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What governs the functional diversity patterns of fishes in the headwater streams of the humid forest enclaves: environmental conditions, taxonomic diversity or biotic interactions?

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Abstract The relationship between functional and taxonomic diversity is a major issue in ecology. Biodiversity in aquatic environments is strongly influenced by environmental gradients that act as dispersion and niche barriers. Environmental conditions act as filters to select functional traits, but biotic interactions also play a role in assemblage structure. In headwater streams, the relationship between functional and taxonomic diversity remains unclear. In this study we investigated how environmental conditions, taxonomic diversity and biotic interactions influence the spatial distribution of traits and functional diversity in stream fish species. Standardized sampling of fish species was carried out in 50 m sections of 16 streams located in rainforest enclaves in a semiarid region of Brazil (Caatinga biome). The functional diversity indices displayed different responses to the predictor variables used. Functional richness was mainly influenced by environmental conditions, while functional evenness was mostly determined by taxonomic diversity. On the other hand, functional dispersion was explained by a combination of environmental conditions and taxonomic diversity. The spatial distribution of fish species with the same functional traits was random, indicating that biotic interactions are not a strong predictor in these ecosystems. Channel width, pH and substrate were the most important variables in the spatial distribution of the functional traits of the fish species. Our results suggest that the functional structure of fish assemblages in headwater streams depends mainly on environmental conditions and taxonomic diversity.

Keywords Fish community · Northeastern Brazil · Functional traits · Environmental filters · Taxonomic diversity

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Introduction

One of the recent issues in Ecology is to understand the relationship between the three different components of biodiversity (taxonomic, functional and phylogenetic). In the last decades, the growing interest in comparing

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these components has increased significantly and a series of studies has compared mainly the taxonomic and functional approaches (Hoeinghaus et al. 2007; Pool et al. 2014). Study area and the sampling scale directly influence the results of such comparisons. As shown by Heino et al. (2007) in large-scale studies, climate, historical and regional factors are the main determinants of taxonomic diversity, while local factors are the main determinants of functional diversity. On the other hand, in small-scale studies conducted in headwater streams, Carvalho and Tejerina-Garro (2015a) showed strong correlation between the patterns of taxonomic and functional diversity although relationships have been differed across habitat types within a catchment.

In aquatic systems, biodiversity is strongly influenced by environmental gradients that act as barriers that limit species dispersal (Olden et al. 2010) or their environmental requirements (Mattos et al. 2014; Terra et al. 2016). Poff (1997) suggested that the local environmental conditions act as filters, selecting the functional traits of the most adapted species. However, environmental conditions are not the only factors influencing biodiversity. At local scales, the effects of biotic interactions via competition and predation are also seen as important agents for the structure of fish assemblages (Taylor 1996; Jackson et al. 2001). From the interaction of these two factors, two ecological processes may be obtained, depending on which of the two forces (environmental or biotic) prevails over the other. Great abundance of redundant species can be observed when environmental conditions act as the main agents of functional diversity (Mouillot et al. 2007). Otherwise, assemblages of functionally complementary species are observed when biotic interactions prevail over environmental conditions (Mouillot et al. 2007).

Headwater streams, located upstream the main rivers, are classified between the first and third orders (Vannote et al. 1980). In these environments, with high environmental heterogeneity and variability, it can be observed that environmental conditions prevail over biotic interactions of species and that the taxonomic diversity is low, presenting less structured assemblages (Jackson et al. 2001). In some cases, however, the association between the environmental conditions and the diversity of functional traits does not present significant relationship (Poff and Allan 1995). In fact, the inconsistency in supposing that the environmental conditions is the main agent of the diversity of functional traits can be explained by its high variability, as well as regional species pool, capable of colonizing a certain region. These observations are explained by studies

that compared assemblages in similar environmental conditions and which have high functional similarity (Lamouroux et al. 2002) with others that present high functional dissimilarity (Carvalho and Tejerina-Garro 2015b). Therefore, there is consensus in inferring that environmental conditions are more important than biotic interactions, as regards patterns of functional diversity, in headwater streams.

