 1911* | - | - | - | 7 | 2.6 | 0.01 | - | - | - | Hbre |
| *Hemigrammus gracilis* (Lütken, 1875) | 38 | 7.92 | 0.58 | 18 | 5.74 | 0.03 | - | - | - | Hgra |
| *Hemigrammus marginatus* Ellis, 1911 | 13 | 2.51 | 0.06 | 14 | 3.6 | 0.01 | - | - | - | Hmar |
| *Hyphessobrycon diastatos* Dagosta. Marinho & Camelier, 2014 | 38 | 3.54 | 0.26 | 11 | 1.6 | <0.01 | - | - | - | Hdia |
| *Hyphessobrycon eques* (Steindachner, 1882)** | - | - | - | 2 | 0.8 | <0.01 | - | - | - | Hequ |
| *Moenkhausia costae* (Steindachner, 1907) | - | - | - | 1 | 0.7 | <0.01 | 22 | 46.36 | 0.63 | Mcos |
| *Moenkhausia sanctaefilomenae* (Steindachner, 1907) | 29 | 31.3 | 1.76 | 3 | 6.3 | 0.01 | - | - | - | Msan |
| **Subfamily Stevardiinae** | | | | | | | | | | |
| *Piabarchus stramineus* (Eigenmann, 1908) | 6 | 24.6 | 0.29 | 1 | 0.2 | <0.01 | - | - | - | Pstr |
| *Piabina argentea* Reinhardt, 1867 | - | - | - | 9 | 10.5 | 0.03 | - | - | - | Parg |
| **Family Triportheidae** | | | | | | | | | | |
| **Subfamily Triportheinae** | | | | | | | | | | |
| *Triportheus guentheri* (Garman, 1890)* | - | - | - | - | - | - | 5 | 22.7 | 0.07 | Tgue |

