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Fish assemblages in Atlantic Forest streams: the relative influence of local and catchment environments on taxonomic and functional species

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Abstract – Streams are under environmental pressures acting at different scales that influence the ecological organisation of their fish assemblages. However, the relative influence of the different scale-related variables on assemblage composition and function is poorly understood. We evaluated the importance of local- and catchment-scale environmental variables, as well as the spatial structure of the sampling sites, in shaping fish assemblages in Atlantic Forest streams. Local-scale variables were those measured at the sampling sites, describing the local habitat conditions (e.g. depth, substrate type, altitude). Catchment-scale variables were those integrating the upstream landscape of the sampling sites (e.g. catchment land use). Spatial distances were calculated from watercourse distance using principal coordinates of neighbour matrices. Altogether, 28 local and seven catchment variables were initially subjected to two processes of eliminating co-linearity. Redundancy analysis was applied to the three matrices (spatial, local and catchment) to quantify the variance in the structure of the fish assemblages explained by each matrix. Local variables explained more variability in both taxonomic and functional assemblage structure, than catchment and spatial variables. Local variables also changed along the longitudinal gradient, which consequently influenced fish assemblage structure. This pattern was also influenced by anthropogenic alteration and non-native species, which were more abundant in downstream sites. These results highlight the need to assess Atlantic Forest streams under different environmental scales, especially through the use of quantitative local-scale metrics, and to consider the effects of longitudinal patterns in structuring fish assemblages when developing and implementing monitoring programmes, impact studies and conservation plans.

Key words: stream habitat; variance partitioning; fish ecology; longitudinal gradient; tropical streams

Introduction

Characterising fish assemblage structure at different scales increases our ability to comprehend ichthyofaunal organisation, which is important for conserving aquatic systems. Studies have indicated that fish assemblage organisation may be determined not only by local processes, but also by large-scale environmental variables (e.g. Magalhães et al. 2002; Hoeing-haus et al. 2007). Local variables, such as water quality, energy source, substrate and channel morphology, help to determine the structure and composition of fish assemblages and are influenced by catchment-scale factors, such as surficial geology, soil type, bedrock type and depth, watershed topography, land cover and climate (Tonn 1990; Wang et al. 2003). Moreover, local habitat characteristics and catchment environmental factors mediate biotic inter-

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actions, which are inherently local in scale, and may limit the ability of species to persist in a local community (Hoeinghaus et al. 2007). Because rivers are one of the most threatened ecosystems in the world (Dudgeon et al. 2006), with projected high faunal extinction rates, it is vital to develop a consistent understanding of the patterns and processes that determine aquatic diversity at different spatial scales (Ibañez et al. 2007).

The Atlantic Forest biome has high levels of biodiversity and is considered one of the 25 global biodiversity hotspots in regard to endemism and degree of threat (Myers et al. 2000). One of the biggest threats is urbanisation, considering that 58.1% of the Brazilian population lives in the Atlantic Forest, and more than 80% of the original vegetation cover has been removed (SFB 2014). Streams are one of the most threatened components of this biome; most of which are small, highly isolated coastal systems harbouring numerous endemic species (Abilhoa & Bastos 2009; Nogueira et al. 2010). Of the 260 species of fish currently identified in this region, 70% are endemic (Abilhoa et al. 2011).

In these small Atlantic Forest streams, environmental conditions vary considerably longitudinally over relatively short distances ($\approx$200 km, altitudes from 0 to 2000 m) (Aranha & Caramaschi 1999; Lowe-McConnell 1999). Headwater streams have high velocities, waterfalls, boulder substrates, small pools, cool clear water and dense riparian vegetation. Middle reaches have moderate velocities, gravel substrates, runs and larger pools, warmer water and disturbed riparian vegetation. Lower reaches have low velocities, sand and silt substrates, many large pools, warm turbid water and highly fragmented riparian vegetation. In other words, these streams follow the river continuum concept (RCC; Vannote et al. 1980), but with little change in stream order. According to the RCC, changes in food sources along the fluvial continuum constrain the trophic groups of aquatic organisms within communities. Based on this concept, fish species that are generalised invertebrate feeders are expected in upstream reaches, whereas omnivores, detritivores, herbivores and piscivores become more abundant in larger reaches downstream (Vannote et al. 1980). Some tropical stream studies have corroborated this pattern using taxonomic species data (Mazzoni & Lobón-Cerviá 2000; Mazzoni & Iglesias-Rios 2002; Súarez & Petrere-Júnior 2007; Súarez & Lima-Junior 2009; Gonçalves & Braga 2012). These studies suggest that differences along longitudinal gradients in tropical rivers are among the main determinants of fish species distribution (Mazzoni et al. 2006; Araújo et al. 2009; Ferreira & Petrere 2009) and their food sources (Ibañez et al. 2009; Wolff et al. 2013).

Ontogenetic segregation of some fish species is also observed in Atlantic Forest streams. In some populations, small individuals are found in lower reaches, whereas larger individuals and adults concentrate in upper reaches (Abilhoa et al. 2011). During the wet season, eggs, larvae and small individuals of those species are carried to lower reaches, and as they grow, they increase their swimming capability and then explore upstream habitats, where they reproduce (Abilhoa et al. 2011). Such human interventions as dam building, clear-cutting of riparian vegetation and contaminant discharges may create structural, thermal and chemical migration barriers leading to declines of natural populations (Casatti et al. 2006a), dominance of generalist species (Casatti et al. 2006b), establishment of non-native species (Cucherousset & Olden 2011) and modifications in natural longitudinal patterns. However, the wide range in natural variability along the longitudinal gradient confounds our ability to detect the effects of human-induced changes in these streams.

The most influential drivers of fish assemblage organisation in Atlantic Forest streams have been presumed to be local habitat characteristics such as cover, water velocity, substrate, riparian vegetation, depth, current velocity and water quality. In tropical environments, that may be because most studies have focused on local environmental influences on fish assemblages or populations (e.g. Ferreira & Casatti 2006a; Rezende et al. 2010). Catchment-scale variables (e. g. geomorphology, annual precipitation, distance to the estuary, area above the sampling site and land cover) have been pointed out as those that altogether define lower-level, instream properties (Poff 1997). However, some studies suggest that landscape-scale properties, such as catchment land cover, better predict local stream conditions (see Kautza and Sullivan 2012). Human influences, particularly land use and land management practices, also influence reach-scale habitat (Richards et al., 1996). Because the catchment-scale studies are less common, and mostly focused on determinants of species richness (Hoeinghaus et al. 2007; Macedo et al. 2014), our ability to understand catchment-scale controls is limited. However, catchments are the chief management focus in Brazil and are needed for effective management intervention for protecting and recovering ecosystem integrity (Lake et al. 2007).

The use of functional groups along with taxonomic data can be helpful, but they are still largely underused for understanding fish assemblage organisation in tropical ecosystems. Some functional groups (e.g. trophic guilds, water column habitat) have been applied in multimetric biotic indices (Ferreira & Casatti 2006b; Terra et al. 2013). However, because of the scarcity of ecological information (e.g. species

autecology, trophic and reproductive guilds, habitat occupation), biological and ecological traits have been used less for fish than other aquatic groups such as macroinvertebrates (Tupinambás et al. 2014). Both taxonomic diversity and functional diversity must be addressed to understand the structure and function of fish assemblages (Ricotta 2005; Manna et al. 2013), and assessing species functional traits can lead to greater clarity of ecosystem processes, because inter-specific relationships determine species coexistence (Poff & Allan 1995; Villéger et al. 2010; Mouillot et al. 2013).

In this study, we examined the relative importance of local- and catchment-scale (land cover) variables on taxonomic and functional assemblage structure along the longitudinal gradient of Brazilian Atlantic Forest streams. We investigated the relative importance of local and catchment variables on both taxonomic and functional assemblage structure because functional traits are expected to respond better to environmental influences (Marzin et al. 2012). We examined the relationships between functional fish species along an environmental gradient because previous studies have indicated shifts in function (Ibañez et al. 2009; Wolff et al. 2013). Because non-native species can seriously undermine the ecological integrity of freshwater ecosystems (Hermoso & Clavero 2013), we investigated the pattern in native and non-native distribution from a functional perspective. We predicted that local variables would be more important in shaping fish assemblages, that both taxonomic and functional assemblage organisation would respond to a longitudinal gradient, and that habitat alteration would drive fish assemblage organisation, including greater representation by non-native species.

