

# Trophic structure of coastal freshwater stream fishes from an Atlantic rainforest: evidence of the importance of protected and forest-covered areas to fish diet

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**Abstract** The role of riparian forests in the functioning of aquatic ecosystems is well known, and they are recognized as an important food source for riverine fauna. This study investigates the trophic structure of coastal freshwater stream fishes from a large conservation area in an Atlantic rainforest using stomach content and food availability analyses. Four samples were collected from 19 sample sites. Fishes were caught with electrofishing. Prey were sampled with trays, Surber, traps, and electrofishing to evaluate the availability of food resources. The diets of 20 fish species were determined from the stomach contents of 1691 individuals. Terrestrial and aquatic insects and detritus were the most consumed items. Fish diet and prey availability were not seasonally dependent. A cluster analysis showed five trophic functional groups: terrestrial insectivores,

aquatic insectivores, detritivores, carnivores, and omnivores. Insectivores predominated in species richness (60%), abundance (47%) and biomass (39%). Allochthonous and autochthonous items were found in similar proportions in the environment; however, allochthonous items were representative for insectivores and detritivores, whereas autochthonous items were important for primarily aquatic insectivores. The preference for certain insects by insectivorous fishes was associated with food selectivity rather than the availability of the resource and demonstrated the strong relationship between feeding behavior and food preference. The absence of seasonal variation in the diets of the fishes was possibly related to the consistent food supply. Our results confirm the role of the forest as a food provider for stream fishes, such as terrestrial insects and plant debris/detritus (also consumed by aquatic insects, which subsequently serve as food for fish), highlighting the importance of conserving the Brazilian Atlantic rainforests.

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## Introduction

The importance of forested areas in maintaining the function of aquatic ecosystems is well documented, and numerous functions are recognized (Gregory et al. 1991; Osborne and Kovacic 1993; Naiman and

Décamps 1997; Pusey and Arthington 2003). Riparian forests are transition zones between terrestrial and aquatic ecosystems and therefore act in several processes involving the transfer of energy and matter (inorganic and organic) (Pusey and Arthington 2003): they regulate the temperature and the primary aquatic production through shading (Kiffney et al. 2003), they maintain structural characteristics and increase channel stability due to sediment entry control (Lorion and Kennedy 2009b), and they mediate the input and processing of nutrients and organic matter (Cummins 1974; Gregory et al. 1991).

Riparian forests also represent an important food source for fish (Nakano et al. 1999) and macroinvertebrates (Anderson and Sedell 1979). The trunks, branches, leaves, fruits, seeds and invertebrates from the forest are important sources of nutrients for these organisms. Trunks, branches and leaves increase the structural complexity of a stream, serve as refuge (e.g., from predation and stream flow) (Everett and Ruiz 1993; Crook and Robertson 1999), habitat for many animals (Lorion and Kennedy 2009b), and food for detritivores after they have been degraded by physical and biological processes (Murphy and Giller 2000). These structures make the establishment of a greater diversity of aquatic invertebrates possible (Schneider and Winemiller 2008), which, in turn, serve as food for fish (Angermeier and Karr 1984). In lotic systems, fruits, seeds and terrestrial invertebrates provided by riparian forest are important food items for ichthyofauna (Barili et al. 2011). The way in which such resources can serve as terrestrial subsidies for riverine consumers may vary among taxa and sites with different levels of canopy cover (Collins et al. 2016). Among terrestrial invertebrates, insects are widely consumed by several fish species (Esteves and Lobón-Cerviá 2001; Ferreira et al. 2012; Leite et al. 2015), especially if they occur at a higher abundance during a given time of year (Kawaguchi and Nakano 2001).

Because of this strong link between riparian and lotic ecosystems, the removal of forests is expected to disrupt allochthonous resource inputs and negatively affect the trophic structure of ichthyofauna (e.g., Wright and Flecker 2004; Leite et al. 2015). Over the past several years, the advancement of agriculture and cattle farming has been identified as the primary cause of deforestation in Brazilian rainforests (Morton et al. 2006; Santos et al. 2015). The Atlantic rainforest is among the eight hotspots with the highest biodiversity in the world, as

it harbors an exceptional amount of endemic species that are suffering from habitat reduction (Myers et al. 2000). Originally, this biome covered 1 million km<sup>2</sup> along the Brazilian coast, and currently, less than 8% remains due to the destruction caused by agriculture, urbanization and industrial development (Mamede et al. 2004). In the southeastern region, biodiversity is threatened mainly by the disorganized increase in human occupation that causes the illegal removal of the Atlantic forest and consequently habitat loss (Menezes et al. 2007). However, pollution, mining, invasion of exotic species, overfishing and illegal fishing for aquarism are also threats to the native ichthyofauna (Duboc and Menezes 2008; Barrella et al. 2014; Frehse et al. 2016). The Atlantic forest often exhibits a longitudinal gradient of degradation in which lowland areas are deforested, and the hilltops are preserved (e.g., Lobón-Cerviá et al. 2016), which is an important issue to address when evaluating fish diversity along the elevation profile in coastal regions (Terra et al. 2016). Changes in the taxonomic, functional and trophic structure of fishes are expected in the absence of forest cover (Teresa and Casatti 2012; Peressin and Cetra 2014) due to changes in water quality (Souza et al. 2013), habitat diversity and structure (Pusey and Arthington 2003), which consequently alter food availability (or trophic dynamics) (Ferreira et al. 2012) when the riparian forest is suppressed or reduced.

Despite the importance of riparian forests to aquatic organisms, very few studies have been conducted in tropical forested-protected areas to provide a reliable baseline (sensu Alagona et al. 2012) of species composition and biology. Pristine conditions (reference areas, sensu Hughes 1995) are currently very rare but extremely important when they are intended to incorporate biological information into environmental monitoring programs. Although there are studies that show the impact of deforestation on fish (e.g., Leite et al. 2015; Lobón-Cerviá et al. 2016), information about the trophic organization of fishes in pristine streams is still needed, which can also contribute to the evaluation of the protection efficiency of these areas. In this context, we described the trophic structure of coastal freshwater stream fishes in a pristine area of the Atlantic rainforest. Hence, we established that a forest-covered and protected area would be essential and the Juréia-Itatins, one of the largest forest remains in southeastern Brazil, was chosen. Because we studied the streams located in a preserved area of the Atlantic rainforest (Mamede et al. 2004), and because habitat quality is associated with the

degree of integrity of a riparian forest (Casatti et al. 2012), we expect that the pristine condition of the forested streams would be reflected in the trophic structure of studied fish populations. Previous studies elsewhere indicate that riparian forest is one of the most important food sources for riverine fauna, such as fishes and macroinvertebrates (e.g., Gregory et al. 1991; Nakano et al. 1999). Considering the presence of riparian forests and the high diversity of insects in these environments (Colzani et al. 2013), we expect that insectivorous fishes will predominate and that the availability of resources provided by the forest will be constant due to the lack of seasonality in tropical forest (Esteves and Lobón-Cerviá 2001).