In this study, a set of tropical headwater streams was used to evaluate how the patterns of functional diversity and individual distribution of species functional traits respond to environmental conditions, taxonomic diversity and biotic interactions of fish species. We believe that the patterns of functional diversity and the distribution of functional traits will be governed mainly by the environmental conditions, and that these assemblages will be composed of a high proportion of functionally redundant species. In this way, we evaluated (i) the relationship of taxonomic diversity and environmental conditions to functional diversity and individual distribution of functional traits; (ii) the relationship between the environmental variables and the functional traits; and (iii) if the functionally similar species present spatial segregation different than that expected at random.

Materials and methods

Study system and data sampling

This study was conducted in two humid forest enclaves located in semiarid Caatinga biome, Araripe and the Ibiapaba Plateaus, only in rainy season, since most of the rivers are intermittent. Ecosystems usually called Altitude Swamps (*Brejos de Altitude*), due to their climate and hydrological characteristics, are located in these two plateaus. The *Brejos de Altitude* are enclaves of rainforest occurring in the Brazilian Northeast, presenting rainfall indices relatively high (1,000 mm per year) for the semiarid region. These ecosystems have maximum altitude of around 1,000 m, presenting perennial water bodies, meanwhile most of the semiarid Caatinga rivers are intermittent (Rosa et al. 2003). In this study, 16 first through third order streams located at an altitude of 400 to 900 m were sampled, covering three drainage basins (Fig. 1). Application of a PERMANOVA exploratory analysis in software R using the Sørensen's distances showed that the taxonomic and functional composition between the three

basins were significantly similar ($P > 0.05$ for all comparisons). Therefore, we will not evaluate the taxonomic and functional relationship between river basins.

The streams were characterized environmentally, based on physical and chemical variables, according to a standard protocol proposed by Mendonça et al. (2005). In this protocol, stretches of 50 m, initially sealed with 12 mm nets to prevent the fish from escaping, was delimited and subdivided by four equidistant transects, in which average values of environmental conditions were measured. Width (m) was measured at each transect in each stream. At each of four transects we measured depth (m) at 10 cm intervals along each transect across the stream (totalizing 36 subsamples), starting 10 cm from the margin. At the same points, we registered the type of substrate using the classification of Gonçalves and Braga (2012) to pebble/gravel (1-10 mm), coarse sand (0.1-1 mm) and fine sand (0.05-0.1 mm), using ruler. Each class was estimated as the proportion of points of each substrate type in relation to all substrate founds in each stream. The water velocity ($m.s^{-1}$) in the channel was computed three times in each transect, using the distance traveled by the Styrofoam ball. Black and white photographs in North, South, East and West directions to each transect using a SONY Cybershot (A530) camera, with 5.8-23 mm lenses were taken to measure the mean canopy cover (%) in Image J software. Pictures were taken immediately above (about 2.0 m high) in the middle of each transect, by the same photographer. Average values of these variables were obtained from the values computed in each transect. The habitat volume (m^3) was measured using the values for area and average depth of each transect. Water temperature (°C) and dissolved oxygen ($mg.L^{-1}$) were measured with a Hanna HI9146 instrument and the pH with a PHscan 30 instrument only in more downstream point of 50 m. The altitude (m) of the sample point and the geographic coordinates were measured using a Garmim eTrex 10 Portable GPS.

After environmental characterization, fish were caught with a trawl net (5.3 m^2 and mesh size of 14 mm between opposing knots), a sieve net (0.7 m^2 and mesh of 1 mm between opposing knots) and a seine net (1.3 m^2 and mesh of 2 mm between opposing knots), in a fishing effort of four people/hour. The aim of utilizing these three gears was to explore all possible habitats in the stream (i.e. riffles, rapids and pools) and avoid selectivity of each gear (Uieda and Castro 1999). All samples were conduct during daytime. The fish were euthanized by immersion in anesthetic solution of Eugenol, and subsequently fixed in 10% formalin and later preserved in 70% alcohol.

