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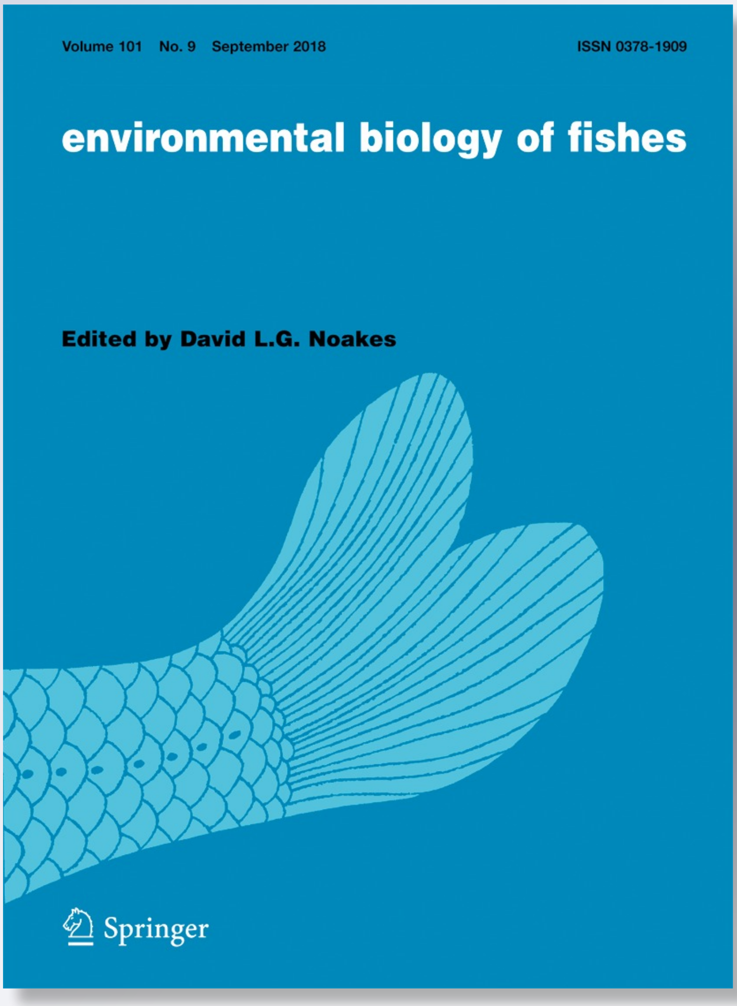

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Using the relationship between taxonomic and functional diversity to assess functional redundancy in streams of an altered tropical watershed

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Abstract The relationship between taxonomic and functional diversity indices has been used to better describe and understand the structure of biological communities. Functional diversity is expected to have an asymptotic relationship with species richness because at some point, the addition of new species will increase some of the already established functional groups (functional redundancy). However, the asymptotic relationship may not be reached in intermediately disturbed systems once many intolerant species that would have played a redundant role or even represented some functional groups have been lost. This study aimed to address such a relationship (taxonomic and functional indices) and to evaluate the functional redundancy in intermediately disturbed streams in the Atlantic Rainforest domain. We expected a positive linear relationship between taxonomic and functional diversity; however, we did not expect to find an asymptotic relationship between richness and functional diversity because of the loss of many intolerant species caused by anthropogenic uses. The taxonomic diversity indices were Species Richness (SR) and Simpson's Diversity (SD), while the functional diversity indices were the Functional Richness (FRic) and Functional Dispersion (FDisp). The two taxonomic and two functional diversity indices showed a significant positive relationship that never reached an asymptote, suggesting low functional redundancy in the fish communities. Our results indicate that care is needed in the management of the studied streams because assemblies with low functional redundancy are more susceptible to loss of functions in the case of species loss.

Keywords Freshwater fishes · Streams · Ecology · Traits

Introduction

Diversity indices based on taxonomic composition have been widely used as descriptors of community structure and as tools to assess environmental changes across changing gradients. Recently, some concerns have been raised about the limitations of these classic taxonomic indices because they consider only species abundance and richness, omitting the identity of species and their role and function in the ecosystem (Mokany et al. 2008). This fact limits their predictive capacity for community structure and functioning (Diaz and Cabido 2001; Ricotta 2005; Cianciaruso et al. 2009). On the other hand, the rise of functional diversity indices enabled the discussion and better understanding of ecosystem

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functioning (Cianciaruso et al. 2009). These indices are related to the functions (e.g., nutrient cycle, defence against predation, resource acquisition and storage) that species develop as part of their role in the ecosystem (Diaz and Cabido 2001; Manna et al. 2013), considering their individual characteristics and their interaction with other species (Mokany et al. 2008). Functional diversity is based on species functional traits that are measurable expressions of the form, physiology, behaviour, ecology or life cycle of an organism in the environment (Frimpong and Angermeier 2010).