Materials and methods

Study area

We conducted this study in five catchments, all of which drain to Guanabara Bay in the Atlantic Forest biome, in the state of Rio de Janeiro, south-eastern Brazil (Guanabara Bay basin area = 4081 km^2). This area is bounded by the Serra do Mar, with altitudes between 800 and 1800 m a.s.l. The climate is warm and humid, with a wet season from October to March, a dry season from April to September, an average annual temperature of 22 °C and mean annual precipitation near 1700 mm (SEMADS 2001). All catchments occur in the same 'environmental macro-region' (MR-1), which is the unit of environmental management and intervention established by Rio de Janeiro State legislation. This macro-region is among seven in the state and the most populous one,

harbouring around 70% (around 12 million people) of the Rio de Janeiro State population (SEMADS 2001; IBGE 2014). Our sampled sites were distributed from extreme upper accessible rivers (altitude = 862 m) to lowland reaches (altitude = 8 m). We did not sample estuarine areas.

Fish sampling

We randomly chose 46 wadeable stream sites ranging from 1.0 to 16.0 m wide and sampled fish during the 2010 and 2011 dry seasons (Fig. 1). Single-pass electrofishing removal was conducted during the daylight through the use of an alternating current generator (Coleman 3000 W, 110/220 V) with two hoop-shaped (440 mm × 300 mm) anodes supporting nets (3 mm mesh). Two people, each with an anode, fished from one edge to the other of each site in an upstream direction removing all fishes detected in the electric field. All the fish we collected were identified to species, counted, weighed (g) and measured for total length (mm). Vouchers were deposited in the fish collection of the Laboratory of Fish Ecology, Universidad Federal Rural do Rio de Janeiro.

Trait classification and functional matrix

Several functional attributes could have been used (i.e. morphology, reproduction, life history strategy); however, we restricted our analyses to the ones directly available and based on published data (Appendix 1). The traits were (i) trophic guild (i.e. piscivore, invertivore, omnivore, detritivore), (ii) vertical habitat use (i.e. water column or benthic) and (iii) mesohabitat affiliation (i.e. pool, fast water or intermediate). As suggested by Erős et al. (2012), besides these three traits, we also differentiated fishes by their native versus non-native status. According to the trait classification, the 68 species caught during the study could be categorised as 17 unique functional species (Appendix 1).

Local variables

Following the USEPA's national protocol (Peck et al. 2006), at each point a site was extended upstream for 40 times the mean wetted channel width, or a minimum of 100 m. In each site, 11 equidistant cross-section transects were marked, defining 10 sections of the same length. In the middle of each section, another transect was marked to replicate a subset of physical habitat and physico-chemical variables. Thus, 21 transects were sampled along each site.

At five equidistant points along each of the 21 transects, we measured depth, substrate size (silt:
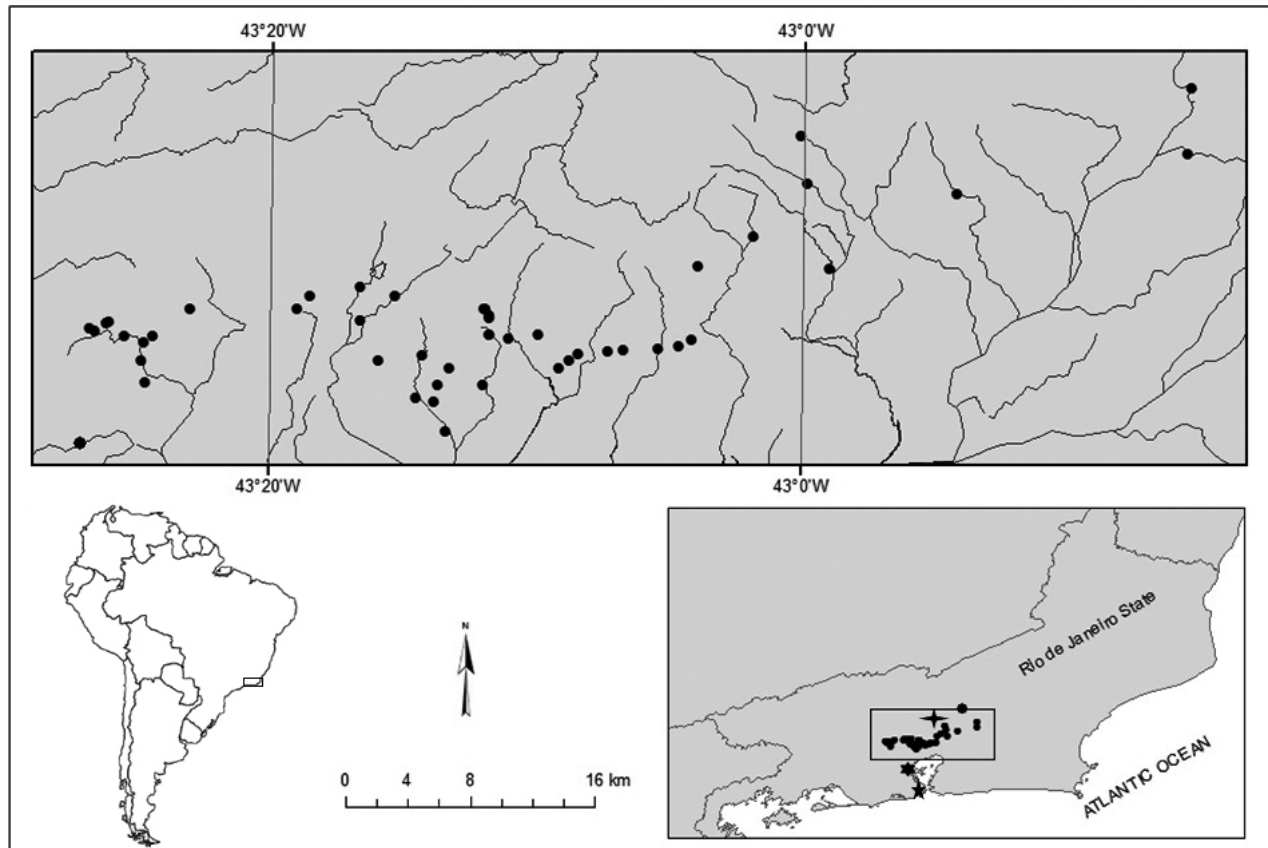
Fig. 1. Locations and distribution of the 46 sites sampled in five basins that drain to Guanabara Bay, Rio de Janeiro, Brazil. The black circles correspond to sample sites. Population size in urban centres close to the sample area: ★ = Rio de Janeiro – 6,320,000; ✦ = Petrópolis – 295,000; ✹ = Teresópolis – 171,482; ✶ = Duque de Caxias – 855,000 (Source: IBGE 2014).

<0.06 mm; sand: 0.06–2.0 mm; small gravel: >2.0–16 mm; large gravel: >16–250 mm; cobble: >250–1000 mm; boulder: >1000–4000 mm; and bedrock: >4000 mm) and current velocity ($m \cdot s^{-1}$ – measured 5 cm above the bottom). We calculated the geometric mean substrate diameter (Dgm) for each site by assigning each particle the geometric mean diameter of the upper and lower bounds of its size class and then calculating the geometric mean as the antilog of the arithmetic mean of the logarithms of those frequency-weighted class mid-point values (Kaufmann et al. 2008).

At each of the 11 transects, we measured or visually estimated a number of physical habitat variables. We measured wetted width, riparian structure (e.g. mid-channel and margin shading), conductivity ($mS \cdot cm^{-1}$), dissolved oxygen ($mg \cdot l^{-1}$), temperature (°C) and turbidity (NTU). We visually estimated the percentage area of flow type (pool, fast water), small/large wood, grass, mean of root areal cover, mean boulder areal cover and canopy cover. We also visually estimated the percentage area of erosion, sewer discharges, construction and agriculture in the riparian zone. We calculated hydromorphological variabil-

ity (HV), as suggested by Sály et al. (2011). The HV equalled a site's first axis value of a principal component analysis (PC1) calculated from the wetted width coefficient of variation (CV), depth CV and current velocity CV.

Catchment variables

We determined land uses and the catchment area (km^2) in each catchment from 1:25,000 scale orthophotos (aerial photograph geometrically corrected from 2008), freely available from the Instituto Brasileiro de Geografia e Estatística. Land uses were determined by visual interpretation and vectorisation directly on the computer screen using ArcGis 10 software packages (ESRI 2007). We identified five major land cover classes (% forest, % secondary vegetation, % agriculture, % pasture and % urban area). Water was not included as a land cover type in analyses. Each class was defined based on the USGS Land Use/Land Cover Classification System. We did not assess geological or climate variables because the available data had too little resolution to detect differences among sites.

Spatial variables

We calculated site spatial variables via principal coordinates of neighbour matrices (PCNM; Borcard & Legendre 2002; Borcard et al. 2004) from watercourse distance. From the resulting matrices, we extracted principal coordinates from truncated matrices (Borcard & Legendre 2002) calculated in the R package PCNM (Legendre et al. 2009). Only the principal coordinates with positive eigenvalues were considered as spatial descriptor variables. According to Borcard & Legendre (2002), negative eigenvalues cannot be used because their axes are formed by complex numbers.

