



Physical habitat as predictor of fish trophic structure in Brazilian Atlantic rainforest streams

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Trophic structure of fish assemblages is one of the most sensitive indicators of changes in streams environments. Since it is crucial to understand the response of trophic groups to habitat alteration, our study aimed to address this research gap by assessing the influence of substrate composition, meso-habitat variability, and bank stability, on the richness, biomass, and number of individuals of carnivores, invertivores, omnivores, and herbivorous-detritivores. Using an electrofishing device, we sampled 13 Atlantic rainforest streams reaches in a degradation gradient, located in the upper Paranapanema river basin. Sample points were ranked using a physical habitat index. More pristine streams had high availability of twigs, trunks, rocks and boulders in the substrate, great meso-habitat variability, and the presence of roots, trunks, and rocks in the margins. Canonical correlations between habitat characteristics and trophic groups explained more than 90% of data variability. Richness and number of individuals of invertivores increased in more preserved stream reaches, while richness of carnivores and number of individuals of omnivores decreased. These results demonstrate that trophic structure varies according to level of degradation, and that invertivore richness represents the best indicator of fish trophic structure responses to physical habitat alterations in streams.

Keywords: Abundance, Environmental Assessment, Invertivores, Richness, Substrate.

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A estrutura trófica da assembleia de peixes é um dos indicadores mais sensíveis a alterações ambientais em riachos. Considerando a relevância de entender a resposta de grupos tróficos à alteração ambiental, este estudo buscou preencher esta lacuna científica avaliando a influência da composição do substrato, variabilidade de meso-hábitats e estabilidade das margens sobre riqueza, biomassa e número de indivíduos de peixes carnívoros, invertívoros, onívoros e herbívoros-detrítivos. Amostramos com pesca elétrica 13 trechos de riachos de Mata Atlântica com estado de conservação variável, localizados na parte superior da bacia do alto rio Paranapanema. Os pontos amostrais foram ranqueados pelo índice de hábitat físico. Riachos mais preservados apresentaram mais galhos, troncos, matacões e blocos no substrato, maior variabilidade de meso-hábitats e maior quantidade de raízes, troncos e rochas nas margens. As correlações canônicas explicaram mais de 90% da variabilidade dos dados. A riqueza e o número de indivíduos de invertívoros aumentaram em riachos mais preservados, enquanto que a riqueza de carnívoros e o número de indivíduos onívoros diminuíram. Estes resultados demonstram que a estrutura trófica varia em resposta ao nível de preservação, e que a riqueza de invertívoros é o melhor indicador de respostas da estrutura trófica às alterações do hábitat em riachos.

Palavras-chave: Abundância, Avaliação Ambiental, Invertívoros, Riqueza, Substrato.

INTRODUCTION

The study of trophic structure is an important tool for evaluating fish assemblage structure (Angermeier, Karr, 1983; Nimet *et al.*, 2015). Since environmental filters act by selecting assemblage species according to their traits, the effects of physical habitat characteristics on trophic structure may be a more accurate predictor than taxonomic composition (Teresa *et al.*, 2016). Additionally, investigating different aspects of trophic structure can help detect patterns and predict assemblage responses to different environmental conditions, which are fundamental aspects to biodiversity conservation (Cruz *et al.*, 2013).

Habitat characteristics promote alterations in trophic structure (Cunico *et al.*, 2011) and in-stream habitat homogenization, often due to anthropogenic causes, is expected to promote less diverse trophic structures (Zeni, Casatti, 2014). Several habitat elements have been shown to influence fish assemblages in streams, including substrate composition and flow heterogeneity (Hugueny *et al.*, 2010; Carvalho, Tejerina-Garro, 2015). Channel morphology variables such as substrate, depth, and velocity alter trophic structure as large carnivores tend to predominate in large pools or streams (Schlosser, 1982). According to Lorion, Kennedy (2009), the impacts caused by the conversion of natural forest to pastures could alter trophic structure by increasing the density of herbivorous-detritivores fish. Additionally, Cross *et al.* (2013) showed that streams subjected to siltation, a form of environmental simplification in which there is

homogenization of the substrate composition, can consequently decrease the diversity of trophic groups. Omnivorous fish tend to thrive after habitat alteration (Karr, 1981), especially in cases where larger substrate particles are replaced by smaller particles (Berkman, Rabeni, 1987). Furthermore, substrate composition can alter food availability for fish, since elements such as branches, leaves, and rocks create microhabitats not only for algae and fungi (Gordon, 1993) but for aquatic insects as well (Reid *et al.*, 2010; Luek, Rasmussen, 2017).

