

Edge-mediated effects of forest fragments on the trophic structure of stream fish

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Abstract The aquatic communities of headwater streams are highly influenced by the surrounding matrix. The edge effects of forest fragments are known to influence terrestrial communities; however, their influence on aquatic communities remains poorly understood. The aim of this study was to investigate whether and how edge effects can influence stream environmental variables and fish trophic structure. We sampled stream reaches located within forest fragments (192–2480 ha) and stream reaches located on the forest edge during wet and dry periods to describe local habitat variables and fish trophic structure. We found high dissimilarity in the trophic structure (>60%) between stream positions and between seasons. Aquatic invertivores contributed to the majority

of the observed dissimilarity. Omnivores and algivores were more abundant on edge reaches and were notably associated with high water temperature. Herbivores and terrestrial invertivores were more abundant in the interior reaches mostly during the wet season and were associated with high dissolved oxygen. The scarcity of riparian forest cover on the edge reaches not only caused physical changes but also influenced the fish trophic structure, therefore providing evidence of edge-mediated effects.

Keywords Edge effect · Fish feeding · Trophic guilds · Riparian vegetation · Agroecosystems · Conservation

Introduction

Habitat fragmentation is a process characterized by the reduction of a natural habitat area into smaller habitat patches with smaller total areas that are isolated from each other by a matrix (Noss et al., 2006). The matrix is the spatially dominant land cover (commonly deforested agricultural areas) in which forest fragments are imbedded and that patch-dependent species cannot sustainably inhabit (Driscoll et al., 2013). In the boundary between forested and deforested areas, temperature, luminosity, and exposure to winds are higher than in core forested areas, modifying the structure and composition at the edge of the forest fragment (Harper et al., 2005). These changes can in

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turn lead to changes in ecological factors, known as edge effects (Pearson, 2002). Henceforth, the mechanisms that influence the ecological processes of edges can be termed as edge-mediated effects, which can be assessed under a trophic perspective because habitat edges can alter cross-boundary subsidies (Fagan et al., 1999).

The effects of forest fragmentation on terrestrial fauna (e.g., Fischer & Lindenmayer, 2007; Cruze & Kumar, 2011; Canale et al., 2012; Prist et al., 2012) are better understood than those on aquatic fauna, which are rarely addressed in the literature (Eikaas et al., 2005). Notwithstanding, terrestrial habitat fragmentation can also pose great threats to stream fishes, which are subject to constrained watercourse connectivity (Eikaas et al., 2005) and limited to a spatially reduced system that is highly influenced by its surroundings. Riparian vegetation conditions, for example, can influence stream habitat quality and food resource availability for fish (Esteves & Aranha, 1999; Gücker et al., 2011; Hogsden & Harding, 2012). It can also alter their trophic structure (Pouilly et al., 2006; Ferreira et al., 2012; Zeni & Casatti, 2014) by supplying an important allochthonous energy source (Uieda & Motta, 2007; Abrantes & Sheaves, 2010; Schneider et al., 2011) that is disrupted when deforestation occurs. In streams located on the edge of forest fragments, the same vegetation that grows in the matrix often occupies the deforested margin (Casatti et al., 2009). This structural change can also affect autochthonous resource availability, mainly as a consequence of increased primary production (due to increased sunlight incidence) and the proliferation of generalist-like aquatic insects, shifting the main energy sources in stream communities from allochthonous to autochthonous (Ceneviva-Bastos & Casatti, 2014). Hence, the trophic structure of stream fish can be subject to edge effects.

Given the current rates of deforestation and the lack of knowledge regarding edge effects on streams, our aim was to investigate whether fish trophic structure at the reach scale varies according to reach position (edge or interior) and across seasons (dry or wet), as well as to describe the relationships among trophic guilds and environmental variables in the set of sampled streams. We hypothesized that fish trophic structure will vary according to reach position (i.e., will be influenced by the edge effect), and that this variation will likely be due to distinct environmental variables between edge and interior stream reaches.

We also hypothesized that seasonality will influence fish trophic structure differently between edge and interior reaches because interior streams' surrounding forest may buffer seasonal events (such as flash floods and droughts, for example) and thus influence stream environmental variables.

Methods

Study area

The stream reaches are located in the northwest region of São Paulo State (Fig. 1), southeastern Brazil. The region belongs to the Serra Geral geological formation and is characterized by a relatively flat slope, with plains of quaternary fluvial sedimentary nature (IPT, 1999). The climate is hot tropical, with maximum temperatures between 31 and 32°C and minimum temperatures between 13 and 14°C; the average annual rainfall is between 1300 and 1800 mm (Silva et al., 2007). Two seasons can be defined: a dry season between June and September with lower rainfall and cooler temperatures, and a wet season between December and March with higher rainfall and temperatures (IPT, 1999). This region was originally covered by semi-deciduous seasonal forest (Silva et al., 2007); in chronological order, the landscape has historically been fragmented for the development of coffee crops, livestock grazing, and sugar cane. Currently, the native vegetation is restricted to less than 4% of its original area, distributed in several unconnected small fragments (more than 60% of the fragments are smaller than 10 ha and thus are entirely influenced by edge effects) and embedded in pasture and sugar cane matrices (Nalon et al., 2008).

Forest fragments were selected based on the presence of water bodies (located either on the edge or in/near the fragment core), preservation status (i.e., least amount of impact as possible), fragment shape (excluding those that were highly indented or elongated), size (>200 ha), and distance from larger urban centers (>10,000 inhabitants). Of the nine forest remnants that fulfilled such criteria, six were selected that contained streams with similar habitat structure and water volume (i.e., could be used as replicates). The sampling set consisted of eight stream reaches: four located on the edge of forest fragments (two in pasture and two in sugar cane matrices; none were completely deforested

