

How are local fish communities structured in Brazilian semiarid headwater streams?

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Abstract Environmental and spatial factors are known as the main determinants of community variation in aquatic organisms. However, historical factors may interact with local processes to regulate community structure patterns. Here we compared historical, environmental, and spatial factors in a multi-scale approach in order to identify the main drivers structuring species composition and functional diversity of fish communities in forest enclaves across three hydrographic basins in semiarid Brazil Caatinga biome. We initially modeled spatial structure within

each basin using asymmetric eigenvector maps (AEM). We then partitioned the explanation of the variation in local community structure into three groups of predictor variables: (1) environmental variables, (2) spatial variables, and (3) phylogenetic history. Biogeographical bias was assessed using a basin identity matrix as covariable. The combination of 1, 2, and 3 explained the variation in species composition, while pure spatial, phylogenetic, and environmental components explained the distribution of functional groups and their nested patterns. Our findings confirmed the importance of phylogenetic history, as well as the usefulness of robust methods in community studies in refining explanations of the processes determining variation in species composition and functional groups.

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Introduction

The assembly of communities is a central issue within ecology, with classical approaches assuming niche-based processes and dispersion as the main drivers structuring communities across spatial scales (Hubbell, 2001; Leibold et al., 2004). In addition, historical processes affect the configuration of the past, defining the spatial arrangement of ecosystems and consequently the regional pool of species capable of colonizing local communities (Cavender-Bares et al., 2009). As a result, the phylogenetic structure of communities, the patterns of species coexistence (Cavender-Bares et al., 2009), and the diversity of functional traits within species pool are closely related to the history of a given region (Olden et al., 2010; Rodrigues-Filho et al., 2018). This view is based on the assumption that biogeography and phylogenetic history are, together, the main structuring forces acting on communities at the regional scale (Peres-Neto et al., 2012; Sternberg et al., 2014). For example, patterns purely linked to species dispersion limitation (mass effect or neutral dynamics) could be due to historical legacies (i.e., tectonic movements; Peres-Neto & Legendre, 2010). Similarly, patterns of species coexistence commonly interpreted as a consequence of environmental filters (sorting) may, in fact, result from allopatric effects (Wiens & Graham, 2005). In this context, the knowledge of phylogenetic history can provide additional information on how niche-based processes and dispersion structure current local communities (Sternberg et al., 2014; Castillo-Escrivà et al., 2017).

Aquatic systems are ideal for testing the effects of historical, niche-based, and dispersion processes, since they show discrete spatial distribution and have extensive environmental gradients (Heino, 2013). In such systems, in addition to the action of historical filters, processes based on niche breadth and dispersion capacity can act together to structure local communities across spatial scales (Tonn, 1990). From

the niche perspective, environmental conditions would select species with similar phenotypic characteristics (Poff, 1997). On the other hand, the dendritic configuration of river systems can act as a barrier to the movement of species with low dispersion capacity (Heino et al., 2015). Thus, taken together, niche-based process and dispersal limitation supposedly are the main factors determining the spatial structure of stream fish communities (Vitorino Júnior et al., 2016).

In headwaters, great hydrological variation coupled with high environmental heterogeneity favors processes based on niche (Landeiro et al., 2011; Zbinden & Matthews, 2017), although contrary results have been reported (Cetra et al., 2017). In part, these contradictory results may be explained by the complex dynamic of colonization and extinction typically found in headwaters, where flash flood events are common (Taylor & Warren, 2001). This dynamic can generate a pattern of nested subgroups in headwater streams. However, to better understand the complexity of this relationship, it is necessary to investigate the other facets of biodiversity (McGill et al., 2006). Functional ecology is an aspect of biodiversity which adds complementary information to taxonomic approaches, especially by providing a mechanistic link to buttress explanations based solely on environmental conditions (Heino et al., 2007; Sternberg et al., 2014; Zorzal-Almeida et al., 2017; Tolonen et al., 2018). In addition, grouping species based on functional traits (related to performance or fitness) has proven useful in the development of generalized ecological models (Teresa & Casatti, 2012; Arantes et al., 2017; Henriques et al., 2017). This is explained by the relation between the functional characteristics of the species and its environmental requirements and dispersion capacity (de Campos et al., 2018). Fish are a good model group with which to examine such relationships since they have a wide range of trophic associations, habitat uses, and body sizes (Villéger et al., 2017).

The South American ichthyofauna is diverse and one of the best models for the assessment of functional relationships (Toussaint et al., 2016). Marine transgressions, tectonics, climate change, and historical connections between river basins have been the principle events shaping fish diversity and distribution in the Neotropics (Hubert & Renno, 2006; Ribeiro,

2006; Dias et al., 2014). Humid forest enclaves in semiarid Brazil (Caatinga biome) are a very particular system due to the long-term disturbances occurring during their formation (Pôrto et al., 2004). However, apart from their high levels of endemism, little is known about the ecology of stream fish in such enclaves (Rodrigues-Filho et al., 2016; but see Gurgel-Lourenço et al., 2017).

In this study, we assessed (i) the relative importance of environmental, spatial, and historical events in taxonomically and functionally structuring stream fish communities, (ii) the relation between environmental gradients and the distribution of species and functional groups, and (iii) whether environmental variation is responsible for the nested patterns of species distribution and functional groups. We expected variations between the communities in humid forest enclaves within Caatinga to be explained by a suite of opposing forces. In the taxonomic approach, historical events should be of primary importance, whereas environmental conditions will be better at explaining functional group distribution. Moreover, considering the importance of basin identity to river fish (Heino et al., 2017), and their association with factors influencing regional biogeographical aspects (Benone et al., 2017), we expected the results of the taxonomic approach to be basin-specific. We also tested whether environmental conditions generate taxonomic and functional nesting patterns and expected spatial determinants to explain the local distribution of species and functional groups within the species pool.