Angermeier, Karr (1983) also suggest that large scale alterations in stream structure may have serious impacts on biodiversity due to the effects of shading, siltation, and changes in available food types. However, identifying the effects of environmental change on the ichthyofauna may depend on the assemblage structure descriptor selected (Casatti *et al.*, 2009a; Krause *et al.*, 2013; Nimet *et al.*, 2015; Feld *et al.*, 2016; Vilmi *et al.*, 2016).

In order to use trophic structure as a viable alternative to taxonomic approaches, the relationships between trophic structure and habitat characteristics must be well understood (Vitule *et al.*, 2017). Therefore, we aimed to answer the question: Does substrate composition, meso-habitat variability, and bank stability correlate with richness, biomass, and number of individuals of each trophic group? We expected to detect variation in trophic group responses to habitat characteristics, especially for invertivores and herbivorous-detritivores in response to substrate composition due to the dependency of most species in these groups on substrates as foraging sites. In addition, when considering possible replacements of species by others from different trophic groups in response to environmental changes, we expected to detect a stronger response in trophic group richness than in number of individuals and biomass.

MATERIAL AND METHODS

Sampling sites. Sampling was carried out once at each of the 13 stream reaches (P1 – P13) between August and December in 2010 and 2011. The sampling sites were located in the southwest region of São Paulo state, Brazil, in streams located on the Upper Paranapanema River (Fig. 1). All sampled streams were of 3rd or 4th order (Strahler, 1957), and were selected due to accessibility and dimensions that allowed the use of electrofishing methods. The streams were located closest to the cities of Pilar do Sul and São Miguel Arcaño in areas surrounded by natural vegetation, *Eucalyptus* spp. plantations, and/or pastures. The natural vegetation covers 15% of the total area of the upper Paranapanema river basin. The vegetation was primarily composed of fragments of Atlantic rainforest, especially from phytophysognomys tropical semi-deciduous forest and floodplain forests. However, there were also some Brazilian savannah fragments, corresponding to 0.3% of the area (Secretaria do Meio Ambiente, 2005). The region presents a humid tropical climate (Type Aw according to Köppen classification) with annual precipitation of 1,200 mm. Geologically, two structural units predominate: the Atlantic Orogenic Belt and the Paraná Sedimentary basin. The altitude varies from 600 to 800 m and the region has mainly low hills with slopes between 20 to 30% (CBH-ALPA, 2016).

Sampling. Based on previous analyses of sampled sites located within the same basin