## Material and methods

### Study area

This study was conducted in the streams of the Juréia-Itatins Ecological Station (JIES), one of the largest conservation areas with Atlantic forest fragments, situated on the Atlantic shore of the state of São Paulo, Brazil (24°25'S, 47°15'W). It is located near the megapolis of São Paulo, one of the most densely populated regions in Latin America with more than 20 million inhabitants, and much closer to Cubatão, one of the worst polluted industrial areas in the world (Por and Imperatriz-Fonseca 1984). The region is threatened by deforestation due to anthropogenic pressure, mostly by burgeoning urbanization. During the 70's and the early 80's, the region suffered from strong pressure from land-plot speculation and was considered by the Brazilian nuclear program for the installation of a nuclear power plant (Marques and Duleba 2004). Despite that, the JIES gained protection in 1987 to protect and ensure the integrity of ecosystems and comprises  $\approx 80,000$  ha of practically untouched Atlantic rainforest (Por and Imperatriz-Fonseca 1984; Marques and Duleba 2004). Due to its harsh access, the area of the JIES is considered one of the best-preserved Atlantic forest remnants (Mamede et al. 2004).

The climate is subtropical humid without a pronounced dry season (Af type, according to Köppen classification). The hotter and rainier season occurs from October to April, and the lesser rainy season occurs from May to September (Tarifa 2004). The mean rainfall and temperature are 2277 mm and 21.4 °C, respectively

(Marques and Duleba 2004). The hydrographic system of the JIES comprises different types of water, according to the topography, soil, and forest type in the drainage. Thus, the mountain streams that drain the Ombrophilous Atlantic Forest (Precambrian terrain) have clear waters and are poor in nutrients (pH  $\sim 5$ ), while the lowland streams have black waters that are rich in humic substances (pH  $\sim 4$ ) due to the typical lowland “restinga” forest soils (alluvial, podzolic, and hydromorphic) (Por 1986, 2004; Por and Lopes 1994).

### Sampling

Four samples were collected over a one-year period (April, July/August, November 2009, and February 2010) at seven streams, totaling 19 sample sites. Fishes were caught with electrofishing gear (500 V, DC) in 50 m-long reaches, according to the methods of Gonçalves and Braga (2012). Voucher specimens were deposited in the fish collection of the Department of Zoology and Botany (DZSJRP), São Paulo State University (UNESP), São José do Rio Preto, State of São Paulo, Brazil (DZSJRP 13234–13,258).

Terrestrial invertebrates and macroinvertebrates, which are considered potential food sources for fish, were sampled in the same 50 m reaches used for electrofishing. For terrestrial items, two pan traps (each with a surface area  $\approx 800$  cm<sup>2</sup>) were partially filled with soapy water, placed at each sample site (one at each wetted edge of the stream) and retrieved after 24 h. Benthic macroinvertebrates were sampled with a Surber net (area 900 cm<sup>2</sup>, 250  $\mu$ m mesh). The area delimited by the sampler was manually disturbed for 5 min. To collect other aquatic items (e.g., crustaceans), four plastic minnow traps (60  $\times$  20 cm) were set near of the bottom of the stream edges for 24 h, totaling 76 samplings. In addition, macroinvertebrates that were sampled with electrofishing were also counted. Invertebrates were fixed and later conserved in 70% ethanol. Food items and macroinvertebrates were identified according to Borror and DeLong (1969), Fernández and Domínguez (2001), Costa et al. (2006), Mugnai et al. (2010) and Triplehorn and Johnson (2011).

In addition to terrestrial invertebrates, another important organic matter (energy) resource from allochthonous origin is plant litter, including leaves, fruits, seeds, flowers and wood (Wantzen et al. 2008). Considering that detritivorous fishes and several aquatic invertebrates that are preyed upon by fishes may feed on these

sources after degradation, the allochthonous vegetal matter input sampled by the pan traps was also analyzed.

### Data analysis

The diet of 20 fish species was determined by analyzing the stomach contents of 1691 individuals under a stereomicroscope. Individuals of species without differentiated stomachs (e.g., members of Loricariidae and Poeciliidae) had the contents of the first portion of the digestive tract analyzed via microscope. To determine the diets of the fishes, food items were grouped into broad categories: Bryozoa, Nematoda, Mollusca, Annelida, Arachnida, Crustacea, Diplopoda, Chilopoda, Collembola, Insecta, Amphibia, Actinopterygii, vegetal matter, periphyton, and detritus (particulate organic matter). A wide range of organic matter, i.e., dead plant and animal material, composed the detritus (Wantzen et al. 2008). The lowest (order) level was used for insects to calculate the *IRI* and *E* indexes (see below). The presence of sand (inorganic matter) was also registered. We analyzed the diet of all species caught with the exception of *Hoplias malabaricus* (Erythrinidae) and *Synbranchus marmoratus* (Synbranchidae), which did not have food content in the stomachs.

The origins of the food resources were evaluated to verify the importance of the riparian forest to the fish diets. Therefore, food items were classified as allochthonous (terrestrial items), autochthonous (aquatic items) or of indeterminate origin. The frequency of occurrence of these resources in the diet of the species and in the environment (i.e., food resource availability considering only streams where the species occurred) was evaluated graphically.