The concept of functional redundancy as the number of taxonomically distinct species that have similar ecological functions (Walker 1992) has become the focus of some ecological questions. Mainly, this is because the level of functional redundancy is related to the susceptibility of communities to the loss of species (Sasaki et al. 2009), and how the loss of diversity affects the ecosystem is not clear (Fetzer et al. 2015). Therefore, determining the relationships between taxonomic and functional diversities that imply the analysis of functional redundancy has important implications for predicting the consequences of disturbance or management regimes for the functioning of a given ecosystem (Sasaki et al. 2009). Although the number of studies that relate taxonomic and functional diversity indices (see Hoeinghaus et al. 2007; Teresa and Casatti 2012; Cheng et al. 2014; Carvalho and Tejerino-Garro 2015; Cilleros et al. 2016) and investigate functional redundancy (see Micheli and Halpern 2005; Halpern and Floeter 2008; Rice et al. 2013; Mouillot et al. 2014; Casatti et al. 2015; Aguilar-Medrano and Calderon-Aguilera 2016) of different communities has grown, there are many questions to be answered about this issue. Some of these questions are, for example, how these indices are related and how this may reflect the functional redundancy of biological communities.

Streams are a good system in which to analyse the relationship between functional and taxonomic diversity and thus to investigate functional redundancy. These systems are suitable to this investigation because they are dynamic water bodies with complex spatial heterogeneity (Schlosser 1991) and high endemism (Ribeiro 2006), and they are highly vulnerable to environmental changes, mainly those that result in habitat homogenization. In the present study, we selected five Neotropical streams that are moderately altered (i.e., although suffering from anthropogenic influences, they still maintain considerable habitat diversity to support fish fauna) to test for relationships between taxonomic and functional diversity indices and their use to detect functional redundancy of fish communities. We hypothesized that these indices are positively related and that intermediately disturbed systems present low redundancy of functional groups, even with increasing species richness.

Materials and methods

Study area

We conducted this study in five streams of the Paraíba do Sul river basin in the Atlantic Rainforest domain, southeastern Brazil. The basin area is approximately 57,000 km^2 and drains one of the most developed industrial areas of Brazil. Its waters are used for industrial and domestic purposes, hydroelectric power generation, and water supply for ca. 15,000,000 people in the cities of Rio de Janeiro and São Paulo. Located in a metropolitan region, the Paraíba do Sul basin has few remnants of Atlantic Rainforest and mostly consists of urban areas interspersed with large areas destined to be used for agriculture and pastures. The climate is mesothermic type Cwa according to Köppen classification, with an average annual temperature of 20.5 °C (18-24 °C) and average annual rainfall of 1500 mm (Carvalho and Torres 2002). The wet season (December to March) has accumulated rainfall between 200 and 250 mm month^{-1}, and the dry season (May to August) has accumulated rainfall less than 50 mm month^{-1} (Marengo and Alves 2005). The streams selected for this study are located along a 30-km stretch in the middle-lower reaches of the Paraíba do Sul basin. These reaches feature an average altitude of 300 m, and the middle-lower section of the Paraíba do Sul River has an extension of approximately 480 km (Marengo and Alves 2005).

Fish collections

Fish sampling was carried out quarterly in two periods: from February 2008 to May 2009 (seven excursions) and from October 2012 to July 2013 (four excursions). Each stream was sampled at two sites (upper and lower stream) in the first period (2008-2009) and at a single site (middle stream) in the second period (2012-2013) (Fig. 1). Sampling effort was standardized to cover a stream length of ca. 100 m. A total of 70 samples were