Data analyses

We used variance partitioning to evaluate the relative contribution of environmental (28 local and seven catchment variables) and spatial variables on fish assemblage structure (taxonomic and functional). To do so, the fish assemblage composition data (response variables) were organised in two different matrices according to the abundance of each species (taxonomic) and according to the sum of species abundances of each functional species by sample site. The explanatory variables were organised in three matrices: (i) local (meso- and microhabitat characteristics), (ii) catchment area and land use for each site and (iii) spatial (generated from the watercourse distance between sites).

We used a Hellinger transformation (Legendre & Gallagher 2001) obtained by dividing the abundance of each taxonomic and functional species at a site by the sample total abundance and taking the square root of the quotient through use of the decostand function in VEGAN (Oksanen et al. 2009). This transformation is recommended by Legendre & Gallagher (2001) for use in linear ordinations. To standardise all variables that were expressed in different units, we transformed those variables. The proportional environmental variables were arcsine $(x/100)^{1/2}$-transformed, and the other environmental variables were logarithmic ($\log x + 1$)-transformed.

We used two steps to eliminate collinear environmental variables. We first calculated the variance inflation factor (VIF) for each variable. Variables with VIF >10 were eliminated (Sály et al. 2011). Then, variables with Pearson correlation values >|0.70| were eliminated, retaining the variable that was least correlated with the other variables within both environmental matrices.

The selected variables in each matrix (local, catchment and spatial) were included in a partial redundancy analysis (pRDA). The pRDA allows one to determine the explanatory fraction of each explanatory matrix for the fish assemblage matrix variability, as well as the shared explanation among those matrices. As suggested by Borcard et al. (2011), we did not detrend the response variables. Instead, we tested the linear trend and, explicitly, incorporated it in the variance-partitioning process. In detrended correspondence analysis (DCA), a gradient length >4 indicates some species have a unimodal distribution along the axis (Ter Braak & Smilauer 2002), and in such cases, canonical correspondence analysis is preferred. We used RDA because the preliminary DCA indicated linear responses to the gradient.

We used forward selection to select the most relevant explanatory variables, setting the significance level to 0.1 to avoid skipping any potentially important variables as suggested by Sály et al. (2011). This function selects variables with the highest R^2 or those with the most explanatory power first. Adjusted R^2 provides an unbiased estimate of the explained fraction of variance (Peres-Neto et al. 2006). The variance partitioning yielded three pure fractions of the explained variance [local], [catchment] and [spatial], four shared fractions [local + catchment], [local + spatial], [catchment + spatial] and [local + catchment + spatial], expressed as percentages of the total variability explained, plus the unexplained or residual fraction of variance [residual]. We tested the significance of the pure fractions with permutation tests (999 permutations) at a significance level of 0.05 (Legendre & Legendre 1998). We ran redundancy analyses (RDA) with the taxonomic and functional assemblages and the environmental variables with the greatest explanatory power to evaluate the degree that each variable group influenced the fish assemblages.

In a second step, we ran an RDA on the local variables only, because they turned out to be the most important fraction in the initial pRDA step. All analyses were conducted in R version 2.15.2 (R Development Team 2013). The forward selection procedure (forward.sel function) was performed in PACKFOR (Dray et al. 2013), and variance partitioning was conducted in VEGAN (Oksanen et al. 2013).

Species richness, abundance, and Shannon and Simpson indices were regressed against altitude, for both taxonomic and functional species. To do so, sites considered less disturbed were selected to contrast the results with all sites regression. Less disturbed sites were based on the Integrated Disturbance Index (IDI) score of each site. The IDI assesses the total disturbance of the sites due to human pressure by combining multiple disturbances measured at local and regional scales into a single index (see Terra et al. (2013) for further details). Species richness and abundance data were $\log_{10}(x + 1)$-transformed.

Results

Taxonomic and functional assemblage structure

We collected 17,906 individuals and 68 species including six aliens (*Poecilia reticulata*, *Xiphophorus* sp. *Crenicichla* cf. *lepidota*, *Oreochromis niloticus*, *Cichla kelberi* and *Cichlasoma* sp.) (Appendix 2). The Siluriforms represented 41.18% of the total species, followed by the Characiforms with 35.29%. We collected seven Perciform species (10.29%), and the Cyprinodontiforms, Gymnotiforms and Synbranchiforms contributed 8.82%, 2.94% and 1.47% of the total species respectively. *Astyanax taeniatus* and *P. reticulata* represented over 20% of the total individual abundance in the total collection. Other species occurring in more than 50% of the sites included *Scleromystax barbatus*, *Geophagus brasiliensis*, *Rhamdia quelen*, *Acentronichthys leptos*, *Schizolecis guntheri* and *Synbranchus marmoratus* (Appendix 2). Species richness ranged from three to 30 per site and was generally greater in the downstream sites. Five species (*A. taeniatus, R. quelen, G. brasiliensis*, *P. reticulata* and *Mimagoniates microlepis*) were collected along the entire longitudinal gradient; however, the latter three species were more abundant and frequent in downstream sites. Patterns of species turnover and addition were apparent from high to low altitudes. Some species (e.g. *Rhamdioglanis transfasciatus*, *Neoplecostomus microps*) were found only in the headwaters. Downstream, those species were replaced by *Pimelodella lateristriga*, *Hypostomus affinnis*, *S. barbatus* and *Rineloricaria* species. Further downstream, we found *Oligosarcus hepsetus* and *Hoplias malabaricus*.

Of the 17 functional species, four represented more than 10% of the total abundance: NOWP (native, omnivorous, water column, pool, 17.9%), NIBF (native, invertivorous, benthic, fast water, 13.5%), NIBI (native, invertivorous, benthic, intermediate, 12.1%) and NNDWP (non-native, detritivorous, water column, pool, 11.8%) (Appendix 1). The functional species turnover was clearer than that for taxonomic species. All fast water combinations and three invertivorous functional species were more abundant and frequent at upstream sites. Native omnivore and detritivore species, and those related to pool mesohabitat were most frequently found at downstream sites. Except for NNDWP, which was collected in upstream sites at low abundances, functional species containing non-natives were found only at low altitudes.

Assemblage structure variability

During the preliminary analysis, seven local environmental variables and two catchment variables were discarded. The forward selection procedure eliminated 14 and 17 (being two regional variables for both groups, taxonomic and functional), leaving 12 and nine local explanatory variables for taxonomic and functional classification respectively (Table 1). Those explanatory variables were significantly correlated with the eliminated variables in the selection process (Table 2). The principal coordinates of neighbour matrices (PCNM) obtained six axes with positive eigenvalues, and all six axes were retained by forward selection for both taxonomic and functional variance-partitioning analysis.

The total explained variability of taxonomic and traits data, for the local, catchment and spatial variables was 31% and 30% respectively. For taxonomic data, local variables (13.1%, $P = 0.005$) had more explanatory power than spatial variables (3.2%, $P = 0.07$) or catchment variables (4.9%, $P = 0.01$). The shared components [local + catchment], [local + spatial], [catchment + spatial] and [local + catchment + spatial] explained 5.5%, 4.7%, 2.5% and 0.2% respectively. For functional species data, local variables (13.7%, $P = 0.005$) also had more explanatory power than spatial variables (5.7% $P = 0.01$) and catchment variables (1.7% $P = 0.18$). The shared components [local + catchment], [local + spatial], [catchment + spatial] and [local + catchment + spatial] explained 7.4%, 1.0%, 0.3% and 2.4% respectively.

Assemblage structure–local variables relationship

Because local variables explained most of the variation in assemblage structure, we evaluated the associations of those local variables with functional and taxonomic species having relative abundances over 0.1% (40 species). The first two local RDA axes explained 14.9% and 9.3% of the taxonomic assemblage total variation respectively (eigenvalues of 0.98 and 0.64) (Fig. 2a). The most important local variables were altitude, turbidity, % grassy riparian and % erosion. The greatest altitudes and rocky substrates were associated with *R. transfasciatus, Hemipsilichthys gobio*, *N. microps*, *Trichomycterus* cf. *zonatus*, *Bryconamericus ornaticeps* and *Kronichthys heylandi*. The Cyprinodontiforms, *Astyanax* species, *S. marmoratus*, and others were correlated positively with % grassy riparian, higher conductivity and turbidity, and absence of rocky substrate. *Rhamdia quelen, M. microlepis* and *S. barbatus* were strongly associated with % erosion and buildings in the riparian area. It is interesting to observe that the *S. barbatus* has not been recognised as a tolerant species; instead, it has been deemed an endangered Atlantic Forest species (Machado et al. 2008).

The first two local RDA axes for the functional assemblages explained 16.2% and 8.7% of the variability respectively, (eigenvalues of 0.08 and 0.04) (Fig. 2b). The local variables contributing most to

Table 1. Median, minimum and maximum values of the local and catchment variables collected for 46 Atlantic Forest stream sites sampled in the dry season (2010 and 2011). FSP indicates variables rejected in the forward selection procedure; F (final) indicates variables selected in the variance-partitioning procedure for pRDA.