The diets were analyzed based on the occurrence (*O*, %), weight (*W*, %), and number (*N*, %) of each food item (*i*). The alimentary index (*AI*, %), proposed by Kawakami and Vazzoler (1980), was calculated with modification (for better accuracy, the volume was replaced by the weight of the food items), as:  $AI_i = O_i * W_i / \sum f = 1^n (O_i * W_i)$ . Since insects are preyed on by several stream fishes, the index of relative importance (*IRI*) (Pinkas et al. 1971) and the index of electivity (*E*) (Ivlev 1961) were used to evaluate the importance and selectivity in the diets of insectivorous fishes, as follows. The *IRI* (%) was calculated to determine the predominant taxon (order level) in the diet of the insectivorous fishes, replacing the volume by the

weight of food items (also for better accuracy), as:  $IRI = (N + W) * O$ . The feeding selectivity of the fish was evaluated using *E*, establishing the proportion of each insect order consumed by the fish species to each insect order available in the environment, as:  $E_i = (r_i - P_i) / (r_i + P_i)$ , where *r<sub>i</sub>* is the frequency of occurrence (%) of each insect order *i* in the stomach contents of the fish, and *P<sub>i</sub>* is the frequency of occurrence (%) of each insect order *i* available in the environment. *E* ranges from -1 to +1, and the selectivity is considered positive when *E* > 0, negative when *E* < 0 and absent when *E* = 0 (Ivlev 1961).

To verify the seasonal dependency of the diet, the values of *AI* obtained from each sample during the study (four samples) were tested by a Kruskal-Wallis test. Similarly, the biomass of the food resources, i.e., availability of prey items from each sample (four samples), was evaluated to verify the seasonal dependency using a Kruskal-Wallis test. The species occurrence was considered to determine the availability of the food resource to each species. These analyses were performed using R, version 3.0.3 (R Development Core Team 2014).

A simple agglomerative hierarchical clustering analysis was applied to determine the feeding habits, considering the *AI* values of each food item consumed by the fish species. The Bray-Curtis index and the single linkage method were used, and the data were standardized to simplify the relationships (Legendre and Legendre 1998). A SIMPROF (similarity profile) permutation test was used to determine the significant differences among the clusters (999 permutations). The null hypothesis considers that samples are not *a priori* divided into groups. The cluster and SIMPROF analyses were performed using PRIMER 6 (Clarke and Gorley 2006).

The significance level  $\alpha = 5\%$  was established for the statistical analyses.

### Results

Of the 24 food items consumed by the fishes, ten were allochthonous, ten were autochthonous and four were of indeterminate origin (Table 1). Terrestrial and aquatic insects and detritus were the most commonly consumed food items and prevailed in the diet of five, ten, and six species, respectively (Table 1). The results of the Kruskal-Wallis tests indicated that the diet and food

**Table 1** Specimens' abundance and number of stomachs analyzed for each fish species in streams of Juréia-Itatins Ecological Station, between April 2009 and February 2010

	Digu	Mmic	Phar	Hmul	Clan	Pobt	Alep
Specimens	1032	853	660	353	171	112	94
Stomachs	492	436	40	272	115	56	60
Allochthonous items							
Nematoda		0.00003		0.004			
Annelida	0.05			0.004			3.27
Arachnida	0.04	0.28		0.52	0.001		0.15
Crustacea	0.0002	0.001		0.0005			0.52
Diplopoda	0.08			0.02			
Chilopoda				0.001			
Collembola	0.0002	0.05		0.0001			0.01
Insecta	<b>17.17</b>	<b>78.76</b>		<b>90.11</b>	0.05		2.96
Vegetal matter	4.95	0.03		0.59			
Detritus/Organic matter	<b>25.97</b>		<b>99.999</b>	0.65		<b>98.53</b>	
Autochthonous items							
Bryozoa	0.003						
Nematoda	0.0001	0.0002		0.002			0.01
Mollusca	0.0001	0.001			0.003		0.02
Arachnida	0.000003	0.00001		0.000003	0.0004		
Crustacea	0.22	0.10		1.75	0.1	0.004	5.24
Insecta	<b>22.35</b>	12.49	0.001	4.15	<b>99.87</b>	0.01	<b>86.49</b>
Amphibia				0.01			
Actinopterygii				0.14			
Vegetal matter	<b>25.40</b>			0.02	0.01		
Periphyton	1.78					1.46	
Indeterminate origin							
Nematoda							0.02
Arachnida		0.00004					
Insecta	1.86	8.29		2.01	0.01		1.29
Vegetal matter	0.12			0.01			0.003
Indeterminate	0.01	0.00001		0.000001			
Sand/Inorganic matter	present	present	present	present		present	present
Trophic guilds	O	IS	D	IS	IS	D	IS
KW test (diet)	H = 1.75 df = 3 p = 0.63	H = 0.27 df = 3 p = 0.97	–	H = 2.98 df = 3 p = 0.39	H = 1.08 df = 3 p = 0.78	H = 4.55 df = 3 p = 0.21	H = 3.35 df = 3 p = 0.34
KW test (food resources)	H = 2.28 df = 3 p = 0.52	H = 1.84 df = 3 p = 0.61	H = 2.56 df = 3 p = 0.46	H = 1.62 df = 3 p = 0.65	H = 1.85 df = 3 p = 0.60	H = 1.82 df = 3 p = 0.61	H = 2.27 df = 3 p = 0.52
	Rque	Ataj	Sgun	Gpan	Hgri	Asan	Csch
Specimens	66	63	58	48	41	39	35
Stomachs	27	20	20	34	18	24	29
Allochthonous items							
Nematoda							
Annelida	<b>44.82</b>	0.25		10.96			
Arachnida	0.03					0.92	