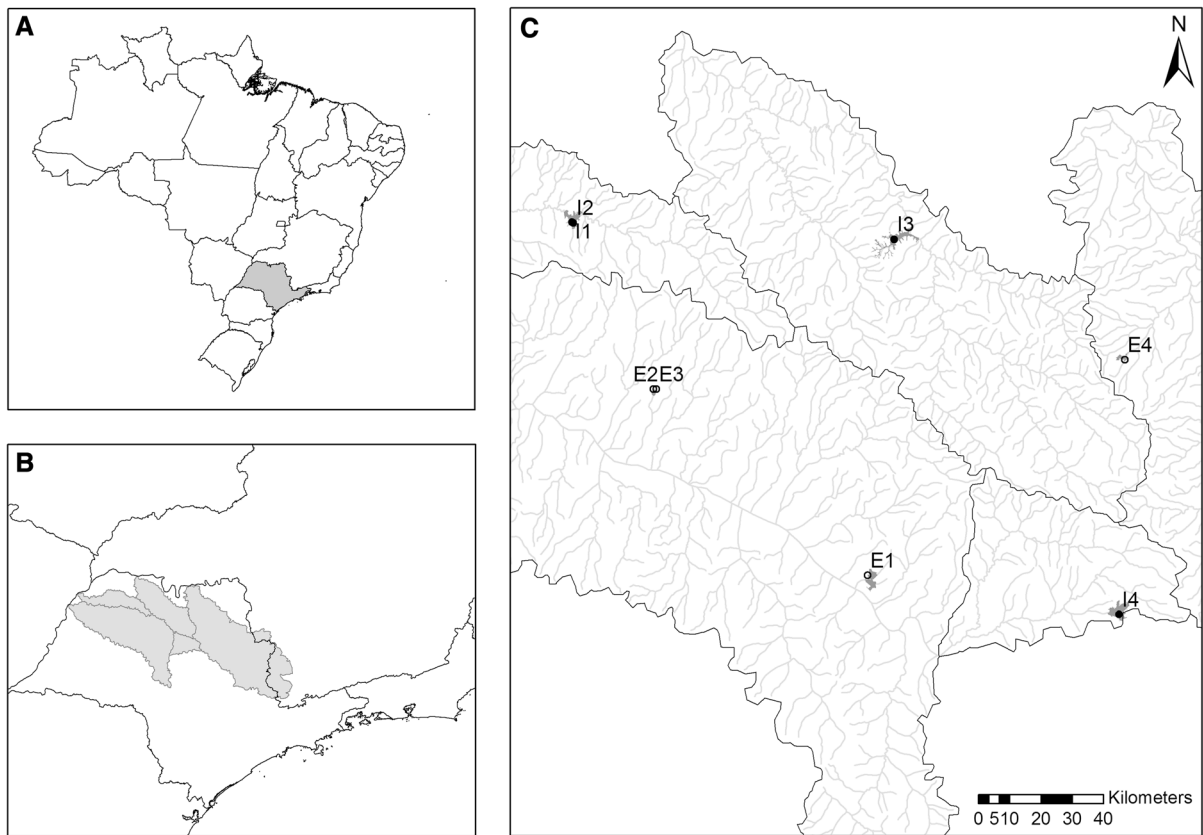


Fig. 1 **A** Location of São Paulo State, Brazil. **B** Study region in São Paulo State. **C** Stream reaches sampled on the edge (**E**) and interior (**I**) of forest fragments

but had only scarce forest cover) and four located in fragment core areas (with dense and well-preserved forest cover) (Table 1; Fig. 1). The length of each selected reach was 75 m, and sampling events were conducted three times during the dry season (June, July, and August 2007) and three times during the wet season (January, February, and March 2008) for a total of 48 sampling events.

Environmental variables and fish sampling

At each sampling location, dissolved oxygen (DO, mg/l), water conductivity ($\mu\text{S}/\text{cm}$, automatically corrected to 25°C), pH, turbidity (NTU), and temperature ($^\circ\text{C}$) were quantified in situ with electronic equipment (Horiba® U-10). Water samples were also collected to obtain the concentration of nitrate (mg/l), ammonia (mg/l), orthophosphate (mg/l), inorganic carbon (IC, mg/l), and non-particulate organic carbon (NPOC, mg/l), which were evaluated at a specialized laboratory by

a trained technician. For habitat structural evaluation, each 75-m reach was divided into 15 sections of 5 m each. Several measurements of width and depth were recorded at each transect, and three measurements of water velocity at the margins and mid-channel were taken with a flowmeter. These measurements were then used to calculate the average surface area, average water velocity, and discharge of the reach. The proportions of each substrate type present in each 5 m section were visually estimated, and the proportion of silt (<0.05 mm) and sand (0.05–2.0 mm) was combined to represent the overall amount of unconsolidated substrate in the reach.

In addition, we measured the following five landscape variables: forest fragment area, perimeter of each fragment, perimeter/area ratio, core area, and distance from the sampling site to the edge. We determined micro-basins from a georeferenced geographic point for each stream. We used Landsat/TM images from the São Paulo State Forest Inventory

Table 1 General description of the sampled reaches: position according to the forest fragment, geographical coordinates, altitude (m), land use in the surrounding matrix, stream order (1:50,000 map scale), area (ha), and perimeter (m) of the forest fragments, perimeter/area ratio for forest fragments, core area

of forest fragments (ha), and distance to core edge (m); distance to core edge was obtained only for the interior reaches to confirm that they were not under the influence of edge effects

Reaches	Coordinates		Altitude	Matrix	Stream order	Area	Perimeter	Perimeter/area ratio	Core area	Distance to core edge
	S	W								
Edge										
E1	21°31'26.2"	49°18'52.7"	375	Sugar cane	1	624.69	14,340	22.95	524.34	–
E2	20°59'25.6"	49°58'50.5"	426	Pasture	1	192.78	6900	35.79	145.62	–
E3	20°59'26.0"	49°58'20.7"	381	Pasture	2	192.78	6900	35.79	145.62	–
E4	20°53'26.9"	48°31'49.8"	482	Sugar cane	3	495.27	26,100	52.70	321.21	–
Interior										
I1	20°30'29.6"	50°14'00.4"	344	Sugar cane	2	1624.86	54,240	33.38	1259.10	880
I2	20°30'36.7"	50°13'43.6"	341	Sugar cane	3	1624.86	54,240	33.38	1259.10	230
I3	20°33'02.5"	49°14'38.7"	467	Citriculture	3	2208.69	43,860	19.86	1893.24	470
I4	21°37'38.2"	48°32'08.6"	498	Citriculture	2	2480.76	173,760	70.04	1383.39	890

Stream reaches E2–E3 and I1–I2 are located in the same forest fragment but in independent stream reaches

(SMA/IF, 2005) to obtain landscape variables with a spatial resolution of 30 m and a mapping scale of 1:50,000, with a map superposition of the prominent lines of São Paulo State using ArcGIS 9, ArcMap version 9.2 software. We generated the forest fragments metrics by Fragstats 4 (McGarigal et al., 2012) and calculated the core area for each fragment after excluding borders of 100 m in width (Table 1).

We sampled fish with an electrofishing alternate current generator (220 V, 50–60 Hz, 3.4–4.1 A, 1000 W) in an upstream direction for 60 min after blocking the upper and lower reach limits with block nets (5 mm mesh). The fish were anesthetized in benzocaine (one gram of benzocaine in 100 ml of 92 GL alcohol and diluted afterward in 5 l of water), fixed in 10% formalin solution for 72 h, and then transferred to a 70% alcohol solution. Samples were deposited in the Fish Collection of the Zoology Department (DZSJRP 13960-14012) at Instituto de Biociências Letras e Ciências Exatas, IBILCE-UNESP, São José do Rio Preto, SP, Brazil.

Analysis

Trophic guild determination was based on diet analysis of the largest individuals of species with at least five specimens per stream ($n = 338$). Despite not being submitted to diet analysis, species with less than five adult specimens were also included in the results section

to illustrate the diversity sampled. After obtaining the weight (g) of each species, we removed the stomachs and identified the diet items as algae, fish, aquatic invertebrates, terrestrial invertebrates, superior vegetal (vegetal tissue, fruits, and seeds), and detritus with the aid of specialized literature (Bicudo & Bicudo, 1970; Borror & DeLong, 1988; and Costa et al., 2006). The food items whose origin (autochthonous or allochthonous) could not be identified were included in the “unknown origin” category. Because most gut contents were small sized, we visually estimated, with the help of a millimetric petri dish, the percentage that each food item occupied from the total stomach volume (as an analog estimation of volume). The frequency of occurrence (Gelwick & Matthews, 1996) and dominance (Hynes, 1950) were calculated for each feeding item. Dominance was measured by the percentage of the number of times in which the item was the main feed item in each stomach per the total number of analyzed specimens.

The dominance values obtained were then used to calculate the index of feeding importance (IA_i) and were adapted from Kawakami & Vazzoler (1980) following Bennemann et al. (2006):

$$IA_i = \frac{F_i \times D_i}{\sum^n (F_i \times D_i)},$$

where F_i is the frequency of occurrence of item i (%), D_i is the dominance of this item, and n is the total number of feeding items for each species. Finally, the

food item with the highest IA_i value was used to determine species trophic guilds at each sampling location.