Methods

Study location and sampling

We sampled 26 streams of the Caatinga highlands of Araripe and Ibiapaba, two plateaus climatically and hydrologically defined as tropical forest enclaves. Such rainforests are typically found in tablelands up to 1000 m elevation, with annual rainfalls (~ 1000 mm) well above the average for semiarid regions. Over the last 25,000 years, these forests have become uncommon due to the synergy between drought and anthropic activity, exacerbated by the short duration of the rainy season (usually from January to May) in northeastern Brazil (Brasil et al.,

2016; Rito et al., 2017). The investigated streams were perennial, despite a considerable decrease in flow during the dry season (Rosa & Groth, 2004). During the rainy seasons in 2011–2013, we sampled streams from three river basins: Jaguaribe (J), São Francisco (F), and Coreaú (C), the first two on the Araripe Plateau, the third on the Ibiapaba Plateau (Fig. 1; Table S1.1 of Online Appendix 1).

Sampling occurred on 50 m stretches of the stream, following a standardized protocol designed by Mendonça et al. (2005). We blocked the extremities of each stretch with 12-mm nets to prevent fish from escaping, and then defined four equidistant transects in which average width (m) and depth (m) were measured. Water velocity ($\text{m} \cdot \text{s}^{-1}$) in the channel was measured three times in each transect using the distance traveled by a Styrofoam ball. We recorded water temperature ($^{\circ}\text{C}$) and dissolved oxygen ($\text{mg} \cdot \text{L}^{-1}$) at once sampling downstream from the stretches. A GPS was used to determine geographic coordinates and elevation (m). Vegetation coverage (%) was calculated based on 16 b/w photographs of the canopy, using a digital camera fitted with 5.8–23 mm lenses (Mendonça et al., 2005). Area (m^2) and average depth (m) of each stretch were used to determine habitat volume (m^3). Relative substrate composition (%) was determined using the classification of de Gonçalves & Braga (2012): pebble/gravel (1–10 mm; Pb), coarse sand (0.1–1 mm; Cs), fine sand (0.05–1 mm; Fs), and silt/clay (< 0.05 mm; Sc) (see Table S1.2 of Online Appendix 1 for a summary of environmental data).

Taxonomic and functional data

Fish were captured with cast nets (5.3 m^2 ; 14 mm mesh), sieves (0.7 m^2 ; 1 mm mesh), and seine nets (1.3 m^2 ; 2 mm mesh) in a fishing effort of four person-hours. Specimens were euthanized by immersion in an anesthetic solution of eugenol and preserved in a 10% formalin solution, followed by storage in 70% alcohol. Specimens were identified to species level (Table S1.3), and voucher specimens deposited in the fish collection of the Universidade Federal do Rio Grande do Norte (UFRN).

Classification of species into functional groups used six traits (diet, feeding tactic, vertical compartment, body mass, current flow, and substrate specificity) and 26 trait categories (Sabino & Zuanon, 1998;