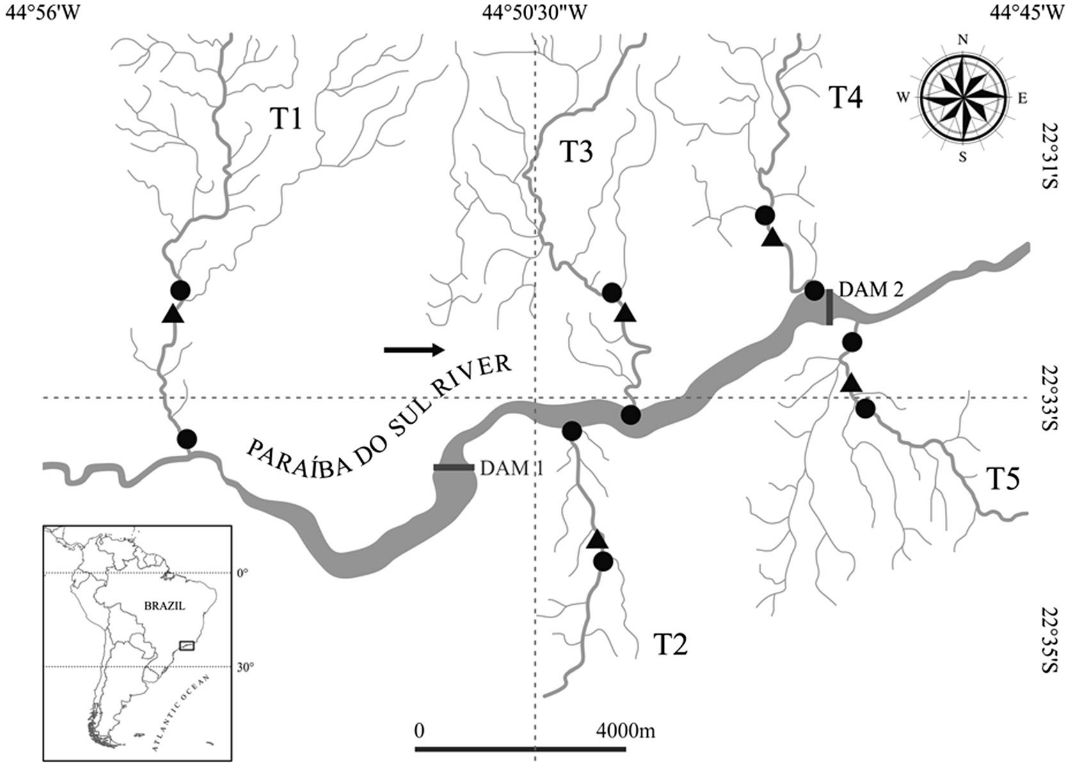

Fig. 1 Study area, Paraíba do Sul river basin, southeastern Brazil. Sampling sites from February 2008 to May 2009 (●), and October 2012 to July 2013 (▲). Streams code: T1, Jacu Stream; T2, Morro Grande Stream; T3, Claro Stream; T4, Entupido Stream; T5, São Roque Stream

performed in the first period (five streams × two sites × seven excursions), and 20 samples were collected in the second period (five streams × one site × four excursions).

In each site, the sampling unit was the sum of all fish collected by using 10 sieves (80 cm diameter; 1 mm mesh size), 10 casting nets (3 m diameter; mesh size from 2 to 3 cm), and approximately one hour of electrofishing with an AC generator (900 W, 220 V, 2.1 A) connected to two hand nets, which were moved from one side of the bank to the other to collect the fish affected by the electric field. The sieve was used to catch fish associated with marginal vegetation, while the casting net collected those species from deep pools.

The fishes that survived the electrofishing procedure and those collected by using other gear were euthanized by hypothermia. After this, the specimens collected were fixed in 10% formalin, and after 48 h, they were preserved in 70% ethanol. Fish were identified to the lowest taxonomic level. Vouchered specimens were deposited in the fish collection of the Laboratório de Ecologia de Peixes, Universidade Federal Rural do Rio de Janeiro, under the numbers LEP-UFRRJ#: 983, 984, 995, 1037, 1039, 1040, 1066, 1072-1075, 1087, and 1088-1090.

Habitat characteristics

In each of the sampled sites, three to five transects were marked. In each transect, at five equidistant points (spaced according to the transect width), we classified the substrate based on its size: mud (<0.06 mm), sand (0.06-2.0 mm), fine gravel (> 2.0-16 mm), pebble (> 16-64 mm), or cobble (> 64-250 mm), following Kaufmann et al. (1999). Moreover, we estimated the types of mesohabitats (cascade, runs/riffles and pools) and types of shelters (macrophytes, twigs, stones and emerging roots). The percentage of different habitat characteristics in each site was estimated visually. After that, we plotted those percentages and visually evaluated the differences in habitat characteristics among streams.

Functional traits

Thirty-two functional traits adapted from Pease et al. (2012) and Villéger et al. (2010) were measured

(Appendix Table S1). Each trait was defined based on the ecological interpretation of morphological characteristics. Twenty-five species were selected according to the abundance and consequent availability of the specimens for measurements of functional traits. For each species, functional traits were measured in 20 adult individuals of a similar size class using a digital calliper. For the species with less than 20 individuals, all collected individuals were measured.