The overall assessment of edge-mediated effects of forest fragments on fish trophic guilds was based on the comparisons of trophic guild biomass according to two factors (position and season) that represent the group of samples (edge vs. interior; dry vs. wet). We conducted a two-way permutational multivariate analysis of variance (PERMANOVA) using the Bray–Curtis coefficient of similarity to test for differences in the biomass of trophic guilds between groups and for the possibility of interaction between these groups. Position and season were considered as fixed factors. A significant pseudo- F ratio resulting from the PERMANOVA indicates differences between groups due to either differences in the position/season in the multivariate space or differences in the dispersion of samples. To uncover the nature of trophic differences that can be revealed in the PERMANOVA, we used a Permutational Analysis of Multivariate Dispersions (PERMDISP; Anderson et al., 2008). PERMDISP calculates the centroid of samples belonging to each group in the multivariate space based on a similarity measure (Bray–Curtis in this case) and then calculates the distance of each sample to their group centroid. To compare average dispersion values between groups, PERMDISP calculates a pseudo- F statistics and P value, similar to the PERMANOVA. A significant pseudo- F ratio from the PERMANOVA and a non-significant difference in dispersion between groups from the PERMDISP indicate that differences in trophic structure are not due to dispersion effects (Anderson et al., 2008).

The PERMANOVA was complemented by the Simper procedure to determine which of the trophic guilds contributed the most to the dissimilarity between groups (edge vs. interior; dry vs. wet). All these procedures were conducted using Primer 6 + Permanova software (Clarke & Gorley, 2006) with 9999 permutations and a 0.05 significance level.

We ran a principal coordinates analysis (PCoA) using Primer 6 + Permanova software (Clarke & Gorley, 2006) to select the environmental variables that explain the most of the variability in the abiotic dataset. The PCoA is an ordination analysis similar to a principal component analysis (PCA); it uses the Euclidean distance matrix to reduce data dimensionality to allow the most relevant structural patterns to be observed (Anderson et al., 2008). Variables were

normalized to even their weight, and the two axes that contributed the most to explain the observed variation were selected. We chose the variables that showed the highest PCoA scores and avoided the correlated values. Then we conducted a PERMANOVA using the Euclidean Distance coefficient to test for differences in the environmental variables between groups (edge vs. interior; dry vs. wet) and also to obtain the interaction between them. Similar to the procedures described above, we ran PERMDISP to detect if the environmental differences could be attributed to the dispersion of samples.

To summarize the variation in trophic guilds which is explained by the most important environmental variables, we used a Redundancy Analysis using Canoco 5 software (ter Braak & Smilauer, 2012). To test the significance of all axes, we performed a Monte Carlo permutation using a full model (4999 permutations). To test the significance of each variable, we used stepwise generalized linear model (GLM) selection to obtain the pseudo- F statistic, with a 0.05 significance level (ter Braak & Smilauer, 2012).

Results

A total of 53 species were recorded. Some species occurred both in edge and interior stream reaches, with 45 species sampled in reaches located at the edge of the forest fragments and 33 in the interior. Trophic guild determination was based on diet analysis of 23 species from edge stream reaches and 15 from interior, which were those species with five or more specimens (Table 2; Appendix 1 in supplementary material). Seven trophic guilds were found at the edge and interior reaches: aquatic invertivores (preyed mostly insect larvae), terrestrial invertivores (preyed mostly on adult insect stages), general invertivores (fed on insect larvae and adults, from aquatic, terrestrial, or unknown origin, and also on other invertebrates), omnivores (fed on basal resources and also preyed upon other consumers), herbivores (fed mostly on seeds and superior plants), detritivores, and algivore-detritivores. The exclusive algivore, represented by *Serrapinnus notomelas* (Eigenmann, 1915), was found only at the edge streams during the wet season; the carnivore, represented by *Hoplias malabaricus* (Bloch, 1794) (preyed on shrimp, fish, snakes, and tadpoles), was found only at the edge streams in the

Table 2 List of all sampled species with trophic guilds and biomass (in parentheses, g) for examined species from edge and interior reaches and from dry and wet seasons

Order and family	Species	Trophic guilds ^a and biomass			
		Edge		Interior	
		Dry	Wet	Dry	Wet
Characiformes					
Anostomidae	<i>Leporinus friderici</i> (Bloch, 1794)	–	–	–	–
	<i>Leporinus lacustris</i> Campos, 1945	–	–	–	–
	<i>Leporinus striatus</i> Kner, 1858	–	–	–	–
Characidae	<i>Astyanax altiparanae</i> Garutti & Britski, 2000	Ter-inv (287.7)	Omn (270.8)	Omn (534.6)	Her (1359.1)
	<i>Astyanax fasciatus</i> (Cuvier, 1819)	Aq-inv (90.1)	Omn (106.3)	Ter-inv (219.6)	Ter-inv (711.6)
	<i>Bryconamericus stramineus</i> (Eigenmann, 1908)	–	–	Aq-inv (9.9)	Gen-inv (7.5)
	<i>Hemigrammus marginatus</i> Ellis, 1911	Gen-inv (88.0)	Gen-inv (24.9)	–	–
	<i>Hyphessobrycon anisitsi</i> (Steindachner, 1882)	Gen-inv (459.5)	Omn (190.1)	–	–
	<i>Hyphessobrycon eques</i> (Steindachner, 1882)	–	–	–	–
	<i>Knodus moenkhausii</i> (Eigenmann & Kennedy, 1903)	–	–	–	–
	<i>Moenkhausia sanctaefilomenae</i> (Steindachner, 1907)	Ter-inv (21.8)	Ter-inv (5.2)	–	–
	<i>Oligosarcus pintoii</i> Campos, 1945	–	–	–	–
	<i>Piabina argentea</i> Reinhardt, 1867	–	Aq-inv (4.9)	Aq-inv (42.7)	Omn (96.4)
	<i>Planaltina britskii</i> Menezes, Weitzman & Burns, 2003	–	–	–	–
	<i>Salminus hilarii</i> Valenciennes, 1850	–	–	–	–
	<i>Serrapinnus heterodon</i> (Eigenmann, 1915)	–	Aq-inv (0.8)	–	Aq-inv (4.3)
<i>Serrapinnus notomelas</i> (Eigenmann, 1915)	Alg-det (325.62)	Alg (72.0)	–	–	
Crenuchidae	<i>Characidium gomesi</i> Travassos, 1956	–	–	–	–
	<i>Characidium</i> aff. <i>lagosantense</i> Travassos, 1947	–	–	–	–
	<i>Characidium zebra</i> Eigenmann, 1909	–	–	Aq-inv (99.6)	Aq-inv (100.4)
Curimatidae	<i>Cheirodon stenodon</i> Eigenmann, 1915	–	–	–	–
	<i>Cyphocharax vanderi</i> (Fernández-Yépez, 1948)	Det (84.6)	Det (49.1)	–	–
Erythrinidae	<i>Hoplias malabaricus</i> (Bloch, 1794)	Car (2103.2)	–	–	–
Lebiasinidae	<i>Pyrrhulina australis</i> Eigenmann & Kennedy, 1903	Gen-inv (123.3)	Ter-inv (196.2)	–	–
Parodontidae	<i>Apareiodon piracicabae</i> (Eigenmann, 1907)	–	–	–	–
	<i>Parodon nasus</i> Kner, 1858	–	–	–	–
Serrasalminidae	<i>Metynnis maculatus</i> (Kner, 1858)	–	–	–	–
Cyprinodontiformes					
Poeciliidae	<i>Phalloceros harpagos</i> Lucinda, 2008	–	–	–	–
	<i>Poecilia reticulata</i> Peters, 1859	–	Det (4.0)	Det (0.8)	Det (0.8)
Gymnotiformes					
Gymnotidae	<i>Gymnotus sylvius</i> Albert & Fernandes-Matioli, 1999	Aq-inv (614.8)	Aq-inv (322.0)	–	–

