Neotropical Ichthyology, 13(3): 579-590, 2015

DOI: 10.1590/1982-0224-20140157

Fish complementarity is associated to forests in Amazonian streams

Carolina Rodrigues Bordignon[1], Lilian Casatti[1] , María Angélica Pérez-Mayorga[1], Fabrício Barreto Teresa[2] and Gabriel Lourenço Brejão[1]

The functional structure of communities is commonly measured by the variability in functional traits, which may demonstrate complementarity or redundancy patterns. In this study, we tested the influence of environmental variables on the functional structure of fish assemblages in Amazonian streams within a deforestation gradient. We calculated six ecomorphological traits related to habitat use from each fish species, and used them to calculate the net relatedness index (NRI) and the nearest taxon index (NTI). The set of species that used the habitat differently (complementary or overdispersed assemblages) occurred in sites with a greater proportion of forests. The set of species that used the habitat in a similar way (redundant or clustered assemblages) occurred in sites with a greater proportion of grasses in the stream banks. Therefore, the deforestation of entire watersheds, which has occurred in many Amazonian regions, may be a central factor for the functional homogenization of fish fauna.

A estrutura funcional das comunidades é comumente medida através da variabilidade nos traços funcionais, que pode demonstrar padrões de complementaridade ou redundância. Testamos a influência de variáveis ambientais na estrutura funcional de peixes de riachos Amazônicos ao longo do gradiente de desmatamento. Para cada espécie, calculamos seis traços ecomorfológicos relacionados ao uso do hábitat e usamos esses traços para calcular o índice de proximidade de táxon (NRI) e o índice do táxon mais próximo (NTI). Os conjuntos de espécies que usam o hábitat de modo distinto (comunidades complementares) ocorreram em trechos de microbacias com maior proporção de florestas, e os conjuntos de espécies que utilizam o hábitat de forma similar (comunidades redundantes) ocorreram em trechos com maior proporção de gramíneas nas margens. Portanto, o desmatamento de microbacias inteiras, como vem acontecendo em muitas regiões Amazônicas, pode ser o fator principal para a homogeneização funcional da ictiofauna.

Keywords: Amazon Forest, Conservation, Ecomorphology, Functional diversity, Habitat use.

Introduction

The functional diversity of a community can be greatly influenced by the loss or addition of species with different traits from most species (*i.e.*, functionally unique) (Cianciaruso *et al.*, 2013). These changes may occur due to different processes, and deforestation has been associated with decreases in functional diversity in different communities (Tilman *et al.*, 1997; Dolédec *et al.*, 2006; Flynn *et al.*, 2009; Barragán *et al.*, 2011). The consequences of these changes can be dramatic, especially in areas of high biodiversity, such as the Amazon (Barletta *et al.*, 2010), one of the most important biomes of the planet due to the extent of its rainforests and drainage network (Krusche *et al.*, 2005). Approximately 735,000 km^2 of the 5 million km^2 that comprised the original Amazon Forest biome have been deforested in Brazil until 2013 (Instituto Nacional de Pesquisas Espaciais (INPE), 2014). This phenomenon is particularly alarming in the state of Rondônia, which has the second highest deforestation rate in Brazil (772 km^2 in 2013), and in 2006 approximately 65.9% of the state area had been cleared (INPE, 2010).

Deforestation at the watershed or at the riparian buffer scale, affect stream characteristics at the local scale (Cruz *et al.*, 2013), such as flow, depth, substrate composition, litter amount, stability of stream banks, and structural complexity (Gorman & Karr, 1978; Lorion & Kennedy, 2009; Casatti *et al.*, 2009). Considering that the influence of these variables on species occurrence depends on their functional traits (Goldstein & Meador, 2005; Teresa & Casatti, 2012), it is presumable that the effects of deforestation on the functional structure of communities are mediated by changes at finer spatial scales.

[1]Universidade Estadual Paulista (UNESP), Departamento de Zoologia e Botânica, Rua Cristóvão Colombo 2.265, 15054-000 São José do Rio Preto, SP, Brazil. (CRB) carolbordi@gmail.com (corresponding author), (LC) licasatti@gmail.com, (MAPM) anyelicaperez@yahoo.com, (GLB) gbrejao@gmail.com
[2]Universidade Estadual de Goiás (UEG), Unidade Universitária de Ciências Exatas e Tecnológicas, BR-153, 3.105, 75132-903 Anápolis GO, Brazil. fabricioteresa@yahoo.com.br

The functional structure of communities is commonly measured through the variability in functional traits (*i.e.,* functional diversity; Mouchet *et al.*, 2010), which may demonstrate complementarity or redundancy patterns (Falk *et al.*, 2006). High functional complementarity occurs in communities with higher functional diversity than expected by chance (Blüthgen & Klein, 2011). Conversely, functional redundancy is the occurrence of functionally similar species which have less functional diversity than expected by chance (Loreau, 2004). The occurrence of complementary or redundant communities may reflect the differential influence of environmental filters (Poff *et al.*, 1997). For example, in highly degraded streams, where the harsh environmental conditions filters species through their traits, so that species with a given set of traits can only survive, it is expected that coexisting species would be functionally more similar (functionally redundant communities). Conversely, higher resource availability and habitat complexity in pristine streams may provide favourable conditions to functionally distinct species to coexist, forming communities with higher functional complementarity.

We tested the influence of environmental variables on the functional structure of Amazonian stream fish communities in watersheds with different degrees of deforestation. We expected to find communities functionally more different in stream reaches embedded in watersheds with higher amounts of forests.

Material and Methods

Study area. This study was conducted in the rio Machado basin (Fig. 1), which drains the most populated area of Rondônia, Northern Brazil, with a total catchment area of 75,400 km^2. The rio Machado is approximately 1,200 km long (Fernandes & Guimarães, 2002) and is formed by the confluence of the Comemoração and Pimenta Bueno rivers. Along its course, it also receives the Rolim de Moura, Urupá, Jaru, Machadinho, and Preto rivers and flows into the right bank of the rio Madeira (Ballester *et al.*, 2003). This region has many terra firme streams, which are intermittent during most of the dry season (Fernandes & Guimarães, 2002).