We used quantitative information (measurements) for the functional traits instead of categorical information, which is commonly used in fish studies (e.g., Erõs et al. 2009; Teresa and Casatti 2012). According to Pease et al. (2012), the use of fish traits measured directly from the species enables characterization of several niche dimensions.

Data analyses

We searched for potential patterns of fish assemblage structure by using non-Metric Multidimensional Scaling (nMDS) based on a Bray-Curtis similarity matrix of fish abundance data to assess four factors: stream (five streams), season (dry and wet), time (2008-2009 and 2012-2013), and stream reaches (upper, middle, and lower). Prior to this analysis, the fish abundance data were $\log_{10}$ (X+1) transformed to decrease the influence of very abundant species. The nMDS procedures were performed using the software PRIMER 6 (Clarke and Gorley 2006).

To analyse the redundancy of the functional traits, we performed a Spearman correlation analysis, since we verified through a Shapiro-Wilk test (Shapiro and Wilk 1965) that the variables did not present a normal distribution. We evaluated the correlation between pairs of traits while considering the ecological interpretation of each one and eliminating the trait with the same interpretation that was highly correlated (> 0.8). To eliminate the influence of size on the functional traits, we used a procedure proposed by Pease et al. (2012). To do so, we regressed each measured character on fish standard length (size) and used the residuals from the regression to carry out the Spearman correlation analysis.

We calculated both taxonomic and functional diversity indices. The taxonomic diversity indices were Species Richness (SR) and Simpson's Diversity (SD) (Magurran 2004). The functional diversity indices were Functional Richness (FRic) and Functional Dispersion (FDisp). FRic represents the amount of functional space occupied by fish assemblages (Villéger et al. 2008). FDisp was proposed initially as a measure of beta diversity but was recently incorporated as a measure of functional diversity (Anderson et al. 2006). This index is an average distance of each species from the centroid in multidimensional trait space, which is influenced by the most abundant species (Laliberté and Legendre 2010). We chose to relate species richness to functional richness because species richness has been used as the main measure in most studies linking species diversity to functional diversity (e.g., Petchey and Gaston 2002; Mayfield et al. 2005; Micheli and Halpern 2005; Petchey et al. 2007; Sasaki et al. 2009). We chose Simpson's Diversity because it is analogous to Rao's quadratic entropy (de Bello et al. 2009), which is similar to Functional Dispersion according to Laliberté and Legendre (2010). Functional Dispersion has advantages over the Rao quadratic entropy, since the former allows more possibilities for statistical tests (see Anderson et al. 2006); thus, we used FDisp in our study. All indices were calculated in R version 3.3.1. (R Development Core Team 2016): Simpson's Diversity by using the Vegan package (Oksanen et al. 2015) and Functional Richness and Functional Dispersion by using the FD package (Laliberté and Legendre 2010; Laliberté et al. 2014).

To investigate the relationship between the taxonomic and functional diversity indices (Species Richness and Functional Richness; Simpson's Diversity and Functional Dispersion), we tested two different regression models based on dispersion plots (linear regression model and logarithmic regression model). The corrected Akaike Information Criterion (AICc) and model weighting were considered to identify the best model (Johnson and Omland 2004; Sasaki et al. 2009). We used AICc instead of AIC to establish the selection criteria, since the number of samples is small compared to the number of predictor variables Burnham et al. (2011). We further calculated Akaike weights (w_i) for each model for comparison purposes. The AICc was calculated by using the AICcmodavg package (Mazerolle 2017). All analyses were conducted in R version 3.3.1 (R Development Core Team 2016).