Table 2 continued

Order and family	Species	Trophic guilds ^a and biomass			
		Edge		Interior	
		Dry	Wet	Dry	Wet
Sternopygidae	<i>Eigenmannia virescens</i> (Valenciennes, 1842)	Aq-inv (56.3)	Aq-inv (44.9)	–	–
	<i>Sternopygus macrurus</i> (Bloch & Schneider, 1801)	Aq-inv (47.7)	Aq-inv (55.1)	–	–
Perciformes					
Cichlidae	<i>Cichlasoma paranaense</i> Kullander, 1983	Her (255.3)	Omn (361.9)	–	–
	<i>Crenicichla britskii</i> Kullander, 1982	–	–	–	–
	<i>Geophagus brasiliensis</i> (Quoy & Gaimard, 1824)	–	–	–	–
	<i>Satanoperca pappaterra</i> (Heckel, 1840)	Aq-inv (60.6)	Omn (120.8)	–	–
Siluriformes					
Auchenipteridae	<i>Tatia neivai</i> (Ihering, 1930)	–	–	–	–
	<i>Trachelyopterus</i> sp.	–	–	–	–
Callichthyidae	<i>Aspidoras fuscoguttatus</i> Nijssen & Isbrücker, 1976	–	–	–	–
	<i>Callichthys callichthys</i> (Linnaeus, 1758)	–	–	–	–
	<i>Corydoras aeneus</i> (Gill, 1858)	–	Omn (20.1)	–	Aqu-inv (34.8)
	<i>Hoplosternum littorale</i> (Hancock, 1828)	–	–	–	–
Heptapteridae	<i>Cetopsorhamdia iheringii</i> Schubart & Gomes, 1959	Aq-inv (27.1)	Aq-inv (15.1)	Aq-inv (5.7)	–
	<i>Imparfinis schubarti</i> (Gomes, 1956)	Aq-inv (202.4)	Aq-inv (41.5)	Aq-inv (153.6)	Aq-inv (103.9)
	<i>Phenacorhamdia tenebrosa</i> (Schubart, 1964)	–	–	–	–
	<i>Pimelodella avanhandavae</i> Eigenmann, 1917	Gen-inv (84.4)	Gen-inv (60.5)	Aq-inv (372.0)	Aq-inv (153.3)
	<i>Rhamdia quelen</i> (Quoy & Gaimard, 1824)	Gen-inv (401.6)	Gen-inv (108.7)	Gen-inv (621.0)	Gen-inv (428.9)
Loricariidae	<i>Hisonotus francirochai</i> (Ihering, 1928)	–	–	–	–
	<i>Hypostomus ancistroides</i> (Ihering, 1911)	Det (246.5)	Det (134.2)	Det (83.2)	Alg-det (161.6)
	<i>Hypostomus nigromaculatus</i> (Schubart, 1964)	–	–	Det (86.9)	Det (150.8)
	<i>Otothyropsis marapoama</i> Ribeiro, Carvalho & Melo, 2005	Det (0.22)	Det (13.7)	–	–
Pseudopimelodidae	<i>Pseudopimelodus</i> aff. <i>pulcher</i> (Boulenger, 1887)	–	–	Aq-inv (35.9)	Aq-inv (69.6)
Synbranchiformes					
Synbranchidae	<i>Synbranchus marmoratus</i> Bloch, 1795	–	–	–	–

Alg algivores, Car carnivores, Alg-det algivore/detritivores, Det detritivores, Her herbivores, Gen-inv general invertivores, Aq-inv invertivores based on aquatic organisms, Ter-inv invertivores based on terrestrial organisms, Omn omnivores

^a Trophic guilds were determined for species with more than five adult specimens; those species that were less abundant are represented by dashes

dry season (Table 2). The number of species and biomass of each trophic guild varied between the interior and edge reaches (Table 2). The carnivore *Hoplias malabaricus* showed the highest biomass in the edge reaches, followed by aquatic invertivores, which were represented by *Gymnotus sylvius* Albert & Fernandes-Matioli, 1999 and *Imparfinis schubarti*

(Gomes, 1956). In the interior reaches, the highest biomass was represented by the herbivore *Astyanax altiparanae* Garutti & Britski, 2000 in the wet season, followed by the aquatic invertivore *Rhamdia quelen* (Quoy & Gaimard, 1824).

The diet analysis showed that some species, particularly small characins [such as *Astyanax*

Table 3 Results from Simper procedures that show the comparison between the biomass of trophic guilds on the edge versus interior reaches and in the dry versus wet seasons

Guilds/position	Edge	Interior	Average biomass \pm standard deviation	% Contribution ^a
Aquatic invertivores	222.7	148.2	13.6 \pm 1.0	21.0
Omnivores	133.8	78.9	11.6 \pm 0.8	17.9
Herbivores	31.9	169.9	9.7 \pm 0.7	15.1
General invertivores	168.9	132.2	8.4 \pm 1.3	12.7
Terrestrial invertivores	63.9	116.4	7.9 \pm 1.0	12.2
Carnivores	262.9	0	6.5 \pm 0.4	10.0
Detritivores	66.5	40.3	4.7 \pm 1.3	7.2
Algivore–detritivores	40.7	20.2	1.9 \pm 0.7	3.0
Algivores	9.0	0	0.6 \pm 0.4	0.9
Guilds/season	Dry	Wet	Average biomass \pm standard deviation	% Contribution ^b
Aquatic invertivores	252.0	118.9	14.9 \pm 1.3	22.2
Omnivores	66.8	145.8	11.4 \pm 0.8	17.0
Herbivores	31.9	169.9	9.8 \pm 0.7	14.5
General invertivores	222.2	78.8	9.4 \pm 1.4	13.9
Terrestrial invertivores	66.1	114.1	8.3 \pm 1.3	12.4
Carnivores	262.9	0	6.5 \pm 0.4	9.7
Detritivores	62.8	44.1	4.4 \pm 1.2	6.6
Algivore–detritivores	40.7	20.2	1.9 \pm 0.7	2.9
Algivores	0	9.0	0.6 \pm 0.4	0.8

Values of biomass are presented as average biomass for each guild (g). % of contribution refers to the contribution to the average dissimilarity between groups

^a Total dissimilarity between edge and interior reaches = 65%

^b Total dissimilarity between dry and wet periods = 67%

altiparanae, *Astyanax fasciatus* (Cuvier, 1819), *Bryconamericus stramineus* (Eigenmann, 1908), *Hyphessobrycon anisitsi* (Steindachner, 1882), *Piabina argentea* (Reinhardt, 1867), and *Serrapinnus notomelas*, and cichlids (such as *Cichlasoma paranaense* (Kullander, 1983) and *Satanoperca pappaterra* (Heckel, 1840)], were classified in distinct trophic guilds according to both reach position and season (Table 2). The interaction between position of stream reaches and seasons was significant for trophic guilds biomass (pseudo- $F = 3.68$, $P = 0.004$). Multivariate dispersion did not vary significantly between position (pseudo- $F = 0.07$, $P = 0.81$) and season (pseudo- $F = 3.65$, $P = 0.11$). These results indicate that differences in trophic structure are not due to dispersion effects. Instead, each combination of samples (edge wet, edge dry, interior wet, and interior dry) had a different trophic structure. According to Simper,

aquatic invertivores contributed the most to separate samples according to reach position and season (contribution of 21.0 and 22.2% to the average dissimilarity between groups, respectively) (Table 3).