Continuation

| Taxonomic list | GRS | | | CRS | | | RRS | | | AS |
|---|---|---|---|---|---|---|---|---|---|---|
| | N | B | *IP* | N | B | *IP* | N | B | *IP* | |
| **Family Iguanodectidae** | | | | | | | | | | |
| *Bryconops* aff. *affinis* (Günther, 1864) | 10 | 117.8 | 2.28 | 74 | 508.35 | 10.48 | - | - | - | Baff |
| **Family Crenuchidae** | | | | | | | | | | |
| **Subfamily Characidiinae** | | | | | | | | | | |
| *Characidium bahiense* Almeida, 1971[DD] | 17 | 3.7 | 0.12 | 1 | 0.2 | <0.01 | - | - | - | Cbah |
| *Characidium* sp.n. aff. Satoi | 13 | 2.85 | 0.07 | 2 | 1.3 | <0.01 | - | - | - | Csat |
| **Order Siluriformes** | | | | | | | | | | |
| **Family Auchenipteridae** | | | | | | | | | | |
| **Subfamily Centromochlinae** | | | | | | | | | | |
| *Centromochlus bockmanni* (Sarmento-Soares & Buckup, 2005)* | - | - | - | 2 | 1.5 | <0.01 | - | - | - | Cboc |
| **Subfamily Auchenipterinae** | | | | | | | | | | |
| *Trachelyopterus striatulus* (Steindachner, 1877) | - | - | - | 2 | 18.7 | 0.01 | - | - | - | Tstr |
| **Family Pseudopimelodidae** | | | | | | | | | | |
| *Microglanis leptostriatus* Mori & Shibatta, 2006* | - | - | - | 3 | 1.4 | <0.01 | - | - | - | Mlep |
| **Family Heptapteridae** | | | | | | | | | | |
| *Cetopsorhamdia iheringi* Schubart & Gomes, 1959 | 6 | 3.3 | 0.04 | 6 | 2.6 | <0.01 | - | - | - | Cihe |
| *Imparfinis minutus* (Lütken, 1874)* | - | - | - | 2 | 1.1 | <0.01 | - | - | - | Imin |
| *Phenacorhamdia tenebrosa* (Schubart, 1964) | - | - | - | 1 | 0.8 | <0.01 | - | - | - | Pten |
| *Pimelodella laurenti* Fowler, 1941* | 3 | 1.8 | 0.01 | 5 | 7.8 | 0.01 | - | - | - | Plau |
| **Family Callichthyidae** | | | | | | | | | | |
| **Subfamily Callichthyinae** | | | | | | | | | | |
| *Hoplosternum littorale* (Hancock, 1828) | - | - | - | - | - | - | 3 | 42.2 | 0.08 | Hlit |
| **Subfamily Corydoradinae** | | | | | | | | | | |
| *Corydoras garbei* Ihering, 1911* | - | - | - | - | - | - | 1 | 0.3 | <0.01 | Cgar |
| *Corydoras multimaculatus* Steindachner, 1907* | - | - | - | 7 | 10.4 | 0.02 | - | - | - | Cmul |
| **Family Loricariidae** | | | | | | | | | | |
| **Subfamily Hypoptopomatinae** | | | | | | | | | | |
| *Hisonotus vespuccii* Roxo. Silva & Oliveira, 2015* | 1 | 0.2 | <0.01 | 18 | 2.37 | 0.01 | - | - | - | Hves |
| *Otocinclus xakriaba* Schaefer, 1997* | - | - | - | 16 | 6.7 | 0.03 | - | - | - | Oxak |
| **Subfamily Loricariinae** | | | | | | | | | | |
| *Harttia* cf. *garavelloi* Oyakawa, 1993[NT] | - | - | - | 3 | 12.8 | 0.01 | - | - | - | Hgar |
| *Harttia longipinna* Langeani, Oyakawa & Montoya-Burgos, 2001 | - | - | - | 2 | 10.8 | 0.01 | - | - | - | Hlon |
| *Rineloricaria* sensu Fischberg | - | - | - | 4 | 25.6 | 0.03 | - | - | - | Rfis |
| **Subfamily Hypostominae** | | | | | | | | | | |
| *Hypostomus* aff. *francisci* (Lütken, 1874) | 1 | 44.5 | <0.01 | 2 | 46.1 | <0.01 | - | - | - | Hafra |
| *Hypostomus francisci* (Lütken, 1874) | 2 | 19.3 | <0.01 | - | - | - | - | - | - | Hfra |
| *Hypostomus lima* (Lütken, 1874)* | - | - | - | 2 | 3.6 | <0.01 | - | - | - | Hlim |
| *Hypostomus macrops* (Eigenmann & Eigenmann, 1888)* | - | - | - | 33 | 444.09 | 4.08 | - | - | - | Hmac |
| **Order Gymnotiformes** | | | | | | | | | | |
| **Family Sternopygidae** | | | | | | | | | | |
| *Eigenmannia microstoma* (Reinhardt, 1852)*[DD] | 8 | 5.3 | 0.08 | 7 | 8.5 | 0.02 | - | - | - | Emic |
| *Sternopygus macrurus* (Bloch & Schneider, 1801) | 1 | 0.3 | <0.01 | 3 | 9.4 | 0.01 | - | - | - | Smac |
| **Order Cyprinodontiformes** | | | | | | | | | | |
| **Family Poeciliidae** | | | | | | | | | | |
| **Subfamily Poeciliinae** | | | | | | | | | | |
| *Pamphorichthys hollandi* (Henn, 1916) | - | - | - | 14 | 2.43 | 0.01 | 4 | 1.4 | <0.01 | Phol |
| **Order Synbranchiformes** | | | | | | | | | | |
| **Family Synbranchidae** | | | | | | | | | | |
| *Synbranchus* cf. *pardalis* | 2 | 6.3 | 0.02 | - | - | - | - | - | - | Spar |
| **Order Perciformes** | | | | | | | | | | |
| **SuperOrder Percoidei** | | | | | | | | | | |
| **Family Sciaenidae** | | | | | | | | | | |
| *Pachyurus francisci* (Cuvier, 1830)*[NT] | - | - | - | 3 | 46.8 | <1 | - | - | - | Pfra |
| **SuperOrder Labroidei** | | | | | | | | | | |
| **Family Cichlidae** | | | | | | | | | | |
| **Subfamily Pseudocrenilabrinae** | | | | | | | | | | |
| *Coptodon rendalli* (Boulenger, 1897)** | - | - | - | - | - | - | 2 | 543.7 | 0.67 | Cren |
| **Subfamily Cichlinae** | | | | | | | | | | |
| *Cichlasoma sanctifranciscense* Kullander, 1983 | 11 | 70.7 | 1.50 | 23 | 179.5 | 1.15 | 7 | 109 | 0.47 | Csanc |
| *Crenicichla* aff. *lepidota* Heckel, 1840 | 3 | 18.7 | 0.11 | 14 | 72.07 | 0.28 | 7 | 82.6 | 0.36 | Clep |
| Total number of specimens | | 495 | | | 862 | | | 332 | | |
| Total number of species | | 34 | | | 58 | | | 21 | | |