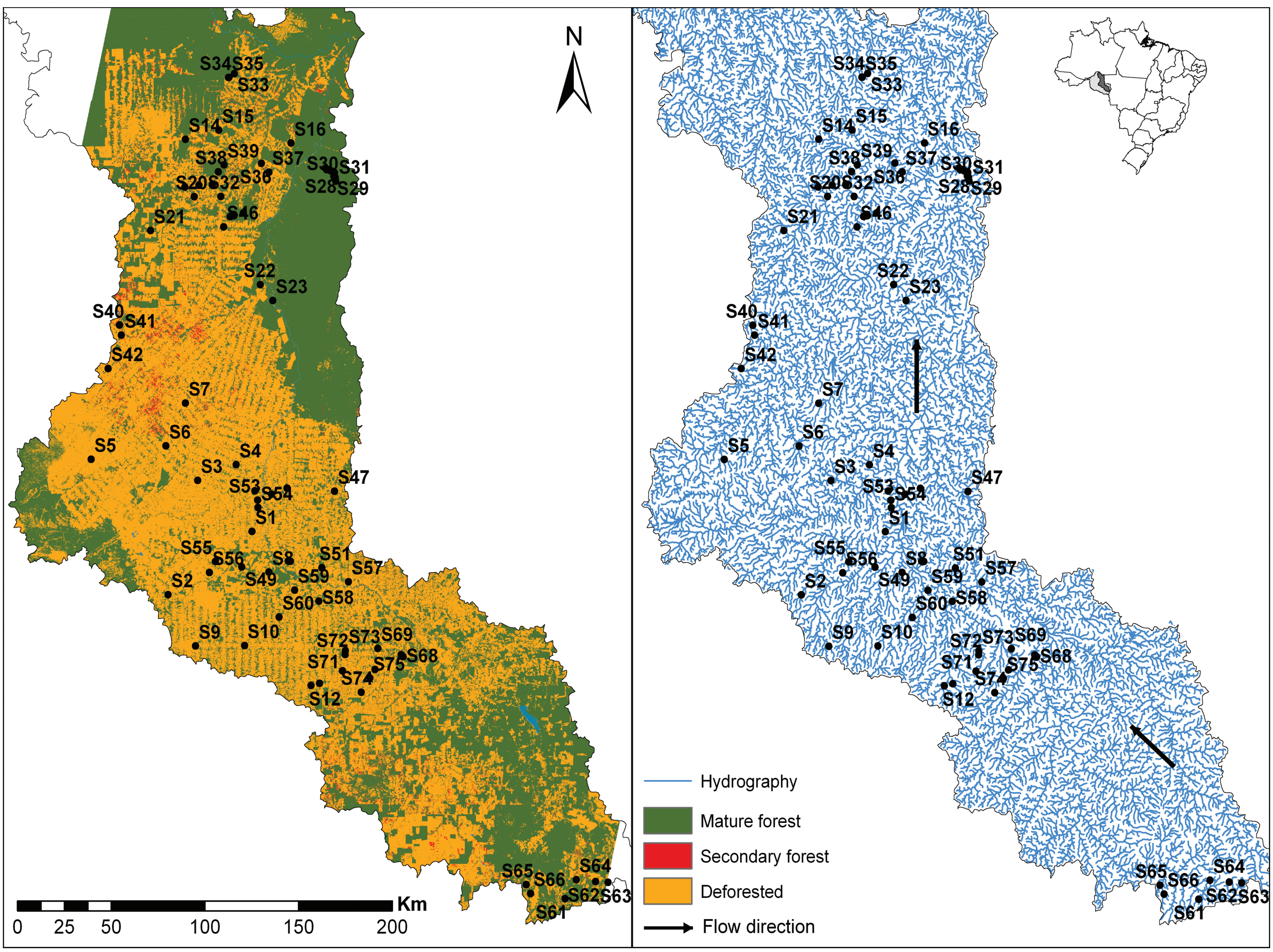

Fig. 1. Sampled sites along the rio Machado basin and the three main types of soil coverage (left). Hydrography of the rio Machado basin and flow direction of the rio Machado (right).

This region has been altered since 1970, with settlements along the highway BR-364. The watersheds that form the rio Machado basin are covered by forests (mature and secondary, ranging from 0 to 100% of coverage) or grasses which are used as pasture for cattle ranching (Fernandes & Guimarães, 2002). Due to this mixed degree of forest cover conditions, the rio Machado basin represents a suitable model for studying the biological consequences of human activities, such as habitat loss and simplification, on diverse aspects of fish ecology, notably on the functional diversity. Samplings were conducted in streams with different degrees of forest cover, from highly degraded to entirely forested, like those inside the protected areas, such as Jaru Biological Reserve and Rio Preto-Jacundá, Castanheira, and Aquariquara Extractive Reserves.

Watersheds selection. We generated the drainage network and the watersheds using the hydrological model S.W.A.T. (Soil and Water Assessment Tools) and satellite images of MDET SRTM (90 x 90 m resolution) from NASA (available at www.usgs.gov) to select the watersheds to be sampled. In order to standardize the stream order (2^{nd} to 4^{th} orders *sensu* Strahler, 1957), we selected watersheds with areas between 1,500 ha and 5,000 ha that represented the forest coverage variation in the watersheds (from 0 to 100% of forests). Overall, we sampled 75 streams reaches (one per watershed), 80-m long, that were definitively selected in situ after following these criteria: accessibility and authorization by the owners, maximum depth of 1.5 m, and the presence of perennial watercourses. We conducted the fieldwork in August and October of 2011 and in June and July of 2012. These months are characterized by low rainfall and in both years the hydrological regime was similar (Agência Nacional das Águas (ANA), 2009).

Environmental variables. As environmental variables we considered landscape and local attributes. The landscape variable was represented by the proportion of forests in the watershed, which was obtained for each site (see Table 1 for procedures). The amount of forests in the watershed influences not only habitat characteristics (Krusche *et al.*, 2005; Gonçalves Jr. & Callisto, 2013), but also diversity patterns (Poole & Downing, 2004), and it is a good surrogate for the watershed's conservation status.

The local variables were obtained during the fieldwork. In each reach, we measured five local variables associated to fish habitat (see Table 1 for the details of how each variable was obtained): percentage of grasses in the riparian banks; percentage of submerged roots in the riparian banks; percentage of consolidate substrate; percentage of large wood debris on the stream bottom; and average depth (Table 1).

Table 1. Scales, variables, codes, mean ± standard deviation, and explanation of how each variable was obtained.

Variables	Codes	Mean ± standard deviation	Explanation
LANDSCAPE SCALE:			
Forest cover in the watershed (proportion)	FO	0.40 ± 0.33	Proportion of forest cover for each watershed based on Landsat images (30 x 30 m resolution, available at www.dgi.inpe.br/CDSR/). The forest cover was classified according to the supervised classification method (Jensen, 2000) in the software ERDAS 9.2.
Local scale: calculated from (at least 20 m) measurements obtained in each stream reach			
Grasses in the stream banks (%)	GRA	35.02 ± 38.00	Percentage of the reach bank extension that was covered by marginal grasses derived from surrounding pasture entering the water. For this calculation, both stream sides were computed.
Submerged roots in the stream banks (%)	ROO	3.43 ± 5.87	Percentage of the reach bank extension that presented roots derived from riparian trees entering the water. For this calculation, both stream sides were computed.
Consolidate substrate (%)	CSU	2.11 ± 3.68	Percentage of gravel and cobbles (particles with 2-256 mm in size) on the bottom of each stream reach (following the classification of Krumbein & Sloss, 1963).
Large wood debris on the stream bed (%)	LWD	11.35 ± 10.77	Percentage of fallen branches and trees, representing large wood debris, on the stream bed of each reach.
Depth (cm)	DEP	27.26 ± 14.03	Average value of depth.