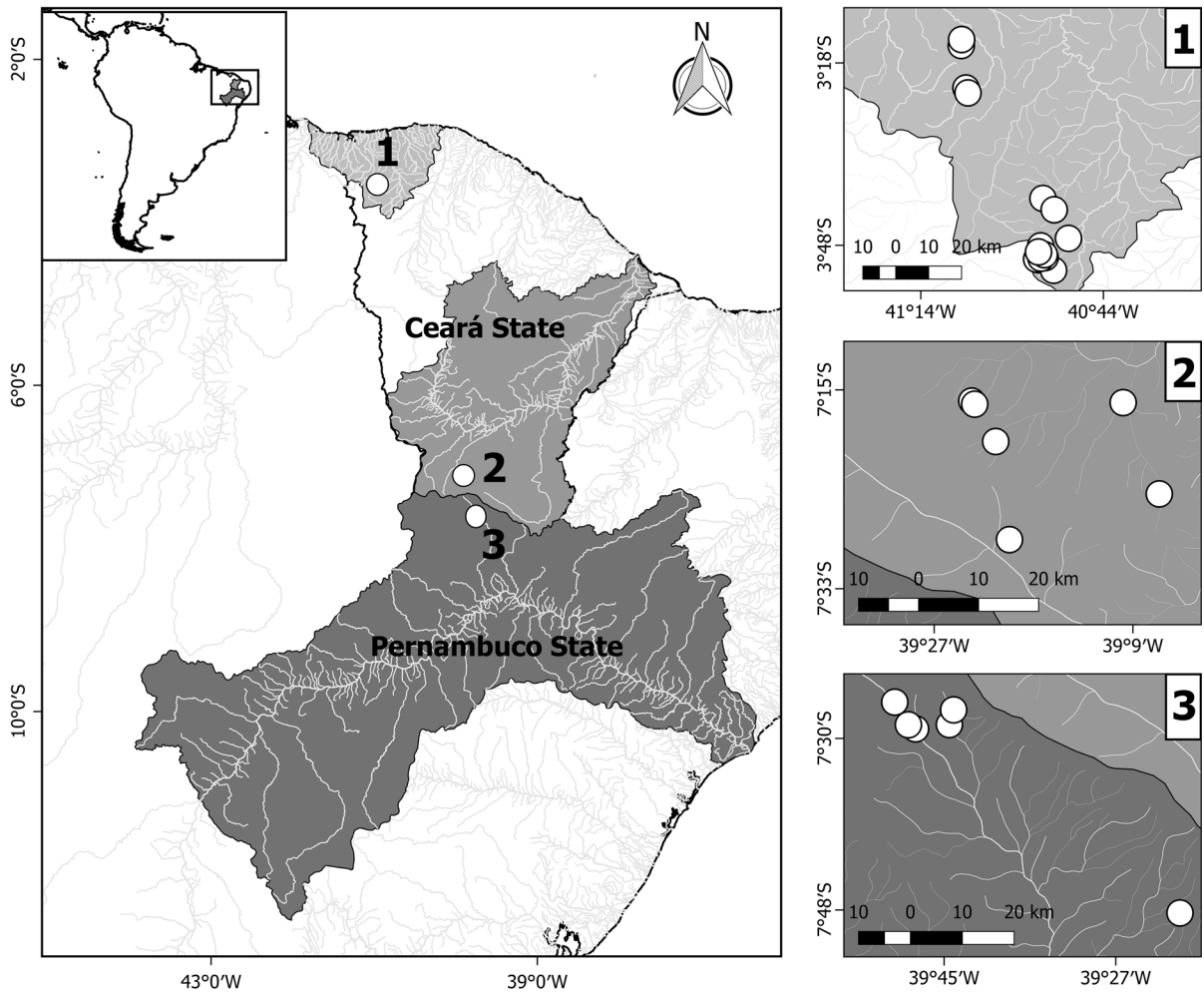


Fig. 1 Sampling points (white circles) and riverine basins (1—Coreaú; 2—Jaguaribe; 3—São Francisco) in forest enclaves in semiarid Brazil

Teresa & Casatti, 2012; Brejão et al., 2013; Tables 1, S3.1 of Online Appendix 3). For trait categories, we adopted a binary approach when characterizing each species. When information at the species level was not available in the literature (30% of the species), we used a genus-level classification. These traits were selected due to their mechanistic relation with species locomotion capacity (Blanchet et al., 2010), resource use, and microhabitat exploration (Teresa & Casatti, 2012; Rodrigues-Filho et al., 2017), these being key aspects in dispersal and niche-based processes.

As recommended by Pillar and Sosinski (2003) and Dumay et al. (2004), functional group classification included three steps, in order to minimize subjectivity bias. We first calculated Pearson correlation

coefficients among trait categories to determine if the selected traits reflected informative and complementary functions within the fish assemblage (Online Appendix 2). Subsequently, and to reduce the dimensionality of functional space, we performed a principal coordinates analysis (PCoA) based on a Gower's distance matrix of species traits (Pavoine et al., 2009). We selected the first nine eigenvectors (broken-stick explanation percentage: 71.7%; Table S3.2 of Online Appendix 3) and submitted it to non-hierarchical cluster analysis (*k*-means clustering). Then, based on functional space, five functional groups were defined by minimizing the sum of squared Euclidian distances between the species and the centroid of the groups (Tables 2, S3.3 and Fig. S3 of Online Appendix 3).

Table 1 Trait and 26 functional categories used to group fish sampled in enclaves of tropical forest in semiarid Brazil, with the abbreviations used in subsequent analyses

Trait	Category	Abbreviation
Diet	Detritivore	det
	Aquatic insectivore	a.ins
	Herbivorous insectivore	h.ins
	Invertivore	inv
	Omnivore	omn
	Piscivore	pis
Feeding tactic	Water column	wcol
	Substrate speculation	sspe
	Ambusher	amb
	Grazer	gra
	Stalker	sta
	Night active	nig
	Surface	sur
Vertical compartment	Nektonic	nek
	Nektobenthic	nekt
	Benthic	ben
Current flow	Slow	slo
	Intermediate	int.flo
	Fast	fas
Body mass	Very light (< 0.001 g)	v.lig
	Light (0.001–1 g)	lig
	Intermediate (1–2.5 g)	int.bod
	Heavy (> 2.5 g)	hea
Specify for substrate	Low	low
	Intermediate	int.sub
	High	hig

Predictor variables

Phylogenetic history

To evaluate the evolutionary history of the humid forest enclaves in the Caatinga, a phylogenetic information matrix was built at the family level, exploring the descriptive aspect rather than the phylogenetic signs (Webb, 2000). Thus, following Sternberg and Kennard (2013), phylogeny of the species were defined from a matrix of sampled streams (lines) versus families (columns). For this, we built a matrix of species richness for each stream. Although phylogenetic predictors are often extracted using phylogenetic trees (Leibold et al., 2010), or paleoecological differences between sampling locations (Castillo-Escrivà et al., 2017), we adopted Webb's classic approach due to the lack of detailed phylogenetic

information for the endemic fauna of the study area, and also because the two humid forest enclaves displayed similar geology and formation history. Although their use may result in information loss, Ricotta et al. (2012) have demonstrated that cladistic relationships are strongly related to distance based on phylogenetic trees.