**Table 1** (continued)

Crustacea				0.001			
Diplopoda	11.27						
Chilopoda							
Collembola					0.05		
Insecta	12.69			9.65	<b>31.93</b>	<b>55.10</b>	4.01
Vegetal matter	0.06			0.56			
Detritus/Organic matter		8.88	<b>93.55</b>				0.001
Autochthonous items							
Bryozoa							
Nematoda							
Mollusca	0.0001	0.18				0.05	
Arachnida						1.18	1.43
Crustacea	12.35	0.63		9.18			
Insecta	5.85	<b>89.93</b>		<b>62.39</b>	<b>23.98</b>	<b>42.29</b>	<b>94.44</b>
Amphibia							
Actinopterygii	10.33			0.01			
Vegetal matter	0.0004	0.11		0.19			
Periphyton		0.02	6.45				0.001
Indeterminate origin							
Nematoda							
Arachnida							
Insecta	2.59	0.00		6.99	<b>43.86</b>		0.11
Vegetal matter	0.0001				0.17		
Indeterminate				0.07		0.46	
Sand/Inorganic matter	present		present	present			present
Trophic guilds	CA	IS	D	IS	IS	IS	IS
KW test (diet)	H = 3.58 df = 3 p = 0.31	H = 2.79 df = 3 p = 0.43	H = 0 df = 2 p = 1	H = 5.53 df = 3 p = 0.14	H = 3.27 df = 2 p = 0.19	H = 1.20 df = 3 p = 0.75	H = 1.30 df = 3 p = 0.73
KW test (food resources)	H = 3.23 df = 3 p = 0.36	H = 3.32 df = 3 p = 0.35	H = 2.36 df = 3 p = 0.50	H = 2.51 df = 3 p = 0.47	H = 0.48 df = 3 p = 0.92	H = 0.33 df = 3 p = 0.95	H = 3.18 df = 3 p = 0.37
	Hret	Khey	Gbra	Epis	Smac	Dmac	
Specimens	27	24	21	18	11	9	
Stomachs	18	4	6	10	8	2	
Allochthonous items							
Nematoda							
Annelida							
Arachnida							
Crustacea							
Diplopoda							
Chilopoda							
Collembola	0.01						
Insecta	9.22		1.46				
Vegetal matter	1.02		0.18				
Detritus/Organic matter		<b>94.61</b>	0.40			<b>96.77</b>	
Autochthonous items							
Bryozoa							
Nematoda	0.01		0.01				
Mollusca			0.04				
Arachnida							
Crustacea			<b>22.32</b>	<b>93.10</b>			
Insecta	4.00		<b>75.48</b>	5.93	<b>99.82</b>	3.23	
Amphibia							
Actinopterygii							
Vegetal matter							
Periphyton		5.39			0.18		



**Table 1** (continued)

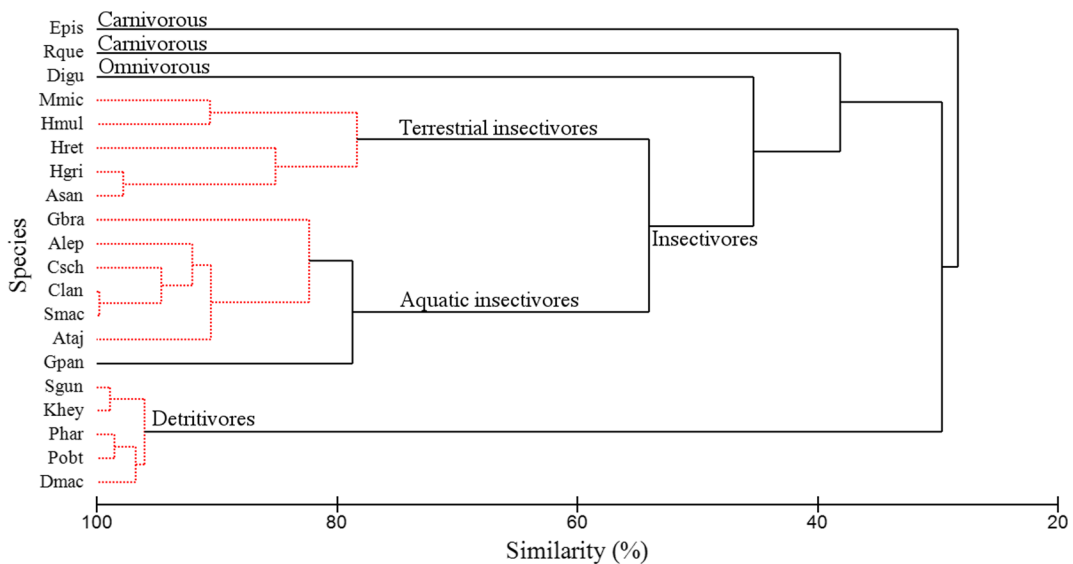
Indeterminate origin						
Nematoda						
Arachnida						
Insecta	<b>80.38</b>		0.12	0.97		
Vegetal matter	5.36					
Indeterminate						
Sand/Inorganic matter						
Trophic guilds	IS	D	IS	CA	present	present
KW test (diet)	–	–	H = 2.75 df = 3 p = 0.43	H = 3.75 df = 3 p = 0.29	–	–
KW test (food resources)	H = 0.74 df = 3 p = 0.86	H = 1.54 df = 3 p = 0.67	H = 1.62 df = 3 p = 0.65	H = 2.36 df = 3 p = 0.50	H = 1.16 df = 3 p = 0.76	H = 1.37 df = 3 p = 0.71

Site-specific columns represent the Alimentary Index (AI) for each food item consumed by fishes, according to its origin (allochthonous, autochthonous or indeterminate). Bold highlights food items with high values of AI. Acronyms: Digu (*Deuterodon iguape*), Mmic (*Mimagoniates microlepis*), Phar (*Phalloceros harpagos*), Hmul (*Hollandichthys multifasciatus*), Clan (*Characidium cf. lanei*), Pobt (*Pseudotothyris obtusa*), Alep (*Acentronichthys leptos*), Rque (*Rhambdia quelen*), Ataj (*Awaous tajasica*), Sgun (*Schizolecis guntheri*), Gpan (*Gymnotus pantherinus*), Hgri (*Hyphessobrycon griemi*), Asan (*Atlantirivulus santensis*), Csch (*Characidium schubarti*), Hret (*Hyphessobrycon reticulatus*), Khey (*Kronichthys heylandi*), Gbra (*Geophagus brasiliensis*), Epis (*Eleotris pisonis*), Smac (*Scleromystax macropterus*), Dmac (*Dormitator maculatus*). Trophic guilds determined by cluster analysis: detritivores (D), omnivores (O), carnivores (CA), and insectivores (IS). Results of Kruskal-Wallis (KW) test to verify the seasonal dependency of the diets and food resources are also presented, except when fish were not sampled more than once

resource availability were not seasonally dependent for any of the species (Table 1).