Fish data and ecomorphological traits. To collect fish, firstly we used two blocking nets (2 mm mesh) to isolate the stream reach. Two people collected fish using the most appropriate technique according to the reach characteristics. A hand seine (2 mm mesh) was used for portions without marginal vegetation with a sandy or clay bottom; a dip net (2 mm mesh) was used for portions with trunks, branches, and gravel. The sampling effort was standardized in one hour for each reach. Fish were fixed in 10% formalin and transferred to 70% ethanol. Voucher specimens were deposited at the fish collection of the Departamento de Zoologia e Botânica (DZSJRP), Universidade Estadual Paulista, São José do Rio Preto, Sao Paulo, Brazil (for voucher numbers, see Appendix).

We considered ecomorphological traits related to habitat use as functional traits. From the set of 139 species (Appendix) sampled in the 75 streams, we measured 137 species, except for *Potamotrygon orbignyi* and *Synbranchus marmoratus* that were excluded from this analysis due to the absence of pectoral fins. We took 11 measurements from each specimen, which were used to calculate six ecomorphological traits (Table 2) related to adaptations to water flow, swimming ability, and position in the water column, following Gatz (1979), Mahon (1984), and Watson & Balon (1984). We obtained linear measurements, area, and width with a stereomicroscope (Zeiss Discovery V12 SteREO), coupled with an imaging software (AxioVision Zeiss) and digital caliper to the nearest 0.01 mm. For larger species, we obtained areas of fins and body by drawing their profiles on graph paper (Beaumord & Petrere Jr., 1994).

Functional structure. We calculated the net relatedness index (NRI) and the nearest taxon index (NTI) for each fish assemblage by using the functional dendrogram. To obtain the functional dendrogram we assembled a standardized matrix of ecomorphological traits (with zero mean and unit variance) by species and used the function "dist.ktab" in the software R (R Development Core Team, 2011), based on the distance matrix obtained by the generalization of Gower's distance. We used the unweighted pair-group method using arithmetic averages (UPGMA) clustering method (Pavoine *et al*., 2009). NRI and NTI were originally described by Webb (2000) for phylogenetic diversity and are considered relevant to represent the functional structure (Hidasi-Neto *et al*., 2012). We decided to use these indexes because they are based on presence/absence and, therefore, more sensitive to rare species that are more vulnerable in the degradation context. Positive values of NRI and NTI indicate functional redundancy and negative values indicate functional complementarity. The NRI and NTI correspond, respectively, to the standardized effect size of functional diversity indexes MPD (mean pairwise distance) and MNTD (mean nearest taxon distance) (Webb, 2000), multiplied by -1 and calculated in relation to 1,000 randomly generated communities using an independent swap algorithm, maintaining the observed species richness and occurrence frequency in the null communities (Gotelli & Entsminger, 2001). For this analysis, we used the functions 'ses.mpd' and 'ses.mntd' in the R (R Development Core Team, 2011) package 'picante' (Kembel *et al*., 2010).

Data analysis. We used a partial regression analysis to relate the landscape and local variables (explanatory variables) with the NRI and NTI (response variables). Prior to the analysis, we standardized the explanatory variables (with zero mean and unit variance). In order to guarantee spatial independence of data (Legendre & Fortin, 1989; Legendre & Legendre, 1998), we evaluated the spatial autocorrelation in the residuals generated in the partial regressions described previously. New partial regressions were carried out using the regression residuals as response variable and the spatial filters as predictor, taking the effect of environmental variables into account. The spatial filters were generated by eigenvector-based spatial filtering approach (Griffith, 2003) based on a matrix of fluvial distance among all pairs of sampled reaches. The spatial filters with significant spatial structure as measured by Moran's *I* coefficients, at the first distance class, higher than 0.5) were retained. We performed these analyses in the software SAM (Rangel *et al*., 2010).

Table 2. Codes, calculations and ecological significance of ecomorphological traits related to habitat use. For details of how measurements were taken see Cochran-Biederman & Winemiller (2010). All measurements were taken in millimeters (mm).

Traits	Codes	Calculation	Ecological significance
Relative depth	RD	Maximum height of the body divided by standard length.	Lower values indicate fishes inhabiting fast waters. It is directly related to the ability to perform vertical spins (Gatz, 1979).
Index of ventral flattening	IVF	Middle line height divided by maximum body height.	Low values indicate fishes inhabiting environments with high hydrodynamism, able to maintain their position even when stationary (Hora, 1930).
Relative area of pectoral fin	APF	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 upwards and thereby, maintain themselves firmly attached to the substrate (Mahon, 1984; Watson & Balon, 1984).
Pectoral fin aspect ratio	PFA	Maximum length of the pectoral fin divided by its maximum width.	High values indicate long fins, typical of fish that swim long distances (Watson & Balon, 1984), or pelagic fish that swim constantly (Casatti & Castro, 2006).
Relative eye position	EP	Distance from the middle of the eye to the base of the head, divided by head height.	Position of eyes is related to vertical habitat preference (Gatz, 1979); high values indicate dorsally located eyes, typical of benthic fish (Mahon 1984; Watson & Balon, 1984).
Fineness ratio	FC	Standard length divided by the square root of the maximum height of body, multiplied by the maximum body width.	The influence of body shape on the ability to swim; values from 2 to 6 indicate low drag, the optimum ratio for swimming efficiency is 4.5 (Blake, 1983).

In order to identify the set of environmental variables that discriminate streams, we used the distance based Redundancy Analysis (dbRDA, as described by Legendre & Anderson, 1999). In dbRDA, a Principal Coordinate Analysis (PCoA) is used to extract the principal coordinates of a calculated matrix of distances. These principal coordinates are Euclidean representations of the distances and are suitable for analysis by linear models. Due to this, and because significance testing is by permutation, there was no need for an assumption of normality (Anderson, 2006). We conducted dbRDA in the Primer 6 software (Clarke & Gorley, 2006). In the resulting biplot, we identified *a posteriori* the stream reaches according to NTI values, and informed the most important variables.