Results

A total of 50 species of fish belonging to 13 families and six orders and totalling 3,206 individuals were collected (Appendix Table S2). The order Siluriformes showed the greatest richness (22), followed by Characiformes (16). The order Characiformes, however, contributed higher values of abundance (43.1%), followed by Siluriformes (36.1%). The families Characidae and Loricariidae were the most representative in terms of numerical abundance, with each contributing 37.2% or 26.6% of the total number of individuals, respectively. The Characidae and Loricariidae families also had the highest number of species, with 12 and nine species, respectively. The species *Astyanax bimaculatus* was the most abundant (25.5%), followed by *Ancistrus multispinis* (20.9%) and *Astyanax scabripinnis* (6.6%). Thirty-seven species presented a percentage of the total number of individuals captured of less than 1.0% (Appendix Table S2). The species *Astyanax bimaculatus*, *Astyanax parahybae*, *Geophagus brasiliensis*, *Gymnotus carapo*, *Phalloceros caudimaculatus* and *Rineloricaria* sp. 1 were common to all sampled streams. Ten species occurred in only one of the streams: *Astyanax taeniatus*, *Characidium alipioi*, *Neoplecostomus variipictus*, and *Pimelodella eigenmanni* (Entupido Stream); *Kronichthys* sp., *Poecilia* sp., and *Trichomycterus* sp. 2 (Jacu Stream); and *Pseudocorynopoma heterandria*, *Pimelodus fur* and *Oreochromis niloticus* (São Roque Stream). The species *Kronichthys heylandi* and *Imparfinis minutus* were caught only during the second collection period (2012-2013), while *Corydoras nattereri* was caught only in the first (2008-2009). Entupido Stream presented the greatest richness and abundance, containing 39 species and 35.6% of the specimens collected. Rio Claro Stream presented the lowest values of richness and abundance, with only 18 species and 3.8% of the total number of individuals.

Habitat characteristics

The habitat characteristics were variable among streams. In streams 1, 3, and 4, run/riffle mesohabitat and pebble substrate predominated. The greatest shelter availability in these three streams was composed of rocks. On the other hand, streams 2 and 5 presented similar proportions of mesohabitat composed of pools and runs/riffles. Sand was the predominant substrate (Appendix Table S3) (Fig. 2).

Functional and taxonomic relationship

The nMDS for species abundance (stress: 0.19) did not depict a clear pattern of species distribution for any of the tested factors (stream, period, season, or reaches) (Fig. 3). Twenty-one traits were selected from the Spearman correlation, and 11 traits were eliminated for showing redundancy with other traits.

The functional and taxonomic indices showed slight variation among streams in both periods sampled (Appendix Table S4). The model selected according to the AICc for both pairs of taxonomic and functional indices was the linear regression model (AICc: SR and FRic = 420.67; SD and FDisp = 102.32) (Table 1). The models were selected with a low amount of uncertainty because in both pairs, the model selected was five (SR and FRic) or 10 (SD and FDisp) times more likely to be a better model than the second one (Table 1a and 1b for the evidence ratio). Our hypothesis of a positive taxonomic-functional indices relationship was supported by both pairs of indices tested (Species Richness and Functional Richness: $R^2_{adj} = 0.607$; Simpson's Diversity and Functional Dispersion: $R^2_{adj} = 0.5137$) (Fig. 4).

Discussion

In this study, we found a significant positive relationship between functional and taxonomic indices. This finding indicates low functional redundancy (see Micheli and Halpern 2005; Sasaki et al. 2009). In a highly redundant community, the loss of one species does not necessarily mean the loss of a given function, since highly redundant functions would be more persistent than the species that are lost (Lundberg and Moberg 2003; Guillemot et al. 2011). Redundant species are considered necessary to ensure ecosystem resilience to perturbation (Walker 1992, 1995; Sasaki et al. 2009). However, in a community with low functional redundancy, such as the assemblages studied here, the loss of a few species may in fact represent the loss of a function, since a function can be represented by very few species or even a single species (Guillemot et al. 2011). Examples of a few species with a specific function in our study are those in Gymnotiformes (*Gymnotus carapo* (Linnaeus 1758) and *Gymnotus pantherinus* (Steindachner 1908) and Synbranchiformes (*Synbranchus marmoratus* Bloch 1795). They are very specialized species with specific