Functional traits

We have selected four functional categories to describe the functional structure of headwater stream fish. These categories were divided into 20 functional traits, which gave basic information about diet, feeding tactic, use of the habitat and biomass (Table 1). These functional traits were used to calculate the indexes of functional richness, evenness and dispersion (Villéger et al. 2008; Laliberté and Legendre 2010). Functional richness (FRic) was obtained using the convex hull volume (Cornwell et al. 2006) and represents the multifunctional space occupied by an assemblage. High values of convex hull indicate assemblages with high functional richness. FRic does not have a limit value since it quantifies the absolute value of convex hull filled by each assemblage. Functional evenness (FEve) measures the regularity with which the functional space is occupied by species abundance. FEve decreases when species abundance is not regularly distributed or when the functional distance between the species is less regular. Functional dispersion (FDis) represents the average distance of the species in the multifunctional space to the centroid of all species. The centroid of the species in the FDis is displaced in the multifunctional space, weighted by the abundance of species. Both FEve and FDis vary between 0 and 1. The relationship between FEve and FDis reveals if the assemblages are composed of complementary species (FEve and FDis are low) or redundant species (FEve and FDis are high). FRic, FEve and FDis were calculated using the FD function (Laliberté and Legendre 2010) from the R statistical package, version 3.1.2 (The R Foundation for Statistical Computing). To resume of environmental conditions and biotic data per stream see Appendix Table S1.

Statistical analysis

The relationships between the indices of functional diversity and traits (dependent variables) to taxonomic diversity, obtained through the taxonomic distinctness measure (Warwick and Clarke 1995) and the environmental conditions (predictor variables) were carried out by multiple linear regression. The functional trait matrix was obtained by multiplying the species-trait and site-
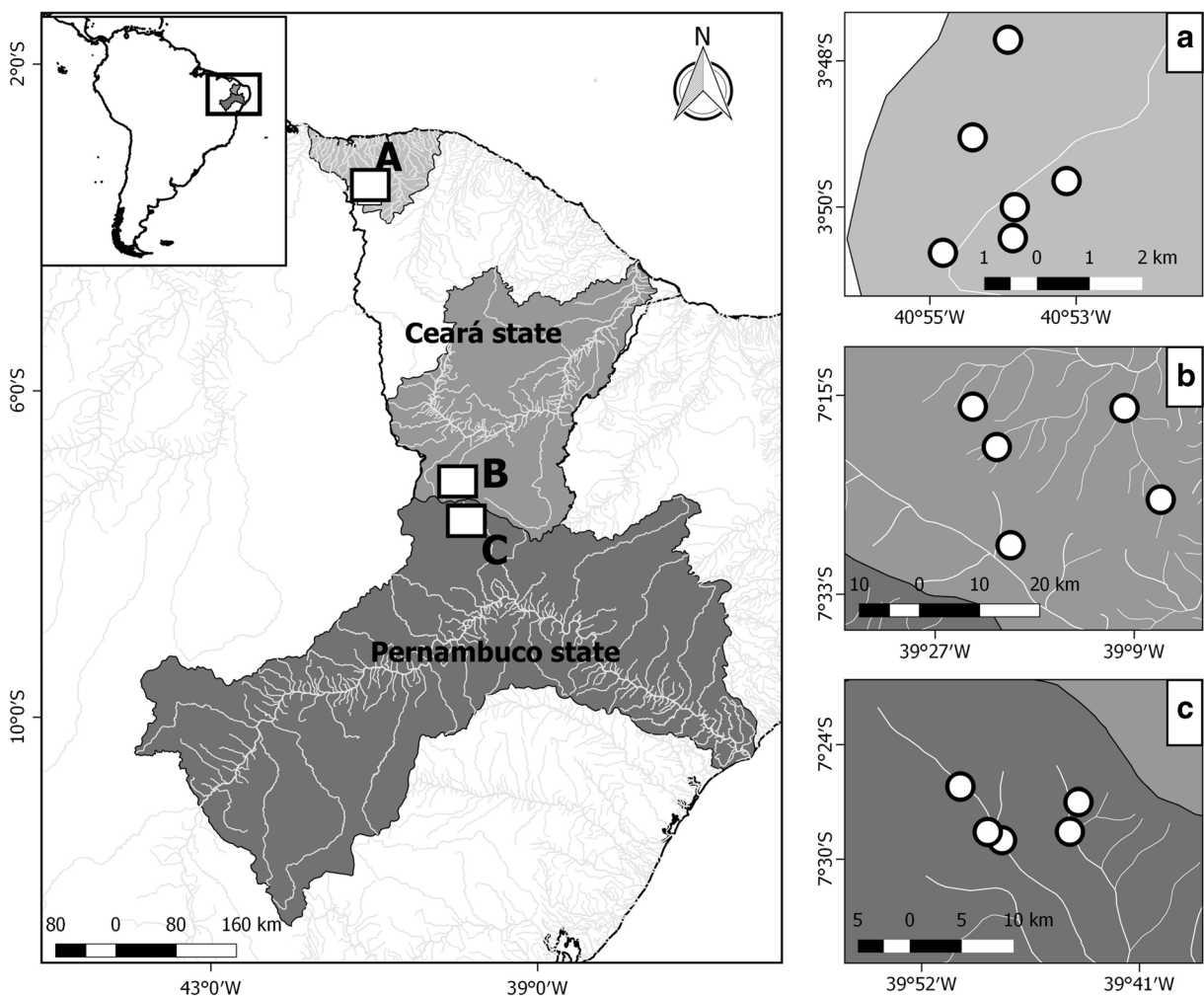
Fig. 1 Sampling in the three drainage basins in the Ibiapaba (northwest of Ceará state *A*) and Araripe (south of Ceará state *B*; and North of Pernambuco state *C*) plateaus. Coreaú River basin (**a**), Jaguaribe River basin (**b**) and São Francisco River basin (**c**)