Results

The partial regression with the NRI and NTI showed that explanatory variables only explained the NTI. The variables that significantly explained the NTI were the percentage of forest cover in the watershed, the percentage of grasses in the stream banks, and depth (Table 3), indicating that most of variation in functional diversity can be explained by the combined effects of landscape and local environmental predictors. The residuals from these regressions did not presented spatial structure, since the correlation between spatial filters and regression residuals were non-significant ($P > 0.51$). This indicates that there was no spatial autocorrelation in our database, which would inflate the type I error.

The first two axes of dbRDA accounted for 51.9% of the explained variation. The coefficients for linear combinations of environmental variables in the formation of dbRDA coordinates indicated that the percentage of forest cover in the watershed (axis 1 = 1.623, axis 2 = -0.680), the percent of submerged roots in the stream banks (axis 1 = 0.034, axis 2 = -0.008), the percentage of grasses in the stream banks (axis 1 = -0.016, axis 2 = -0.002), and depth (axis 1 = -0.003, axis 2 = 0.056) were the variables that contributed the most for stream variation.

By pooling the partial regression with the dbRDA results (Fig. 2), it is shown a gradient in which the more complementary communities were located in watersheds with higher proportions of forests. The more redundant communities were located in stream reaches with large amounts of grasses in the stream banks.

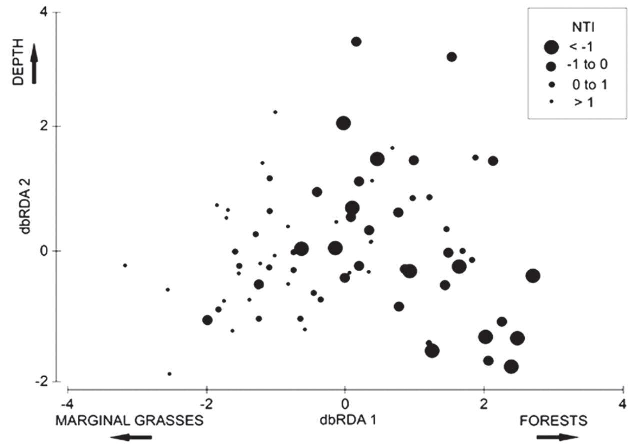

Fig. 2. Biplot resulting from the distance based Redundancy Analysis with seven variables (landscape and local). The proportion of forest cover in the watershed, the proportion of grasses in the stream banks, and depth significantly explained the NTI (nearest taxon index) in the studied communities and therefore are represented here. Each community is identified by circles with different sizes according to the NTI values.

Table 3. Results from the partial regression analysis, including NRI and NTI as dependent variables. For variables codes, see Table 1. Bold numbers of *P* indicate variables that significantly explain the functional indices.

Variables	Coefficient	Standard coefficient	Variance inflation factor	Standard error	t	*P*
NRI (r^2adj = 0.03, $P = 0.586$)						
Landscape variable:						
FO	-0.003	-0.003	1.535	0.118	-0.023	0.982
Local variables:						
GRA	0.199	0.244	1.803	0.128	1.551	0.126
ROO	0.094	0.115	1.188	0.104	0.902	0.370
CSU	0.069	0.084	1.052	0.098	0.700	0.486
LWD	0.055	0.067	1.104	0.100	0.545	0.587
DEP	0.058	0.071	1.058	0.098	0.588	0.558
NTI (r^2adj = 0.51, $P < 0.001$)						
Landscape variable:						
FO	-0.631	-0.515	1.535	0.124	-5.074	**<0.001**
Local variables:						
GRA	0.304	0.248	1.803	0.135	2.255	**0.027**
ROO	-0.140	-0.114	1.188	0.109	-1.276	0.206
CSU	0.059	0.048	1.052	0.103	0.572	0.569
LWD	0.127	0.104	1.104	0.105	1.202	0.234
DEP	-0.292	-0.239	1.058	0.103	-2.831	**0.006**

Discussion

As predicted, stream reaches in the most forested watersheds encompassed the more functionally complementary assemblages regarding fish habitat use. On the contrary, streams with a greater proportion of marginal grasses in stream banks were represented by more redundant assemblages. Therefore, local and landscape features influenced habitat use by stream fish. This relationship was mediated by functional traits, as revealed by the relationship between functional traits and environmental variables, and highlighted the importance of the habitat structure of streams in determining the patterns of functional diversity and composition.

The forest cover, a landscape predictor, was related to the proportion of submerged roots in the stream banks, a local variable. This relationship revealed the hierarchical influence of landscape features on streams habitat structure. In this same vein, the grasses gradient was the opposite of that for forests. Two implications can be inferred from this fact. First, the deforestation in the rio Machado basin has also probably affected the riparian zone. Otherwise, the riparian forests would control the amount of grasses growing in the stream banks (Bunn & Kellaway, 1997), and this variable would be of less importance for stream structure. Second, the deforestation dynamics in the region and the development of pasture for livestock, despite starting in the 1970's, has been severe enough to promote the functional redundancy of fish communities, as demonstrated here.

The greater complementarity in forested stream reaches can be attributed to the occurrence of species with functionally unique traits, a characteristic of complementary assemblages (Petchey & Gaston, 2002). The occurrence of these species is probably due to the availability of shelter, food resources associated to the riparian vegetation, and litter packs (Carvalho *et al.*, 2013). Accordingly, functionally unique species tend to be lost with the removal of vegetation in the watershed (Devictor *et al.*, 2008). If we assume that functionally unique species perform functions not carried out by other species (Mouillot *et al.*, 2011, 2013), these results suggest that vegetation removal, one of the major threats to biodiversity in the region, could potentially impair ecosystem structure and functioning in streams (Turner, 1996; Laurance *et al.*, 1998).

In our study, the NRI was not explained by the environmental variables, contrary to NTI. To explain such results we must understand the properties of these indexes. NRI is an index more sensitive to species present in deep branches of the dendrogram, i.e., functionally distinct species, whereas the NTI is more sensitive to variations towards the tips of the functional dendrogram (Webb, 2000; Hidasi-Neto *et al.*, 2012). Our results show that communities along the environmental gradient were equally represented by species from different branches of the functional dendrogram (and then NRI did not vary). However, the number of species within each branch varied along the environmental gradient and, thus, they were detected by NTI.

Our results reinforced the need to preserve native forests, not only in the vicinity of streams, but also in the whole watershed because their forest elements can be transported downstream (Ferraz *et al.*, 2005; Galas, 2013). Forest cover in the watershed influences habitat use by fish in streams and, consequently, the overall functional diversity of fish assemblages. The removal of forest can be a severe environmental filter (in the sense of Kraft *et al.*, 2015) because it favors generalist species at the expense of functionally unique species, and therefore increases functional redundancy, at least on a reach scale.