Environmental variables	Median	Min.	Max.	Discarded	Taxon FSP	Taxon F	Functional FSP	Functional F
Catchment-scale variables								
Catchment area (km^2) (CA)	6.0	0.1	56.7			x		x
% Secondary vegetation (SV)	3.3	0	68.2	x				
% Forest (FO)	77.7	0	100		x		x	
% Forest + secondary vegetation	90.7	0.1	100	x				
% Agricultural area (AA)	0.0	0	85.4			x	x	
% Urban area (UA)	0.8	0	45.6		x			x
% Pasture (PA)	4.5	0	41			x		x
Local-scale variables								
Altitude (m) (AL)	37.5	8	340			x		x
Depth (m)	0.2	0.1	0.4	x				
Current velocity (cm·s^{-1})	0.1	0.0	2.5		x		x	
Wetted width (WW – m)	4.7	1.0	14.7	x				
Hydromorphological variability (HV)	0	−1.1	1.6		x		x	
Substrate geometric mean diameter (Dgm)	11.0	0.2	424.9	x				
Temperature (°C)	19.7	16.7	23.8		x		x	
Dissolved oxygen (DO – mg·l^{-1})	8.5	5.0	11.1		x			**x**
Conductivity (mS·cm^{-1}) (CON)	4.0	0	23.0			x		x
Turbidity (TU – NTU)	1.6	0	13.5			**x**	x	
% Pool	42.0	0	100		x		x	
% Fast water flows	56.8	0	99		x		x	
% Riparian canopy (>2 m high) cover	87.5	0	57.5	x				
% Grassy riparian (GR)	0.3	0	72.5			x	x	
% Silt +sand (SS)	32	7	100		x			**x**
% Small gravel (SG – 2 to 16 mm)	5	0	37		x		x	
% Cobble (250–1000 mm)	2	0	41	x				
% Boulders (1000–4000 mm) (BO)	0	0	22			**x**	x	
% Bedrock (BE) (>4000)	1	0	20			x		x
% Shading	30	0	58	x				
% Small wood areal cover (SW)	8	0	30.5		x		x	
% Large wood areal cover (LW)	1	0	18.5		x		x	
% Root areal cover (RO)	5.5	0	37.5			x		x
% Boulder areal cover	38	0	75	x				
% Erosion (ER)	10.3	0	57.5			**x**	x	
% Sewer discharge (SD)	0	0	70		x		x	
% Construction (CO)	0	0	80			**x**	x	
% Agriculture	0	0	30		x		x	

X = shows in which test the variables failed and the final variables selected.

functional species were altitude and conductivity. All functional species deemed insectivorous and fast water were associated with higher altitudes. All omnivorous pool species were associated with % silt and sand substrates. All non-native functional species were negatively associated with altitude. Altitude was negatively associated with sewer discharges and temperature, and those two variables also were correlated with higher conductivity, turbidity and erosion, and less riparian cover. Those sites were where non-native species were found and/or more abundant. We calculated the proportion of non-native functional and taxonomic species per each quadrant of the RDAs (Fig. 2a,b). The non-native proportion is clearly higher in sites with poorer water quality and physical habitat structure.

For both, taxonomic and functional species, the first axis of the RDAs explained more than 15%

(15% and 16% respectively) of the variability. Altitude was an important local variable for both groups. In general, the same pattern existed for both groups: species related to fast water and rocks were associated with higher altitudes, whereas more tolerant species were associated with higher conductivity and turbidity. Moreover, non-native species were linked to downstream reaches, where the human influence was greater. Clearly, local variables changed along the longitudinal gradient and influenced fish assemblage structure and function (Fig. 2).

Functional structure and diversity along the longitudinal gradient

On the same RDA ordinal diagram with functional species and selected local variables, we plotted each

Table 2. Pairwise Pearson correlations between discarded and selected explanatory environmental variables. Significant correlations in bold $P < 0.05$.

Discarded variables	Final catchment variables				Final local variables										
	CA	AA	UA	PA	AL	†DO	CON	†SS	BE	RO	‡TU	‡GR	‡BO	‡ER	‡CO
% Secondary veg. (SV)	0.05	**0.37**	**0.64**	**0.70**	−0.48	−0.06	0.20	0.26	−0.08	0.07	**0.49**	**0.62**	−0.15	**0.30**	0.26
% Forest	0.22	**−0.60**	−0.26	**−0.50**	**0.35**	0.00	−0.09	−0.08	0.08	−0.18	−0.19	**−0.30**	0.12	−0.21	−0.05
% Forest + SV	0.16	**−0.67**	−0.17	**−0.45**	0.28	0.16	0.01	−0.17	0.20	−0.02	−0.14	**−0.39**	0.26	−0.18	0.08
% Agricultural area	0.18	−0.01	0.05	0.14	0.14	0.19	0.02	−0.13	0.13	0.12	−0.16	−0.03	**0.32**	0.10	0.23
HV	0.06	**−0.49**	**−0.30**	**−0.47**	**0.33**	0.27	−0.20	**−0.60**	**0.35**	−0.07	**−0.54**	**−0.44**	**0.35**	−0.25	−0.01
% Sewer release area	0.26	0.24	**0.68**	**0.44**	**−0.40**	−0.01	**0.49**	0.20	0.04	**−0.34**	**0.36**	**0.46**	−0.25	0.16	**0.39**
% Boulder areal cover	0.16	**−0.67**	**−0.35**	**−0.49**	**0.47**	**0.32**	−0.19	**−0.60**	**0.32**	0.17	**−0.70**	**−0.60**	**0.54**	−0.21	0.10
% Shading	−0.24	**−0.33**	**−0.54**	**−0.43**	**0.47**	0.24	**−0.30**	−0.24	0.11	0.27	**−0.43**	**−0.61**	**0.37**	0.05	0.07
% Small wood areal cover	−0.07	−0.18	**−0.45**	**−0.30**	**0.41**	0.21	−0.21	−0.17	−0.09	0.27	−0.28	**−0.35**	0.19	0.13	−0.16
% Large wood areal cover	0.09	0.03	−0.28	−0.09	0.26	0.16	−0.08	−0.08	**−0.31**	**0.33**	−0.22	−0.16	0.00	0.09	**−0.36**
% Small gravel	0.11	−0.26	**−0.42**	**−0.31**	**0.33**	0.26	−0.22	−0.14	−0.16	**0.32**	**−0.50**	**−0.36**	0.00	0.19	−0.04
% Cobble	**0.32**	**−0.38**	−0.18	−0.23	**0.48**	0.28	−0.15	**−0.58**	0.20	0.07	**−0.36**	**−0.46**	**0.67**	**−0.34**	0.00
% Pool	0.08	−0.10	−0.03	−0.27	0.07	0.06	−0.04	−0.15	**0.30**	−0.09	**−0.33**	−0.28	0.18	−0.07	−0.24
% Fast water flows	0.20	−0.11	−0.04	0.04	0.10	−0.05	−0.04	−0.20	0.00	−0.06	−0.04	−0.15	0.03	0.00	0.24
% Riparian canopy cover	**−0.43**	−0.20	**−0.44**	**−0.43**	**0.32**	0.14	−0.29	−0.17	0.20	0.23	−0.27	**−0.49**	**0.34**	0.06	0.07
Depth	**0.78**	0.07	**0.31**	0.22	0.05	−0.17	0.05	**−0.37**	0.06	**−0.40**	0.08	0.13	0.23	−0.25	−0.05
Current velocity	0.29	0.09	0.28	0.13	−0.16	−0.06	0.28	0.11	0.13	**−0.29**	0.28	0.16	−0.02	0.05	−0.01
Wetted width	**0.76**	−0.16	0.04	−0.04	0.19	0.06	−0.15	**−0.36**	0.05	−0.19	−0.28	−0.19	0.22	0.03	0.18
Substrate Dgm	0.19	**−0.50**	−0.24	**−0.37**	**0.48**	0.20	−0.22	**−0.81**	**0.44**	0.04	**−0.58**	**−0.57**	**0.73**	**−0.42**	0.19
Temperature	0.08	**0.32**	**0.64**	**0.42**	**−0.68**	−0.23	**0.52**	**0.45**	−0.16	−0.21	**0.59**	**0.51**	**−0.53**	**0.29**	0.06

Variable codes in Table 1.

†Variables selected only for functional species pRDA.

‡Variables selected only for taxonomic species pRDA.

functional species separately (Fig. 3). The distribution of each functional species responded to a longitudinal gradient, with invertivores and fast water habitat species more abundant at higher altitudes and almost nonexistent in downstream sites [except for native, invertivorous, benthic, intermediate mesohabitat – NIBI species (see Appendix 1)]. On the other hand, omnivorous and detritivorous species became more frequent and abundant at lower altitudes, with omnivore and detritivore pool habitat species more abundant in downstream sites. Non-native species, regardless of trophic guild or habitat, were common at low altitudes, mainly in those sites where human disturbances were more evident. Piscivorous species and water column or benthic habitat species were found through the whole longitudinal gradient; however, they were more abundant in intermediate altitudes.