Spatial

A spatial predictor matrix was constructed using spatial analysis generating eigenvectors capable of capturing complex patterns in taxonomic and functional composition; eigenvectors with high eigenvalues are associated with large-scale spatial effects, while eigenvectors with low eigenvalues represent fine-scale effects (Griffith & Peres-Neto, 2006). We used asymmetric eigenvector maps (AEMs) to reflect

Table 2 Taxonomic composition within each functional group and their behavioral profile, and number of individuals collected according to river basin (Jaguaribe = *J*, São Francisco = *F* and Coreaú = *C*)

Group	Species	Behavioral profile	<i>J</i>	<i>F</i>	<i>C</i>
1	<i>Astyanax bimaculatus</i> <i>Astyanax fasciatus</i> <i>Phenacogaster calverti</i> <i>Poecilia reticulata</i> <i>Poecilia</i> sp. <i>Serrapinnus heterodon</i> <i>Serrapinnus piaba</i>	Mostly small nektonic fish feeding predominantly on insects in the water column or on the surface. They have no specific substrate preference and thrive in streams with low current flows	441	767	1776
2	<i>Hoplias malabaricus</i> <i>Synbranchus marmoratus</i>	Piscivorous species, which ambush their prey. Nektonic or nektobentonic, they prefer streams with low current flows	3	1	14
3	<i>Aspidoras menezesi</i> <i>Aspidoras rochai</i> <i>Aspidoras spilotos</i> <i>Corydoras garbei</i>	Small nektobentonic fish, which sift through the substrate for food (usually aquatic invertebrates), preferably in faster-flowing streams	14	67	119
4	<i>Hypostomus</i> sp. <i>Hypostomus jaguribensis</i> <i>Parotocinclus cearensis</i> <i>Parotocinclus haroldoi</i>	Benthic grazers feeding mostly on detritus. Most abundant in streams with riffles	49	0	71
5	<i>Characidium bimaculatum</i> <i>Cichlasoma orientale</i> <i>Coptodon rendalli</i> <i>Crenicichla menezesi</i> <i>Rhamdia quelen</i> <i>Trachelyopterus galeatus</i> <i>Steindachnerina notonota</i>	Species with great trophic plasticity, feeding on plant debris, detritus, insects, and fish. Some stalk or pursue their prey, usually at twilight. The detritivore <i>S. notonota</i> is an exception	14	64	64

the unidirectional flow of aquatic systems (Blanchet et al., 2008), at the hydrographic basin level (Declerck et al., 2011). Such eigenvectors are capable of modeling the distribution of species and functional groups within each basin but, to avoid bias related to the number of spatial predictors, only spatially structured vectors were selected (initially, 25) (Dray et al., 2012). To do so, Moran's *I* coefficients were calculated for each AEM, selecting those with significant spatial autocorrelation ($p < 0.05$) (Blanchet et al., 2011). Subsequently, five eigenvectors representing large-scale forces were selected (AEM-1, AEM-2, AEM-3, AEM-4, AEM-6; Online Appendix 4).

Environmental

Using PCoA for the $\log(x + 1)$ -transformed data (except pH), the selected environmental variables

were tested for redundancy. The purpose of the procedure was to identify variables with high collinearity in the PCoA biplot. After visual identification of obvious collinearities, we tested the variance of inflation (VIF) factor, excluding values > 10 from further analysis. The following variables were retained for the subsequent analyses: width, depth, elevation, temperature, pebble/gravel, coarse sand, fine sand, silt/clay, and pH.

Data analysis

The importance of environmental (E), spatial (S), and phylogenetic (P; streams vs. family) components for taxonomic and functional structure was determined by partitioning the variance in a partial analysis of redundancy (pRDA), using Hellinger-transformed data (Borcard et al., 1992; Anderson & Gribble,

1998). Variables selected by forward selection were included in the pRDA as long as they did not exceed $p = 0.05$ (based on 999 Monte Carlo permutations). Previous selection of variables allows for a more reliable interpretation of the importance of the predictor variables.

Once the predictors were associated, the total variance was partitioned into eight components: (i) pure environmental (Ep), (ii) pure spatial (Sp), (iii) pure phylogenetic (Pp), (iv) spatially structured environmental (SE), (v) phylogenetically structured environmental (PE), (vi) spatially structured phylogenetic (SP), (vii) spatially and phylogenetically structured environmental (SPE), and (viii) unexplained (U). Following the recommendations of Peres-Neto et al. (2006), we estimated the adjusted coefficients of determination (R_{adj}^2). Biplot ordinations were tested based on 10,000 permutations, assuming $\alpha = 0.05$. Nestedness of the first axis of functional and taxonomic RDA (only for environmental variables) was determined with the nestedness overlap and decreasing fill index (*NODF*) (Almeida-Neto et al., 2008). We tested whether the observed *NODF* differed from the *NODF* derived from 1000 permutations of the species matrix of species and functional groups (SIM9 algorithm, Gotelli, 2000). We adopted this pattern based on the environmental conditions responsible for functional or taxonomic nestedness (observed *NODF* significantly different from expected *NODF*).

To control for biogeographical differences, an identity matrix was built for each hydrographic basin and used as covariable in a new partitioning analysis (PERMANOVA). Hydrographic basin-level analysis suggested a homogeneous taxonomic (Pseudo- $F_{2,24} = 1.01$; $p > 0.38$), and functional composition (Pseudo- $F_{2,24} = 1.07$; $p > 0.35$). The process consists of relating the predictive matrixes with the identity vector of the hydrographic basin of each stream in a residual environmental matrix (E_r) and a residual phylogenetic matrix (P_r). The identity of the hydrographic basin was controlled during the extraction of spatial eigenvectors (AEM). Finally, pRDA analyses were performed with the predictor matrixes E_r , P_r , and S and the response matrixes of species composition and functional groups, evaluating the influence of the hydrographic basin. All analyses were performed in R, version 3.4.2 (The R Foundation for Statistical Computing, 2017).

