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More of the Same: High Functional Redundancy in Stream Fish Assemblages from Tropical Agroecosystems

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Abstract In this study, we investigated the influence of environmental variables (predictor variables) on the species richness, species diversity, functional diversity, and functional redundancy (response variables) of stream fish assemblages in an agroecosystem that harbor a gradient of degradation. We hypothesized that, despite presenting high richness or diversity in some occasions, fish communities will be more functionally redundant with stream degradation. Species richness, species diversity, and functional redundancy were predicted by the percentage of grass on the banks, which is a characteristic that indicates degraded conditions, whereas the percentage of coarse substrate in the stream bottom was an important predictor of all response variables and indicates more preserved conditions. Despite being more numerous and diverse, the groups of species living in streams with an abundance of grass on the banks perform similar functions in the ecosystem. We found that riparian and watershed land use had low predictive power in comparison to the instream habitat. If there is any interest in promoting ecosystem functions and fish diversity, conservation strategies should seek to restore forests in watersheds and riparian buffers, protect instream habitats from siltation, provide wood debris, and mitigate the proliferation of grass on stream banks. Such actions will work better if they are planned together with good farming practices because these basins will continue to be used for agriculture and livestock in the future.

Keywords Conservation · Local variables · Landscape variables · Species diversity

Introduction

Agroecosystems are ecological and socioeconomic systems where biological communities interact with human-modified environments that are used to produce food and other products for human use (Conway 1987).

Currently, these systems represent more than 38 % of the planet's surface (Ramankutty et al. 2008), and they are the main factor associated with global biodiversity losses (Tscharntke et al. 2005; Dolédec and Statzner 2010). Agricultural impacts on the environment include the replacement of naturally forested areas by the expansion of crops and pasture lands, as well as the intensification of increased production through irrigation, fertilizers, biocides, and mechanization on areas that have previously been altered (Foley et al. 2012). When compared to natural ecosystems, agroecosystems demonstrate high fluidity, high vulnerability, spatiotemporal differences, poor stability, and low biodiversity (Zhu et al. 2012). In this scenario, both agricultural expansion and intensification can affect aquatic ecosystems in different ways and levels (Harding et al. 1998; Feld 2013), such as by causing the loss of biodiversity and ecosystem services (Foley et al. 2007), by generating excessive nutrient inputs (Canfield et al. 2010; Woodward et al. 2012), by shifting the main energy sources (from C3 to C4) for aquatic food webs (Bunn et al. 1997), and by increasing pesticide runoff (Bareswill et al. 2013).

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The expansion of agribusiness in many tropical regions has been conducted at the cost of natural resource degradation. An example is the recent approval of the new Brazilian forest code, which provided amnesty for illegal deforestation and relaxed restoration requirements in riparian preservation areas (Soares-Filho et al. 2014). In this context of land use and exploitation, a more accurate picture of stream habitat quality can be provided by the functional approach, which is a way to express the functional differences between species, differently than species richness or diversity that assume that all species contribute in the same manner to the ecosystem functioning (Díaz and Cabido 2001). This approach may be particularly useful in cases in which simplified, poor quality habitats result in habitat constraints that filter out fish species that rely on habitat types that are no longer represented or fish species that are sensitive to harsh environmental conditions, such as grass-dominated, deforested, and heavily silted sites (e.g., Casatti et al. 2009).

Descriptions of communities using functional perspectives have recently been receiving increased attention (Cadotte et al. 2011). The increased attention is partly due to the high predictive power of functional diversity descriptors regarding ecosystem processes (Tilman et al. 1997; Díaz and Cabido 2001), such as the robust habitat-trait relationship observed for different taxa in different environmental gradients (Flynn et al. 2009; Villéger et al. 2008; Mouchet et al. 2010). Measuring functional diversity can provide information that is complementary to that traditionally obtained through taxonomic diversity metrics. In estuarine systems, for example, Villéger et al. (2010) verified that intensified degradation led to increased species richness but decreased functional divergence and specialization, which was explained by the decrease in specialist species and by the fact that the added species were redundant in relation to those that were previously established. In fact, the relationship between species richness and functional diversity can vary (Mayfield et al. 2010), thus revealing the actions of distinct ecological processes (Pavoine and Bonsall 2011).

Agroecosystems can lead to environmental alterations that limit the occurrence of species that have functional traits incompatible with local conditions (Devictor et al. 2008). According to the niche-filtering hypothesis, coexisting species are functionally more similar to one another than would be expected by chance (redundancy) because environmental conditions act as a filter, allowing only species with traits compatible with local conditions to survive (Zobel 1997). In this context, different environmental variables at local and landscape scales would represent environmental filters in agroecosystems (see Pease et al. 2012 for an environmental filtering support for trait-environment relationships in stream fish assemblages).

Burcher et al. (2008) found that functional diversity was lower in streams that were surrounded by pasture in the past or streams with scarce riparian plant cover when compared to streams with forested riparian zones. Such findings can be more complex, however, because the presence/absence of forests can interact with other factors at finer scales (Strayer et al. 2003) to determine assemblage's diversity patterns (Teresa and Casatti 2012; Cruz et al. 2013).

In this study, we investigated the influence of environmental variables on species richness, species diversity, functional diversity, and functional redundancy of stream fish assemblages in agroecosystems. It is known that environmental variables are related to the gradient of structural habitat quality (Wang et al. 1997; Diana et al. 2006). However, severe degradation can represent limiting conditions to the occurrence of species with more specialized niches, even though they can support high species diversity under certain circumstances (Villéger et al. 2010). We conducted our study in river basins that harbors streams that vary from relatively preserved to extremely degraded (Casatti et al. 2009) and we hypothesized that, despite presenting high richness or diversity in some occasions, fish communities will be more functionally redundant in the most degraded conditions. With the aim of exploring this hypothesis, we also determined the functional similarity among species, identified the species-habitat relationships, and tested the relationship of the selected variables with the response variables. Through this approach, we also expected to identify the habitat variables and species traits that are of interest to watershed management and stream restoration efforts in the basin and comparable locations.