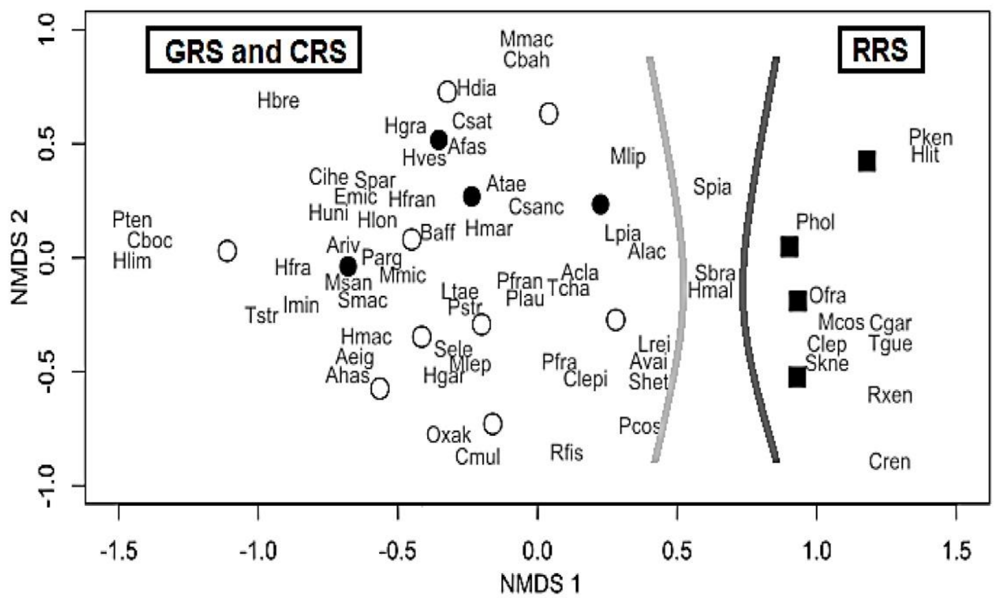


**Figure 2.** NMDS analysis for species sampled in Grande (GRS - ○), Corrente (CRS - ●) and Rãs (RRS - ■) rivers sub-basins at Middle São Francisco. Stress = 0.13.

**Table 3.** PERMANOVA of fish assemblages among the Grande (GRS), Corrente (CRS) and Rãs (RRS) rivers sub-basins at Middle São Francisco River. Significant differences are in bold.

| Permutations = 9999 | Pseudo-*F* = 2.82 | *P* = 0.0001* |
|---|---|---|
| Sub-basins | Pseudo-*F* | *P*-valor |
| GRS:CRS | 1.459 | 0.731 |
| GRS:RRS | **3.392** | **0.029** |
| CRS:RRS | **3.946** | **0.001** |

The Grande and Corrente rivers sub-basins are discrete geographic units, with a distance of 250 km between their confluences with the main channel of São Francisco River. For aquatic organisms which have their dispersion limited by hydrography, such as fish, it is expected that major spatial differentiation occurs (Beisner *et al*., 2006). However, the fish species assemblages of these sub-basins showed high similarity. This result can be explained by the physiographic similarity characteristics of habitats in these sub-basins, which probably were determinant factors for colonization and persistence of species (Martin-Smith, 1998; Súarez *et al*., 2007; Valério *et al*., 2007).

Fish species composition is influenced by an interaction of the regional variable altitude with local variables such as width, substrate and water velocity. *H. diastatos, H. vespuccii,* and *H. gracilis* have preferences for environments located in high altitude, faster waters, and substrates of larger size, typical conditions found in Cerrado River. Larger substrates promote high