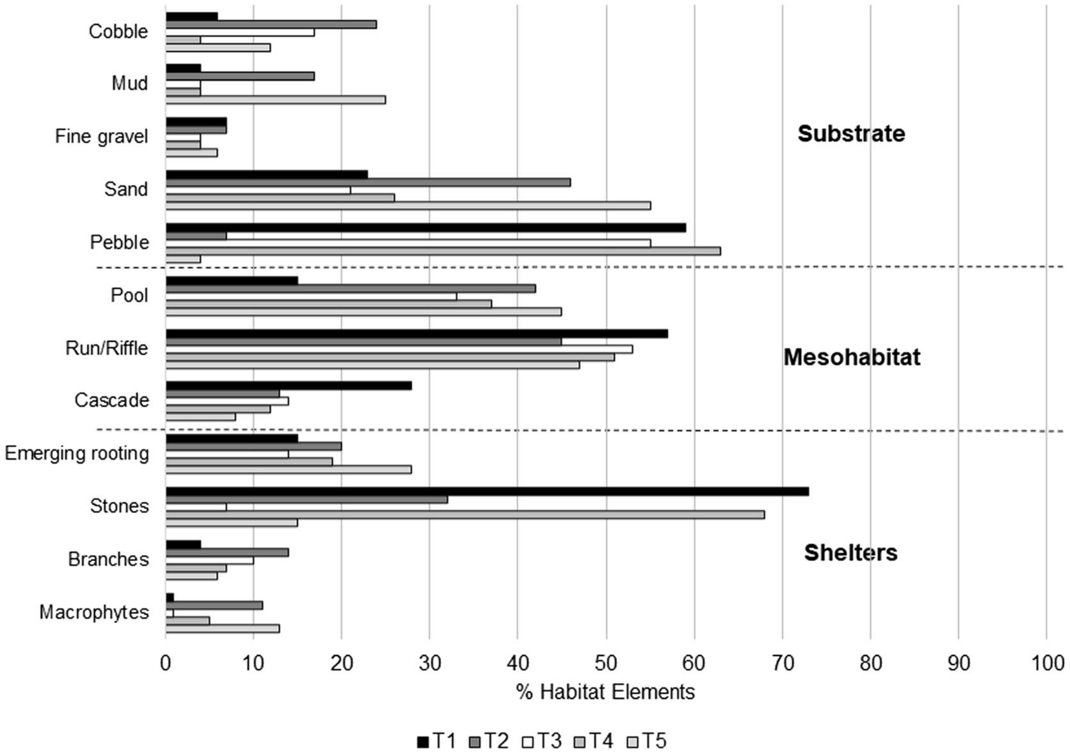

Fig. 2 Graph representing the habitat characteristics of the five streams of the Paraíba do Sul River, southeastern Brazil, sampled in February 2008 to May 2009 and October 2012 to July 2013. Streams code: T1, Jacu Stream; T2, Morro Grande Stream; T3, Claro Stream; T4, Entupido Stream; T5, São Roque Stream

functions in communities, and their extinction could mean the loss of their function in the system.

The examined streams still support a richness of 50 species in 13 families, which is a good representation of the regional ichthyofauna. The high richness may be associated with habitat heterogeneity that still offers suitable conditions to support a fish assemblage. The main anthropogenic changes to the studied streams were the change from forest to pasture and the loss of riparian woody vegetation. However, physical habitat heterogeneity (e.g., different types of substrate; pool, run and rapid mesohabitats; and shelters made by wood and rocks) was preserved, especially in sites far from the main river channel at higher altitudes. The habitat hypothesis (Simpson 1949; MacArthur and Wilson 1967) states that habitat diversity is the best predictor of species richness, even more so than the species-area relationship (Gaston and Blackburn 2000). This is because heterogeneous environments can accommodate more species and support greater variation in their traits since they have higher amounts of microhabitats and thus improved availability of spatial niches (MacArthur and MacArthur 1961; Bazzaz 1975; Willis et al. 2005). Thus, the habitat diversity our sites provide for fish species works to maintain a certain species diversity. This diversity reflects a growing functional diversity (as much as the species richness increased, functional diversity followed the increment). However, it is not sufficient to support the more sensitive species, such as *Taunayia bifasciata* (Eigenmann & Norris 1900) and *Harttia loricariformis* Steindachner 1877, which have been listed for preserved streams from the Paraíba do Sul river basin by Menezes et al. (1998), Pinto et al. (2009) and Rondineli et al. (2011). These results corroborate studies such as that of Teresa and Casatti (2012) that analysed the influence of riparian vegetation on taxonomic and functional diversities in stream fish. In the study carried out by those authors, they found greater functional diversity in streams with deforested margins (but that still had a diversity of mesohabitats, as in the case of our streams) compared to streams with forested margins. This high functional diversity can be explained by the availability of different instream habitats, despite deforestation and the replacement of