Taxonomic and functional species richness increased from higher to lower altitudes (Fig. 4). Contrary to expectations, abundance and diversity (Shannon and Simpson indices) did not follow the same pattern when all of our sites were included in the simple regression. However, when the most disturbed sites (IDI scores > 0.5; Terra et al. 2013)

were eliminated from the regression, diversity indices were negatively associated with altitude (Figs 3 and 4).

Discussion

Explained variability

We found that the fish assemblages of Atlantic Forest streams were structured mainly by local environmental variables. Regional or catchment variables have had less explanatory power than local variables in other temperate and tropical regions also (Wang et al. 2003; Johnson et al. 2007; Sály et al. 2011; Macedo et al. 2014). Exceptions were reported when landscapes were dominated by human land use (Roth et al. 1996; Allan et al. 1997; Wang et al. 2006; Daniel et al. 2014). In those cases, basin-scale conditions were more important to stream fishes than local environmental conditions. Although the streams included in our study were near a large metropolitan region, the catchment land use above the sample sites was predominantly forest (median 88.7%), minimising the human influences at the catchment scale and consequently on fish assemblage organisation. Essel-
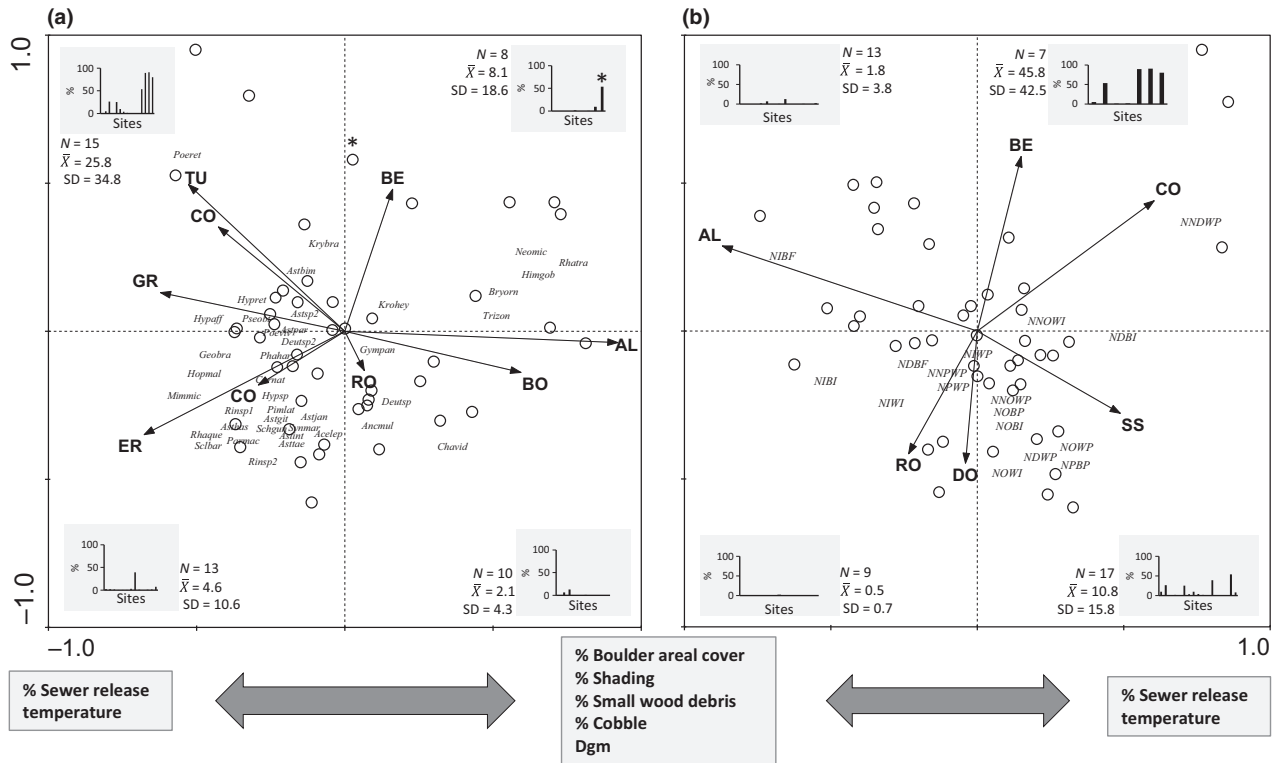
Fig. 2. Results of the redundancy analysis (RDA) with distribution of the sampling sites (O). (a) Relationship between selected local variables and taxonomic species (RDA1, 14.9%; RDA2, 9.3%). (b) Relationship between selected local variables and functional species (RDA1, 16.2%; RDA2, 8.7%). Bar graphs show the proportion of non-native individuals per site falling in the quadrant of the RDA (N = number of sites into the quadrant; $\bar{X}$ = mean of % non-native individuals; SD = standard deviation). See Appendix 1 for trait codes, Appendix 2 for species code and Table 1 for variable codes. *Identifying the position of the only site with high non-native individuals in the first quadrant of the Figure 2a.

man & Allan (2010) explained that regional variables were more important in their study because they included catchments from different biogeographic regions. Such study scales could favour greater importance of regional variables because regional geologic and climatic variability can strongly limit species dispersion, colonisation and persistence (Whittier et al. 1988; Tonn 1990; Rathert et al. 1999). This also helps to explain why spatial variables explained less than three per cent of the variation in our study versus the multi-ecoregion studies of Pinto et al. (2009) and Van Sickle & Hughes (2000). The fact that shared component [local + catchment] explained more taxonomic and functional variability than catchment variables alone suggests that catchment variables had their major influences via local variables.

In our study, the total fraction of variability explained by all explanatory variables together (local, catchment and spatial) was <50% of the variation. In European streams, Ferreira et al. (2007) and Sály et al. (2011) found that environmental variables explained up to 70% of species distribution or assemblage structure variability. Sály et al. (2011) argued that this greater explanation may have been

attributable to incorporating spatial variables in their analyses. However, we included spatial variables in our study and it did not add much more explanation for both taxonomic and functional species variation. Macedo et al. (2014) did not include spatial variables and also explained only 47% of fish species richness in two Brazilian Cerrado basins (variable sets: geophysical landscape variables, land use and land cover, site habitat). Likewise, Wang et al. (2003) explained only 40% of the variation in fish species richness with environmental variables. Cleary & Gennert (2004) argued that low levels of explained variance are common in ecological studies and attributed this, at least in part, to important unmeasured variables. The inclusion of additional unmeasured catchment variables and local gradients, such as geological morphology, soil type, slope and precipitation, would enhance variance explanation and lead to a greater understanding of factors structuring fish communities. The low level of explanation found in our study might also be associated with neutral and/or stochastic processes and biotic factors that are unrelated to environmental variables. In addition to abiotic factors, biotic factors or relationships expressed through morphological and physiological adaptation to local
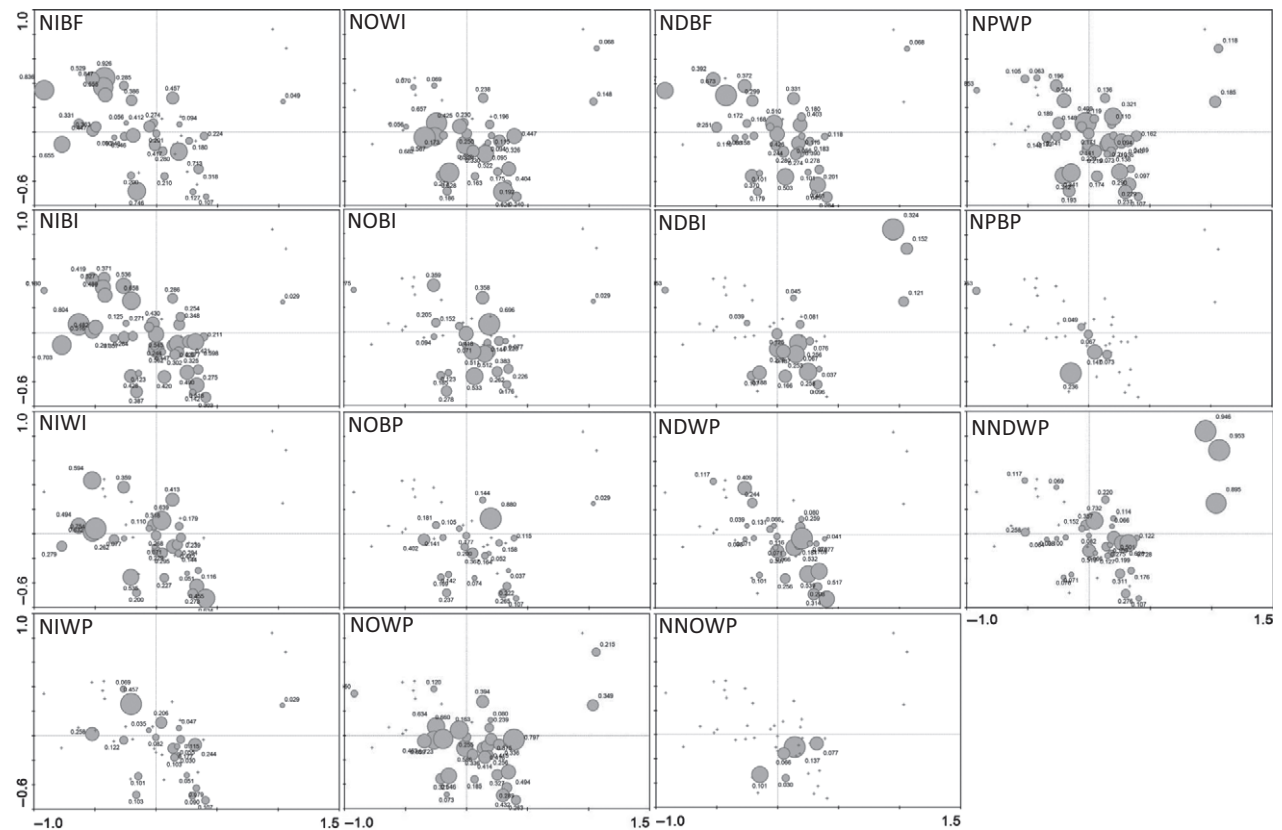
Fig. 3. Redundancy analysis (RDA) ordination diagram with each functional species as a sample attribute. The symbols represent the distribution of attribute values, and the diameter of the symbols is proportional to the attribute value for this particular site. Sites and axes as in Fig. 2a; + indicates the non-occurrence of that functional species in that site. See Appendix 1 for trait codes.