Results

The forest enclave ichthyofauna

Fish sampled comprised 23 species belonging to five orders and 11 families (Table S1.3 of Online Appendix 1). Siluriformes and Characiformes were the most strongly represented orders. Coreaú had the greatest number of species (17), followed by Jaguaribe and São Francisco (14 each). On average, 5.6 species (2–12) were captured per stream. Two of the registered species were non-native to the Caatinga. One of these, *Poecilia reticulata* Peters 1859, was widely distributed across samples sites, occurring in 69.2% of them. The most commonly captured native species was *Astyanax bimaculatus* (Linnaeus, 1758), occurring in 73.0% of the sites. Nektonic fish feeding on insects in the water column (Group 1) and ambushers with high trophic plasticity (Group 5) were the most species-rich and abundant groups in all basins (Table 2). In contrast, detritivorous and piscivorous species with strong substrate preferences had low abundances, occurring in specific environmental and elevational gradients. According to rarefaction procedures, the number of sites used ($n = 26$) allowed complete sampling of the species richness of the study region (Fig. S1 of Online Appendix 1).

Relative contribution of structuring factors (environment, space, and phylogeny)

Following forward selection, three spatial eigenvectors (AEM-1, AEM-2, and AEM-4), phylogenetic information on the clades Characidae and Poeciliidae, and two environmental variables (elevation and channel width) (Table 3) together explained, respectively, 29% and 24% of the total variation in species composition and functional groups (Table 4). The components most important for the taxonomic approach were those spatially and phylogenetically structured by the environment (SPE) and the phylogenetically structured environmental (PE) (17% and 7%, respectively). In contrast, composition of functional groups was explained primarily by the pure spatial component (Sp = 13%; $p = 0.001$), followed by the pure phylogenetic component (Pp = 7%; $p = 0.021$).

The identity of the basins had little influence on taxonomic variation but was important for the

Table 3 Spatial, environmental, and phylogenetic predictors retained after forward selection for the taxonomic and functional approaches

Determinant	Variable	Taxonomic		Functional	
		Cumulative R_{adj}^2 (%)	p	Cumulative R_{adj}^2 (%)	p
Spatial	AEM-1	17.4	0.02	0.28	0.07
	AEM-2	10.5	0.01	29.7	0.21
	AEM-3	18.1	0.33	17.8	0.08
	AEM-4	17.7	0.31	12.7	0.02
	AEM-6	17.6	0.46	23.1	0.08
Environmental	Width	15.7	0.01	14.7	0.11
	Depth	16.2	0.85	11.6	0.60
	Elevation	28.4	0.01	5.2	0.01
	Temperature	29.2	0.14	18.1	0.16
	Pebble/gravel	31.8	0.59	9.8	0.12
	Coarse sand	32.4	0.06	7.1	0.91
	Fine sand	30.0	0.72	1.7	0.96
	Silt/clay	28.5	0.70	14.2	0.91
	pH	31.2	0.50	16.2	0.55
Phylogenetic history	Auchenipteridae	29.3	0.08	18.8	0.28
	Callichthyidae	31.3	0.37	12.9	0.26
	Characidae	19.3	0.01	8.6	0.04
	Cichlidae	30.2	0.64	18.7	0.34
	Crenuchidae	26.0	0.13	10.4	0.83
	Curimatidae	28.9	0.60	4.4	0.93
	Erythrinidae	27.1	0.78	19.1	0.34
	Heptapteridae	31.2	0.14	14.3	0.24
	Loricariidae	21.4	0.90	12.1	0.15
	Poeciliidae	23.8	0.03	18.6	0.13
Synbranchidae	24.6	0.80	15.1	0.72	

The Cumulative R_{adj}^2 (%) corresponds to the R_{adj}^2 values of each variable within the RDA models which contain all the other variables. Statistically significant ($p < 0.05$) variables, highlighted in bold, were retained

functional groups (Table 4). For example, after controlling for basin identity, the phylogenetic component structured by the environment (PE = 6%) and the pure phylogenetic component (Pp = 5%; $p = 0.03$) explained most of the functional distribution (Table 4). Moreover, the pure environmental component increased in importance (Ep = 3%, $p = 0.003$), while the pure spatial component decreased (Sp = 2%; $p = 0.02$) when compared to the results of the analysis without controlling for hydrographic basin identity.

A moderate proportion (28.8%) of the species distribution was explained by the environmental

variables (Pseudo- $F = 1.47$; $p = 0.03$), especially channel width and elevation (Table 3). The first RDA axis (11.7%) was constituted by elevational gradient, with positive scores corresponding to narrow streams and negative scores to wide streams. Temperature (negative scores) and depth (positive scores) explained the second RDA axis (4.7%). Most species occurred in wider and moderately elevated streams (< 250 m a.s.l) (RDA axis 1; Fig. 2a), without a nested distribution ($NODF = 48.11$; $p = 0.75$; Fig. 3a). The distribution of functional groups was associated mainly with elevation (Fig. 2b). Small species feeding mainly on small insects (Group 1) and

Table 4 Summary of results of variation partitioning of environmental, spatial, and phylogenetic history factors (%) on taxonomic and functional approaches with and without control for basin identity