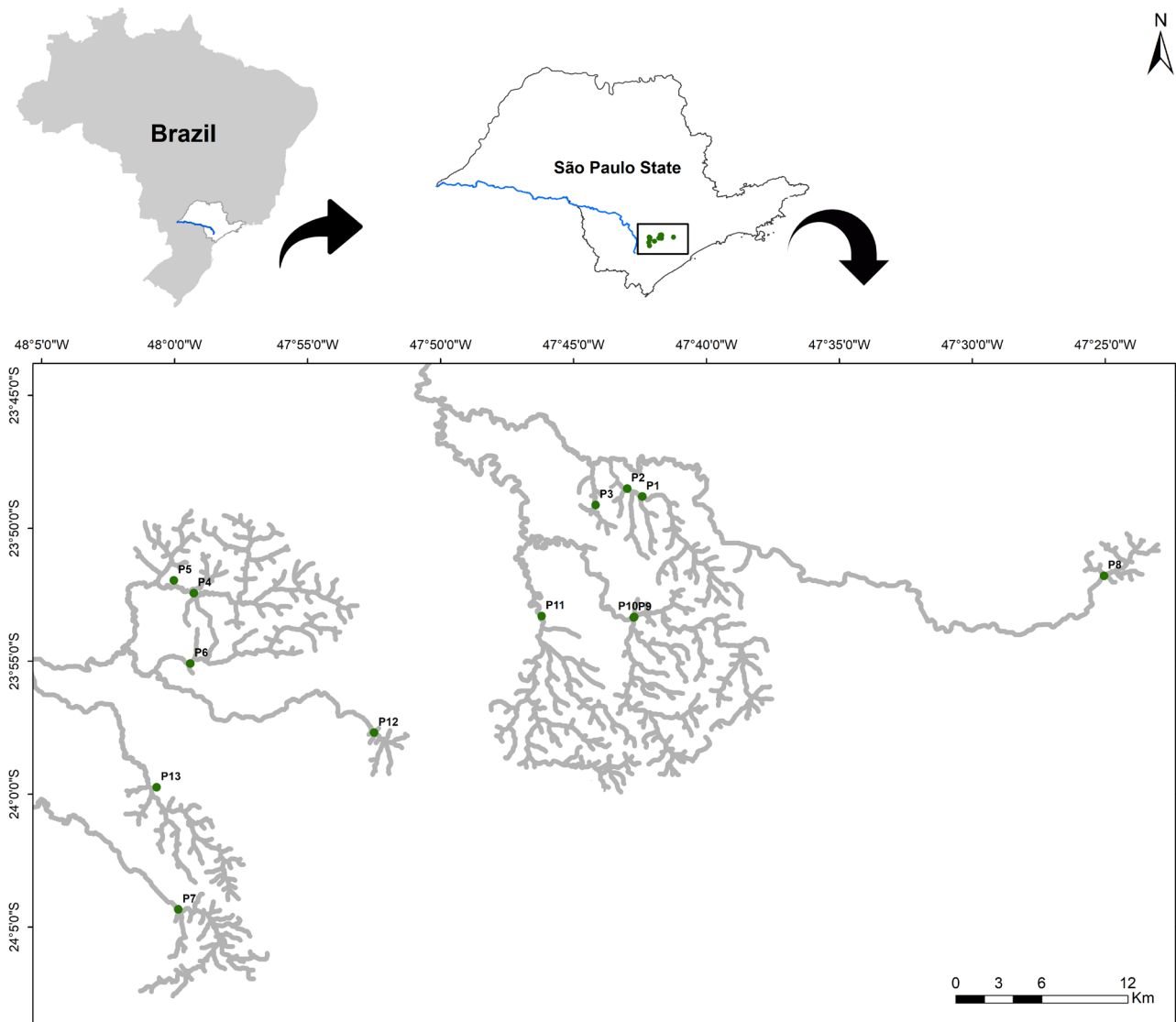


FIGURE 1 | Sampling sites located in the Paranapanema river basin, São Paulo state, Brazil. The Paranapanema river is highlighted in blue.

(see Peressin, Cetra, 2014 and Peressin *et al.*, 2018 for more details), we considered the following habitat characteristics: substrate composition (SC), meso-habitat variability (MH), and bank stability (BS). We established three equidistant transverse transects across each stream and recorded depth, velocity, and substrate composition in one-meter intervals along each transect. In these same transects, we recorded the composition of both sides of the river. Classification of the SC, MH, and BS parameters was based on substrate elements (silt, twigs, rocks, etc.), velocity and depth combinations, and bank composition following the protocols adapted from Barbour *et al.* (1999) (Tab. 1). High SC scores indicate high availability of larger substrate particles such as twigs, trunks, and large substrate particles such as rocks and boulders. High MH scores indicate a great meso-habitats diversity such as alternations between shallow and deep reaches and also between high and low velocities. Elevated BS scores denote an increase of elements such as roots, trunks, and rocks in the river margins. Overall, high scores

for these habitat parameters indicated more pristine streams while low scores indicated streams that were more affected by anthropogenic impacts. Fish sampling took place between 8 am and 5 pm, using an electrofishing apparatus. We sampled fish along a 70 m reach of each stream with a single electrofishing pass from downstream to upstream, without the use of block nets. This distance is considered sufficient to encompass the diversity of meso and micro-habitats of tropical streams (Mazzoni *et al.*, 2000). In a laboratory, fishes were identified to the lowest possible taxonomic level. Representative ichthyofauna specimens were deposited at the fish collection of Ichthyology Laboratory of the Department of Zoology and Botany of Universidade Estadual Paulista in São José do Rio Preto, Brazil (DZSJRP) under the catalog numbers: DZSJRP 13642–43, 13645–46, 13648, 13650, 13652–53, 13655–57, 13663–67, 13673–74, 13676–77, 13681–83, 13685–88, 13690–95, 13699, and 13701.