conditions, interactions among different species and coevolution among them have been considered major agents affecting species occurrence in a given environment (Mazzoni et al. 2006). Tropical systems are known for having greater species diversity than temperate systems, and one hypothesis for this is that more predictable climates led to greater importance of biotic interaction, which contributed to the origin and maintenance of greater diversity than in temperate systems (Schemske et al. 2009).

Local environmental variables and ichthyofauna

Stream fish assemblages displayed patterns of longitudinal structure within the Atlantic Forest (e.g. Petry & Schulz 2006; Araújo et al. 2009; Ferreira & Petrere 2009) and elsewhere in the tropics (e.g. Winemiller & Leslie 1992; Esselman et al. 2006). The higher altitude sites had rocky bottoms and shallower and faster waters and were characterised by *R. transfasciatus*, *T.* cf. *zonatus*, *B. ornaticeps* and *N. microps*. The downstream sites had grassy riparian vegetation, higher temperatures and silt and sand substrates and were characterised by Characiforms, *Astyanax*, *M. microlepis* and *H. malabaricus*. Species turnover in taxonomic species and functional species was

apparent in fish assemblages from higher altitudes to lowland streams. Omnivores and detritivores and pool species were numerically dominant in downstream sites, whereas invertivores and fast water species were most abundant in upstream sites. Such longitudinal patterning is described by such concepts as the river continuum (Vannote et al. 1980), fish zonation (Thorp et al. 2006), riverscape (Fausch et al. 2002) and species–discharge relationship (McGarvey & Hughes (2008). The streams located in the higher altitudes were covered by riparian vegetation that blocked sunlight and periphyton growth; therefore, the food chain was based on allochthonous inputs (Barrella et al. 2000), invertebrates and invertivores. In the downstream sites, the canopy cover was less dense, sunlight reached the water surface, and periphyton growth was extensive, leading to a food chain based on autochthonous inputs, omnivores and detritivores. Although omnivores were more abundant further downstream, they were found along the entire longitudinal gradient, which corroborates the expectation for tropical streams where a high number of omnivores are considered natural (Lowe-McConnell 1999; Ibañez et al. 2009).

The longitudinal pattern also was influenced by anthropogenic alterations. In our study, richness was
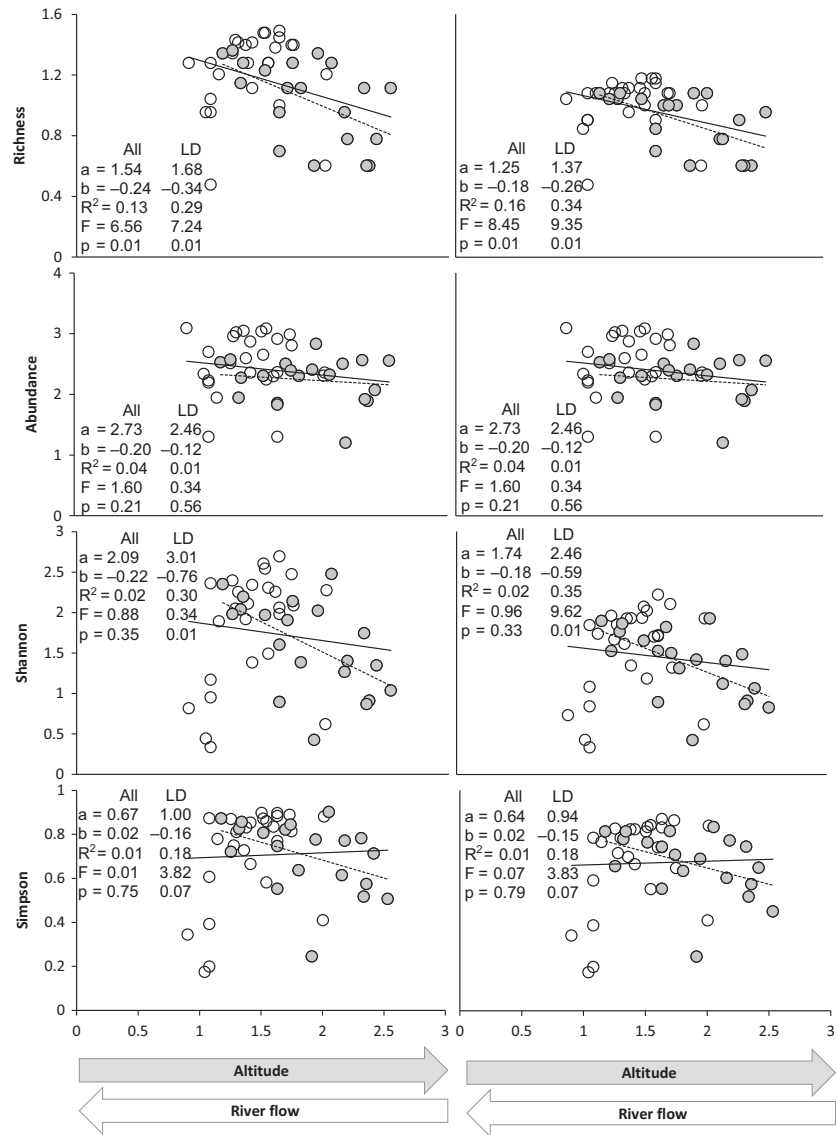
Fig. 4. Regression of species richness, abundance, and Shannon and Simpson indices on altitude for taxonomic (left column) and functional species (right column). Each graph shows the regression including all sites (solid line and open circle) and less disturbed (LD) sites (dashed line and filled circle) based on the Integrated Disturbance Index (IDI) score of each site (Terra et al. 2013). All parameters of the regression and F and P values from ANOVA are shown in each graph.

negatively associated with altitude, that is, more species were found downstream. We expected that diversity indices would follow the same pattern, as predicted by the RCC (Vannote et al. 1980), River Habitat Template (Townsend & Hildrew 1994) and fish zonation (Thorp et al. 2006), in which complexity and diversity increase from headwaters to downstream. However, diversity indices were negatively associated with altitude only when the most disturbed sites were eliminated from the analysis, for both taxonomic and functional species. Clearly, sites with greater human alteration can change the longitudinal pattern of these streams (Humphries et al. 2014). Those eliminated sites had the highest IDI scores (see Terra et al. 2013 for details) because of habitat modification (small dams, channelisation, sewage discharges, trash, little riparian woody vegetation and human habitation in the riparian zone). Often, such highly disturbed sites supported few species and were dominated by a few disturbance-tolerant species such as *G. brasiliensis*, *P. reticulata* and *R. quelen* (e.g. Casatti et al. 2006b; Araújo et al. 2009; Terra & Araújo 2011).