species matrices, producing a matrix of frequency distribution for the functional traits of the assemblages per stream. To avoid overestimating the importance of environmental conditions (multicollinearity) in the regression models, the following procedure was used for the selection of environmental variables: (i) the variance inflation factor (VIF) was calculated for each variable, and those presenting values above 10 were not used; (ii) a forward selection was conducted using multiple regressions between the dependent variables and those selected by the VIF (width, depth, pH, pebble/gravel, coarse sand and fine sand) in order to select only the significant environmental variables ($P < 0.05$; Blanchet et al. 2008). This procedure is one the two suggested by Friedman

(1991) for the correct selection of models in regression analysis because the use of forward selection only can prevent the identification of a better set of explanatory variables.

In the case of significant relationship between the dependent and predictor variables, partial multiple regressions were conducted in order to quantify the relative effects of the environmental conditions and taxonomic diversity on indices for functional diversity and individual distribution of functional traits (Borcard et al. 1992). This analysis makes it possible to decompose the variance of the dependent matrix into [a] taxonomic diversity only, [b] shared with environmental conditions and taxonomic diversity, [c] environmental conditions only and

Table 1 Functional categories and 20 functional traits used to the fishes sampled in headwater streams in Araripe and Ibiapaba plateaus, with the abbreviations used in subsequent analyses

Trait	Trait categories	Abbreviation
Diet	detritivore	det
	allochthonous insectivore	ali
	autochthonous insectivore	auti
	invertivore	inv
	omnivore	omn
	piscivore	pis
Feeding tactic	water column	wcol
	substrate filterer	ssub
	ambusher	amb
	grazer	gra
	stalker	sta
	night active	nig
	surface	sur
Habitat preference	nektonic	nek
	nektobenthic	nec
	benthic	ben
Biomass	reduced biomass (<0.1g)	rbio
	low biomass (0.1-1g)	lbio
	average biomass (1-5g)	abio
	big biomass (>5g)	bbio

Fig. 2 Explanation variance of significant results for variance partitioning into purely environmental, purely taxonomic (Δ^+), taxonomic environment (Environmental/Δ^+) and unexplained (U) for the indices and for the species individual functional traits. See Table 1 for the abbreviations of functional traits

[d] unexplained variance. Adjusted R^2 was used in order to determine the importance of each fraction of variance partitioning (Peres-Neto et al. 2006).

Since the environmental conditions explained most of the variance of functional trait distribution (Fig. 2 and Table 2), the trait-environment relationship was evaluated using a direct-ordering technique. A Canonical Correspondence Analysis (CCA) was selected to verify the trait-environment relationship using the variables selected by the VIF only. In our analysis, CCA performing the ordination of the species traits (reciprocal average) to be constrained by a multiple regression with overall environmental variables (Johnson 1998), allowed global interpretations of the factors that govern the distribution of functional traits. Similar to the procedure for the selection of multiple regression variables, forward selection was carried out in the CCA to determine the most important environmental variables for the general distribution of the functional traits. Monte Carlo permutation tests with 999 randomizations were carried out to test the meaning of the CCA axes.