From the 13 environmental variables sampled for habitat evaluation (Table 4), four (dissolved oxygen, temperature, orthophosphate, and unconsolidated substrate) explained most of the variability among streams (Table 4). The environmental variables were significantly different between edge and interior stream reaches (PERMANOVA pseudo- $F = 3.46$, $P = 0.0009$) and between dry and wet seasons (pseudo- $F = 3.29$, $P = 0.0014$), with no interaction between position and season (pseudo- $F = 0.71$, $P = 0.734$). The explanatory variables included in the RDA accounted for 27.7% of the total variation in the trophic guilds matrix; the fitted explanation of the first two RDA axes was 74.0%, and according to the

Table 4 Average values of local variables measured for each sampling reach (*E* edge, *I* interior). PCoA 1 and 2 are the correlation values resulting from the first two axes of principal coordinates analysis, which together explained 49.3% of environmental data variability

Variables	Units	E1	E2	E3	E4	I1	I2	I3	I4	PCoA1	PCoA2
Dissolved oxygen	mg/l	6.96	5.68	7.12	6.88	8.08	6.89	8.84	8.09	<i>-0.85</i>	<i>-0.13</i>
Water conductivity	μS/cm	37.67	32.33	27.83	66.67	129.67	123.33	82.17	100.17	<i>-0.77</i>	<i>-0.09</i>
pH	–	8.42	6.70	7.91	8.10	8.25	8.18	8.39	8.24	<i>-0.24</i>	<i>0.44</i>
Turbidity	NTU	38	27	3	17	22	12	20	23	<i>-0.13</i>	<i>-0.27</i>
Temperature	°C	21.58	23.57	22.63	20.53	18.85	19.52	19.72	18.50	<i>0.68</i>	<i>0.48</i>
Nitrate	mg/l	0.64	1.42	0.66	0.44	0.48	0.59	0.54	2.45	<i>0.33</i>	<i>0.33</i>
Ammonia	mg/l	0.57	0.69	0.61	0.43	0.42	0.42	0.44	0.51	<i>0.610</i>	<i>0.71</i>
Orthophosphate	mg/l	0.03	0.01	0.01	0.05	0.01	0.03	0.08	0.09	<i>0.29</i>	<i>0.84</i>
Inorganic carbon	mg/l	21.88	31.91	16.29	24.72	80.30	76.62	48.82	47.28	<i>-0.53</i>	<i>-0.10</i>
Non-particulate organic carbon	mg/l	0.84	0.88	1.47	1.10	1.76	1.77	1.10	8.83	<i>-0.44</i>	<i>0.32</i>
Stream reach surface area	m ²	87.70	204.80	122.20	154.20	103.60	229.20	120.50	108.60	<i>0.26</i>	<i>0.08</i>
Proportion of unconsolidated substrate	%	73	95	52	67	52	34	38	38	<i>0.71</i>	<i>0.03</i>
Current	m/s	0.18	0.06	0.17	0.30	0.23	0.16	0.27	0.20	<i>-0.32</i>	<i>0.44</i>

The PCoA scores selected for further analysis are shown in italics

GLM models, dissolved oxygen (pseudo- $F = 13.69$, $P < 0.00063$), temperature (pseudo- $F = 70.86$, $P < 0.00001$), and unconsolidated substrate (pseudo- $F = 22.39$, $P = 0.00006$) exhibited significant relationships with trophic guilds. The dissolved oxygen was particularly higher in the interior reaches, and demonstrated high association with terrestrial invertivores. The temperature was correlated with omnivores and algivores; the omnivores presented greater biomass on the edge reaches during the wet season, and the algivores were exclusive to edge reaches during the wet season. The proportion of unconsolidated substrate was associated with detritivores, which had greater biomass in the edge reaches (Table 3; Fig. 2).

Discussion

As predicted, the edge effects of forest fragments altered the environmental variables and trophic structure of the stream fish community. Trophic structure also demonstrated spatiotemporal variation because reach position and season exhibited a significant interaction. The increase in solar radiation in the edge streams, as a consequence of partial deforestation, increased the water temperature and decreased the dissolved oxygen. Moreover, the deforestation has jeopardized the retention of sand arising from land use activities on the matrix and increased the proportion of unconsolidated substrate, particularly during the wet

season. Aquatic invertivores, omnivores, detritivores, and algivores showed higher biomass in the edge streams, whereas terrestrial invertivores and herbivores showed higher biomass in the interior streams, wherein terrestrial invertivores were notably associated with higher dissolved oxygen conditions. The increased temperatures, increased unconsolidated substrate, and decreased dissolved oxygen in the edges are conditions that can influence not only the rates of organic matter processing (Ferreira & Chauvet, 2011), fish metabolism (Pang et al., 2011; Ohlberger et al., 2012), and fish behavior (Biro et al., 2010), but also the trophic structure, as demonstrated by the edge-mediated effects found in this study.

Aquatic invertivores, omnivores, herbivores, general invertivores, and terrestrial invertivores contributed up to approximately 78% of the dissimilarity between the edge and interior stream reaches. The aquatic invertivores contributed the most to the dissimilarity between both stream position (edge vs. interior) and seasons (dry vs. wet), with greater biomass at the edge reaches in dry season. In these deforested streams, marginal grasses from the surrounding matrix proliferate due to increased sunlight (Pusey & Arthington, 2003) and may have provided spatial refugia against predation in these simplified environments (Ceneviva-Bastos & Casatti, 2014). Invertebrates are tolerant to physical degradation and many Diptera and Ephemeroptera are often associated