Non-native species were more abundant at low-altitude stream sites. *Poecilia reticulata,* originally from north-eastern South America (Endler & Houde 1995), represented 40% of the total abundance at three of five sites with IDI scores >1.35, and IDI and *P. reticulata* abundance were positively correlated ($R^2 = 0.43$, $F = 6.83$, $P = 0.02$). Some non-native species may be favoured by environmental changes (high conductivity and turbidity, channel homogenisation, absence of instream cover) where they find open niches to reproduce and grow. Although *P. reticulata* was collected at higher altitudes, it comprised more than 80% of total abundance in highly disturbed downstream sites, where it totally replaced native Poeciliids.

Conservation of Atlantic Forest streams

Changes in local habitat directly affect fish faunal composition and structure, so small changes in stream channel and riparian vegetation may affect fish faunas more than moderate catchment land use changes in the short term. Furthermore, because fish assemblage structure is related to local changes along the longitudinal gradient, preserving only upstream areas in the Guanabara Bay Basin will not protect faunal diversity along the entire gradient. Effective Brazilian legislation should consider the longitudinal organisation of streams and rivers in government planning and management. The current legislation requires protection of riparian vegetation widths proportional to river width (e.g. 30 m for streams up to 10 m wide), and a minimum of 50 m around springs, and hill tops with average heights of 100 m and slopes > 25°. Those areas should be preserved as Permanent Preservation Areas (Law no 12.651, de 25 May 2012). Furthermore, Law no 9433/97 (The National Water Resources Plan) guides water management in Brazil, defines catchments as management units and requires that water resource management protects biotic diversity. However, it does not ensure the ecological functioning of aquatic systems, and it prioritises those systems as sources of water supply rather than sources of biodiversity, leading to biodiversity losses (Casatti et al. 2006b; Abilhoa et al. 2011).

Although the Atlantic Forest is recognised as a globally important biome, few of its aquatic systems have been studied. Most of the studies conducted so far have been concentrated in São Paulo, Rio de Janeiro and Paraná States, with little information from other states. Moreover, even in the most studied areas, there is little basic information about the autoecology of many species. Dozens of species are being catalogued every year, and many others are being redescribed or repositioned in their groups. Buckup et al. (2007) reported that 64 new freshwater fish species were described in 2006 in Brazil, an average rate of five new species per month. The use of traits (e.g. ecological, morphological, life history strategy) for classifying functional species is an important and challenging step in freshwater fish ecology (Frimpong & Angermeier 2010). However, assessment of functional group richness is useful because functional groups are directly related to the roles that species play within the ecosystem and the capacity of organisms to provide ecosystem services (Blaum et al. 2011 and references therein). Understanding how ecological processes and patterns are related and how we can use our knowledge to preserve them are important goals for ecology in this century. This study, although using a simple functional classification based on trophic guild, vertical habitat and mesohabitat use, pointed out the importance of functional structure in understanding stream organisation. Therefore, we should focus on filling knowledge gaps and advancing basic information when conducting research on Atlantic Forest streams, including exploration of functional traits and functional diversity to answer more complex questions and better understand ecosystem functioning.

Another important issue is the increased abundance of non-native species in downstream reaches where human influences are intensified by easier access. Non-native species can change water transparency, the behaviour, distribution, and abundance of native species (Hughes & Herlihy 2012), ecosystem function (Simon & Townsend 2003), hybridisation rates, unique gene pools and trophic state, and introduce diseases and parasites (Olden et al. 2004; Vitule et al. 2009; Strayer 2010). According to Olden et al. (2004), such modifications lead to native species extinctions, biodiversity losses and biotic homogenisation. Unfortunately, Brazil has encouraged the introduction of freshwater fish species by sports fishermen and state agencies for sport and aquaculture (Vitule et al. 2009).

From the perspective of conservation biology, our results highlight the need to evaluate Atlantic Forest streams under different spatial scales and to consider the existence of longitudinal changes in fish assemblage structure. Moreover, we should consider the influence of natural altitudinal gradients, as seen in this study, in developing and implementing monitoring programmes, impact studies, conservation plans, and mitigation and rehabilitation activities.

Acknowledgements

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Appendix 1. Species categorised as functional species based on origin (categories: 2), trophic guild (categories: 4), vertical habitat (categories: 2) and mesohabitat use (categories: 3).

Species	Origin	Trophic Guild	Vertical Habitat	Mesohabitat Use	Code
Astyanax taeniatus	Native	Omnivorous	Water column	Pool	NOWP
Hyphessobrycon reticulatus	Native	Omnivorous	Water column	Pool	
Geophagus brasiliensis	Native	Omnivorous	Water column	Pool	
Astyanax bimaculatus	Native	Omnivorous	Water column	Intermediate	NOWI
Astyanax giton	Native	Omnivorous	Water column	Intermediate	
Astyanax hastatus	Native	Omnivorous	Water column	Intermediate	
Astyanax intermedius	Native	Omnivorous	Water column	Intermediate	
Astyanax janeiroensis	Native	Omnivorous	Water column	Intermediate	
Astyanax parahybae	Native	Omnivorous	Water column	Intermediate	
Astyanax sp.	Native	Omnivorous	Water column	Intermediate	
Astyanax sp.1	Native	Omnivorous	Water column	Intermediate	
Astyanax sp.2	Native	Omnivorous	Water column	Intermediate	
Brycon opalinus	Native	Omnivorous	Water column	Intermediate	
Deuterodon parahybae	Native	Omnivorous	Water column	Intermediate	
Deuterodon sp.	Native	Omnivorous	Water column	Intermediate	
Deuterodon sp.2	Native	Omnivorous	Water column	Intermediate	
Pimelodella lateristriga	Native	Omnivorous	Benthic	Pool	NOBP
Awaous tajasica	Native	Omnivorous	Benthic	Intermediate	NOBI
Callichthys callichthys	Native	Omnivorous	Benthic	Intermediate	
Rineloricaria sp.1	Native	Omnivorous	Benthic	Intermediate	

Appendix 1 *(continued)*

Species	Origin	Trophic Guild	Vertical Habitat	Mesohabitat Use	Code
Rineloricaria sp.2	Native	Omnivorous	Benthic	Intermediate	
Phalloceros aff *anisophalos*	Native	Detritivorous	Water column	Pool	NDWP
Phalloceros harpagos	Native	Detritivorous	Water column	Pool	
Poecilia vivipara	Native	Detritivorous	Water column	Pool	
Hoplosternum littorale	Native	Detritivorous	Benthic	Intermediate	NDBI
Hypostomus affinis	Native	Detritivorous	Benthic	Intermediate	
Hypostomus sp.	Native	Detritivorous	Benthic	Intermediate	
Loricariichthys castaneus	Native	Detritivorous	Benthic	Intermediate	
Ancistrus multispinnis	Native	Detritivorous	Benthic	Fast water	NDBF
Heptapterus sp.	Native	Detritivorous	Benthic	Fast water	
Hisonotus notatus	Native	Detritivorous	Benthic	Fast water	
Paratocinclus maculicauda	Native	Detritivorous	Benthic	Fast water	
Parotocinclus sp.	Native	Detritivorous	Benthic	Fast water	
Kronichthys heylandi	Native	Detritivorous	Benthic	Fast water	
Pseudotothyris obtusa	Native	Detritivorous	Benthic	Fast water	
Schizolecis guntheri	Native	Detritivorous	Benthic	Fast water	
Homodiaetus passarellii	Native	Detritivorous	Benthic	Fast water	
Listura nematopteryx	Native	Detritivorous	Benthic	Fast water	
Gymnotus sylvius	Native	Invertivorous	Water column	Pool	NIWP
Gymnotus pantherinus	Native	Invertivorous	Water column	Pool	
Bryconamericus microcephalus	Native	Invertivorous	Water column	Intermediate	NIWI
Bryconamericus ornaticeps	Native	Invertivorous	Water column	Intermediate	
Bryconamericus tenuis	Native	Invertivorous	Water column	Intermediate	
Mimagoniates microlepis	Native	Invertivorous	Water column	Intermediate	
Kryptolebias brasiliensis	Native	Invertivorous	Water column	Intermediate	
Scleromystax barbatus	Native	Invertivorous	Benthic	Intermediate	NIBI
Corydoras nattereri	Native	Invertivorous	Benthic	Intermediate	
Acentronichthys leptos	Native	Invertivorous	Benthic	Intermediate	
Rhamdioglanis transfasciatus	Native	Invertivorous	Benthic	Intermediate	
Hemipsilichthys gobio	Native	Invertivorous	Benthic	Fast water	NIBF
Characidium interruptum	Native	Invertivorous	Benthic	Fast water	
Characidium vidali	Native	Invertivorous	Benthic	Fast water	
Trichomycterus cf paquequerensis	Native	Invertivorous	Benthic	Fast water	
Trichomycterus sp.	Native	Invertivorous	Benthic	Fast water	
Trichomycterus zonatus	Native	Invertivorous	Benthic	Fast water	
Neoplecostomus microps	Native	Invertivorous	Benthic	Fast water	
Crenicichla lacustris	Native	Piscivorous	Water column	Pool	NPWP
Oligosarcus hepsetus	Native	Piscivorous	Water column	Pool	
Rhamdia quelen	Native	Piscivorous	Benthic	Pool	NPBP
Hoplerythrinus unitaeniatus	Native	Piscivorous	Benthic	Pool	
Hoplias malabaricus	Native	Piscivorous	Benthic	Pool	
Synbranchus marmoratus	Native	Piscivorous	Benthic	Pool	
Poecilia reticulata	Non-native	Detritivorous	Water column	Pool	NNDWP
Xiphophorus sp.	Non-native	Omnivorous	Water column	Pool	NNOWP
Cichla kelberi	Non-native	Omnivorous	Water column	Pool	
Oreochromis niloticus	Non-native	Omnivorous	Water column	Intermediate	NNOWI
Crenicichla cf. *lepdota*	Non-native	Piscivorous	Water column	Pool	NNPWP
Cichlassoma sp.	Non-native	Piscivorous	Water column	Pool	

Appendix 2. Species, species code, frequency of occurrence (FO%), abundance (N), biomass (g) and trophic guild (TG) of fish species.