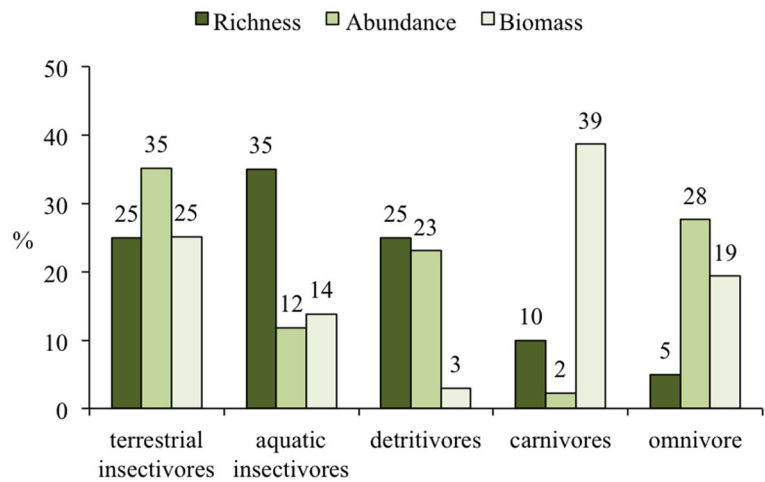
The cluster analysis categorized the fish feeding habits according to the similarity of the food categories preyed upon (Fig. 1). The dendrogram showed five significant trophic guilds (SIMPROF,  $p < 0.05$ ): terrestrial insectivores (predominance of terrestrial insects), aquatic insectivores (predominance of aquatic insects), aquatic

insectivores (predominance of immature aquatic insects), detritivores (predominance of detritus), carnivores (if the diet included fish or shrimp in addition to other invertebrates) and omnivorous (plant/animal food resources and detritus in similar proportions) species (Fig. 1, Table 1). Insectivores predominated in species richness (60%), abundance (47%) and biomass (39%) (Fig. 2).



**Fig. 1** Dendrogram resulted from the cluster analysis, indicating the fish trophic guilds. Dotted lines connect fish species that do not differ in terms of feeding habits (SIMPROF,  $p > 0.05$ ). See Table 1 for species acronyms

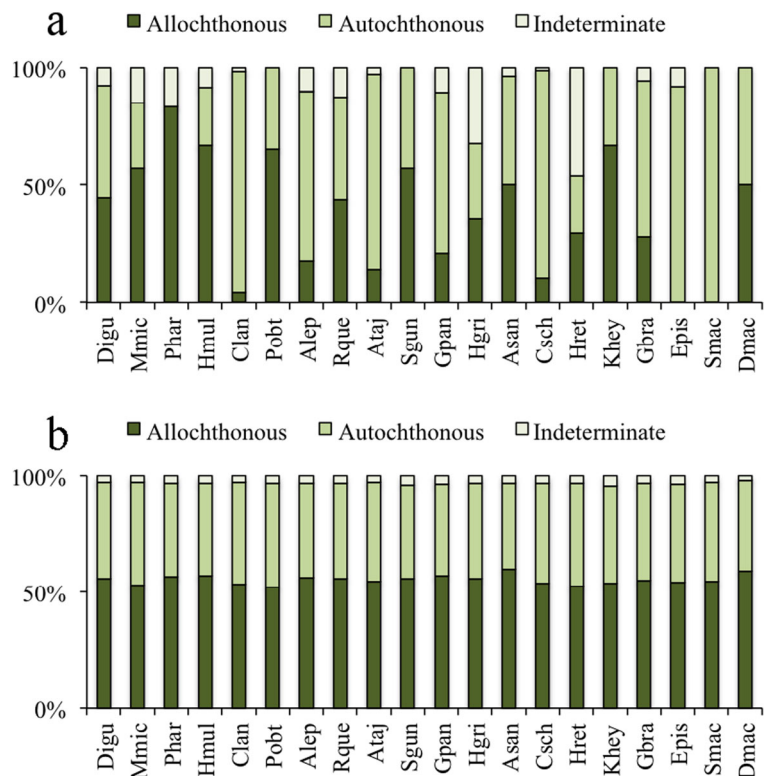
**Fig. 2** Species richness, abundance and biomass of fish trophic guilds



Food items of allochthonous origin were representative in the diets of *Mimagoniates microlepis* (Characidae), *Phalloceros harpagos* (Poeciliidae), *Hollandichthys multifasciatus* (Characidae), *Pseudotothyris obtusa* (Loricariidae), *Schizolecis guntheri* (Loricariidae) and *Kronichthys heylandi* (Loricariidae), whereas items of autochthonous origin were important for *Characidium lanei* (Crenuchidae), *Acentronichthys leptos* (Heptapteridae), *Awaous*

*tajasica* (Gobiidae), *Gymnotus pantherinus* (Gymnotidae), *C. schubarti* (Crenuchidae), *Geophagus brasiliensis* (Cichlidae), *Eleotris pisonis* (Eleotridae) and *Scleromystax macropterus* (Callichthyidae) (Fig. 3a). Food items of both origins were consumed in similar proportions by *Deuterodon iguape* (Characidae), *Rhamdia quelen* (Heptapteridae), *Schizolecis guntheri* (Loricariidae), *Hyphessobrycon griemi* (Characidae) and *Atlantirivulus santensis* (Rivulidae) (Fig. 3a).

**Fig. 3** Food resources consumed by fish species (a), and available in the environment for each species (b), according to its origin. See Table 1 for species acronyms





Considering the availability of food resources, allochthonous and autochthonous items were found in similar proportions in the environment for all species (Fig. 3b).

Diptera, Hymenoptera and Ephemeroptera were the most abundant insect orders in the environments (Table 2). For all fish species (except *S. macropterus*), the most frequently consumed food resource was also considered the most important by the *IRI* (Table 2). Overall, many insectivorous species ingested items considered important by the *IRI* that were positively selected ( $E > 0$ ) (Table 2). Most insectivorous fish presented specialized diets: terrestrial insectivores (*M. microlepis* and *H. multifasciatus*) preferentially consumed ( $E \geq 0.5$ ) allochthonous insects and avoided ( $E < 0$ ) the intake of autochthonous insects, while aquatic insectivores (*C. lanei*, *A. leptos*, *A. tajasica*, *C. schubarti*, *S. macropterus*) preferentially consumed ( $E \geq 0.5$ ) autochthonous insects and avoided ( $E < 0$ ) the ingestion of allochthonous insects (Table 3). No evident pattern was detected for the insectivores that fed on insects of indeterminate origin (*H. reticulatus*) or of allochthonous and autochthonous origin in similar proportions (*H. griemi*, *A. santensis*) (Table 3).