Trophic groups. The trophic group of each fish species was assigned based on a review of available literature and diet analysis. We considered the following trophic groups: carnivores – species that consume mainly invertebrates and fish; invertivores – species that consume insects and other invertebrates such as molluscs, crustaceans, and annelids; omnivores – species that consume items of plant and animal origin, and may also include detritus; and herbivorous–detritivores – species that consume mainly detritus (particulate organic matter at different stages of decomposition) and algae, including periphyton.

TABLE 1 | Criteria selected to determine the habitat score based on the substrate composition, meso-habitat variability, and bank stability habitat characteristics (Adapted from Barbour *et al.*, 1999).

Habitat characteristic	Category of condition																				
	Optimal					Suboptimal					Marginal					Poor					
Substrate composition	More than 50% of the substrate favours the colonization of epifauna and fish; can include trunks, branches, banks with exposed roots, rocks, or other stable habitats that allow full potential for colonization (<i>i.e.</i> , permanent trunks and branches).					30-50% stable habitat with good colonization potential; adequate habitat to maintain populations; presence of additional forest substrate, but not yet ready for colonization					10-30% stable habitat; availability of less than desirable habitat; substrate often removed or disturbed.					Less than 10% stable habitat; clear lack of habitat; unstable or absent substrate.					
Score	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0
Meso-habitat variability	All 4 speed/depth combinations present (slow-deep, slow-shallow, fast-deep and fast-shallow) (slow = <0.3 m/s, deep = > 0.5 m).					Only 3 of the 4 pool types present (note: if fast-shallow is absent, the score is less than with the absence of other pool types).					Only 2 of the 4 pool types present (note: the score is less if fast-shallow or slow-shallow are absent).					Dominated by one pool type (generally slow-deep).					
Score	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0
Bank stability	Stable margins; absence or minimal evidence of erosion or collapse; low potential for future problems; <5% of the margin affected.					Moderately stable; small areas of erosion exist but are infrequent and are usually stable; 5-30% of the margin affected by erosion.					Moderately unstable; 30-60% of the margin affected by erosion; high erosion potential at flow peaks.					Unstable; many eroded areas; frequent exposed areas (<i>i.e.</i> , without cover); 60-100% of the margin affected by erosion.					
Score	Right margin	10	9			8	7	6			5	4	3			2	1				0
	Left margin	10	9			8	7	6			5	4	3			2	1				0

We carried out stomach content analysis for 12 individuals of *Neoplecostomus selenae*, an endangered species (São Paulo, 2018) for which there was no diet data in the literature. We identified stomach contents to the lowest taxonomic level possible and then classified each item into the following alimentary categories: vegetal material, algae, detritus, insects, and other invertebrates. For each item per stomach sample, we assigned values according to the method of Degree of Food Preference (DFP) (Braga, 1999). Only stomachs with full contents were considered. To calculate the DFP, we assigned values of importance for each item recorded in a sample. If only one item type was present in the stomach, it was assigned a value of 4. For samples with more than one item type, the most abundant item was allocated the value 3, while the values 1 and 2 were assigned to the least abundant and the intermediate items, respectively. For samples with more than 3 items, multiple items were assigned the same value, following the same procedure described above.

Statistical analyses. Considering the values assigned in the stomach content analysis, a DFP value was calculated for each alimentary category using the equation: $DFP = S(i)/N$, where $S(i)$ is the sum of the values assigned to each item (i) in each stomach, and N is the total number of analyzed stomachs.