Materials and Methods

Study Area and Site Selection

We conducted this study in non-urban areas of the hydrographic basins of the São José dos Dourados and Turvo-Grande Rivers in the northwest region of the State of São Paulo, located in southeastern Brazil (Fig. 1). This region was originally covered by semi-deciduous seasonal forest (Silva et al. 2007). Since the second half of the nineteenth century, this region has experienced high rates of deforestation: first for the development of coffee cultivation and second, from 1929 on, for the creation of pasture for livestock grazing that replaced the coffee crops (Monbeig 1998). Currently, only 4 % of the original vegetation coverage remains (Nalon et al. 2008) and is distributed in small and isolated fragments (Silva et al. 2007). For this study, we selected only streams that were embedded in
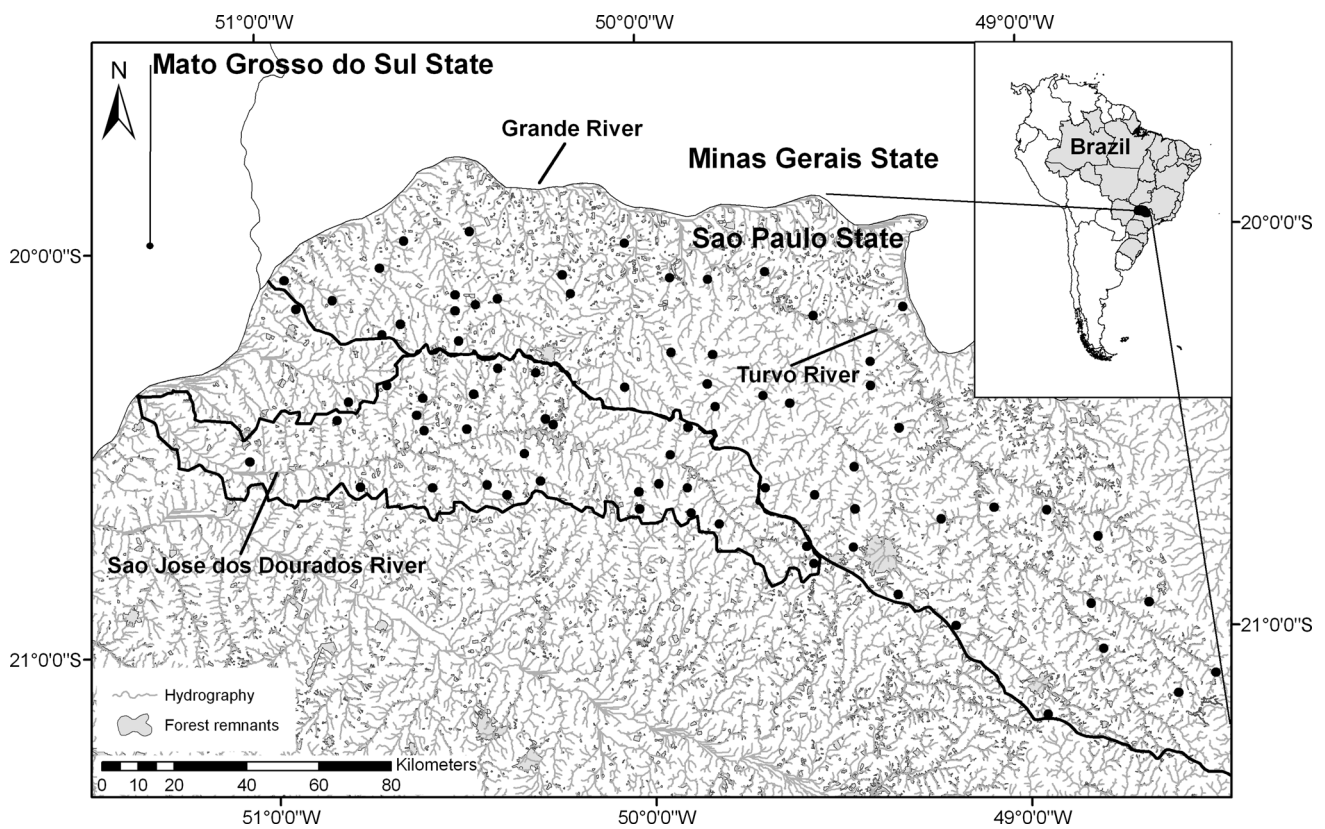
Fig. 1 Location of the sampled stream reaches in the José dos Dourados and Turvo-Grande river basins, São Paulo State, Brazil

agricultural lands, which were mostly used for livestock grazing or sugarcane plantations, and avoided direct urban influence. The soil of the region is characterized by unconsolidated sand and clay sediments, which have a high erosive potential (IPT 1999). The climate is hot and tropical, with maximum average temperatures between 31 and 32 °C, minimum average temperatures between 13 and 14 °C, and an annual rainfall between 1300 and 1800 mm (Silva et al. 2007). There are two well-defined climatic periods: a dry period with lower rainfall between June and August and a wet period with higher rainfall between December and January (IPT 1999).

We selected the sampling sites using a randomized approach (Kasyak 2001). We selected one site for each 100 km of a specific length order (from first to third order determined in a 1:50,000 map scale, sensu Sthraler 1957), with one sampled reach in each stream. Overall, we sampled 95 stream reaches on one occasion during the dry seasons from 2003 to 2005 to limit the effects of seasonal differences.

Environmental Variables

At each 75 m long sampling reach, we obtained 21 environmental variables, which represented the local riparian, and watershed scales (Table 1). At local scale we measured dissolved oxygen, conductivity, pH, temperature, and turbidity with a portable multiparameter probe. Nitrate, orthophosphate, and ammonia were dosed at a specialized laboratory; ammoniacal nitrogen and orthophosphate were determined by a spectrophotometry technique using MERCK® reagents and nitrate by following the APHA Standard Methods (method 4500-NO_3). We used the average width and depth of each reach to calculate habitat volume (=average width × reach length × average depth). We calculated the average current from three measurements with a mechanical flowmeter taken side by side across the mesohabitat (pools, runs, riffles) present in the reach. Using visual inspection, we obtained the percent of silt, sand and coarse substrate (particle size based on Krumbein and Sloss's 1963 classification), the percentage of wetted area covered by woody debris, and the percentage of stream bank length occupied by grass.