Acknowledgments

ICMBio/SISBIO provided collecting permits (3604-1, 4355-1) and logical support. The "Secretaria de Estado do Desenvolvimento Ambiental" and "Escritório Regional de Gestão Ambiental de Machadinho d'Oeste" allowed us to conduct the surveys in the study areas. Financial funding was provided by "Fundação de Amparo à Pesquisa do Estado de São Paulo" (FAPESP 2010/17494-8). Fellowships were granted to CRB (PIBIC CNPq/UNESP), MAPM (AUIP/PAEDEX/UNESP), GLB (FAPESP 2011/11677-6), FBT (PROBIP/UEG), and LC (CNPq). Fernando R. Carvalho, Francisco Langeani, Bárbara B. Callegari, Fernanda Martins, Ilana Fichberg, Leandro Sousa, Manoela M. F. Marinho; Marcelo Britto, Marcelo Carvalho, and Willian Ohara helped with fish identification. Diogo B. Provete helped with a former revision of the manuscript. Felipe Rossetti de Paula helped with watersheds selection and fieldwork. Fernando R. Carvalho, Mateus Ferrareze, Angelo R. Manzotti, Igor D. Costa, Wesclen Vilar, and Vanessa Bressan helped during fieldwork. We are grateful to Fernando Pelicice, and two anonymous referees for comments and suggestions on the manuscript.

References

Agência Nacional das Águas (ANA). 2009. Inventário das estações fluviométricas. Available from: http://arquivos.ana.gov.br/infohidrologicas/InventariodasEstacoesFluviometricas.pdf (09/October/2014).

Anderson, M. J. 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics, 62: 245-253.

Ballester, M. V. R., D. de C. Victoria, A. V. Krusche, R. Coburn, R. L. Victoria, J. E. Richey, M. G. Logsdon, E. Mayorga & E. Matricardi. 2003. A remote sensing/GIS-based physical template to understand the biogeochemistry of the Ji-Paraná river basin (Western Amazônia). Remote Sensing of Environment, 87: 429-445.

Barletta, M., A. J. Jaureguizar, C. Baigun, N. F. Fontoura, A. A. Agostinho, V. M. F. Almeida-Val, A. L. Val, R. A. Torres, L. F. Jimenes-Segura, T. Giarrizzo, N. N. Fabré, V. S. Batista, C. Lasso, D. C. Taphorn, M. F. Costa, P. T. Chaves, J. P. Vieira & M. F. M. Corrêa. 2010. Fish and aquatic habitat conservation in South America: a continental overview with emphasis on Neotropical systems. Journal of Fish Biology, 76: 2118-2176.

Barragán, F., C. E. Moreno, F. Escobar, G. Halffter & D. Navarrete. 2011. Negative impacts of human land use on dung beetle functional diversity. PLoS ONE, 6: e17976 (p. 1-8).

Beaumord, A. C. & M. Petrere Jr. 1994. Comunidades de peces del rio Manso, Chapada dos Guimarães, MT, Brasil. Acta Biológica Venezuelica, 15: 21-35.

Blake, R. W. 1983. Functional design and burst-and-coast swimming in fishes. Canadian Journal of Zoology, 61: 2491-2494.

Blüthgen, N. & A. M. Klein. 2011. Functional complementarity and specialisation: the role of biodiversity in plant-pollinator interactions. Basic and Applied Ecology, 12: 282-291.

Buckup, P. A., N. A. Menezes & M. S. Ghazzi (Eds.). 2007. Catálogo das espécies de peixes de água doce do Brasil. Rio de Janeiro, Museu Nacional. 195p. (Série Livros, 23).

Bunn, S. E., P. M. Davies & D. M. Kellaway. 1997. Contributions of sugar cane and invasive pasture grass to the aquatic food web of a tropical lowland stream. Marine & Freshwater Research, 48: 173-179.

Calcagnotto, D., S. A. Schaefer & R. DeSalle. 2005. Relationships among characiform fishes inferred from analysis of nuclear and mitochondrial gene sequences. Molecular Phylogenetics and Evolution, 36: 135-153.

Carvalho, L. N., L. Fidelis, R. Arruda, A. Galuch & J. Zuanon. 2013. Second floor, please: the fish fauna of floating litter banks in Amazonian streams and rivers. Neotropical Ichthyology, 11: 85-94.

Casatti, L. & R. M. C. Castro. 2006. Testing the ecomorphological hypothesis in a headwater riffles fish assemblage of the rio São Francisco, southeastern Brazil. Neotropical Ichthyology, 4: 203-214.

Casatti, L., C. P. Ferreira & F. R. Carvalho. 2009. Grass-dominated stream sites exhibit low fish species diversity and dominance by guppies: an assessment of two tropical pasture river basins. Hydrobiologia, 632: 273-283.

Cianciaruso, M. V., M. A. Batalha & O. L. Petchey. 2013. High loss of plant phylogenetic and functional diversity due to simulated extinctions of pollinators and seed dispersers in a tropical savanna. Natureza & Conservação, 11: 36-42.

Clarke, K. R. & R. N. Gorley. 2006. PRIMER v6: User manual/ Tutorial. Plymouth, UK. Plymouth Marine Laboratory.

Cochran-Biederman, J. L. & K. O. Winemiller. 2010. Relationships among habitat, ecomorphology and diets of cichlids in the Bladen River, Belize. Environmental Biology of Fishes, 88: 143-152

Cruz, B. B., L. E. Miranda & M. Cetra. 2013. Links between riparian landcover, instream environment and fish assemblages in headwater streams of south-eastern Brazil. Ecology of Freshwater Fish, 22: 607-616.

Devictor, V., R. Julliard & F. Jiguet. 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos, 117: 507-514.

Dolédec, S., N. Phillips, M. Scarsbrook, R. H. Riley & C. R. Townsend. 2006. Journal of the North American Benthological Society, 25: 44-60.

Falk, D. A., M. A. Palmer & J. B. Zedler (Eds). 2006. Foundations of restoration ecology. Washington, D.C., Island Press.

Fernandes, L. C. & S. C. P. Guimarães. 2002. Atlas geoambiental de Rondônia. Porto Velho, SEDAM.

Ferraz, S. F. B., C. A. Vettorazzi, D. M. Theobald & M. V. R. Ballester. 2005. Landscape dynamics of Amazonian deforestation between 1984 and 2002 in central Rondônia, Brazil: assessment and future scenarios. Forest Ecology and Management, 204: 67-83.

Flynn, D. F. B., M. Gogol-Prokurat, T. Nogeire, N. Molinari, B. T. Richers, B. B. Lin, N. Simpson, M. M. Mayfield & F. DeClerck. 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters, 12: 22-33.

Galas, J. 2013. Detritus in small streams of the Tatra mountains - the role of abiotic factors. International Review of Hydrobiology, 98: 199-205.

Gatz, A. J., Jr. 1979. Ecological morphology of freshwater stream fishes. Tulane Studies on Zoology and Botany, 21: 91-124.