From SC, MH, and BS scores, we calculated a physical habitat index (PHI), following an adaptation from the method used in Casatti *et al.* (2006). Calculations of these metric scoring thresholds were based on the distribution of total values, with the lowest threshold established at the 25th percentile and the upper threshold at the 75th percentile where the former would score 1 and the latter case would score 5. Intermediate conditions, *i.e.*, between the 75th and 25th percentiles of the reference sites, would score 3. From the sum of metric scoring for each habitat parameter, we define a PHI for each stream. Again, sample points at the 25th percentile were considered less pristine, points at 75th percentile were considered more pristine and the remaining were considered in an intermediate condition.

To evaluate the relationship between habitat parameters and trophic groups, we conducted a canonical correlation analysis (CCorA). In this analysis, we used the three habitat characteristics as predictors for proportions within the four trophic groups at each sample point (Sherry, Henson, 2005; Legendre, Legendre, 2012). We ran three CCorA analyses: one with trophic group richness (S), another with biomass (B), and another for the number of individuals (N) in each trophic group. Because Wilks' λ represents the variance unexplained by the model, $1-\lambda$ yields the full model effect size in an r^2 metric. Wilks' Lambda values were calculated from the eigenvalues and converted to F statistics. With the F value we tested H_0 ; the canonical correlations in the current row and all that follow are zero. For emphasis, structure (r_s) and communality coefficients (h^2) above 0.45 are in bold, following a convention in many factor analyses (Sherry, Henson, 2005). All analyses were performed using statistical software R version 3.0.0. We used the CCorA, Candisc, and Vegan R packages (R Core Team, 2018).

RESULTS

According to PHI, sampled points P2, P6, P7 and P11 were considered more pristine, while P5, P8 and P10 were less pristine; the remaining were considered at intermediate preservation level (Tab. 2). The average width and depth of the sampling points were 4.64 and 0.34 m, respectively.

In total, 1,356 fishes were sampled, representing 31 species. Degree of food preference values for stomachs of *Neoplecostomus selenae* were 0.08 for vegetal material, 1.33 for algae, 2.33 for detritus and 0.58 for insects. Three species were considered carnivores, twelve invertivores, eleven omnivores, and five herbivorous-detritivores (including *N. selenae*) (Tab. 3). *Hoplias malabaricus* had the highest number of individuals and also presented the highest biomass for the carnivore trophic group. Similarly, *Pimelodella avanhandavae* had both the highest number of individuals and biomass for the invertivore group. For omnivores, *Phalloceros reisi* had the highest number of individuals, while *Geophagus brasiliensis* presented the highest biomass. *Hypostomus ancistroides* was the herbivorous-detritivore with the highest number of individuals and biomass (Tab. 3). In general, omnivores and invertivores were dominant in terms of richness and number of individuals in our streams. However, herbivorous-detritivores had the highest biomass and highest number of individuals in the P9 and P12 streams, respectively, while carnivores presented the highest biomass in P1, P5 and P13 (Fig. 2).

TABLE 2 | Habitat characteristics in each stream reach. Substrate composition = area covered by boulders, rocks, branches, trunks, and leaves. Meso-habitat variability = combination of water velocity and depth: slow and deep, fast and shallow, and slow and shallow (deep: > 0.5 m; fast: > 0.3 m/s). Bank stability = percentage of banks covered by rocks, vegetation and logs. PHI = physical habitat index. Stream order determined according to Strahler (1957).

Stream	Order	Substrate composition	Meso-habitat variability	Bank stability		PHI
				Right bank	Left bank	
P1	3	9.6	8.5	4.0	1.8	9
P2	3	9.8	20.0	0.5	1.0	11
P3	3	0.0	5.0	6.7	6.7	9
P4	4	8.0	16.7	0.3	0.7	9
P5	4	1.3	7.4	0.7	0.2	5
P6	3	9.1	17.0	0.7	0.7	11
P7	3	16.0	16.0	10.0	10.0	13
P8	3	4.3	4.1	2.0	5.0	5
P9	4	13.0	4.3	2.0	4.3	9
P10	4	11.5	4.3	0.8	0.5	5
P11	4	13.0	15.2	6.2	6.2	13
P12	3	4.8	14.8	4.0	3.5	9
P13	4	12.5	4.3	4.3	4.8	7
Minimum	3	0.0	4.1	0.3	0.2	5
Maximum	4	16.0	20.0	10.0	10.0	13