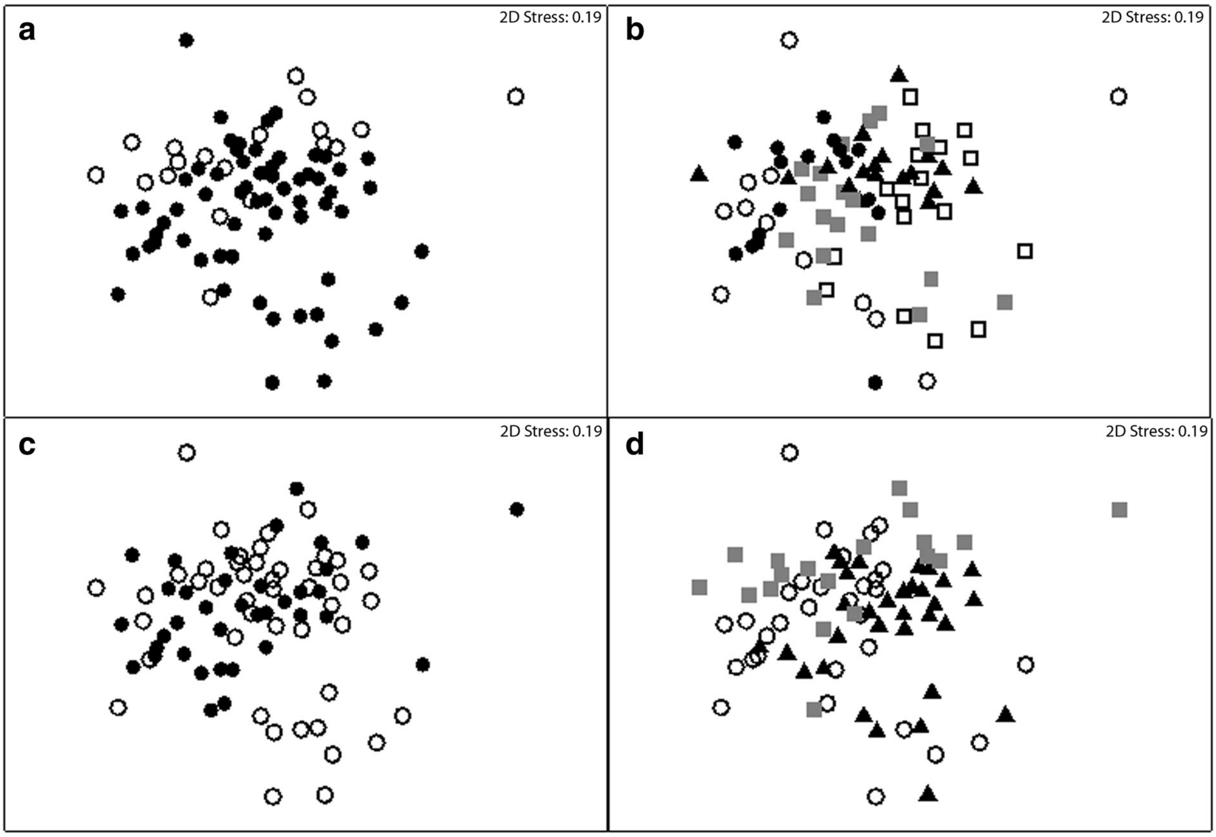

Fig. 3 nMDS analysis of the fish assemblages of the five tributaries of the Paraíba do Sul River. Samples are indicated by: A - Sampling periods: ● – 2008-2009, ○ – 2012-2013; B – streams: □ – Jacu Stream, ■ – Morro Grande Stream, ○ – Claro Stream, ▲ – Entupido Stream, ● – São Roque Stream; C - Seasons: ● – wet season, ○ – dry season; D - stream reaches: ▲ – upper, ■ – middle, ○ – lower

sensitive species by generalist and tolerant species (Teresa and Casatti 2012).

Low functional redundancy in intermediately disturbed systems was a main finding of the present study. Our results confirm our initial hypothesis and indicate that care is needed in the management of the studied streams, since assemblages with low functional redundancy are more susceptible to loss of functions in the case of species loss. Thus, we recommend that indices of taxonomic and functional diversity be used together to evaluate functional redundancy as part of monitoring, impact assessment, and plans for creation of new

Table 1 Results of model selection for the relationship between taxonomical and functional indices and test statistics from the best models, listing the corrected Akaike Information Criterion (AICc), the difference from the 'best fit' model (ΔAICc), the Akaike weight (w_i), and the evidence ratio (w_i/w_i; w_i from the best fitted model/w_i from the second model) for each best fitted model

Models	AICc	ΔAICc	w_i	w_i/w_i	dF	F*stat*	P*value*
Species richness *vs.* Functional Richness							
Linear model	420.67	0	0.85	5.66	59	64.39	<0.001
Logarithmic model	424.13	3.56	0.15		59	57.59	<0.001
Simpson´s diversity *vs.* Funcional dispersion							
Linear model	102.32	0	0.91	10.11	59	93.63	<0.001
Logarithmic model	107.03	4.71	0.09		59	82.2	<0.001