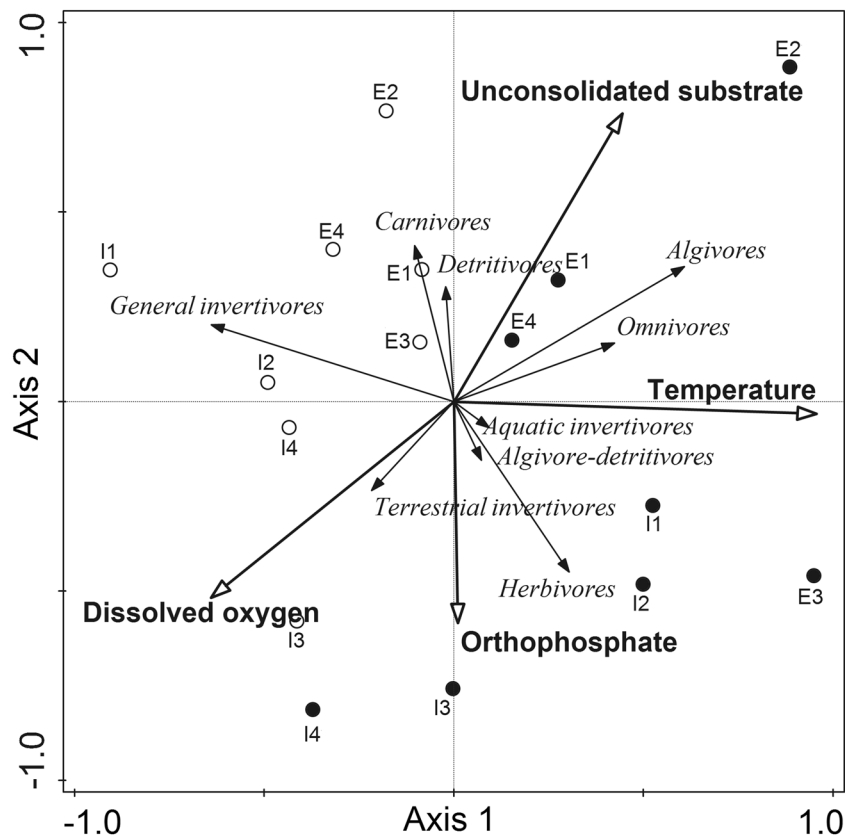


Fig. 2 Biplot resulting from redundancy analysis, representing the ordination of samples according to the environmental variables (open arrows), trophic guilds (dark arrows), and stream reaches sampled on the edge (E) and interior (I) of forest

fragments during dry (open circles) and wet (black circles) periods (permutation test on all axes: pseudo- $F = 1.10$, $P = 0.417$)

with these marginal grasses (Bonato et al., 2012; Wang et al., 2012; Marques et al., 2013; Ceneviva-Bastos & Casatti, 2014). In fact, these insects were the most frequent and abundant food item for fishes that fed on aquatic invertebrates. According to Zeni & Casatti (2014), marginal grasses from pastures contributed to the increased abundance and biomass of aquatic insectivores and may be a key factor in trophic homogenization. Despite the presence of one margin of forested area, the edge streams in this study were influenced by edge effects and presented features that indicate some degree of ecological impairment, with a higher proportion of marginal grasses. Thus, indirect edge effects can influence the physical habitat and mediate changes in trophic organization.

Terrestrial invertivores and herbivores showed greater biomass in the interior streams, particularly during the wet season. These results corroborate many

other studies that demonstrated that the lateral dimension of a stream segment plays a fundamental role in fish species diet (Uieda & Motta, 2007; Abrantes & Sheaves, 2010; Schneider et al., 2011; Ferreira et al., 2012). The input of allochthonous items from riparian vegetation, such as terrestrial insects and seeds, represents an additional source of energy for the aquatic systems (Chang et al., 2008) and a food source of great importance for stream fishes (Nakano & Murakami, 2001; Small et al., 2011, 2013), which may contribute to consumer abundance and biomass (Kawaguchi et al., 2003), as found in this study. The scarcity of riparian vegetation in one stream bank, as found in our edge streams, is thus sufficient to cause changes that promote substantial alterations in the diet of the fish fauna. Therefore, according to Small et al. (2011), fish that eat terrestrial insects have one important role to nutrient recycling by their capacity

to absorb, retain, and provide nitrogen and phosphorus to the stream environment and food web system. In deforested streams, the abundance of these food resources is lower (Ferreira et al., 2012); consequently, Neotropical fish tend to change their diet to consume the most abundant item in the environment (Zeni & Casatti, 2014), but the consequences of this change to the nutrient cycle remains unexplored. These results emphasize the importance of well-preserved riparian vegetation in providing terrestrial food inputs that influence the trophic organization of stream fish, which are different in the edge and interior reaches and suggest edge-mediated effects.

The presence of riparian vegetation can also differently influence the allochthonous resource availability based on the season, and consequently, the use of such resources by fish. The inputs of terrestrial insects and seeds are usually higher during the wet season due to washout (Rezende & Mazzoni, 2005), which explains the higher biomass of terrestrial invertivores, herbivores, and omnivores instead of aquatic invertivores in this season, independently from the stream location in our study. Similarly, Ortaz (2000) observed a high consumption of aquatic insects in the dry season and a high consumption of terrestrial insects and seeds during the wet season in a forested tropical stream. However, resource diversity in streams with no riparian forest can be reduced and, depending on the magnitude of feeding resource homogenization, the seasonal variability can be suppressed (Rocha et al., 2009). Hence, even the scarce and degraded forest cover of the edge streams may have buffered the effects of seasonality (as the occurrence of flash floods during the rainy season, for example, which can increase macroinvertebrate drift) in the fish trophic structure.

Algivores were associated with water temperature and were exclusive to the edge reach, which was located in a pasture edge that is frequently used as a water source for cattle. These factors promote a high entry of nutrients in organic form (cattle feces) into the stream, particularly during the wet period (Brodie & Mitchell, 2005). Moreover, the increased solar radiation on the edge stream (Pusey & Arthington, 2003) along with the high entry of nutrients most likely stimulates primary productivity, favoring species, such as *Serrapinnus notomelas*, that feed on algae (Casatti et al., 2003; present study).

In our study, omnivores had a slightly higher contribution to the edge reaches; thus, the edge effects may not be the main factor influencing this guild. According to Kratina et al. (2012), omnivory is very common in biological systems (Kratina et al., 2012) and can be explained by various mechanisms (see Singer & Bernays, 2003 for examples). Although the effects of omnivory on overall community dynamics can be controversial (see revision in Kratina et al., 2012), it can be considered a community-stabilizing factor because it can reduce the propagation of a given effect across trophic levels (Thompson et al., 2007). It can also be directly related to density-dependent foraging, particularly regarding tropical fish assemblages, where the high omnivory that is commonly reported (Winemiller, 1990; Ceneviva-Bastos et al., 2012; Davis et al., 2012; González-Bergonzoni et al., 2012) can be a result of stream fish dietary flexibility, which allows them to consume other items when a preferred prey source is in short supply (Jepsen & Winemiller, 2002; Uieda & Motta, 2007). In the present study, this trophic group was principally composed by nektonic species that swim in the water column, catching items that are dragged by the current (Casatti et al., 2003); such traits would explain why omnivores exhibited a larger contribution to fish biomass in the wet period, when the loading of feeding items by water is higher (Rezende & Mazzoni, 2005).

Despite the importance of resource origin (autochthonous or allochthonous) and seasonality, we can illustrate the greater fish biomass associated with the interior sites by a brief exercise. After restricting the biomass comparison only to the species that were common to the edge and interior reaches [*Astyanax altiparanae*, *Astyanax fasciatus*, *Hypostomus ancistroides* (Ihering, 1911), *Imparfinis schubarti*, *Pimelodella avanhandavae* Eigenmann, 1917, and *Rhamdia quelen*] regardless of the season, the fish biomass from the interior samples is approximately two times the biomass of edge samples. From this perspective, it can be presumed that these fishes receive benefits by being located in the stream reaches within the forest fragments, where both autochthonous and allochthonous resources are abundant (as in deforested streams), particularly in the wet period.