Goldstein, R. M. & M. R. Meador. 2005. Multilevel assessment of fish species traits to evaluate habitat degradation in streams of the Upper Midwest. North American Journal of Fisheries Management, 25: 180-194.

Gonçalves Jr., J. F. & M. Callisto. 2013. Organic-matter dynamics in the riparian zone of a tropical headwater stream in Southern Brasil. Aquatic Botany, 109: 8-13.

Gorman, O. T. & J. R. Karr. 1978. Habitat structure and stream fish communities. Ecology, 59: 507-515.

Gotelli, N. J. & G. L. Entsminger. 2001. Swap and fill algorithms in null model analysis: rethinking the Knight's Tour. Oecologia, 129: 281-291

Griffith, D. A. 2003. Spatial autocorrelation and spatial filtering: gaining understanding through theory and scientific visualization. Springer-Verlag, Berlin Heidelberg.

Hidasi-Neto, J., J. Barlow & M. V. Cianciaruso. 2012. Bird functional diversity and wildfires in the Amazon: the role of forest structure. Animal Conservation, 15: 407-415.

Hora, S. L. 1930. Ecology, bionomics and evolution of the torrential fauna, with special reference to the organs of attachment. Philosophical Transactions of the Royal Society of London, series B, 218: 172-282.

Instituto Nacional de Pesquisas Espaciais (INPE). 2010. Projeto PRODES: Monitoramento da Floresta Amazônica Brasileira por Satélite. Available from: http://www.obt.inpe.br/prodes/index.html (05 February 2014).

Instituto Nacional de Pesquisas Espaciais (INPE). 2014. Projeto PRODES.Available from: http://www.obt.inpe.br/prodes/prodes_1988_2013.htm (04 February 2014).

Jensen, J. R. 2000. Introductory digital image processing: a remote sensing perspective. Upper Saddle River, N. J., Prentice Hall.

Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg & C. O. Webb. 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics, 26: 1463-1464.

Kraft, N. J. B., P. B. Adler, O. Godoy, E. C. James, S. Fuller & J. M. Levine. 2015. Community assembly, coexistence, and the environmental filtering metaphor. Functional Ecology, 29: 592-599.

Krumbein, W. C. & L. L. Sloss. 1963. Stratigraphy and sedimentation. 2nd ed. San Francisco, W. F. Freeman. 660p.

Krusche, A. V., M. V. R. Ballester, R. L. Victoria, M. C. Bernardes, N. K. Leite, L. Hanada, D. C. Victoria, A. M. Toledo, J. P. Ometto, M. Z. Moreira, B. M. Gomes, M. A. Bolson, S. Gouveia Neto, N. Bonelli, L. Deegan, C. Neill, S. Thomas, A. K. Aufdenkampe & J. E. Richey. 2005. Efeitos das mudanças do uso da terra na biogeoquímica dos corpos d'água da bacia do rio Ji-Paraná, Rondônia. Acta Amazonica, 35: 197-205.

Laurance, W. F., L. V. Ferreira, J. M. Rankin-De Merona & S. G. Laurance. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology, 79: 2032-2040.

Legendre, P. & M. J. Anderson. 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. Ecological Monographs, 69: 1-24.

Legendre, P. & M. J. Fortin. 1989. Spatial pattern and ecological analysis. Vegetatio, 80: 107-138.

Legendre, P. & L. Legendre. 1998. Numerical ecology. 2nd ed. Amsterdan, Elsevier. 853p.

Loreau, M. 2004. Does functional redundancy exist? Oikos, 104: 606-611.

Lorion, C. M. & B. P. Kennedy. 2009. Riparian forest buffers mitigate the effects of deforestation on fish assemblages in tropical headwater streams. Ecological Applications, 19: 468-479.

Mahon, R. 1984. Divergent structure in fish taxocenes of north temperate streams. Canadian Journal of Fisheries and Aquatic Sciences, 41: 330-350.

Mouchet, M. A., S. Villéger, N. W. H. Mason & D. Mouillot. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology, 24: 867-876.

Mouillot, D., D. R. Bellwood, C. Baraloto, J. Chave, R. Galzin, M. Harmelin-Vivien, M. Kulbicki, S. Lavergne, S. Lavorel, N. Mouquet, C. E. T. Paine, J. Renaud & W. Thuiller. 2013. Rare species support vulnerable functions in high-diversity ecosystems. PLoS Biology, 11: e1001569 (p. 1-11).

Mouillot, D., S. Villéger, M. Scherer-Lorenzen & N. W. H. Mason. 2011. Functional structure of biological communities predicts ecosystem multifunctionality. PLoS ONE, 6: e17476 (p. 1-9).

Pavoine, S., J. Vallet, A. -B. Dufort, S. Gachet & H. Daniel. 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. Oikos, 118: 391-402.

Petchey, O. L. & K. J. Gaston. 2002. Functional diversity (FD), species richness and community composition. Ecology Letters, 5: 402-411.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. Sparks & J. C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience, 47: 769-784.

Poole, K. E. & J. A. Downing. 2004. Relationship of declining mussel biodiversity to stream-reach and watershed characteristics in an agricultural landscape. Journal of the North American Benthological Society, 23: 114-125.

R Development Core Team. 2011. R: A language and environment for statistical computing. Viena, Austria, R Foundation for Statistical Computing.

Rangel, T. F., J. A. F. Diniz-Filho & L. M. Bini. 2010. SAM: a comprehensive application for Spatial Analysis in Macroecology. Ecography, 33: 46-50.

Reis, R. E., S. O. Kullander & C. J. Ferraris (Orgs.). 2003. Check list of the freshwater fishes of South and Central America. Porto Alegre, Edipucrs. 729p.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Transactions of the American Geophysical Union, 38: 913-920.

Teresa, F. B. & L. Casatti. 2012. Influence of forest cover and mesohabitat types on functional and taxonomic diversity of fish communities in Neotropical lowland streams. Ecology of Freshwater Fish, 21: 433-442.

Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie & E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. Science, 277: 1300-1302.

Turner, I. M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. Journal of Applied Ecology, 33: 200-209.

Watson, D. J. & E. K. Balon. 1984. Ecomorphological analysis of fish taxocenes in rainforest streams of northern Borneo. Journal of Fish Biology, 25: 371-384.

Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. The American Naturalist, 156: 145-155.

Submitted April 30, 2014
Accepted April 13, 2015 by Fernando Pelicice
Published September 25, 2015

Appendix. Species registered in the sampled streams, their voucher number and abundances (N). *Potamotrygon orbignyi* and *Synbranchus marmoratus* were not included in the present analysis. Classification follows Reis *et al.* (2003); except for Serrasalmidae that follows Calcagnotto *et al.* (2005) and *Parauchenipterus porosus* that follows Buckup *et al.* (2007). *Provisionally included in *Cheirodon*.