## Discussion

The presence of insectivorous fishes in the JIES was expressive and reflected what was expected since many insectivores and few omnivores were expected in this high-integrity forest. We studied microbasins with very little anthropogenic interference and were, therefore, covered by high-quality forests, including a riparian buffer. Thus, the high quality of the riparian buffer is transferred to the aquatic environment. In these conditions, the fish fauna is predominantly composed of species with specialized habits and insectivorous diets, as opposed to degraded environments, where generalist habits predominate and omnivory, as well as trophic redundancy, is more frequently observed (Casatti et al. 2012; Lobón-Cerviá et al. 2016; Ceneviva-Bastos et al. 2017).

The importance of riparian forests for maintaining the quality of the aquatic environment is well documented in the literature (e.g., Sweeney and Newbold 2014). Many stream fish species require specific conditions and resources and depend on the importation of material from the surrounding forest (Schlosser 1991). Microhabitat preference is closely related to the morphological

traits of fishes (Manna et al. 2017). In the JIES streams, different micro and mesohabitats that are formed by combinations of substrate types, depths and water velocities (Gonçalves and Braga 2012) can be exploited by fish from different groups. Indeed, the 12 insectivores were distributed in two functional feeding groups. They were represented by the terrestrial insectivores that explore the entire water column (e.g., *Hollandichthys multifasciatus* and *Mimagoniates microlepis*) and are frequently found in deep pools with lentic waters and sandy substrates (Sabino and Castro 1990) and by species that predominantly exploit the bottom, such as aquatic insectivores (e.g., *Characidium lanei* and *C. schubarti*) who prefer environments with opposite characteristics that are common in lotic reaches (Sabino and Silva 2004; Terra et al. 2016). The in-stream variability provided by higher habitat complexity can harbor more diverse aquatic food webs (Ceneviva-Bastos et al. 2017). Therefore, functional complementarity is evident in forested streams (Bordignon et al. 2015), unlike deforested streams where the communities are redundant (Casatti et al. 2015).

In addition to the diversity of habitats, food availability is an important factor for ichthyofauna organization (Uieda and Pinto 2011; Leite et al. 2015). In lotic ecosystems, many processes are determined by their interface with riparian ecosystems, and this link is more accentuated in streams because they are naturally narrow (Gregory et al. 1991). The contribution of organic matter is higher in closed canopy sites (see Wantzen et al. 2008 for examples). We are aware that the implications of this allochthonous contribution to the energy flow through aquatic food chains in tropical streams are still unclear (Wantzen et al. 2008). Despite this, we agree that this potential input of terrestrial energy derived mainly from trunks, branches and leaves of the riparian forest (while in degraded environments the proliferation of macrophytes occurs and the source of organic matter is autochthonous) may favor the presence of detritivorous organisms, such as fish and macroinvertebrates. Forest litter may not be consumed directly by detritivores, but after its degradation, this source of organic matter becomes available as particulate organic matter (POM) or fine particulate organic matter (FPOM). In the JIES, *P. obtusa* and *S. guntheri* are relatively abundant species (Gonçalves and Braga 2012), and the occurrence of these detritivorous fish was probably favored by the food supply.

**Table 2** Frequency of occurrence of each food item *i* available in environment ( $P_i$ , %), frequency of occurrence of each food item *i* in fish stomach contents ( $r_i$ , %), index of relative importance ( $IRI_i$ , %), and index of electivity ( $E_i$ )

Food item ( <i>i</i> )	Mimic			Hmul			Clan			Alep						
	$P_i$	$r_i$	$IRI_i$	$E_i$	$P_i$	$r_i$	$IRI_i$	$E_i$	$P_i$	$r_i$	$IRI_i$	$E_i$	$P_i$	$r_i$	$IRI_i$	$E_i$
Ephemeroptera	10.30	2.80	0.24	-0.57	9.10	4.20	1.25	-0.37	9.40	45.60	73.09	0.66	9.40	38.80	81.08	0.61
Odonata	8.80	0.30	0.01	-0.94	6.30	1.00	0.05	-0.72	5.90	0.60	0.00	-0.83	6.60	3.00	0.18	-0.38
Orthoptera	2.70	0.90	0.03	-0.50	3.50	3.10	0.79	-0.06	2.60			-1.00	2.90	1.50	0.11	-0.32
Dermoptera				0.00		0.30	0.00	1.00				0.00				0.00
Plecoptera	2.70	0.30	0.00	-0.80	2.90	0.50	0.00	-0.69	2.70	0.60	0.00	-0.66	2.90	1.50	0.05	-0.32
Isoptera	0.30	0.90	0.01	0.50	0.10	0.80	0.10	0.70	0.10			-1.00	0.20			-1.00
Blattodea	2.90	0.90	0.05	-0.54	3.30	5.50	3.43	0.25	2.20			-1.00	2.50	4.50	1.44	0.28
Hemiptera	4.10	4.60	0.62	0.05	5.30	2.60	0.20	-0.34	6.00			-1.00	4.70	4.50	1.19	-0.02
Thysanoptera	0.30	0.10	0.00	-0.33	0.30			-1.00	0.30			-1.00	0.40			-1.00
Coleoptera	7.40	12.40	4.15	0.25	6.70	19.80	12.18	0.50	6.50	0.60	0.00	-0.84	7.60	7.50	1.25	-0.01
Neuroptera	0.30			-1.00	0.30	0.30	0.01	-0.02	0.40			-1.00	0.20			-1.00
Hymenoptera	13.90	48.70	82.64	0.56	17.20	45.30	77.90	0.45	16.80	2.80	0.09	-0.72	15.40	3.00	0.09	-0.68
Trichoptera	12.70	1.30	0.04	-0.81	10.20	2.10	0.15	-0.66	11.00	13.90	4.26	0.12	10.10	4.50	0.61	-0.39
Lepidoptera	1.80	1.00	0.11	-0.26	1.20	3.40	0.88	0.47	1.60			-1.00	1.40			-1.00
Diptera	31.90	25.70	12.09	-0.11	33.60	11.20	3.07	-0.50	34.60	36.10	22.54	0.02	35.70	31.30	13.98	-0.06
Food item ( <i>i</i> )	Ataj			Gpan			Hagri			Asan						
Ephemeroptera	9.80	44.00	62.97	0.64	40.00	18.90	21.88	-0.36	16.80	10.00	2.61	-0.25	16.90	19.00	13.07	0.06
Odonata	4.70	4.00	0.37	-0.08	2.10	5.70	1.18	0.47	5.20			-1.00	2.00			-1.00
Orthoptera	3.30			-1.00	1.10	1.90	0.17	0.25	1.20	5.00	3.09	0.62	2.40			-1.00
Dermoptera				0.00		1.90	0.05	1.00								
Plecoptera	3.00			-1.00	1.30	1.90	0.09	0.19	1.10			-1.00		2.40	0.15	1.00
Isoptera	0.10			-1.00	0.03			-1.00	0.10			-1.00				-1.00
Blattodea	2.60			-1.00	1.40	7.50	10.50	0.69	2.70			-1.00	3.20			-1.00
Hemiptera	6.10			-1.00	1.90			-1.00	1.70			-1.00	2.20	9.50	4.61	0.62
Thysanoptera	0.20			-1.00	0.03			-1.00								
Coleoptera	6.70	4.00	0.07	-0.25	2.40			-1.00	3.30	5.00	2.01	0.21	3.60	7.10	0.84	0.33
Neuroptera	0.50			-1.00	0.20			-1.00	0.10			-1.00	0.10			-1.00
Hymenoptera	17.40			-1.00	9.30	7.50	0.82	-0.10	11.60	35.00	45.16	0.50	15.80	47.60	74.28	0.50
Trichoptera	9.80	4.00	0.14	-0.42	9.70	18.90	13.42	0.32	23.20			-1.00	17.70	4.80	1.01	-0.58
Lepidoptera	1.50			-1.00	0.20	1.90	0.48	0.77	0.30			-1.00	0.30			-1.00