The riparian corridor (Table 1) was represented by the percentage of the stream corridor covered by shrubs and trees, obtained by visual inspection, and the riparian canopy cover, which was based on the degree of coverage at both margins of the sampled reach (0, without coverage; 1, from 1 to 25 % of coverage; 2, from 26 to 50 %; 3, from 51 to 75 %; 4, more than 75 %). The watershed scale

Table 1 Units, means, and range values of environmental variables sampled from the 77 stream reaches

Variables	Units	Mean (range)
Local scale		
Dissolved oxygen	mg/l	7.8 (1.1–13.4)
Conductivity	mS/cm	0.1 (0.02–0.4)
pH	–	7.3 (5.62–8.4)
Turbidity	NTU	70.7 (1.0–511.0)
Nitrate	mg/l	0.5 (<0.001–2.7)
Ammonia	mg/l	0.1 (<0.001–1.8)
Orthophosphate	mg/l	0.1 (<0.001–1.2)
Habitat volume	m^3	67.6 (1.1–280.5)
Current	m/s	26.2 (0.1–75.8)
Percentege of the bottom covered by silt (0.004-0.05 mm)	%	2.0 (0–20.0)
Percentege of the bottom covered by sand (0.05–2 mm)	%	91.5 (60–100.0)
Percentege of the bottom covered by coarse substrate (2 to >256 mm)	%	6.5 (0–40.0)
Percentege of the bottom covered by woody debris	%	6.2 (0–40.0)
Percentege of the stream banks covered by grass	%	33.8 (0–90.0)
Riparian corridor		
Percentege of the stream corridor covered by shrubs and trees	%	24.4 (0–100.0)
Canopy cover	–	1.6 (0–4.0)
Watershed		
Percentege of forest area in the riparian buffer (30 m wide)	%	11.9 (0–49.9)
Percentege of forest area in the watershed	%	5.6 (0–21.1)
Distance from the reach to the headwaters	km	3.1 (0.1–11.8)
Dams upstream to the sampled reach	n°	2.2 (0–12.0)
Road density	km/km^2	1.9 (0–29.3)

(Table 1) included the land use and coverage, obtained through the analysis of Landsat 5 TM (2010, 30 × 30 m^2 resolution) satellite images, made available by the National Institute for Space Research (INPE). We conducted the classification according to the supervised classification using the maximum likelihood algorithm (Jensen 2000) in the software Erdas Imagine 9.2. The watershed limits and the drainage network were generated using the hydrological model ArcSWAT (Soil and Water Assessment Tool) and satellite images from the Digital Elevation Model (DEM) SRTM (90 × 90 m^2 resolution) generated by the National Aeronautics and Space Administration (NASA), made available by the United States Geological Survey (USGS). We generated the watersheds using georeferenced points taken during the sampling period considering a minimum contribution area of 150 ha, using the ArcMap module of the software ArcGIS version 9.3 (ESRI 2008). We calculated the percentage of forest in the riparian buffer zone (30-m wide on each side), the percentage of the watershed covered by forest, the distance of each sampled reach to its headwaters, and the number of dams upstream of the reach for each watershed. We calculated the road density through the extension of paved roads (km) divided by the watershed area (km^2), according

to Kautza and Sullivan (cited by them as Regional Development Index, 2012).

Fish Sampling and Functional Trait Measurement

We sampled fish with standardized sampling efforts at all reaches. We started the collection 15 min after blocking the upstream and downstream limits of each reach with block nets (5 mm mesh) by using two electrofishing passes for 60 min combined. Three collectors conducted the electrofishing; the first handled an electrified dip net (220 V, 50–60 Hz, 3.4–4.1 A, 1000 W), the second a grill-shaped electrode, and the third a regular dip net. We fixed fish in a 10 % formalin solution and transferred them to a 70 % ethanol solution after 48 h. They were identified, counted, weighed, and deposited at the Fish Collection of the Department of Zoology and Botany of São Paulo State University (DZSJRP 5833–6190, 7264–7443), São José do Rio Preto, São Paulo, Brazil.

We measured nine functional traits (see Table 2 for details and Appendix Table 5 for the matrix of traits) in 36 species that were represented by a sufficient number of specimens (≥10) to obtain quantitative traits. Traits were associated with vertical habitat use, body size, trophic

Table 2 Functional traits examined from the fish fauna

Traits	Types	Descriptions/interpretations
Compression index	Quantitative	Maximum height of the body divided by its maximum width
		High values may indicate a laterally compressed fish inhabiting lentic habitats[a]
Relative area of pectoral fin	Quantitative	Pectoral fin area divided by body area. High values indicate slow swimmers, which use pectoral fins to perform maneuvers and breakings, or fish inhabiting fast waters, which use them as airfoils to deflect the water current upward to remain firmly attached to the substrate[a]
Pectoral fin aspect ratio	Quantitative	Maximum length of the pectoral fin divided by its maximum width. High values indicate long fins, typical of fish that swim for long distances[a]
Eye position	Quantitative	Distance from the middle of the eye to the base of the head, divided by head height. High values indicate dorsally located eyes, typical of benthic fish[a]
Standard length classes	Ordinal	Values of 1, 2, or 3 were assigned to each species, according to the most common size class for adults, cited in Graça and Pavanelli (2007), Froese and Pauly (2013): 1 = up to 50 mm, 2 = from 51 to 100 mm, 3 = greater than 100 mm
Diet	Fuzzy	Feeding items were fish (fish), algae (algae), periphyton (per), plants (plan), detritus (det), autochthonous invertebrates (autinv), and allochthonous invertebrates (allinv). Each feeding item was coded as 0, 1, or 2, depending on its predominance in the stomachs of each species sample. 0 = item absent or rare in species diet, 1 = item consumed, although not the most representative in species diet, 2 = dominant item in the diet
Velocity preference	Ordinal	Values of 0, 1, or 2 were assigned to each species, according to its preference for current speed: 0 = slow, 2 = intermediate, 3 = fast[b]
Substrate preference	Binary	Values of 0 or 1 were assigned to each species, according to its preference for different substrates: 0 = mostly sand substrate; 1 = coarse substrates, mostly gravel and cobbles[b,c]
Feeding tactics	Ordinal	Values of 1–9 were assigned to each species to represent its main feeding tactic: 1 = grubber excavating while moving, feeding on bottom animals[d]; 2 = picker of items in the water column[e]; 3 = crepuscular to nocturnal predator of bottom animals[d]; 4 = ambush predator among roots of submerged vegetation[e]; 5 = digger of localized excavations, feeding on bottom animals[d]; 6 = grazer[e]; 7 = surface picker[d]; 8 = sit-and-wait predator of bottom animals[d]; 9 = mud-eater[d]