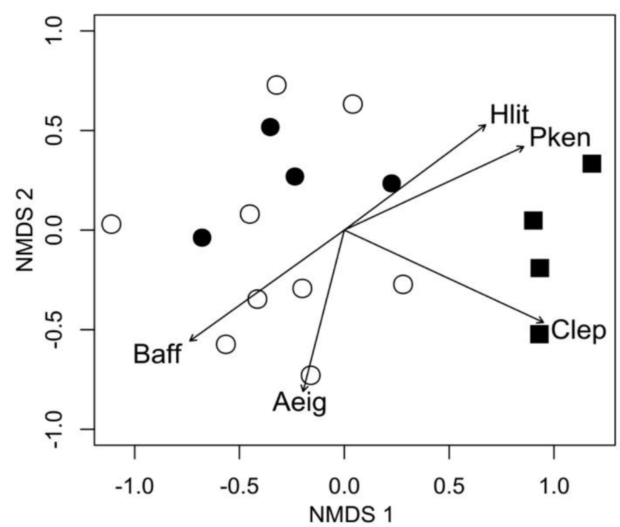


**Figure 3.** Resuls of nMDS from species occurrence with an overlap of IP index matrix of species using the function *Envfit* of *Vegan* package. Only significant species to ordination were plotted. Stress = 0.13. Hlit: *Hoplosternum littorale*, Pken: *Psellogrammus kennedyi*, Baff: *Bryconops* aff. *Affinis*, Aeig: *Astyanax aff. Eigenmanniorum*, Clep: *Crenicichla lepidota.* Grande (○), Corrente (●) and Rãs (■) rivers sub-basins at Middle São Francisco.

environmental heterogeneity because they provide proportionate cover, food and places for spawning (Casatti *et al*., 2006). Thus the high water velocity allows major habitat diversity (Barbour *et al*., 1999). However, these geomorphologic and hydrologic characteristics can be adverse for the permanence of other

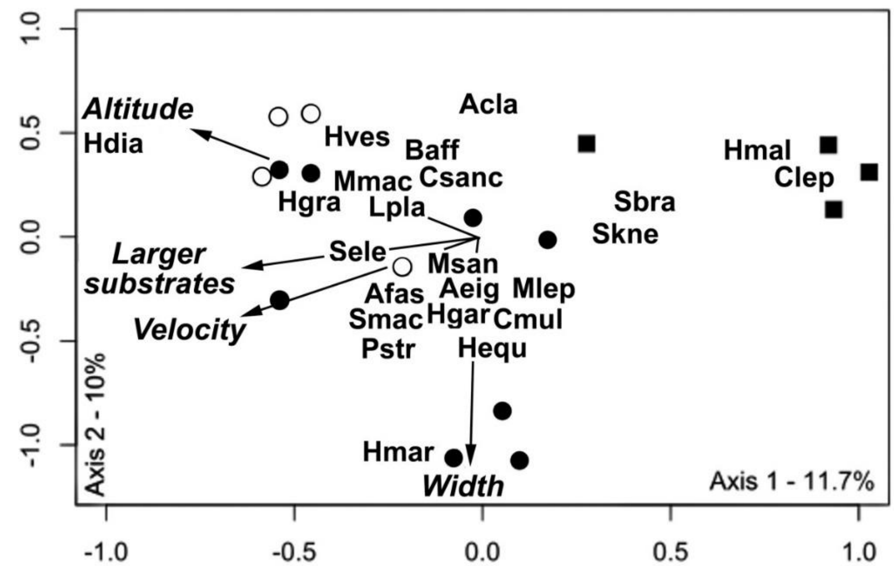


**Figure 4.** RDA analysis using data of species importance (*IP*) and environmental variables sampled in Grande (○), Corrente (●) and Rãs (■) rivers sub-basins at Middle São Francisco. Species with low importance were not present in this biplot.

**Table 4.** Results of RDA with variance partition performed to quantify the contribution of factors. a) Environmental pure, b) environmental and geographic combined, c) geographic pure, and d) residual for distribution of fish assemblages in Grande, Corrente and Rãs rivers sub-basins in the Middle São Francisco. Permutation = 9999; Pseudo-$F$ = 1.5; $P$ = 0.04.

| Partition | $R^2$ | $R^2$adj | % Explained variation |
|---|---|---|---|
| Environmental (a+b) | 0.32 | 0.09 | 9 |
| Geographic (b+c) | 0.21 | 0.10 | 10 |
| Environmental and geographic (a+b+c) | 0.47 | 0.16 | 16 |
| Individual factor | | | |
| Environmental pure | | 0.06 | 6 |
| Combined | | 0.03 | 3 |
| Geographic pure | | 0.07 | 7 |
| Residual | | 0.84 | 84 |

species (Vieira & Shibatta, 2007), as for *Crenicichla* aff. *lepidota* and *Hoplias* gr. *malabaricus*, which find more favorable conditions in Caatinga river. The relevance of altitude in the pattern of species distribution was observed by Súarez & Lima-Junior (2009), in which even with low altimetry variation, altitude in association with other variables was important to the definition of richness and local composition of species.