On the other hand, the partial multiple regression was conducted to evaluate the relative effects of environmental conditions and taxonomic diversity specifically on indices for func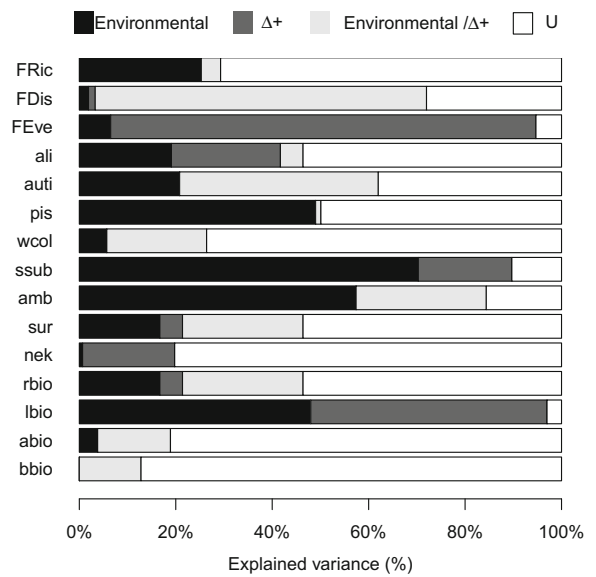tional diversity and individual distribution of functional traits. The value of the partial coefficient for one independent variable (environmental conditions or taxonomic diversity) vary, in general, depending upon the other specific independent variables included in the regression equation (functional diversity and individual distribution of functional trait).

Biotic interactions are also important determinants of the structure of assemblages (Jackson et al. 2001), and part of the variance not explained by any of the variables is probably due to this effect. Co-occurrence analyses based on null models were carried out (Gotelli and Graves 1996) in order to test if negative interactions among species presenting the same functional trait influence their distribution patterns. We tested if species that have same functional trait present non-random pattern of co-occurrence in the three drainage basins in presence-absence matrices, using the C-score index and randomizations using the sequential swap randomization algorithm (Gotelli and Entsminger 2003). All the statistical analyses were conducted in the R software (R Core Team 2013).

Results

Twenty species were collected in the 16 streams. The two families with more species were Characidae and

Table 2 Summary of the multiple regression analyses of the environmental conditions and taxonomic diversity, with the functional diversity indices and for each line separately. (wid) width; (dep) depth; (p_g) pebble/gravel; (c_s) coarse sand; (f_s) fine sand; (tax) taxonomic diversity. See Table 1 for the abbreviations of functional traits