Table 2 (continued)

Food item ( <i>i</i> )	$P_i$	$r_i$	IRI	$E_i$	$P_i$	$r_i$	IRI	$E_i$	$P_i$	$r_i$	IRI	$E_i$	$P_i$	$r_i$	IRI	$E_i$
Diptera	<b>34.30</b>	<b>44.00</b>	36.46	0.12	30.40	<b>34.00</b>	<b>51.40</b>	0.06	<b>32.80</b>	<b>45.00</b>	<b>47.13</b>	0.16	<b>35.90</b>	9.50	6.04	-0.58
Food item ( <i>i</i> )	Csch				Hret				Gbra				Smac			
Ephemeroptera	<b>33.10</b>	<b>32.80</b>	<b>49.22</b>	-0.01	9.20	5.60	0.60	-0.25	9.20	<b>20.00</b>	<b>27.27</b>	<b>0.37</b>				
Odonata	1.20			-1.00	11.00	11.10	5.92	0.01	5.70			-1.00	<b>25.00</b>			-1.00
Orthoptera	0.50			-1.00	3.10			-1.00	2.30			-1.00	2.30			-1.00
Dermoptera																
Plecoptera	2.20	1.70	1.13	-0.12	2.60			-1.00	2.90			-1.00				
Isoptera					0.40			-1.00								
Blattodea	0.30			-1.00	3.50			-1.00	1.50			-1.00	4.50			-1.00
Hemiptera	3.70			-1.00	3.90			-1.00	6.10			-1.00	2.30			-1.00
Thysanoptera	0.10			-1.00				-1.00	0.40			-1.00				
Coleoptera	3.00	3.40	0.14	0.07	7.00	5.60	0.60	-0.12	6.70	10.00	4.22	0.20	4.50			-1.00
Neuroptera	0.50			-1.00	0.40			-1.00	0.20			-1.00				
Hymenoptera	7.90	1.70	0.04	-0.64	14.90	<b>27.80</b>	<b>39.37</b>	<b>0.30</b>	15.80	10.00	1.24	-0.22	13.60			-1.00
Trichoptera	7.40	<b>32.80</b>	<b>30.33</b>	<b>0.63</b>	14.00	5.60	0.96	-0.43	9.50	<b>20.00</b>	<b>17.11</b>	<b>0.36</b>	18.20	<b>40.00</b>	<b>53.36</b>	<b>0.38</b>
Lepidoptera	0.80			-1.00	0.90			-1.00	1.90	10.00	1.65	<b>0.68</b>				
Diptera	<b>39.20</b>	<b>27.60</b>	19.15	-0.17	<b>28.90</b>	<b>44.40</b>	<b>52.54</b>	<b>0.21</b>	<b>37.80</b>	<b>30.00</b>	<b>48.52</b>	-0.12	<b>29.50</b>	<b>60.00</b>	<b>46.64</b>	<b>0.34</b>

Numbers in bold represent the most frequent food resource in environment and fish stomachs, the most important food resource consumed by fish considering IRI, and the positive and negative feeding selectivity considering  $E_i$ . Fish acronyms are showed in Table 1

**Table 3** The most frequent insect orders available in environment (Environment) and in fish stomach contents (Stomach), insect orders with the highest values of *IRI* (index of relative importance), and the highest and the lowest (in decreasing order of availability in the environment) values of *E* (index of electivity)