Orders and families	Species and authors	Voucher	N
Myliobatiformes			
Potamotrygonidae	*Potamotrygon orbignyi* (Castelnau, 1855)	DZSJRP 17112	1
Characiformes			
Parodontidae	*Parodon nasus* Kner, 1859	DZSJRP 14506	4
Curimatidae	*Curimatopsis macrolepis* (Steindachner, 1876)	DZSJRP 16692	6
	Cyphocharax plumbeus (Eigenmann & Eigenmann, 1889)	DZSJRP 17238	1
	Cyphocharax spiluropsis (Eigenmann & Eigenmann, 1889)	DZSJRP 16630	40
	Steindachnerina cf. *dobula* (Günther, 1868)	DZSJRP 14512	4
	Steindachnerina fasciata (Vari & Géry, 1985)	DZSJRP 14661	57
	Steindachnerina guentheri (Eigenmann & Eigenmann, 1889)	DZSJRP 16782	3
Prochilodontidae	*Prochilodus nigricans* Spix & Agassiz, 1829	DZSJRP 16799	1
Anostomidae	*Anostomus ternetzi* Fernández-Yépez, 1949	DZSJRP 14664	5
	Leporinus friderici (Block, 1794)	DZSJRP 14763	36
Crenuchidae	*Characidium* aff. *gomesi* Travassos, 1956	DZSJRP 14704	7
	Characidium aff. *zebra* Eigenmann, 1909	DZSJRP 14703	762
	Characidium sp.	DZSJRP 14335	8
	Elachocharax pulcher Myers, 1927	DZSJRP 15057	79
	Microcharacidium aff. *weitzmani* Buckup, 1993	DZSJRP 16653	38
	Microcharacidium sp.	DZSJRP 14986	50
	Melanocharacidium dispilomma Buckup, 1993	DZSJRP 17205	1
	Melanocharacidium pectorale Buckup, 1993	DZSJRP 16678	1
Hemiodontidae	*Hemiodus unimaculatus* (Block, 1794)	DZSJRP 14672	2
Gasteropelecidae	*Carnegiella strigata* (Günther, 1864)	DZSJRP 14886	40
Characidae	*Amazonspinther dalmata* Bührnheim, Carvalho, Malabarba & Weitzman, 2008	DZSJRP 14947	7
	Astyanax cf. *bimaculatus* (Linnaeus, 1758)	DZSJRP 14419	108
	Astyanax cf. *maximus* (Steindachner, 1876)	DZSJRP 14460	18
	Astyanax maculisquamis Garutti & Britski, 1997	DZSJRP 14700	43
	Bario steindachneri (Eigenmann, 1893)	DZSJRP 15090	3
	Brachychalcinus copei (Steindachner, 1822)	DZSJRP 14769	147
	Bryconella pallidifrons (Fowler, 1946)	DZSJRP 14628	695
	Bryconops caudomaculatus (Günther, 1864)	DZSJRP 17278	912
	Bryconops piracolina Wingert & Malabarba, 2011	DZSJRP 16651	23
	**Cheirodon troemneri* Fowler, 1942	DZSJRP 14668	62
	Creagrutus petilus Vari & Harold, 2001	DZSJRP 14733	1021
	Hemigrammus aff. *ocellifer* (Steindachner, 1882)	DZSJRP 15009	62
	Hemigrammus bellotti (Steindachner, 1882)	DZSJRP 14524	152
	Hemigrammus melanochrous Fowler, 1913	DZSJRP 15100	1418
	Hemigrammus neptunus Zarske & Géry, 2002	DZSJRP 14710	60
	Hemigrammus sp.	DZSJRP 15101	14
	Hyphessobrycon aff. *heterorhabdus* (Ulrey, 1894)	DZSJRP 16929	144
	Hyphessobrycon agulha Fowler, 1913	DZSJRP 15103	1131
	Hyphessobrycon bentosi Durbin, 1908	DZSJRP 15011	178

Orders and families	Species and authors	Voucher	N
	Hyphessobrycon copelandi Durbin, 1908	DZSJRP 14673	151
	Jupiaba citrina Zanata & Ohara, 2009	DZSJRP 14701	273
	Jupiaba poranga Zanata, 1997	DZSJRP 15107	9
	Jupiaba zonata (Eigenmann, 1908)	DZSJRP 19916	55
	Knodus cf. *smithi* Fowler, 1913	DZSJRP 14715	827
	Knodus heteresthes Eigenmann, 1908	DZSJRP 14651	736
	Microschemobrycon guaporensis Eigenmann, 1915	DZSJRP 14476	166
	Moenkhausia aff. *gracilima* Eigenmann, 1908	DZSJRP 16817	1
	Moenkhausia cf. *bonita* Benine, Castro & Sabino, 2004	DZSJRP 14717	339
	Moenkhausia pankilopteryx Bertaco & Lucinda 2006	DZSJRP 14526	60
	Moenkhausia collettii (Steindachner, 1882)	DZSJRP 14639	1924
	Moenkhausia cotinho Eigenmann, 1908	DZSJRP 14478	259
	Moenkhausia comma Eigenmann, 1908	DZSJRP 14962	11
	Moenkhausia mikia Marinho & Langeani, 2010	DZSJRP 14447	105
	Moenkhausia oligolepis (Günther, 1864)	DZSJRP 14479	330
	Odontostilbe fugitiva Cope, 1870	DZSJRP 14545	307
	Phenacogaster retropinnus Lucena & Malabarba, 2010	DZSJRP 14450	386
	Serrapinus aff. *notomelas* (Eigenmann, 1915)	DZSJRP 14659	3642
	Serrapinnus microdon (Eigenmann, 1915)	DZSJRP 14658	1901
	Tetragonopterus argenteus Cuvier, 1816	DZSJRP 17040	2
	Triportheus angulatus (Spix & Agassiz, 1829)	DZSJRP 14456	2
	Tyttocharax madeirae Fowler, 1913	DZSJRP 14945	32
Serrasalmidae	*Myleus* sp.	DZSJRP 14741	12
	Serrasalmus rhombeus (Linnaeus, 1766)	DZSJRP 14695	1
Acestrorhynchidae	*Acestrorhynchus falcatus* (Bloch, 1794)	DZSJRP 17072	3
Erythrinidae	*Erythrinus erythrinus* (Bloch & Schneider, 1801)	DZSJRP 16650	11
	Hoplerythrinus unitaeniatus (Spix & Agassiz, 1829)	DZSJRP 16764	3
	Hoplias malabaricus (Bloch, 1794)	DZSJRP 14538	88
Lebiasinidae	*Nannostomus trifasciatus* Steindachner, 1876	DZSJRP 14963	1
	Pyrrhulina cf. *australis* Eigenmann & Kennedy, 1903	DZSJRP 14634	193
	Pyrrhulina cf. *brevis* Steindachner, 1876	DZSJRP 15115	65
	Pyrrhulina cf. *zigzag* Zarske & Géry, 1997	DZSJRP 17280	9
Siluriformes			
Cetopsidae	*Denticetopsis seducta* (Vari, Ferraris & de Pinna, 2005)	DZSJRP 14887	4
	Helogenes gouldingi Vari & Ortega, 1986	DZSJRP 15099	22
Aspredinidae	*Pseudobunocephalus amazonicus* (Mees, 1989)	DZSJRP 14940	37
Trichomycteridae	*Ituglanis amazonicus* (Steindachner, 1882)	DZSJRP 14676	108
	Miuroglanis platycephalus Eigenmann & Eigenmann, 1889	DZSJRP 14963	1
	Paracanthopoma sp.	DZSJRP 14905	19
Callichthyidae	*Corydoras acutus* Cope, 1872	DZSJRP 15023	5
	Corydoras aff. *ambiacus* Cope, 1872	DZSJRP 17229	3
	Corydoras bondi Gosline, 1940	DZSJRP 17263	1
	Corydoras cf. *melanistius* Regan, 1912	DZSJRP 15124	55
	Corydoras elegans Steindachner, 1876	DZSJRP 14422	7
	Corydoras stenocephalus Eigenmann & Allen, 1942	DZSJRP 16757	5
	Corydoras trilineatus Cope, 1872	DZSJRP 14755	82