In conclusion, the edge effects of forest fragments affect not only the terrestrial biota (see Cox et al., 2012; Robinson & Sherry, 2012; Santos-Filho et al., 2012; Silva et al., 2012; and Sundarapandian &

Karoor, 2013, for examples, in which different biological groups are used to assess edge effects) but also stream fish. The removal of part of the forest cover on the edge streams studied herein not only caused physical and structural changes but also influenced fish trophic structure and demonstrated edge-mediated effects. As many of the fish species from the studied region are generalists regarding feeding habits, their biomass (higher in the forested fragment core) and trophic structure can be influenced by the presence of well-preserved riparian forest. This is because stream ecosystems are directly linked to the adjacent terrestrial ecosystems, and reciprocal subsidies traded between these two environments can influence physical stream features (Pusey & Arthington, 2003) and the entire food web (Nakano & Murakami, 2001). We demonstrated that streams can be physically and biologically influenced by edge effects. These findings provide additional information for the future restoration of aquatic ecosystems and stream fish conservation.

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References

Abrantes, K. G. & M. Sheaves, 2010. Importance of freshwater flow in terrestrial–aquatic energetic connectivity in intermittently connected estuaries of tropical Australia. *Marine Biology* 157: 2071–2086.

Anderson, M. J., R. N. Gorley & K. R. Clarke, 2008. PERMANOVA+ for PRIMER: guide to Software and Statistical Methods. Plymouth Marine Laboratory, Plymouth.

Bennemann, S. T., L. Casatti & D. C. Oliveira, 2006. Alimentação de peixes: proposta para análise de itens registrados em conteúdos gástricos. *Biota Neotropica* 6: 1–8.

Bicudo, C. E. M. & R. M. T. Bicudo, 1970. *Algas de Águas Continentais Brasileiras*. FBDDe, São Paulo.

Biro, P. A., C. Beckmann & J. A. Stamps, 2010. Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proceedings of the Royal Society B: Biological Sciences* 277: 71–77.

Bonato, K. O., R. L. Delariva & J. C. Silva, 2012. Diet and trophic guilds of fish assemblages in two streams with different anthropic impacts in the northwest of Paraná, Brazil. *Zoologia* 29: 27–38.

Borror, D. J. & D. M. DeLong, 1988. *Introdução ao Estudo de Insetos*. Edgard Blücher, São Paulo.

Brodie, J. E. & A. W. Mitchell, 2005. Nutrients in Australian tropical rivers: changes with agricultural development and implications for receiving environments. *Marine and Freshwater Research* 56: 279–302.

Canale, G. R., C. A. Peres, C. E. Guidorizzi, C. A. F. Gatto & M. C. M. Kierulff, 2012. Pervasive defaunation of forest remnants in a tropical biodiversity hotspot. *PLoS ONE* 7: 1–9.

Casatti, L., H. F. Mendes & K. M. Ferreira, 2003. Aquatic macrophytes as feeding site for small fishes in the Rosana reservoir, Paranapanema river, southeastern Brazil. *Brazilian Journal of Biology* 63: 213–222.

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

Ceneviva-Bastos, M. & L. Casatti, 2014. Shading effects on community composition and food web structure of a deforested pasture stream: evidences from a field experiment in Brazil. *Limnologia* 46: 9–21.

Ceneviva-Bastos, M., L. Casatti & V. S. Uieda, 2012. Can seasonal differences influence food web structure on preserved habitats? Responses from two Brazilian streams. *Community Ecology* 13: 243–252.

Chang, E. K. W., Y. Zhang & D. Dudgeon, 2008. Arthropod ‘rain’ into tropical streams: the importance of intact riparian forest and influences of fish diets. *Marine and Freshwater Research* 59: 653–660.

Clarke, K. R. & R. N. Gorley, 2006. *PRIMER v6: user manual/tutorial*. Plymouth Marine Laboratory, Plymouth, UK.

Costa, C., S. Ide & C. E. Simonka, 2006. *Insetos Imaturos: Metamorfose e Identificação*. Editora Holos, São Paulo.

Cox, W. A., F. R. Thompson & J. Faaborg, 2012. Landscape forest cover and edge effects on songbird nest predation vary by nest predator. *Landscape Ecology* 27: 659–669.

Cruze, N. D. & S. Kumar, 2011. Effects of anthropogenic activities on lizard communities in northern Madagascar. *Animal Conservation* 14: 542–552.

Davis, A. M., M. L. Blanchette, B. J. Pusey, T. J. Jardine & R. G. Pearson, 2012. Gut content and stable isotope analyses provide complementary understanding of ontogenetic dietary shifts and trophic relationships among fishes in a tropical river. *Freshwater Biology* 57: 2156–2172.

Driscoll, D. A., S. C. Banks, P. S. Barton, D. B. Lindenmayer & A. L. Smith, 2013. Conceptual domain of the matrix in fragmented landscapes. *Trends in Ecology and Evolution* 28: 605–613.

Eikaas, H. S., A. R. Mcintosh & A. D. Kliskey, 2005. Catchment and site-scale influences of forest cover and longitudinal forest position on the distribution of a diadromous fish. *Freshwater Biology* 50: 527–538.