[a] Watson and Balon (1984), [b] Teresa and Casatti (2012), [c] Romero and Casatti (2012), [d] Sazima (1986), [e] Casatti (2002)

ecology, velocity preference, hard substrate preference, and feeding tactics. We obtained fish measurements with a digital caliper and pectoral fin areas with a Zeiss® SteREO Discovery V12 stereomicroscope and AxioVision Zeiss® image software. For specimens larger than 80 mm, we obtained fin areas by contouring the fins over graph paper (according to Beaumord and Petrere 1994) due to the view limitation of the optic equipment field in such cases. For species with accentuated sexual dimorphism, such as *Poecilia reticulata* and *Phalloceros harpagos*, we measured only females for procedure standardization. Despite being observed in the sampled streams, we excluded *Synbranchus marmoratus* from the functional analysis because the absence of fins precludes the application of the proposed indexes. We obtained the body size of each species from the literature to code this trait so that it could represent the predominant size class of adult individuals. We adopted this procedure to avoid underestimating the species' characteristic size as an adult if there were a large number of juveniles present in the samples. We obtained the functional traits related to feeding through stomach content analysis and treated them as fuzzy variables. We determined velocity, substrate preference, and feeding tactic traits according to previous studies (e.g., Teresa and Casatti 2013) and our own underwater observations.

Selection of Environmental Variables

We selected environmental variables according to their contribution to the variability among streams using principal component analysis (PCA), performed with the SAM 4.0 software (Rangel et al. 2010). We normalized variables to present the same weight (mean = 0, standard deviation = 1), and the axes that contributed the most to explain the observed variation were selected according to the Broken-Stick model, one of the methods with the most consistent results in ecological studies (Jackson 1993). This model constructs a null distribution of eigenvalues and compares it with observed ones; a principal component is interpretable if it exceeds the eigenvalue randomly generated by the Broken-Stick model (Legendre and Legendre 1998). Because some variables were correlated, we considered the most important variables to be those that presented the highest loadings (loadings <−0.7 or >0.7 at least in one axis).

Data Analysis

We represented the functional similarity among species in a graph resulting from PCoA according to Pavoine et al. (2009), in which a matrix of functional distance among species is generated through the generalization of Gower's Distance (Pavoine et al. 2009). We conducted this analysis with the function "dist.ktab" in the "vegan" and "ade4" packages of R software (R Development Core Team 2011), according to Pavoine et al. (2009). To aid in the interpretation of the results, we added the main functional characteristics of each species group to the graph.

To evaluate the relationship between the fish abundance and environmental variables, we used the redundancy analysis (RDA), a constrained ordination technique, which directly analyzes the relationships between multivariate ecological datasets (ter Braak and Smilauer 2012). Based on the results of the PCA, we included the (normalized) variables with the highest contribution to the between-stream variability. To test the significance of the first axis, we performed a Monte Carlo permutation, under full model (4999 permutations, $P < 0.05$). To test the significance of each variable, we used stepwise model selection of the

Generalized Linear Models to obtain F statistics, again using a 0.05 significance level. We conducted all these procedures in the software CANOCO 5 (ter Braak and Smilauer 2012).

We followed the procedures of Pillar et al. (2013) to calculate species diversity (D, Gini-Simpson index for species diversity), functional diversity (Q, Rao's quadratic entropy), and functional redundancy (FR). FR is defined as the difference between species diversity and functional diversity (de Bello et al. 2007), given by the formula FR = D − Q (Pillar et al. 2013). We calculated D and Q in the "vegan" and "ade4" packages of R software (R Development Core Team 2011). If FR = 0, the species have completely different traits; if FR = 1, all the species have identical traits; this second condition should be expected in redundant assemblages (Pillar et al. 2013).

To investigate the determinants of the diversity patterns on assemblages, we generated multiple regression models. The response variables were species richness, species diversity, functional diversity, and FR and the explanatory variables were the set of selected environmental. Overall, 31 models were generated for each response variable and they were compared according to the Akaike information

Table 3 Loadings resulting from the principal component analysis for the environmental variables in the sampled stream reaches

Variables	Axis 1	Axis 2
Dissolved oxygen	−0.129	0.654
Conductivity	0.151	−0.617
pH	−0.062	−0.242
Turbidity	0.073	−0.413
Nitrate	0.037	−0.075
Ammonia	−0.258	−0.535
Orthophosphate	0.173	−0.581
Habitat volume	−0.329	−0.355
Current	0.017	0.411
Percentege of the bottom covered by silt	−0.210	−0.187
Percentege of the bottom covered by sand	**0.806**	0.060
Percentege of the bottom covered by coarse substrate	**−0.811**	0.003
Percentege of the bottom covered by woody debris	**−0.729**	−0.161
Percentege of the stream banks covered by grass	**0.757**	−0.054
Percentege of the stream corridor covered by shrubs and trees	**−0.815**	−0.01
Canopy cover	**−0.777**	0.138
Percentege of forest area in the riparian buffer	−0.240	−0.122
Percentege of forest area in the watershed	0.120	−0.449
Distance from the reach to headwaters	−0.153	0.143
Dams upstream to the sampled reach	0.116	0.223
Road density	0.149	−0.043
Eigenvalue proportion	0.196	0.174
Broken stick model	0.111	0.126