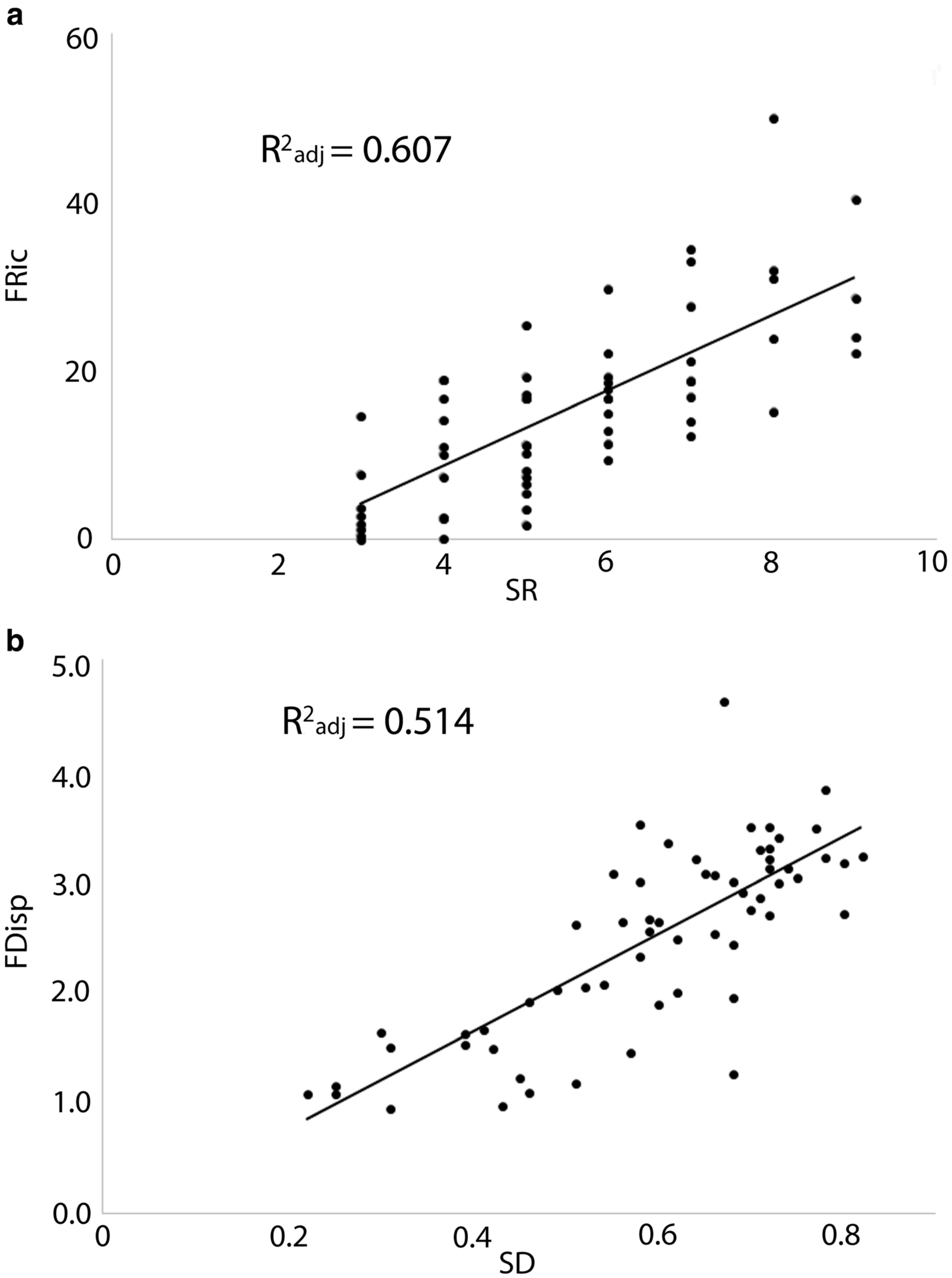

Fig. 4 Comparison of the relationships between taxonomic and functional diversity indices for the pooled data from all five streams of the Paraíba do Sul River sampled in February 2008 to May 2009 and October 2012 to July 2013. SR, Species Richness; SD, Simpson's Diversity; FRic, Functional Richness; FDisp, Functional Dispersion

conservation units. Thus, functional redundancy should be used as a key component of management (conservation, recovery or intervention) decisions. Management and conservation strategies for protecting biodiversity in these systems should seek to enhance resources and habitat availability. This will ultimately increase functioning and contribute to increased redundancy. Additionally, identifying vulnerable functional groups and their redundancy levels and highlighting which species are needed to maintain functions is crucial to reach these goals (Micheli and Halpern 2005). We also recommend that consideration be given to careful selection of functional traits as well as intraspecific variation in future studies.

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Compliance with ethical standards

Ethical approval All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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