Dependent variable	Model	R^2	F	P
FRic	$y = -7.25 + 1.47\ \text{pH} - 1.33\ \log(\text{wid})$	0.294	4.13	**0.04**
FDis	$y = 10.38 + 4.24\ \log(\text{dep}) - 0.10\ \Delta^+$	0.720	20.36	**<0.01**
FEve	$y = 1.77 + 1.77\ \log(\text{dep}) - 0.09\ \log(\text{p\_g}) + 0.12\ \log(\text{c\_s}) - 0.01\ \Delta^+$	0.499	4.75	**0.01**
det	$y = 13.56 - 0.98\ \text{pH} - 0.46\ \log(\text{p\_g}) - 0.04\ \Delta^+$	0.189	2.16	0.14
ali	$y = 27.89 - 12.62\ \log(\text{c\_s}) - 29.10\ \log(\text{wid}) + 8.29\ \log(\text{p\_g}) - 150.30\ \log(\text{dep}) - 12.62\ \Delta^+$	0.465	3.61	**0.03**
auti	$y = -5.52 + 0.69\ \log(\text{c\_s}) + 2.61\ \log(\text{wid})$	0.621	13.29	**<0.01**
inv	$y = -1.32 + 1.45\ \log(\text{c\_s})$	0.034	1.54	0.23
omn	$y = -46.60 - 3.02\ \log(\text{c\_s}) + 7.30\ \text{pH}$	0.178	2.63	0.10
pis	$y = -0.64 + 0.18\ \log(\text{wid}) + 3.00\ \log(\text{dep})$	0.502	8.58	**<0.01**
wcol	$y = -69.97 + 9.47\ \text{pH}$	0.265	6.42	**0.02**
ssub	$y = 16.26 - 24.53\ \log(\text{dep}) + 3.30\ \log(\text{c\_s}) + 7.86\ \text{pH} - 25.30\ \log(\text{wid}) - 0.38\ \Delta^+$	0.352	4.07	**<0.01**
amb	$y = 7.15 - 0.29\ \log(\text{c\_s}) - 0.31\ \log(\text{p\_g}) + 0.65\ \log(\text{wid}) - 1.66\ \log(\text{f\_s})$	0.845	21.54	**<0.01**
gra	$y = 29.53 - 2.22\ \text{pH} - 0.91\ \log(\text{p\_g}) - 0.10\ \Delta^+$	0.081	1.44	0.27
nig	$y = -0.66 + 0.24\ \log(\text{wid}) + 1.48\ \log(\text{dep})$	0.222	3.14	0.07
sta	$y = -0.48 + 0.06\ \log(\text{p\_g}) + 0.01\ \Delta^+$	0.001	0.68	0.52
sur	$y = 26.47 - 11.84\ \log(\text{c\_s}) - 29.51\ \log(\text{wid}) + 7.77\ \log(\text{p\_g}) - 144.93\ \log(\text{dep}) + 0.95\ \Delta^+$	0.465	3.61	**0.03**
ben	$y = 8.19 - 0.45\ \log(\text{p\_g}) - 0.06\ \Delta^+$	0.034	1.26	0.31
nek	$y = 16.83 - 23.42\ \log(\text{dep}) + 3.28\ \log(\text{c\_s}) + 7.62\ \text{pH} - 24.70\ \log(\text{wid}) - 0.38\ \Delta^+$	0.609	5.68	**<0.01**
nec	$y = -54.59 - 156.58\ \log(\text{dep}) + 1.26\ \Delta^+$	0.210	2.99	0.08
rbio	$y = 26.47 - 11.84\ \log(\text{c\_s}) - 29.51\ \log(\text{wid}) + 7.77\ \log(\text{p\_g}) - 144.93\ \log(\text{dep}) + 0.95\ \Delta^+$	0.465	3.61	**0.03**
lbio	$y = 93.75 - 18.55\ \log(\text{wid}) - 0.64\ \Delta^+$	0.507	8.73	**<0.01**
abio	$y = -60.84 + 8.26\ \text{pH}$	0.190	4.52	**0.05**
bbio	$y = 1.12 + 0.24\ \log(\text{wid}) - 0.21\ \text{pH} + 1.67\ \log(\text{dep})$	0.410	4.48	**0.02**

Callichthyidae (with four species each) and seven families had a single species (Appendix Table S2). The most abundant species was *Poecilia reticulata* (52.4% all individuals) occurring in three basins sampled. The species were characterized functionally by individuals of low biomass and nektonic and nektobenthic habits. The most representative trophic guilds, in number of species, were invertivorous (seven species), omnivores (three species) e piscivores (three species; Appendix Table S2).

The multiple regression models (after the forward selection) for FRic, FEve and FDis showed values between 29.4% and 72.0% in variability (Table 2). Narrower streams or with high pH values presented high and low FRic, respectively. FEve and FDis were negatively influenced by taxonomic diversity, and positively by depth. FEve also presented negative and positive relationships with pebble/gravel and coarse sand, respectively. As for the functional traits, the final multiple regression models showed variability between 0.1% and 84.5%, with the substrate characteristics and the channel dimensions being the most important variables for the explanation of the models (Table 2).