Broken stick model indicates that axis 1 should be retained for interpretation. The values that contributed the most for the first axis are represented in bold (loadings <−0.7 or >0.7)
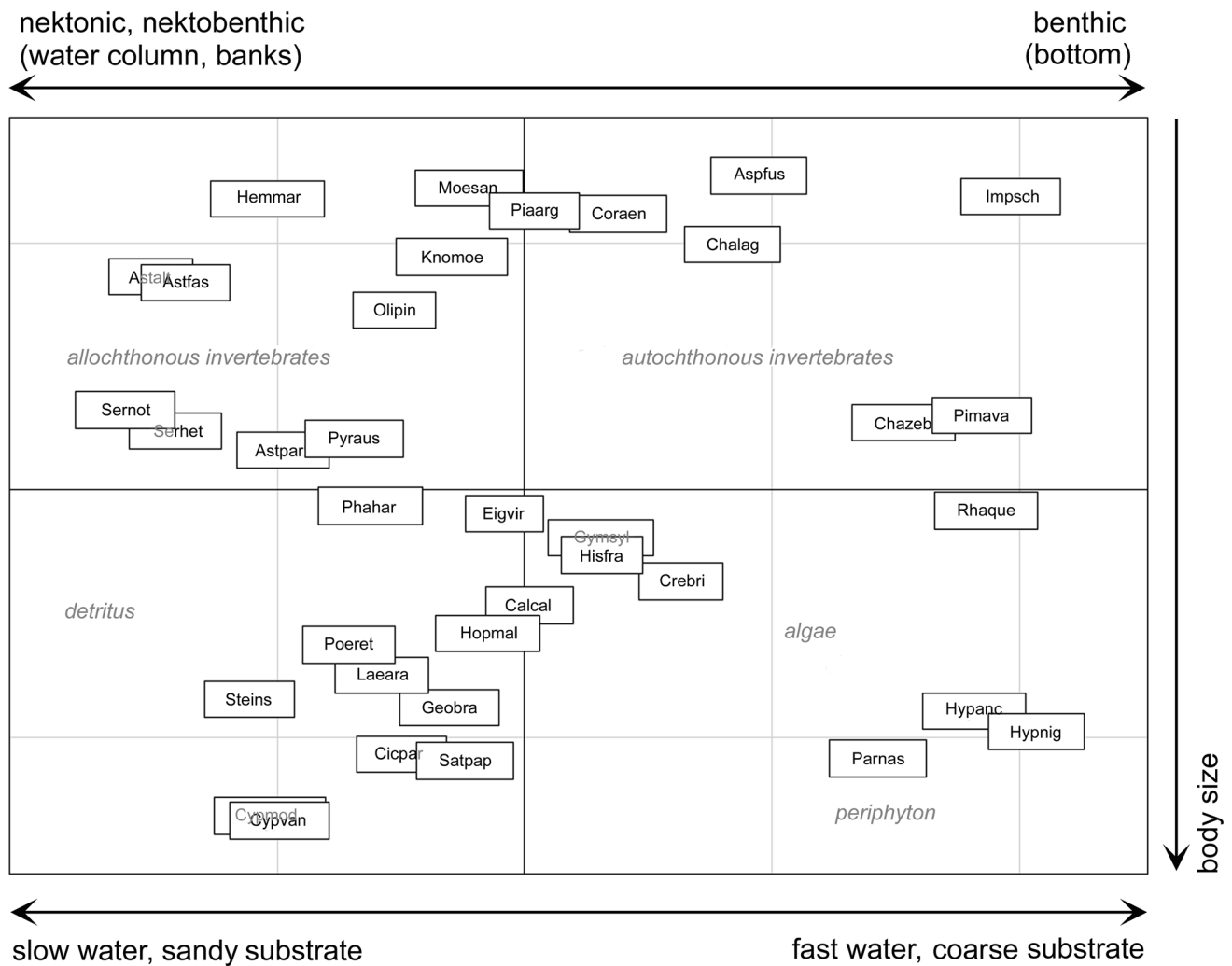
nektonic, nektobenthic
(water column, banks)

benthic
(bottom)

slow water, sandy substrate

fast water, coarse substrate

Fig. 2 Bidimensional *graph* from Principal Coordinates Analysis that represents the global functional distance among species. Some characteristics have been added to the graph to aid interpretation. Characteristics that represent habitat use are on the *horizontal axis*, and body size is represented on the *vertical axis*. The diet items that influenced the most the fish fauna were added a posteriori to the biplot, following their importance for each species (see Table 5). For species codes see Table 6

criterion (AIC) corrected by the sample size and the number of parameters in the model (AICc according to Burnham and Anderson 2002). The relative importance of each variable was estimated based on by averaging summing the AIC weights across all the models, using AIC weights in the set where the given variable occurs. These analyses were conducted with the software SAM 4.0 (Rangel et al. 2010).

Results

Of all variables, only six, which were related to physical characteristics at local and riparian corridor scales, contributed the most to among-stream variation (Table 3). However, some of these varied in the same way (Table 3).

The percentage of coarse substrate, the percentage of woody debris, the percentage of shrubs and trees, and canopy cover showed negative component loadings and demonstrated correspondence at local and riparian corridor scales; in turn, the percentage of sand and the percentage of grass showed positive component loadings (Table 3).

Overall, 13,245 individuals belonging to 60 fish species were sampled (Appendix Table 6). The first PCoA axis ordered the 36 selected species according to their swimming ability in faster or slower running waters, preference for coarse or sand substrate, and the use of vertical strata (Fig. 2). The feeding traits influenced the similarity/dissimilarity among species according to the predominant consumption of the different prey items. Allochthonous invertebrates and detritus are common for species that live in slow water and sandy bottom and that explore the water

column (nektonic), occasionally exploring the stream bed (nektobenthics). In this left portion of the PCoA bliplot are most of the tetras, knifefishes, livebearers, and cichlids. Autochthonous invertebrates, algae, and periphyton are important items for benthic species that are commonly found in fast waters and bottom covered by coarse substrate. These fish species are represented by catfishes, armored catfishes, and South American darters. The second PCoA axis ordered species according to body size (Fig. 2).

Among the ordination axes extracted from RDA, the first one was significant and accounted for 44 % of the variance in species-environment relationships (eigenvalue of first axis = 0.032, pseudo $F = 2.3$, $P = 0.043$). All variables explained the assemblage's structure (sand, $F = 107.42$, $P < 0.0001$; coarse substrate, $F = 212.20$, $P < 0.0001$; woody debris, $F = 44.2$, $P < 0.0001$; grass, $F = 336.04$, $P < 0.0001$; shrubs and trees, $F = 60.15$, $P < 0.0001$). According to axis 1 in the RDA representation, a greater number of species was associated with grassy and sandy conditions (see left side of the biplot in Fig. 3) than to the opposite, which is coarse substrate, woody debris, or shrubs and trees.

All the response variables were predicted by the percentage of coarse substrate on the streambed; species richness, species diversity, and functional redundancy were also predicted by the percentage of grass on the banks (Table 4). Such results indicate that, despite presenting

higher richness or diversity in some instances, species occurring in this type of stream (occupied by grasses in the banks) play similar functional roles in the community.