	Without basin identity control				With basin identity control			
	Taxonomic		Functional		Taxonomic		Functional	
	R^2_{adj} (%)	p	R^2_{adj} (%)	p	R^2_{adj} (%)	p	R^2_{adj} (%)	p
Ep	3	0.209	2	0.231	4	0.134	3	0.003
Sp	< 0	0.403	13	0.001	1	0.326	2	0.020
Pp	1	0.279	7	0.021	2	0.220	5	0.003
SE	1	–	1	–	2	–	4	–
PE	7	–	2	–	5	–	6	–
SP	< 0	–	< 0	–	2	–	2	–
SPE	17	–	1	–	20	–	< 0	–
U	71	–	76	–	80	–	80	–

Statistically significant components appear in bold ($p < 0.05$). Negative R^2_{adj} values are shown by < 0 (see Table 3 for variables selected by forward selection)

Ep pure environmental, Sp pure spatial, Pp pure phylogenetic history, SE spatially structured environmental, PE phylogenetically structured environmental, SP spatially structured phylogenetic, SPE spatially and phylogenetically structured environmental, U unexplained

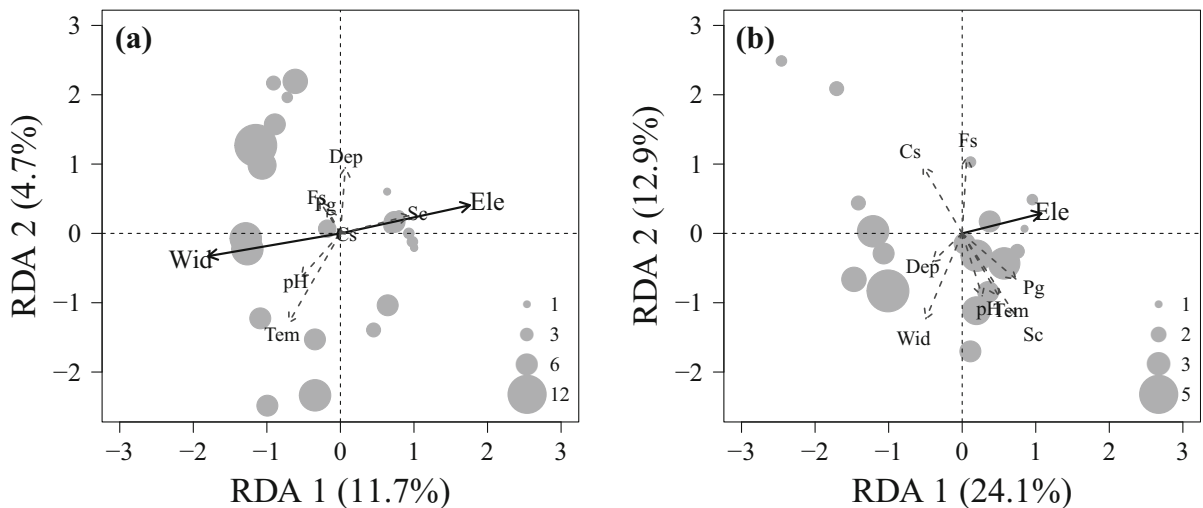


Fig. 2 Ordination of 26 stream fish assemblages from forest enclaves in semiarid Brazil, based on the taxonomic structure (a) and functional groups (b). Loadings of significant and non-significant environmental determinants are represented by

continuous and dashed arrows, respectively. The size of the circle represents the taxonomic richness and the functional groups in each sampling unit

carnivorous species (Group 2) occurred predominantly at intermediate to elevated altitudes (RDA axis 1; Fig. 4), while small nektobenthic substrate-sifting species (Group 3) and benthic grazers feeding mostly on detritus (Group 4) predominated in wider streams with fine sandy substrates (intermediate elevation;

Fig. 4). Piscivorous and nocturnal species (Group 5) were markedly common in low-elevation streams (< 200 m; Fig. 4). These distribution patterns followed the different elevational zones and explained the observed functional nesting patterns ($NODF = 76.23$; $p = 0.007$; Fig. 3b).

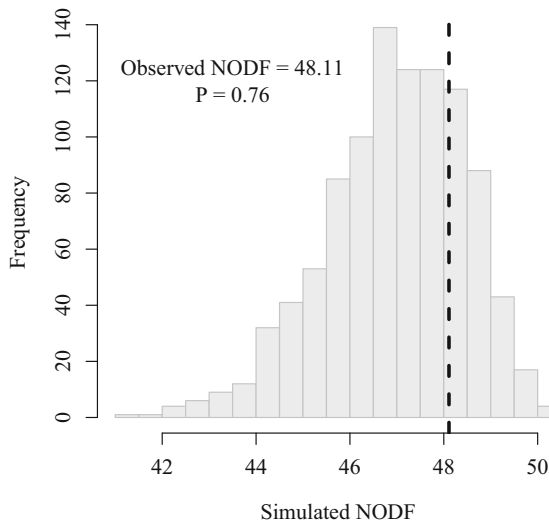
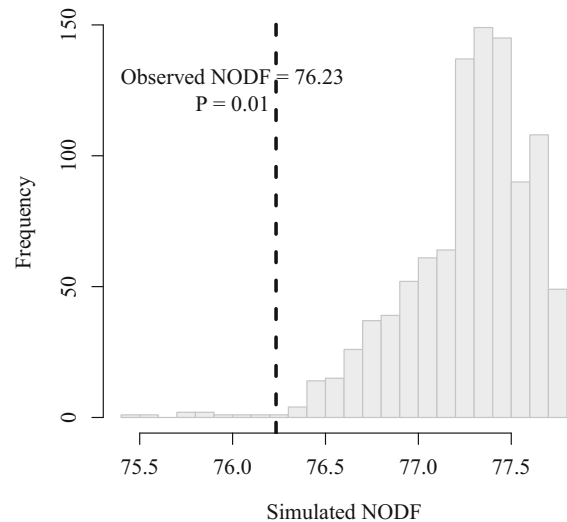
(a) Taxonomic**(b) Functional**