Orders and families	Species and authors	Voucher	N
	Hoplosternum littorale (Hancock, 1828)	DZSJRP 14423	7
	Megalechis picta (Müller & Troschel, 1849)	DZSJRP 16753	49
Loricariidae	*Ancistrus lithurgicus* Eigenmann, 1912	DZSJRP 14418	290
	Farlowella cf. *oxyrryncha* (Kner, 1853)	DZSJRP 14671	120
	Hypostomus pyrineusi (Miranda Ribeiro, 1920)	DZSJRP 14424	34
	Hypostomus sp.	DZSJRP 17290	1
	Lasiancistrus schomburgkii (Günther, 1864)	DZSJRP 14697	61
	Loricaria cataphracta Linnaeus, 1758	DZSJRP 14499	4
	Otocinclus hoppei Miranda Ribeiro, 1939	DZSJRP 14685	119
	Parotocinclus aff. *aripuanensis* Garavello, 1988	DZSJRP 14895	24
	Rineloricaria heteroptera Isbrücker & Nijssen, 1976	DZSJRP 14427	164
	Rineloricaria sp.	DZSJRP 14635	6
	Spatuloricaria evansii (Boulenger, 1892)	DZSJRP 14511	4
	Squaliforma emarginata (Valenciennes, 1840)	DZSJRP 14712	22
Pseudopimelodidae	*Batrochoglanis* cf. *raninus* (Valenciennes, 1840)	DZSJRP 14969	16
	Batrochoglanis villosus (Eigenmann, 1912)	DZSJRP 14665	5
	Microglanis poecilus Eigenmann, 1912	DZSJRP 16655	1
Heptapteridae	*Cetopsorhamdia* sp. 1	DZSJRP 17295	24
	Cetopsorhamdia sp. 2	DZSJRP 17279	8
	Cetopsorhamdia sp. 3	DZSJRP 17216	6
	Imparfinis cf. *hasemani* Steindachner, 1917	DZSJRP 14714	124
	Imparfinis stictonotus (Fowler, 1940)	DZSJRP 14471	49
	Phenacorhamdia cf. *boliviana* (Pearson, 1924)	DZSJRP 14688	4
	Phenacorhamdia sp.	DZSJRP 15019	70
	Pimelodella cf. *howesi* Fowler, 1940	DZSJRP 14656	55
	Pimelodella sp.	DZSJRP 14527	11
	Rhamdia quelen (Quoy & Gaimard, 1824)	DZSJRP 14770	6
Doradidae	*Acanthodoras cataphractus* (Linnaeus, 1758)	DZSJRP 16687	19
Auchenipteridae	*Centromochlus* cf. *perugiae* Steindachner, 1882	DZSJRP 17261	1
	Parauchenipterus porosus (Eigenmann & Eigenmann, 1888)	DZSJRP 17038	5
	Tatia aulopygia (Kner, 1858)	DZSJRP 14696	2
Gymnotiformes			
Gymnotidae	*Gymnotus* aff. *arapaima* Albert & Crampton, 2001	DZSJRP 14649	26
	Gymnotus carapo Linnaeus, 1758	DZSJRP 14648	36
	Gymnotus coropinae Hoederman, 1962	DZSJRP 15006	81
Sternopygidae	*Eigenmannia trilineata* López & Castello, 1966	DZSJRP 14406	196
	Sternopygus macrurus (Bloch & Schneider, 1801)	DZSJRP 14484	97
Rhamphichthyidae	*Gymnorhamphichthys petiti* Géry & Vu-Tân-Tuê, 1964	DZSJRP 14631	287
Hypopomidae	*Brachyhypopomus* sp. 1	DZSJRP 14627	2
	Brachyhypopomus sp. 2	DZSJRP 15091	15
	Brachyhypopomus sp. 3	DZSJRP 15092	26
	Hypopygus lepturus Hoedeman, 1962	DZSJRP 14632	128
Apteronotidae	*Apteronotus albifrons* (Linnaeus, 1766)	DZSJRP 14641	6
	Platyurosternarchus macrostomus (Günter, 1864)	DZSJRP 14690	2
Cyprinodontiformes			
Rivulidae	*Rivulus* sp.	DZSJRP 14942	4

Orders and families	Species and authors	Voucher	N
Beloniformes			
Belonidae	*Potamorrhaphis eigenmanni* Miranda Ribeiro, 1915	DZSJRP 14949	2
Synbranchiformes			
Synbranchidae	*Synbranchus marmoratus* Bloch, 1795	DZSJRP 14485	22
Perciformes			
Cichlidae	*Aequidens tetramerus* (Heckel, 1840)	DZSJRP 14626	199
	Apistogramma cf. *resticulosa* Kullander, 1980	DZSJRP 14994	563
	Cichlasoma amazonarum Kullander, 1983	DZSJRP 14462	46
	Crenicichla johanna Heckel, 1840	DZSJRP 14758	2
	Crenicichla santosi Ploeg, 1991	DZSJRP 14757	163
	Geophagus megasema Heckel, 1840	DZSJRP 15004	1
	Satanoperca jurupari (Heckel, 1840)	DZSJRP 14636	60
	Tilapia rendalli (Boulenguer, 1897)	DZSJRP 14431	2