Discussion

The environmental variables predicted fish species richness, species diversity, functional diversity, and functional redundancy in a similar way. Our initial hypothesis was confirmed because functional redundancy was high, even in conditions of high species richness or diversity. The amount of grass on the stream banks was the main predictor of functional redundancy, which indicates that despite being more numerous and diverse, the groups of species living in this condition perform similar functions in the ecosystem. This vegetation comes from adjacent pastures in areas of limited shade from the riparian zone, and it is a good indicator of low habitat integrity (Bunn et al. 1997, Casatti et al. 2009) and habitat homogenization (Zeni and Casatti 2014). The presence of grass at the border and in the instream habitat, as observed herein, can provide additional microhabitats that favor the colonization, reproduction, and feeding of aquatic insects, playing a similar role to that of aquatic macrophytes, which increase macroinvertebrate abundance in streams (Marques et al. 2013) and lakes (Walker et al. 2013). High macroinvertebrate availability can in turn favor the persistence of fish populations, particularly those that are characterized by opportunistic feeding. Among the submerged roots of invasive grass, large amounts of sediment can be trapped with detritus that, together with high respiration rates, may reduce dissolved oxygen (Bunn et al. 1997). In this type of environment, midge larvae are abundant and represent, along with detritus, the most consumed resources by local fish (Zeni and Casatti 2014). Among the species able to live in such conditions, we can cite, for example, the electric knifefish *Gymnotus sylvius*, the tetras *Knodus moenkhausii* and *Serrapinnus notomelas*, the cichlid *Laetacara araguaiensis*, and the guppy *Poecilia reticulata* (see Fig. 3).

Habitat degradation in its multiple forms can represent an important environmental filter, as documented by studies in other ecosystems, such as reefs (Bellwood et al. 2006) and estuaries (Villéger et al. 2010), in which fish assemblages were considered to be functionally clustered with functionally redundant coexisting species. In a similar way, based on the present findings, we can presume that the physical degradation of the stream caused by the establishment of agroecosystems can also represent an important environmental filter, in which the nektonic/nektobenthic individuals, with large body sizes that use slow waters, sandy substrate, and marginal portions occupied by grass
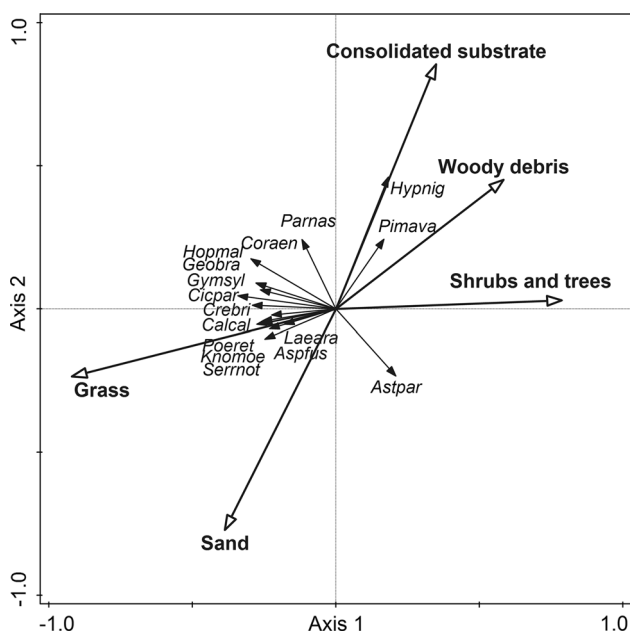

Fig. 3 Bidimensional *graph* from redundancy analysis that represents the relationship between species and environmental variables. For *species codes* see Table 6. Only the 20 species that best fit the environmental variables are displayed

Table 4 Model results of parameter estimates averaged across all 31 models, using Akaike weights for species richness, species diversity, functional diversity, and functional redundancy as response variables

Variables	Importance	Coefficient	Standard coefficient	Standard error	95 % Lower	95 % Upper
Species richness (r^2: 0.122)						
Percentege sand	0.590	1.748	0.492	0.736	0.306	3.190
Percentege coarse substrate	**0.953**	2.436	0.685	1.197	0.090	4.783
Percentege woody debris	0.251	−0.120	−0.034	0.122	−0.359	0.118
Percentege grass	**0.874**	1.183	0.333	0.414	0.373	1.994
Percentege shrubs and trees	0.32a	−0.436	−0.123	0.172	−0.774	−0.099
Species diversity (r^2: 0.129)						
Percentege sand	0.389	−0.002	−0.022	0.014	−0.029	0.025
Percentege coarse substrate	**0.781**	0.041	0.403	0.016	0.010	0.072
Percentege woody debris	0.304	0.010	0.100	0.004	0.002	0.019
Percentege grass	**0.896**	0.035	0.342	0.012	0.011	0.059
Percentege shrubs and trees	0.266	−0.005	−0.047	0.004	−0.013	0.004
Functional diversity (r^2: 0.111)						
Percentege sand	0.421	−0.004	−0.157	0.003	−0.009	<0.002
Percentege coarse substrate	**0.716**	0.008	0.361	0.003	0.003	0.014
Percentege woody debris	0.431	0.004	0.165	0.001	0.001	0.006
Percentege grass	0.253	<0.001	0.018	<0.001	−0.001	0.002
Percentege shrubs and trees	0.36	0.003	0.136	0.001	<0.001	0.005
Functional redundancy (r^2: 0.138)						
Percentege sand	0.391	−0.001	−0.017	0.012	−0.024	0.021
Percentege coarse substrate	**0.737**	0.033	0.372	0.013	0.007	0.059
Percentege woody debris	0.281	0.007	0.079	0.003	<0.001	0.014
Percentege grass	**0.949**	0.034	0.386	0.011	0.012	0.057
Percentege shrubs and trees	0.279	−0.007	−0.079	0.004	−0.014	<0.001

Values in bold identify the variables of greater importance for the best model, according to the Akaike information criterion (AICc)

and that feed mainly on detritus and aquatic invertebrates, predominate (see Fig. 2). From the results obtained herein, it is also possible to conclude that such assemblages are redundant and include many species with functional traits that indicate a generalist strategy.

The percentage of coarse substrate was a good predictor for all the response variables, but does not necessarily indicate a degraded condition. In our sites, coarse substrate is a good predictor for riffle mesohabitat (pers. obs.). Although presenting high fish diversity, riffles are characterized by hydraulic conditions that select species able to live in such a harsh habitat (Teresa and Casatti 2012). Fish able to live and persist in fast-flowing waters normally present morphological adaptations (Martin-Smith 1998), such as periphytivorous benthic grazers like the armored catfishes (*Hypostomus ancistroides* and *H. nigromaculatus*), which attach to the bottom substrate or wood debris, and the scrapetooth (*Parodon nasus*), which has a hydrodynamic body. Other fish in riffles include invertivorous species, which feed on the streambed using sit-and-wait predation (e.g., the South American darter *Characidum zebra*), and crepuscular to nocturnal predator species (e.g., the catfishes *Imparfinis*

schubarti, *Rhamdia quelen*, and *Pimelodella avanhandavae*), which explore the water layer close to the bottom where they are minimally affected by the current. This filtering process selects groups of species with similar functions and therefore explains the high functional redundancy in such conditions, with this process occurring even in preserved sites (Teresa and Casatti 2012).