The partitioning of variability for FRic, FEve and FDis showed that the environmental conditions and the taxonomic diversity have different influence on the functional volume, species relative abundance and dispersion in the functional volume (Fig. 2). The environmental conditions showed greater explanatory power (average of 18.7%, minimum of 0.0%, and maximum of 70.3%) for the distribution of functional traits than the taxonomic diversity (average of 7.7%, minimum of 0.0%, and maximum of 88.2%) (Fig. 2).
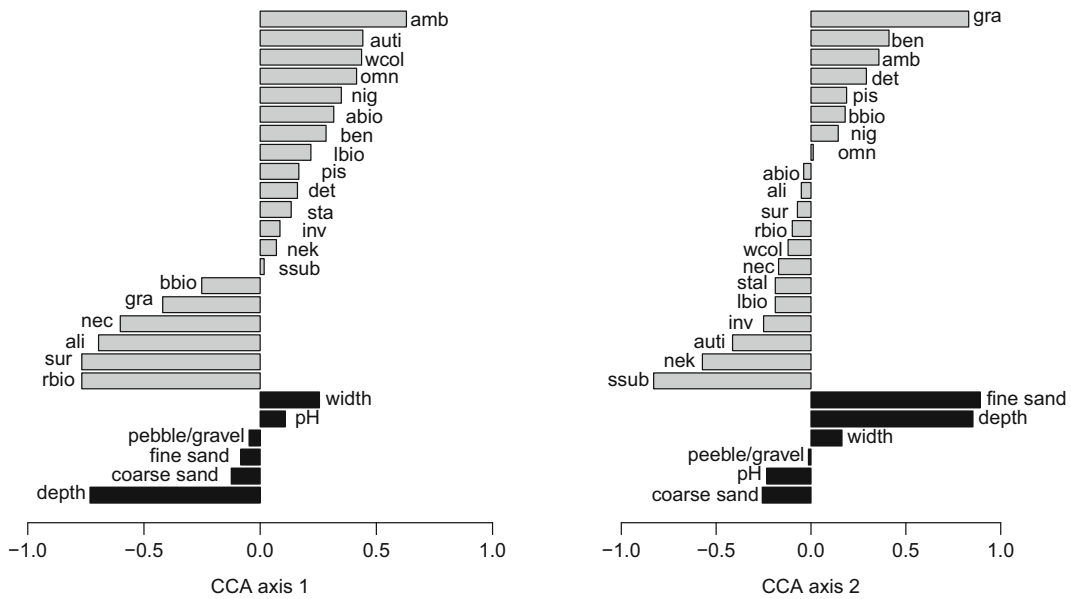
Fig. 3 Plot of the first axis (left) and second axis (right) of the CCA, relating the species functional traits (gray bars) to the environmental variables (black bars). See Table 1 for the abbreviations of functional traits

The first two axes of the CCA explained 29.7% and 12.2% of the variance of functional traits ($P = 0.01$; Monte Carlo test), respectively. The variables width, pH and coarse sand were the only significant variables according to the forward selection ($r^2 = 79.8\%$ and $P = 0.0001$, $r^2 = 74.4\%$ and $P = 0.001$, and $r^2 = 59.0\%$ and $P = 0.01$, respectively). The first axis of the CCA revealed that species of aquatic insectivores present high dominance in deeper streams, while the other guilds occurred more frequently in larger streams. Overall, the two CCA axes showed that functional traits of the same category occur in different environmental conditions (Fig. 3). The co-occurrence analysis showed a non-random pattern of species distribution in the drainage basins (P = 0.03, C-Score$_{obs}$ = 4.73, C-Score$_{simu}$ = 4.40), in contrast to the functional traits, presenting a random pattern of distribution ($P > 0.05$).

Discussion

Our results suggest that environmental conditions influenced the richness and diversity of functional traits, while taxonomic diversity affected mainly the evenness, and together with the environmental conditions, the functional dispersion. The co-occurrence analyses revealed that the interspecific competition between taxa that have the same functional traits show low relevance in the formation of the functional structure of these assemblages. These results suggest that, in the headwater streams analyzed, the functional traits present broad spatial distribution, modifying only their relative frequencies of occurrence according to the environmental conditions or taxonomic diversity. In fact, it has been widely reported in the literature that the environmental conditions are more important for the structure of the fish assemblages than the interspecific competition in various aquatic environments (Hoeinghaus et al. 2007; Erös et al. 2009; Terra et al. 2016). These results can be extended to other regions and taxa, since this has been a recurring pattern for headwater streams (Ostrand and Wilde 2002; Heino et al. 2005). However, the taxonomic relationship among species has been set-aside in studies using the same approach. In this study, this variable showed to be important for evenness and dispersion, important components of functional diversity.

Various theories have been proposed to explain the relationship between the species functional traits and the local environmental conditions. The two best-known ones were proposed by Townsend and Hildrew (1994) and Poff (1997), which affirm that individuals having functional traits that facilitate their occurrence in certain