Fig. 3 Simulated (bars) and observed (dashed line) values from the analysis of nestedness overlap and decreasing fill (*NODF*) for taxonomic **(a)** and functional **(b)** composition of stream fish

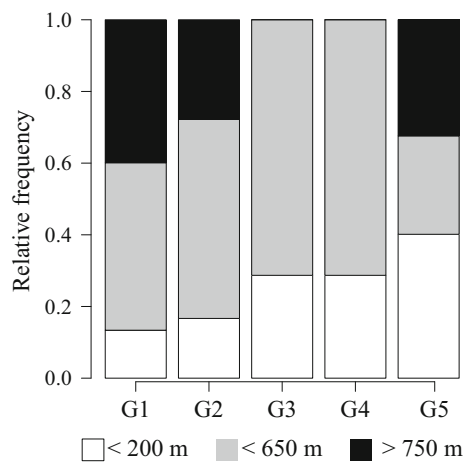


Fig. 4 Relative frequency of individuals from each functional group of stream fish (G1–G5) at each elevational zone from forest enclaves in semiarid Brazil. For details of each group, see Table 2

Discussion

Our study brings new information about community structure in headwater streams, where niche-based processes are expected to predominate (Landeiro et al., 2011; Siqueira et al., 2012; Schmera et al., 2017; Zbinden & Matthews, 2017). By partitioning the variance of taxonomic structure, we separated the

assemblages from forest enclaves in semiarid Brazil. Dashed lines are *NODF* when rows of the incidence matrices were reordered following the first RDA axis (see “Data analysis”)

purely phylogenetic history (P_p) from the spatially and environmentally structured fish fauna. We demonstrated that the inclusion of phylogenetic history as a predictor can generate relevant information on the main factors structuring local communities. We also found that elevation gradients promote functional group nestedness, probably due to the differential dispersal capacity of species from different clades and environmental affinities. Taken together, our results help to clarify the relationship between historical and contemporary determinants in current patterns of fish biodiversity in headwater streams from semiarid Brazil.

Fish community assembly

Recent studies on fish community have identified environmental variability (E_p , in this study) as the main component in explaining patterns of biodiversity (Cottenie, 2005; Sternberg et al., 2014; Viana et al., 2016). However, in our study, environmental conditions were not more important than the phylogenetically structured environmental component (PE). The importance of the phylogenetic history is reflected in the wide distribution of the clades Characidae and Poeciliidae, which may also be one of the explanations for the low importance of the spatial components in the

taxonomic approach (spatial homogenization). Two major geological events were likely responsible for these findings in elevated streams in semiarid Brazil: marine incursions during Plio-Pleistocene in coastal areas, and the confluence of river systems resulting from subsequent headwater captures (Hubert & Renno, 2006; Dias et al., 2014). Headwater captures consists of connecting different river basins after a historical event (Dias et al., 2014). In the studied region, the geographic isolation of the three river basins was interrupted 400,000 years ago when, after a glacial event, the course of the São Francisco river was modified, generating a dispersion corridor to the Jaguaribe and Coreau river basins (Mabessone, 1994). These historical events appear to be responsible for the similarity of the three basins in terms of the phylogenetic and spatial structure of their fish faunas. Based on the known history of the evolutionary radiation of the South American ichthyofauna (Lévêque et al., 2008), it was expected that species from the Characidae family would be very important in structuring local communities. However, the selection of the clade Poecilidae (explained by the high occurrence of the introduced species *P. reticulata*) alerts us to the role of anthropic interventions in modifying the dynamics of local communities. Indeed, introduction of non-native species cannot be ruled out as a driver of taxonomic homogenization (Villéger et al., 2014). This becomes still more serious in view of the ability of such species to interfere directly in ecosystem functioning (Reznick, 1982).

Species composition was weakly explained by the identity of the hydrographic basin. Similar results were found by Heino et al. (2017), suggesting that spatial-environmental heterogeneity increases with increasing sampling scale. In fact, Rodrigues-Filho et al. (2016) found that the biotas of these two humid enclaves have similar species composition. However, variation in functional group composition was dependent on the biogeographic factor of the drainage basins. Therefore, we agree with Heino et al. (2017) that measuring biogeographical effects on local community variation is a difficult task. Thus, we suggest that further assessments should explore the main factors determining the composition of the functional groups after controlling for the hydrographic basin.

Pure components (Ep, Sp, and Pp) in partitioning analyses should be interpreted with caution because the environmental gradients capable of influencing the

community are difficult to quantify: variances are underestimated, whereas the spatial component is overestimated (Smith & Lundholm, 2010; Vellend et al., 2014). This problem has been documented mainly for environmental and spatial components, but it probably applies to other components as well (e.g., phylogenetic, biogeographical, connectivity). Nevertheless, our findings suggest the opposite pattern: large-scale spatial factors (AEM-4) and phylogenetic history were of greater importance in determining functional group composition. This may be due to functional differences in terms of dispersal capacity, associated with strong environmental selection and the complexity of the drainage network in headwater regions (Tonkin et al., 2018).