Our results indicate that in the homogeneous agroecosystem landscape, the functional patterns of fish assemblages are greatly influenced by the local variables, such as substrate composition and bank condition. In such basins, which were deforested in the distant past, riparian and watershed forests are not well represented on the landscape and hence these variables do not account for the environmental gradient. Conservation strategies for aquatic biodiversity in these systems should seek to restore and conserve riparian and landscape diversity (but see a context dependence evaluation by Nislow 2005). Through this way, it is possible to protect instream habitats from siltation (Sweeney and Newbold 2014), provide woody debris for instream habitat (Paula et al. 2011, 2013), and mitigate the proliferation of grass on stream banks (Bunn et al. 1997). This last goal is the main factor associated

with functional redundancy in the studied region. Notably, riparian restoration in small tributaries can introduce additional benefits, since riparian restoration in small tributaries is most likely to result in improved environmental conditions that may extend downstream and consequently improved the quality of larger rivers (Pracheil et al. 2013), thus securing benefits for terrestrial ecosystems in several ways (e.g., Fukui et al. 2006; Chan et al. 2008; Lorion and Kennedy 2009; Gonçalves et al. 2012).

It is noteworthy that according to several authors (e.g., Harding et al. 1998; Teels et al. 2006; Lévêque et al. 2008), the maintenance of aquatic biodiversity and ecological processes depends on the protection of a large percentage of the watershed area. This implies that restoration of the riparian forest alone is not sufficient to improve the integrity of the entire system, although it can maintain the ecological integrity of streams (Lorion and Kennedy 2009) and mitigate impacts on the remaining catchment area (Sweeney and Newbold 2014). The studied basins are located in one of the most productive areas in the most developed state of Brazil. For this reason, it is highly unlikely that these areas will be entirely recovered. Thus, to promote ecosystem functioning and fish diversity, reforestation and rural land management need to be planned together and include sustainable farming practices (Tilman et al. 2002). All of these benefits have great ecological value, particularly in landscapes fragmented by agriculture and livestock expansion.

Appendix

See Tables 5 and 6.

Table 5 Functional traits for each species

Species	CI	RPA	PAR	EP	SL	Diet							VEL	SUB	TAC
						Fish	Algae	Per	Pla	Det	Autinv	Allinv			
Aspfus	1.10	0.16	1.96	0.76	1	0	0	0	0	0	2	0	2	0	1
Astalt	3.11	0.04	3.69	0.58	1	0	0	0	1	1	1	2	0	0	2
Astfas	2.93	0.04	3.47	0.61	1	0	0	0	0	1	1	2	0	0	2
Astpar	2.50	0.06	2.56	0.59	2	0	0	0	0	1	1	2	0	0	2
Calcal	0.97	0.10	1.33	0.73	2	0	0	0	1	2	2	0	0	0	3
Chalag	2.03	0.04	2.58	0.57	1	0	0	0	0	0	2	0	2	1	8
Chazeb	1.50	0.15	2.43	0.65	2	0	0	0	0	0	2	0	2	2	8
Cicpar	2.29	0.14	2.27	0.62	3	0	1	0	0	1	1	0	0	0	5
Coraen	1.32	0.15	2.08	0.71	1	0	0	0	0	0	2	0	1	0	1
Crebri	1.68	0.18	1.76	0.70	3	0	0	0	0	0	2	0	1	0	4
Cypmod	2.18	0.03	2.78	0.54	3	0	0	0	0	2	0	0	0	0	9
Cypvan	1.91	0.04	3.08	0.56	3	0	0	0	0	2	0	0	0	0	9
Eigvir	2.58	0.03	2.39	0.62	3	0	0	0	0	0	2	1	1	0	4
Geobra	2.49	0.15	2.31	0.70	3	0	0	0	0	1	2	0	0	0	5
Gymsyl	2.02	0.02	1.49	0.67	3	0	0	0	0	0	2	1	1	0	4
Hemmar	2.72	0.04	3.69	0.52	1	0	0	0	0	0	0	2	1	0	2
Hisfra	0.80	0.22	2.37	0.68	1	0	1	2	0	1	0	0	1	0	6
Hopmal	1.58	0.09	1.74	0.72	3	1	0	0	0	0	1	2	0	0	4
Hypanc	0.76	0.25	1.92	0.76	2	0	1	1	0	2	0	0	2	2	6
Hypnig	0.71	0.37	1.86	0.82	2	0	0	1	0	2	0	0	2	2	6
Impsch	1.25	0.17	1.32	0.80	1	0	0	0	0	0	2	0	2	2	1
Knomoe	2.37	0.08	2.11	0.60	1	0	1	0	1	1	2	1	1	0	2
Laeara	1.92	0.13	2.13	0.62	2	0	0	0	1	2	1	0	0	0	5
Moesan	2.74	0.06	2.70	0.61	1	0	0	0	0	1	1	2	2	0	2
Olipin	3.17	0.06	3.07	0.61	2	0	0	0	0	0	1	1	1	0	2

Table 5 continued

Species	CI	RPA	PAR	EP	SL	Diet							VEL	SUB	TAC
						Fish	Algae	Per	Pla	Det	Autinv	Allinv			
Parnas	1.59	0.12	1.77	0.58	3	0	1	2	0	1	0	0	2	2	6
Phahar	1.57	0.07	2.47	0.59	1	0	0	0	0	1	2	0	0	0	7
Piaarg	2.08	0.09	1.64	0.63	1	0	0	0	0	0	2	1	1	0	2
Pimava	1.19	0.17	1.70	0.79	2	0	0	0	0	0	2	0	2	1	3
Poeret	1.37	0.10	2.12	0.61	1	0	0	0	0	2	0	0	0	0	7
Pyraus	1.86	0.08	2.14	0.61	1	0	0	0	0	0	1	2	0	0	7
Rhaque	1.16	0.12	1.38	0.82	3	0	0	0	0	0	2	2	2	1	3
Satpap	2.42	0.11	3.08	0.71	3	0	0	0	0	2	0	0	1	0	5
Serhet	2.66	0.05	2.87	0.51	1	0	1	0	0	2	0	0	0	0	2
Serrnot	3.23	0.03	3.55	0.56	1	0	1	0	0	2	0	0	0	0	2
Steins	2.12	0.04	3.16	0.58	2	0	0	0	0	2	0	0	0	0	9