Species	Code	FO%	Abundance	Biomass	TG	References
Characidium interruptum	Chaint	6.5	11	14.4	I	[†]Braga & Gomiero (2009)
Characidium vidali	Chavid	52.2	1301	3107.637	I	Rezende et al. (2011)
Oligosarcus hepsetus	Olihep	10.9	8	270.51	P	Araújo et al. (2005)
Astyanax bimaculatus	Astbim	8.7	39	337.33	O	[†]Menezes et al. (2007)
Astyanax giton	Astgit	52.2	512	3254.85	O	[†]Menezes et al. (2007)
Astyanax hastatus	Asthas	47.8	431	1455.53	O	[†]Menezes et al. (2007)
Astyanax intermedius	Astint	32.6	241	1282.99	O	[†]Menezes et al. (2007)
Astyanax janeiroensis	Astjan	39.1	545	4672.83	O	Mazzoni & Costa (2007)
Astyanax parahybae	Astpar	4.3	33	99.38	O	[†]Menezes et al. (2007)

Appendix 2 *(continued)*

Species	Code	FO%	Abundance	Biomass	TG	References
Astyanax sp.	Astsp	4.3	3	37.94	O	[†]Menezes et al. (2007)
Astyanax sp.1	Astsp1	8.7	5	28	O	[†]Menezes et al. (2007)
Astyanax sp.2	Astsp2	15.2	31	606.14	O	[†]Menezes et al. (2007)
Astyanax taeniatus	Asttae	54.3	2346	16,544.61	O	Manna et al. (2012)
Brycon opalinus	Bryopa	4.3	8	0.77	O	Gomiero et al. (2008)
Bryconamericus microcephalus	Brimic	2.2	1	3.56	I	Mazzoni & Rezende (2009)
Bryconamericus ornaticeps	Bryorn	34.8	655	1534.89	I	[†]Mazzoni & Rezende (2009)
Bryconamericus tenuis	Bryten	2.2	1	0.08	I	[†]Mazzoni & Rezende (2009)
Deuterodon parahybae	Deupar	2.2	2	5.83	O	[†]Mazzoni & Rezende (2003)
Deuterodon sp.	Deutsp	17.4	28	296.42	O	Mazzoni & Rezende (2003)
Deuterodon sp.2	Deutsp2	6.5	37	65.76	O	[†]Mazzoni & Rezende (2003)
Hyphessobrycon reticulatus	Hypret	6.5	74	49.35	O	Barreto & Aranha (2006)
Mimagoniates microlepis	Mimmic	41.3	396	243.28	I	Mazzoni & Costa (2007)
Hopleritrinus unitaeniatus	Hopuni	4.3	2	251.7	P	
Hoplias malabaricus	Hopmal	37.0	56	8063.58	P	Rolla et al. (2009)
Kryptolebias brasiliensis	Krybra	13.0	46	43.96	I	[†]Abilhoa et al. (2010)
Phalloceros aff. *anisophalos*	Phaani	4.3	10	2	D	Ferreira & Casatti (2006a,b,c)
Phalloceros harpagos	Phahar	47.8	427	111.49	D	Souza et al. (2009)
Poecilia reticulata	Poeret	69.6	2108	442.41	D	Ferreira & Casatti (2006a,b,c)
Poecilia vivipara	Poeviv	23.9	417	77.75	D	[†]Ferreira & Casatti (2006a,b,c)
Xiphophorus sp.[‡]	Xiphso	8.7	10	17.02	O	
Gymnotus carapo	Gymcar	17.4	13	269.79	I	Rolla et al. (2009)
Gymnotus pantherinus	Gympan	32.6	66	818.81	I	Esteves & Lobón-Cervía (2001)
Crenicichla cf. *lepidota*[‡‡]	Crelepd	2.2	1	7.97	P	Gurgel et al. (1998)
Oreochromis niloticus	Orenil	2.2	3	19.8	O	
Cichla kelberi[‡]	Cickel	2.2	2	428.39	P	
Cichlasoma sp.[‡]	Cichsp	2.2	1	8.89	O	
Geophagus brasiliensis	Geobra	56.5	785	14,655.07	O	Mazzoni & Costa (2007)
Crenicichla lacustris	Crenlac	6.5	14	148.56	P	Araújo et al. (2009)
Awaous tajasica	Awataj	10.9	9	76.07	O	Sabino & Castro (1990)
Callichthys callichthys	Calcal	4.3	3	68.21	O	Ferreira & Casatti (2006a,b,c)
Corydoras nattereri	Cornat	28.3	77	202.37	I	[†]Ferreira & Casatti (2006a,b,c)
Hoplosternum litoralle	Hoplit	4.3	3	338.11	D	
Scleromystax barbatus	Sclbar	56.5	1226	4261.3	I	
Pimelodella lateristriga	Pimlat	47.8	407	2720.6	O	Rezende et al. (2011)
Rhamdia quelen	Rhaque	69.6	422	17,834.05	P	Brazil-Sousa et al. (2009)
Acentronichthys leptos	Acelep	58.7	433	833.29	I	Esteves & Lobón-Cervía (2001)
Rhamdioglanis transfasciatus	Rhatra	30.4	431	5191.45	I	Brazil-Sousa et al. (2009)
Heptapterus sp.	Hepsp	2.2	1	1.71	I	
Ancistrus multispinis	Ancmul	47.8	303	1327.49	D	
Hemipsilichthys gobio	Himgob	15.2	194	1104.54	D	Araújo et al. (2009)
Hisonotus sp.	Hisnot	2.2	5	3.43	D	
Parotocinclus maculicauda	Parmac	39.1	220	239.6	D	
Parotocinclus sp.	Parsp	2.2	1	0.16	D	
Hypostomus affinis	Hypaff	41.3	116	1978.49	D	Araújo et al. (2009)
Hypostomus sp.	Hypsp	10.9	43	46.56	D	[†]Araújo et al. (2009)
Kronichthys heylandi	Krohey	17.4	95	214.32	D	Esteves & Lobón-Cervía (2001)
Loricariichthys castaneus	Lorcas	2.2	6	309.4	D	Araújo et al. (2009)
Neoplecostomus microps	Neomic	6.5	34	122.87	I	Braga & Gomiero (2009)
Pseudotothyris obtusa	Pseobt	15.2	47	13.82	D	
Rineloricaria sp.1	Rinsp1	47.8	1235	6071.8	O	Araújo et al. (2009)
Rineloricaria sp.2	Rinsp2	23.9	235	1080.97	O	Araújo et al. (2009)
Schizolecis guntheri	Schgun	56.5	503	233.7	D	Esteves & Lobón-Cervía (2001)
Homodiaetus passarellii	Hompas	4.3	8	2.05	D	
Listrura nematopteryx	Listnem	2.2	1	0.2	D	
Trichomycterus cf. *paquequerense*	Tripaq	2.2	2	8.67	I	[†]Esteves & Lobón-Cervía (2001), Braga & Gomiero (2009)
Trichomycterus sp.	Trisp	2.2	4	16.01	I	[†]Esteves & Lobón-Cervía (2001), Braga & Gomiero (2009)
Trichomycterus cf. *zonatus*	Trizon	47.8	1061	1120.6	I	[†]Esteves & Lobón-Cervía (2001), Braga & Gomiero (2009)
Synbranchus marmoratus	Synmar	65.2	112	5433.32	P	Ferreira & Casatti (2006a,b,c)
Total			17,906	110,134.3		

P, Piscivorous; I, invertivorous; O, omnivorous; D, detritivorous.
[†]Reference for the trophic guilds of species of the same genus or family.
Non-native species.