environmental conditions were more abundant. In the headwater streams studied, the channel dimensions (width and depth), pH and the characteristics of the substrate were the main conditions influencing the species functional traits. Among those, substrate diversity is seen as a key factor, since it offers a wider variety of food resources and refuges for the local fish assemblage (Kemenes and Forsberg 2014). The importance of the environmental filters may be observed in the distribution of functional traits related to the species feeding habits, with increased abundance of aquatic insectivores in deeper streams, while the other trophic guilds decrease. On the other hand, taxonomic diversity influenced mainly the functional traits related to species biomass. The abundance of smaller species (rbio) was related to more taxonomically diverse streams, while less diverse streams presented greater abundance of small species (lbio). Despite the fact that in the first axis of the CCA these two traits are influenced by different environmental conditions, the effect of the taxonomic diversity presented greater relevance in their distributions. Irz et al. (2007) argued that the environmental filters are the main promoters of functional convergence among biogeographic regions. This study was conducted in the same ecoregion, and the environmental conditions, as mentioned by the author, were important to determine the functional structure of these ecosystems. However, the taxonomic diversity appears as a promising measure to understand the distribution patterns of functional diversity.

Functional richness did not present any relationship with taxonomic diversity, while functional evenness and dispersion presented negative relationship, according to multiple regression analyses. Functional richness was influenced by pH and channel width, in a way that streams that have higher values of acidity and a wider channel had lower functional richness. It was observed in an experiment carried out by Dangles et al. (2004) that the natural acidity of aquatic systems promote the decrease in taxonomic richness. Considering that in headwater streams the taxonomic approach presents results similar to the functional approach (Carvalho and Tejerina-Garro 2015a), the increase in acidity can also promote the decrease in functional richness. According to the ecosystem services provided by the functional richness and the increasing habitat degradation, these results are important to help develop plans for the maintenance of functional richness in

these headwater environments, known for their importance in the dynamics of larger river systems (Vannote et al. 1980; Finn et al. 2011).

Streams with lower values of taxonomic diversity presented higher values of functional evenness and dispersion, indicating that the functional space is equally occupied by functionally complementary species. Contrarily, streams with high values of taxonomic diversity have assemblages where the functional space is filled unevenly by functionally similar species, resulting in assemblages with a high proportion of redundant species. Similar results were found for assemblages of macroinvertebrates and fish of headwater streams (Heino et al. 2008; Carvalho and Tejerina-Garro 2015b), indicating that the repetition of the same pattern in other ecosystems and taxa, we can affirm that in those systems the increase in taxonomic diversity promotes the increase in the number of redundant species. This result does not corroborate the low diversity of species and less structured assemblages found in those environments (Jackson et al. 2001), suggesting that the assemblages in headwater streams present a complex functional dynamics, different than what has been proposed by Vannote et al. (1980). In fact, in this study, the taxonomic diversity varied between the minimum and maximum values, indicating assemblages composed exclusively of one single species and assemblages composed of totally different species (different orders).

The effect of interspecific competition has been considered important in small-scale studies of freshwater fish assemblages (Jackson et al. 2001), being essential for various structural processes (Angermeier and Winston 1998). In this study, the effect of the interspecific competition did not present any influence on the distribution pattern of species that have the same functional trait. Our result has been corroborated by others that show greater importance of the environmental conditions for fish structures in streams (Peres-Neto 2004; Erös et al. 2012; Carvalho and Tejerina-Garro 2015c). Since this study was carried out in headwater streams, known for presenting high environmental heterogeneity and low species richness, the effects of interspecific competition are minimized, favoring the coexistence of functionally similar species (Grenouillet et al. 2004).

Most studies about headwater streams evaluate the taxonomic and functional structures along altitude gradients, with few of those strictly exploring those high-altitude environments (comprising exclusively first and third order streams). Specifically in the case

of headwater streams of the Caatinga's humid forest enclaves, the relationship between taxonomic and functional diversity is strong, indicating that one approach may substitute the other. In this study, the environmental conditions and the taxonomic diversity influenced different components of functional diversity. Overall, the environmental conditions were more important for the traits and richness functional, while taxonomic diversity was more important for functional evenness and dispersion, together with environmental conditions. The importance of these two factors for the distribution of the functional traits and the FRic, FEve and FDis patterns prevailed over the species biotic interactions, indicating that the interspecific competition in those headwater streams is low. These results, together with others conducted in headwater streams (Heino et al. 2005; Carvajal-Quintero et al. 2015), guide the efforts to better understand how they work. To understand how the fauna in these regions is organized both in a taxonomic and functional way appears as a promising topic for future research, since headwater streams are important to maintain the diversity of a wide range of aquatic systems (Vannote et al. 1980; Meyer et al. 2007).

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