*Bryconops* aff. *affinis* and *Astyanax* aff. *eigenmanniorum* were the most important species for the Corrente River sub-basin, besides showed a significant association with the area comprised by the Cerrado biome. *Bryconops* aff. *affinis* has a preference for lotic systems with clear waters (Chernoff & Machado-Allison, 2005; Santos *et al.*, 2015), which explain its limitation to the Grande and Corrente rivers sub-basins. The high importance of *B. affinis* to the Corrente sub-basin can also be explained by the preference of its juveniles to predate on *Piabina argentea* (Santos *et al.,* 2015), which is restricted to this sub-basin.

The species *H. diastatos* was recently described (Dagosta *et al.*, 2014), with its occurrence for the São Francisco River basin recorded only in the Grande River sub-basin, but this species also occurs in the middle and high Tocantins River basin. The distribution of this species must be associated with places at high altitudes, clear waters and fast velocity (Dagosta *et al.*, 2014). *H. vespuccii* belong to the family Loricariidae. This family has as characteristic the dorso-ventrally compressed body and nektobenthic or benthic habits (Langeani *et al.*, 2005). These characteristics favor the presence of this species in fast water velocity environments, as found in the sampled area comprised by the Cerrado.

*Crenicichla* aff. *lepidota* was the most important species for the Rãs River sub-basin, probably because they had suitable conditions for development. The typical representatives of its family, Cichlidae, have the habit of foraging on sandy bottoms (Uieda, 1984; Bührnheim, 2002; Casatti, 2004), and a preference for habitat with lentic waters (Uieda, 1984). Another species associated with this sub-basin was the piscivorous *Hoplias* gr. *malabaricus*, which is a well-adapted species for lentic environments (Barbieri, 1989), and is also commonly found in small, medium and large size rivers (Bialetzki *et al.*, 2008; Oliveira *et al.*, 2015). Studies showed a high abundance of this fish during dry periods, when the water volume is small (Resende *et al*., 1996; Resende, 2000; Carvalho *et al*., 2002). Thus, the characteristic of retraction of Caatinga River must not be an unfavorable condition for this species.

The analysis of the spatial factor influence on the distribution of fish species is relevant in studies of the Brazilian ichthyofauna since geographic factors contributed to the formation of several endemism points distributed in an aggregated pattern (Hubert *et al*., 2007). The "diagonal dry" corresponds to a wide area located in South America, between the northeast of Brazil and northwest of Argentina, which includes the biogeographic provinces of Chaco, Cerrado, and Caatinga (Ab'Saber, 1977). The synthesis by Zanella (2011) on the biota evolution highlighted the dissimilarity of fauna between Cerrado and Caatinga, although was based in adjacent areas.

Silva (1995) also points out that the relationship between the endemic fauna of the Caatinga and the Cerrado is weak. The results of the present study corroborated with these studies, since the composition of the fish fauna showed a significant difference between the areas comprised by the Cerrado and Caatinga biomes.

The uplift of the Brazilian Central Plateau at the end of the Tertiary period elevated this region to the current levels of altitude (Silva, 1995), and seems to be relevant to the differentiation of Cerrado biota, as also as for the region occupied by Caatinga, because it determines a great denudation of Brazilian Northeast in the driest conditions. Also, alterations in the pluviometric regime and increase of aridity in glacial periods of the Pleistocene resulted in modifications of the distribution of biota (Zanella, 2011).

Fish species from Caatinga are adapted for the climate conditions and hydrological regime of this region because many tributaries are intermittent and associated with high hydric evaporation (Stanley *et al*., 1997; Rosa *et al.*, 2003). These characteristics made the associated systems function as a mosaic of dry and water stains (Stanley *et al*., 1997; Barbosa *et al*., 2012), and acts as drivers of important processes in the maintenance of diversity (Maltchick & Florín, 2002). The hydric dynamics of this biome can lead to extreme situations for many fish species (Medeiros & Maltchik, 2001), which can explain the low richness of species found in Caatinga in relation to Cerrado.

The fish species distribution was limited by factors acting at different scales (Poff & Allan, 1995). The differences in the environment characteristics among drainages of different biomes limited the dispersion of fish species adapted for a specific conjunct of environmental variables (Matthews, 1987). As in the sub-basin scale, the geographical factors were determinant in the structure of species assemblages (Lewis *et al*., 1996).

The difference in the fish species assemblages sampled in different biomes reveals important implications for conservation strategies, management or biodiversity evaluation, once it is essential to consider the spatial distribution of species and its limiting factors. The differences found in our study point to a distribution determined by an interaction of the regional variable altitude (geographic factor) with local environmental variables: width, substrate and superficial velocity of the water).

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