- Esteves, K. E. & J. M. R. Aranha, 1999. Ecologia trófica de peixes de riachos. In Caramaschi, E. P., R. Mazzoni & P. R. Peres-Neto (eds), *Ecologia de Peixes de Riachos*. Série Oecologia Brasiliensis, Rio de Janeiro: 157–182.
- Fagan, W. F., R. S. Cantrell & C. Cosner, 1999. How habitat edges change species interactions. *The American Naturalist* 153: 155–182.
- Ferreira, V. & E. Chauvet, 2011. Synergistic effects of water temperature and dissolved nutrients on litter decomposition and associated fungi. *Global Change Biology* 17: 551–564.
- Ferreira, A., F. R. Paula, S. F. B. Ferraz, P. Gerhard, E. A. L. Kashiwaqui, J. E. P. Cyrino & L. A. Martinelli, 2012. Riparian coverage affects diets of characids in neotropical streams. *Ecology of Freshwater Fish* 21: 12–22.
- Fischer, J. & D. B. Lindenmayer, 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* 16: 265–280.
- Gelwick, F. P. & W. J. Matthews, 1996. Trophic relations of stream fishes. In Lambertini, G. & R. Hauer (eds), *Methods in stream ecology*. Academic, New York: 475–492.
- González-Bergonzoni, I., M. Meerhoff, T. A. Davidson, F. Teixeira-de-Mello, A. Baattrup-Pedersen & E. Jeppesen, 2012. Meta-analysis shows a consistent and strong latitudinal pattern in fish omnivory across ecosystems. *Ecosystems* 15: 492–503.
- Gücker, B., M. Brauns, A. G. Solimini, M. Voss, N. Walz & T. Puschnig, 2011. Urban stressors alter the trophic basis of secondary production in an agricultural stream. *Canadian Journal of Fisheries and Aquatic Sciences* 68: 74–88.
- Harper, K. A., S. E. Macdonald, P. J. Burton, J. Chen, K. D. Brosnoff, S. C. Saunders, E. S. Euskirchen, D. Roberts, M. S. Jaiteh & P. A. Esseen, 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* 19: 768–782.
- Hogsden, K. L. & J. S. Harding, 2012. Anthropogenic and natural sources of acidity and metals and their influence on the structure of stream food webs. *Environmental Pollution* 162: 466–474.
- Hynes, H. B. N., 1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. *Journal of Animal Ecology* 19: 36–57.
- IPT (Instituto de Pesquisas Tecnológicas do Estado de São Paulo), 1999. Diagnóstico da situação atual dos Recursos Hídricos e estabelecimento de diretrizes técnicas para a elaboração do Plano da Bacia Hidrográfica do Turvo/Grande. Relatório n° 40.515. Secretaria de Recursos Hídricos, Saneamento e Obras, São Paulo.
- Jepsen, D. B. & K. O. Winemiller, 2002. Structure of tropical river food webs revealed by stable isotope ratios. *Oikos* 96: 46–55.
- Kawaguchi, Y., Y. Taniguchi & S. Nakano, 2003. Terrestrial invertebrate inputs determine the local abundance of stream fishes in a forest stream. *Ecology* 84: 701–708.
- Kawakami, E. & G. Vazzoler, 1980. Método gráfico e estimativa de índice alimentar aplicado no estudo de alimentação de peixes. *Boletim do Instituto Oceanográfico* 29: 205–207.
- Kratina, P., R. M. LeCraw, T. Ingram & B. R. Anholt, 2012. Stability and persistence of food webs with omnivory: is there a general pattern? *Ecosphere* 3: 1–50.
- Marques, L. C., M. Ceneviva-Bastos & L. Casatti, 2013. Progressive recovery of a tropical deforested stream community after a flash flood. *Acta Limnologica Brasiliensia* 25: 111–123.
- McGarigal, K., S. A. Cushman & E. Ene, 2012. FRAGSTATS v4: spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst.
- Nakano, S. & M. Murakami, 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America* 98: 166–170.
- Nalon, M. A., I. F. A. Mattos & G. A. D. C. Franco, 2008. Meio físico e aspectos da fragmentação da vegetação. In Rodrigues, R. R. & V. L. R. Bononi (eds), *Diretrizes para a Conservação e Restauração da Biodiversidade no Estado de São Paulo* Secretaria do Meio Ambiente e Instituto de Botânica, São Paulo: 17–21.
- Noss, R., B. Csuti & M. J. Groom, 2006. Habitat fragmentation. In Groom, M. J., G. K. Meffe, C. R. Carroll, et al. (eds), *Principles of Conservation Biology*. Sinauer Associates Inc., Sunderland: 213–251.
- Ohlberger, J., T. Mehner, G. Staaks & F. Hölker, 2012. Intraspecific temperature dependence of the scaling of metabolic rate with body mass in fishes and its ecological implications. *Oikos* 121: 245–251.
- Ortiz, M., 2000. Diet seasonality and food overlap in fishes of the upper Orinoco stream, northern Venezuela. *Revista de Biología Tropical* 49: 191–197.
- Pang, X., C. Zhen-Dong & F. Shi-Jian, 2011. The effects of temperature on metabolic interaction between digestion and locomotion in juveniles of three cyprinid fish (*Carassius auratus*, *Cyprinus carpio* and *Spinibarbus sinensis*). *Comparative Biochemistry and Physiology, Part A: Molecular & Integrative Physiology* 159: 253–260.
- Pearson, S. M., 2002. Interpreting landscape patterns from organism-based perspectives. In Gergel, S. E. & M. G. Turner (eds), *Learning Landscape Ecology*. Springer, New York: 187–198.
- Pouilly, M., S. Barrera & C. Rosales, 2006. Changes of taxonomic and trophic structure of fish assemblages along an environmental gradient in the Upper Beni microbasin (Bolivia). *Journal of Fish Biology* 68: 137–156.
- Prist, P. R., F. Michalski & J. P. Metzger, 2012. How deforestation pattern in the Amazon influences vertebrate richness and community composition. *Landscape Ecology* 27: 799–812.
- Pusey, B. J. & A. H. Arthington, 2003. Importance of the riparian zone to the conservation and management of freshwater fish: a review. *Marine and Freshwater Research* 54: 1–16.
- Rezende, C. F. & R. Mazzoni, 2005. Seasonal variation in the input of allochthonous matter in an Atlantic Rain Forest stream, Ilha Grande-RJ. *Acta Limnologica Brasiliensia* 17: 167–175.
- Robinson, W. D. & T. W. Sherry, 2012. Mechanisms of avian population decline and species loss in tropical forest fragments. *Journal of Ornithology* 153: S141–S152.
- Rocha, F. C., L. Casatti, F. R. Carvalho & A. M. Silva, 2009. Fish assemblages in stream stretches occupied by cattail

- (Typhaceae, Angiospermae) stands in Southeast Brazil. *Neotropical Ichthyology* 7: 241–250.
- Santos-Filho, M., C. A. Peres, D. J. Silva & T. M. Sanaïotti, 2012. Habitat patch and matrix effects on small-mammal persistence in Amazonian forest fragments. *Biodiversity Conservation* 21: 1127–1147.
- Schneider, M., P. D. P. U. Aquino, M. J. M. Silva & C. P. Fonseca, 2011. Trophic structure of a fish community in Bananal stream sub-basin in Brasília National Park, Cerrado biome (Brazilian Savanna), DF. *Neotropical Ichthyology* 9: 579–592.
- Silva, A. M., L. Casatti, C. A. Alvares, A. M. Leite, L. A. Martinelli & S. Durrant, 2007. Soil loss risk and habitat quality in streams of a meso-scale river basin. *Scientia Agricola* 64: 336–343.
- Silva, F. R., T. A. L. Oliveira, J. P. Gibbs & D. C. Rossa-Feres, 2012. An experimental assessment of landscape configuration effects on frog and toad abundance and diversity in tropical agro-savannah landscapes of southeastern Brazil. *Landscape Ecology* 27: 87–96.
- Singer, M. S. & E. A. Bernays, 2003. Understanding omnivory needs a behavioral perspective. *Ecology* 84: 2532–2537.
- SMA/IF (Secretaria do meio Ambiente e Instituto Florestal), 2005. Inventário florestal da vegetação natural do Estado de São Paulo. Secretaria do Meio Ambiente e Instituto Florestal, São Paulo.
- Small, G. E., C. M. Pringle, M. Pyron & J. H. Duff, 2011. Role of the fish *Astyanax aeneus* (Characidae) as a keystone nutrient recycler in low-nutrient Neotropical streams. *Ecology* 92: 386–397.
- Small, G. E., P. J. Torres, L. M. Schweizer, J. H. Duff & C. M. Pringle, 2013. Importance of terrestrial arthropods as subsidies in lowland neotropical rain forest stream ecosystems. *Biotropica* 45: 80–87.
- Sundarapandian, S. & P. J. Karoor, 2013. Edge effects on plant diversity in tropical forest ecosystems at Periyar Wildlife sanctuary in the Western Ghats of India. *Journal of Forestry Research* 24: 403–418.
- ter Braak, C. J. F. & P. Smilauer, 2012. CANOCO Reference manual and CanoDraw for Windows user's guide: software for Canonical Community Ordination (version 5). Microcomputer Power, Ithaca, NY.
- Thompson, R. M., M. Hemberg, B. M. Starzomski & J. B. Shurin, 2007. Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. *Ecology* 88: 612–617.
- Uieda, V. S. & R. L. Motta, 2007. Trophic organization and food web structure of southeastern Brazilian streams: a review. *Acta Limnologica Brasiliensia* 19: 15–30.
- Wang, B., D. Liu, S. Liu, Y. Zhang, D. Lu & L. Wang, 2012. Impacts of urbanization on stream habitats and macroinvertebrate communities in the tributaries of Qiangtang River, China. *Hydrobiologia* 680: 39–51.
- Winemiller, K. O., 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs* 60: 331–367.
- Zeni, J. O. & L. Casatti, 2014. The influence of habitat homogenization on the trophic structure of fish fauna in tropical streams. *Hydrobiologia* 726: 259–270.