Fish	Environment	Stomach	Highest <i>IRI</i>	Highest <i>E</i>	Lowest <i>E</i>
Mmic	Diptera	Hymenoptera	Hymenoptera	Hymenoptera	Odonata, Neuroptera
Hmul	Diptera	Hymenoptera	Hymenoptera	Dermaptera, Isoptera, Coleoptera, Lepidoptera, Hymenoptera	Trichoptera, Odonata, Plecoptera, Thysanoptera
Clan	Diptera	Ephemeroptera	Ephemeroptera	Ephemeroptera	Hemiptera, Orthoptera, Blattodea, Lepidoptera, Neuroptera, Thysanoptera, Isoptera
Alep	Diptera	Ephemeroptera, Diptera	Ephemeroptera	Ephemeroptera	Hymenoptera, Lepidoptera, Thysanoptera, Isoptera, Neuroptera
Ataj	Diptera	Diptera, Ephemeroptera	Ephemeroptera	Ephemeroptera	Hymenoptera, Hemiptera, Orthoptera, Plecoptera, Blattodea, Lepidoptera, Neuroptera, Thysanoptera, Isoptera
Gpan	Ephemeroptera	Diptera, Ephemeroptera, Trichoptera	Diptera, Ephemeroptera	Dermaptera, Lepidoptera, Blattodea	Coleoptera, Hemiptera, Neuroptera, Isoptera, Thysanoptera
Hgri	Diptera	Diptera, Hymenoptera	Diptera, Hymenoptera	Orthoptera, Hymenoptera	Trichoptera, Odonata, Blattodea, Hemiptera, Plecoptera, Lepidoptera, Isoptera, Neuroptera
Asan	Diptera	Hymenoptera, Ephemeroptera	Hymenoptera, Ephemeroptera	Plecoptera, Hemiptera, Hymenoptera	Blattodea, Orthoptera, Odonata, Lepidoptera, Neuroptera
Csch	Diptera, Ephemeroptera	Ephemeroptera, Trichoptera, Diptera	Ephemeroptera, Trichoptera	Trichoptera	Hemiptera, Odonata, Lepidoptera, Orthoptera, Neuroptera, Blattodea, Thysanoptera
Hret	Diptera	Diptera, Hymenoptera	Diptera, Hymenoptera	Hymenoptera, Diptera	Hemiptera, Blattodea, Orthoptera, Plecoptera, Lepidoptera, Isoptera, Neuroptera
Gbra	Diptera	Diptera, Ephemeroptera, Trichoptera	Diptera, Ephemeroptera, Trichoptera	Lepidoptera, Ephemeroptera, Trichoptera	Hemiptera, Odonata, Plecoptera, Orthoptera, Blattodea, Thysanoptera, Neuroptera
Smac	Diptera, Odonata	Diptera, Trichoptera	Trichoptera, Diptera	Trichoptera, Diptera	Odonata, Hymenoptera, Blattodea, Coleoptera, Orthoptera, Hemiptera

Fish acronyms are showed in Table 1

On the other hand, aquatic insectivorous fishes indirectly benefit from the contribution of organic matter from the forest, since many aquatic insects, mainly immature forms, feed on debris and plant remains (Boulton and Lake 1992), especially POM and FPOM that are carried by the runoff and accumulate at the bottom of the stream (Galdean et al. 2001). Thus, riparian forests sustain the aquatic food webs through the detritus chain, as they provide organic matter for the consumption of detritivorous invertebrates (and fishes), which will serve as food for insectivorous fishes (Rosemond et al. 2001). Although the origins of the detritus were not determined by laboratory analysis, the pristine condition of the forest cover of the JIES (Mamede et al. 2004) and the non-significant presence of macrophytes in the studied streams (personal observation) allow us to assume that the forest acts as the main donor of these resources. In addition, terrestrial insects were important in the diet of most Characidae species, such as *H. multifasciatus*, *M. microlepis*, *D. iguape*, and *H. griemi* (except *H. reticulatus*), which is consistent with previous findings in other coastal Brazilian streams (e.g., Sabino and Castro 1990; Esteves and Lobón-Cerviá 2001; Deus and Petrere Jr 2003; Wolff et al. 2013) and is also a good indicator of the donation of food resources by the riparian forest.

Allochthonous and autochthonous items were available in very similar quantities. Despite the similarity, these items were differently consumed by fish, which in some extent reveals the preferences for certain food resources. Indeed, most insectivorous fish presented food selectivity. For example, allochthonous items were important for characins (*M. microlepis* and *H. multifasciatus*) that fed mostly on terrestrial insects that fell on the water surface. These fish are extremely active in the water column, easily attracted by materials from the riparian forest that fall on the water surface (Sabino and Sazima 1999; Gomiero et al. 2008), and are frequently classified as surface pickers (Sazima 1986), which explains their high consumption of terrestrial insects. Autochthonous resources, by contrast, were important mainly for *C. lanei*, *A. leptos*, *A. tajasica*, *C. schubarti* and *S. macropterus*, which fed mostly on benthic insects. These fish occupy a bottom position in the stream channel (Sabino and Castro 1990; Sabino and Silva 2004; Gonçalves and Cestari 2013), which facilitates the foraging and consumption of insects that inhabit the substrate. They also

have several foraging tactics to explore the stream bottom (e.g., grubbers excavating while moving, sit-and-wait and crepuscular predators of bottom animals, sensu Sazima 1986).

In this study, we did not observe temporal variations in fish diet, nor in the availability of food resources. In the coastal Atlantic rainforest, the absence of seasonality is common due to high humidity and low variation in the rainfall regime (Talora and Morellato 2000). Although streams are highly dynamic environments where torrential rains can increase water flow over short periods, rainfall in the Atlantic rainforest is high and well distributed throughout the year (Esteves and Lobón-Cerviá 2001). These characteristics were reported for the JIES (Marques and Duleba 2004; Tarifa 2004) and contributed to the seasonally independent distribution of ichthyofauna (Gonçalves and Braga 2012). These findings agree with other records for tropical coastal streams (Esteves and Lobón-Cerviá 2001; Lorion and Kennedy 2009b) and for macroinvertebrates (Lorion and Kennedy 2009a), which is in agreement with our prediction that resource availability would be constant throughout of the year. Therefore, the absence of seasonal variation in the fish diet is possibly related to the consistent food supply over time.

We were able to provide evidence on the role of the riparian forest as a food provider for stream fishes. For example, several terrestrial insects besides ants, a very common terrestrial food resource for insectivorous fishes in deforested tropical streams (Ceneviva-Bastos and Casatti 2007; Lobón-Cerviá et al. 2016), and detritus derived mainly from degraded woody debris and fallen leaves (also consumed by many aquatic insects, which subsequently serve as food for fish) were important food sources, highlighting the importance of adjacent forest-covered areas as donor systems, especially to oligotrophic headwater streams such as those in the JIES. Many human activities alter land use and degrade the environment, which can reduce or even disrupt the connection between fish and the forest. Considering the increasing human population in the coastal region, our results emphasize the importance of protecting the Atlantic forest areas with conservation units such as the JIES to maintain the function, quality and integrity of the aquatic ecosystems and consequently the associated biota such as fish. Finally, our study provides a reliable baseline scenario to subsidize ecological restoration projects in similar environments within the Atlantic biome.

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