This result is not in agreement with the hypothesis of the drainage network position, which predicts greater importance for environmental conditions in headwater streams (Brown & Swan, 2010). This is indicated by the high importance of processes based on dispersion and phylogenetic history, reinforcing the emerging topic of context dependence in aquatic systems (Tonkin et al., 2016; Schmera et al., 2017). In fact, spatial structuring driven by dispersion (e.g., dispersions limitation and mass effect) has also been observed in headwater streams, to be an important structuring factor (Mykrä et al., 2007; Cetra et al., 2017). Thus, our results highlight the importance of combining environmental, spatial, and historical (SPE) factors when analyzing the factors shaping the structure of current local fish communities. While our results agree with the major community assembly theories, in which phylogenetic history and spatial connectivity are key to selecting the regional species pool that will be filtered by local environmental conditions (Emerson & Gillespie, 2008), they are novel because they apply to communities of fish from headwaters of streams in a semiarid area.

Nesting patterns in headwater streams

As expected, species richness was greatest at intermediate altitudes and lowest in narrow and elevated streams (see Fig. 2a). Wider streams generally offer more diversified habitats, an important feature in the structuring of fish communities (Mattos et al., 2014), and tend to be slightly warmer and deeper, so favoring greater species diversity (Ibanez et al., 2007; Báldi, 2008). However, the gradients of elevation and width

do not show nested patterns in species composition. On the other hand, we observed nesting patterns for functional groups which could be the result of (1) physical isolation preventing dispersal (Hill et al., 2017); (2) local communities being connected, but functional groups containing species with varying dispersal capacities (Thompson & Townsend, 2006; Heino, 2011, 2013), and (3) strong environmental gradients (Schmera et al., 2017). Based on the result of the partitioning analysis (while recognizing its limitations) and RDA, we believe the second and third options provide the most plausible explanation: the functional groups include species with varying dispersal capacities responding differently to the environmental gradient. Furthermore, the selection of eigenvectors with wide distribution (AEM-4) suggests that dispersal limitation is more important than mass effect when explaining the local community structure within each basin (Heino et al., 2015).

Studies using functional traits to evaluate the influence of niche or dispersal-based processes in local communities usually classify fish as either good and bad dispersers (e.g., Padiál et al., 2014; Tolonen et al., 2018; but see Wojciechowski et al., 2017). Bad dispersers have spatially structured distribution, while good dispersers will spread as far as environmental conditions permit. In the current study, species were grouped canonically according to functional traits. We could thus explore functional traits responsible for the phylogenetic structure of fish communities, in line with habitat complexity (stream width/elevation relationship). Despite adopting a non-conventional functional approach to specifically explore the factors responsible for local fish community structure, our results also agree with those of studies that simply classified species into good and bad dispersers.

In river ecosystems, elevation gradients are well known for promoting species composition modifications in terms of habitat use, feeding, and locomotion (Jaramillo-Villa et al., 2010). In streams at lower altitudes (< 200 m), nocturnal species that capture their prey by ambush were more strongly represented. These lowland streams were wider, favoring species with high maneuverability (e.g., Cichlidae), that rely on macrophytes for ambushing their prey (Ribeiro et al., 2016). At intermediate elevations (> 200 and < 650 m), streams were generally narrower and substrate composed of pebble and gravel were more common. Here detritivorous and invertivorous species

occurred in greater abundance. Species of these two groups show high adaptive specificity to riffles habitats, and both of them have low dispersal capacity (Pagotto et al., 2011). An abiotic and biotic transition occurs in streams located above 750 m, as there are smaller numbers of pools, fewer macrophytes, and greater inputs of allochthonous material (Rodrigues-Filho, pers. obs.). In such streams, nektonic species that feed on small insects carried along by the stream are more commonly found. Due to their fusiform shape, these species have high dispersion capacity (Makrakis et al., 2010), which explains their often extensive distribution in streams at other altitudes. Similar patterns were observed by Jaramillo-Villa et al. (2010), and reflect the adaptation of these species to highly hydrological complexity of headwater streams (Pusey et al., 2010). Lomolino (2001) proposes that the modification of the diversity and species composition along altitudinal gradients occurs because higher regions are more isolated. Such isolation together with the low dispersion capacities and high environmental affinities of the species present in such regions promotes differentiation of functional composition, thus explaining the nesting patterns for the streams within the forest enclaves studied here. Indeed, similar results were reported by Taylor & Warren Jr. (2001). According to these authors, extirpations of populations at higher altitudes promote significant nestedness at lower altitudes.

Conclusions

We highlight the joint action of space, environment, and phylogenetic history in determining the fish community structure in the highlands of semiarid Brazil. Together with environmental and spatial predictors, phylogenetic history shapes the taxonomic and functional distributions functional groups of headwater streams. Specifically, we have confirmed that predictive models based solely on environmental conditions are not adequate to understand the functioning of in headwaters. Thus, exploring the true reasons for the phylogenetic history of the study region and the dispersal capacity of the species becomes critical points for an understanding of the local dynamics of headwater fish communities (Eros et al., 2012). Likewise many other articles using variation partitioning to explain community structure,

we usually reported low explanation powers (Landeiro et al., 2011; Cetra et al., 2017; Zbinden & Matthews, 2017), preventing broad generalizations considering determinants in metacommunity structure. Even so, we do highlight the joint action of space, environment and phylogenetic history in determining the fish community structure in the highlands of semiarid Brazil. In addition, we have also shown that a basin's identity is important for the functional approach to community composition analysis, suggesting that idiosyncratic processes are more common than imagined in biological systems. This idiosyncrasy can be explained by the high hydrological variability of headwaters and the rapid response of the functional structure of communities to changes in the environment compared to the taxonomic structure (Poff, 1997).

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