See Table 6 for species codes

CI compression index, *RPA* relative area of pectoral fin, *PAR* pectoral fin aspect ratio, *EP* eye position, *SL* standard length, Diet (*per* periphyton, *pla* fragments of plants, *det* detritus, *autinv* autochthonous invertebrates, *allinv* allochthonous invertebrates), *VEL* velocity preference, *SUB* substrate preference, *TAC* feeding tactics (see details in Table 2)

Table 6 Codes and abundance of fish species collected in 77 stream reaches

Order and families, species and authors	Codes	Abundance
Characiformes		
Parodontidae (scrapetooths)		
Apareiodon piracicabae (Eigenmann, 1907)	Apapir	3
Parodon nasus Kner, 1858	Parnas	100
Curimatidae (toothless characins)		
Cyphocharax modestus (Fernández-Yépez, 1948)	Cypmod	12
Cyphocharax vanderi (Britski, 1980)	Cypvan	84
Steindachnerina insculpta (Fernández-Yépez, 1948)	Steins	40
Prochilodontidae (flannel-mouth characiforms)		
Prochilodus lineatus (Valenciennes, 1836)	Prolin	5
Anostomidae (headstanders)		
Leporinus friderici (Bloch, 1794)	Lepfri	5
Leporinus lacustris Campos, 1945	Leplac	1
Leporinus paranensis Garavello and Britski, 1987	Leppar	1
Leporinus striatus Kner, 1858	Lepstr	7
Crenuchidae (South American darters)		
Characidium gomesi Travassos, 1956	Chagom	2
Characidium aff. *lagosantense* Travassos, 1947	Chalag	14
Characidium zebra Eigenmann, 1909	Chazeb	148
Characidae (tetras)		
Astyanax altiparanae Garutti and Britski, 2000	Astalt	2161
Astyanax bockmanni Vari and Castro, 2007	Astboc	2
Astyanax fasciatus (Cuvier, 1819)	Astfas	293
Astyanax paranae Eigenmann, 1914	Astpar	95
Hemigrammus marginatus Ellis, 1911	Hemmar	179
Hyphessobrycon anisitsi (Eigenmann, 1907)	Hypani	1
Hyphessobrycon eques (Steindachner, 1882)	Hypequ	4

Table 6 continued

Order and families, species and authors	Codes	Abundance
Knodus moenkhausii (Eigenmann and Kennedy, 1903)	Knomoe	1525
Moenkhausia sanctaefilomenae (Steindachner, 1907)	Moesan	35
Oligosarcus pintoi Campos, 1945	Oligpin	384
Piabina argentea Reinhardt, 1867	Piaarg	394
Planaltina britskii Menezes, Weitzman and Burns, 2003	Plabri	5
Serrasalmus maculatus Kner, 1858	Sermac	1
Serrasalmus marginatus Valenciennes, 1837	Sermar	1
Serrapinnus heterodon (Eigenmann, 1915)	Serhet	32
Serrapinnus notomelas (Eigenmann, 1915)	Sernot	603
Acestrorhynchidae (smallscale pike characins)		
Acestrorhynchus lacustris (Lütken, 1875)	Acelac	2
Erythrinidae (trahiras)		
Erythrinus erythrinus (Bloch and Schneider, 1801)	Eryery	2
Hoplias malabaricus (Bloch, 1794)	Hopmal	72
Lebiasinidae (pencilfishes)		
Pyrrhulina australis Eigenmann and Kennedy, 1903	Pyraus	73
Siluriformes		
Callichthyidae (armored catfishes)		
Aspidoras fuscoguttatus Nijssen and Isbrücker, 1976	Aspfus	1035
Corydoras aeneus (Gill, 1858)	Coraen	188
Callichthys callichthys (Linnaeus, 1758)	Calcal	19
Hoplosternum littorale (Hancock, 1828)	Hoplit	2
Lepthoplosternum pectorale (Boulenger, 1895)	Leppec	2
Loricariidae (armored catfishes)		
Hisonotus francirochai (Ihering, 1928)	Hisfra	34
Hypostomus ancistroides (Ihering, 1911)	Hypanc	390
Hypostomus nigromaculatus (Schubart, 1964)	Hypnig	143
Heptapteridae (catfishes)		
Cetopsorhamdia iheringi Schubart and Gomes, 1959	Cetihe	5
Imparfinis schubarti (Gomes, 1956)	Impsch	118
Phenacorhamdia tenebrosa (Schubart, 1964)	Pheten	1
Pimelodella avanhandavae Eigenmann, 1917	Pimava	20
Rhamdia quelen (Quoy and Gaimard, 1824)	Rhaque	149
Gymnotiformes		
Gymnotidae (naked-back knifefishes)		
Gymnotus sylvius Albert and Fernandes-Matioli, 1999	Gymsyl	393
Gymnotus inaequilabiatus (Valenciennes, 1839)	Gymine	1
Sternopygidae (glass knifefishes)		
Eigenmannia virescens (Valenciennes, 1842)	Eigvir	10
Cyprinodontiformes		
Rivulidae (annual fishes)		
Rivulus pictus Costa, 1989	Rivpic	7
Poeciliidae (livebearers)		
Phalloceros harpagos Lucinda, 2008	Phahar	71
Poecilia reticulata Peters, 1859	Poeret	3723
Synbranchiformes		
Synbranchidae (swamp-eels)		
Synbranchus marmoratus Bloch, 1795	Synmar	5

Table 6 continued

Order and families, species and authors	Codes	Abundance
Perciformes		
Cichlidae (cichlids)		
Cichlasoma paranaense Kullander, 1983	Cicpar	121
Crenicichla britskii Kullander, 1982	Crebri	78
Geophagus brasiliensis (Quoy and Gaimard, 1824)	Geobra	197
Laetacara aff. *araguaiae* Ottoni and Costa, 2009	Laeara	186
Oreochromis niloticus (Linnaeus, 1758)	Orenil	6
Satanoperca pappaterra (Heckel, 1840)	Satpap	47
Tilapia rendalli (Boulenger, 1897)	Tilren	8

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