TABLE 3 | Data used to assess trophic group descriptors. Car = Carnivore; Inv = Invertivore; Omn = Omnivore; H-D = Herbivorous-Detritivores. References: 1 – Motta, Uieda (2004); 2 – Oliveira, Bennemann (2005); 3 - Gealh (2007); 4 – Gomiero, Braga (2008); 5 - Casatti *et al.* (2009B); 6 - Lobon-Cerviá, Bennemann (2000); 7 - Rondinelli *et al.* (2011); 8 - Casatti *et al.* (2012); 9 - Silva *et al.* (2012); 10 – Montenegro *et al.* (2012); 11 - Lujan *et al.* (2012); 12 - Smith *et al.* (2013); 13 – This study.

Taxon	Number of individuals	Biomass (g)	Trophic group	Reference
Characiformes				
Characidae				
<i>Astyanax lacustris</i> (Lutken, 1875)	19	167.9	Omn	8
<i>Astyanax bockmanni</i> Vari, Castro, 2007	95	157.6	Omn	8
<i>Astyanax fasciatus</i> (Cuvier, 1819)	99	718.3	Omn	8
<i>Astyanax paranae</i> Eigenmann, 1914	23	123.3	Omn	8
<i>Piabarchus stramineus</i> (Eigenmann, 1908)	26	33.2	Inv	8
<i>Hyphessobrycon anisitsi</i> (Eigenmann, 1907)	55	40.2	Omn	2
<i>Piabina argentea</i> Reinhardt, 1867	26	48.2	Inv	5
Crenuchidae				
<i>Characidium gomesi</i> Travassos, 1956	33	37.5	Inv	8
<i>Characidium schubarti</i> Travassos, 1955	20	35.0	Inv	1
<i>Characidium zebra</i> Eigenmann, 1909	23	29.2	Inv	8
Erythrinidae				
<i>Hoplias malabaricus</i> (Bloch, 1794)	20	1209.6	Car	8
Parodontidae				
<i>Apareiodon piracicabae</i> (Eigenmann, 1907)	18	34.9	Omn	3
<i>Parodon nasus</i> Kner, 1859	4	9.5	Omn	4
Gymnotiformes				
Gymnotidae				
<i>Gymnotus sylvius</i> Albert, Fernandes-Matioli, 1999	8	226.6	Inv	8
Siluriformes				
Heptapteridae				
<i>Cetopsorhamdia iheringi</i> Schubart, Gomes, 1959	24	28.1	Inv	8
<i>Imparfinis borodini</i> Mees, Cala, 1989	25	494.7	Inv	7
<i>Imparfinis mirini</i> Haseman, 1911	206	348.1	Inv	8
<i>Phenacorhamdia tenebrosa</i> (Schubart, 1964)	6	2.6	Inv	8
<i>Pimelodella avanhandavae</i> Eigenmann, 1917	241	644.5	Inv	8
<i>Rhamdia quellen</i> (Quoy, Gaimard, 1824)	15	266.4	Car	9
<i>Trichomycterus</i> sp.	17	26.0	Inv	9
Loricariidae				
<i>Hisonotus</i> sp.	40	13.4	HD	11
<i>Hypostomus ancistroides</i> (Ihering, 1911)	62	458.2	HD	2
<i>Hypostomus nigromaculatus</i> (Schubart, 1967)	5	49.3	HD	11
<i>Neoplecostomus selenae</i> Zawadzki, Pavanelli, Langeani, 2008	25	130.7	HD	13
<i>Neoplecostomus</i> sp.	7	11.5	HD	11
<i>Rineloricaria pentamaculata</i> Langeani, Araújo, 1994	37	140.2	Omn	9
Pimelodidae				
<i>Pimelodus maculatus</i> La Cepède, 1803	2	105.9	Omn	6
Cyprinodontiformes				
Poeciliidae				
<i>Phalloceros reisi</i> Lucinda, 2008	108	44.9	Omn	12
Synbranchiformes				
Synbranchidae				
<i>Synbranchus marmoratus</i> Bloch, 1795	8	193.1	Car	10
Cichliformes				
Cichlidae				
<i>Geophagus brasiliensis</i> (Quoy, Gaimard, 1824)	59	1050.9	Omn	8
Total	1356	6879.2		

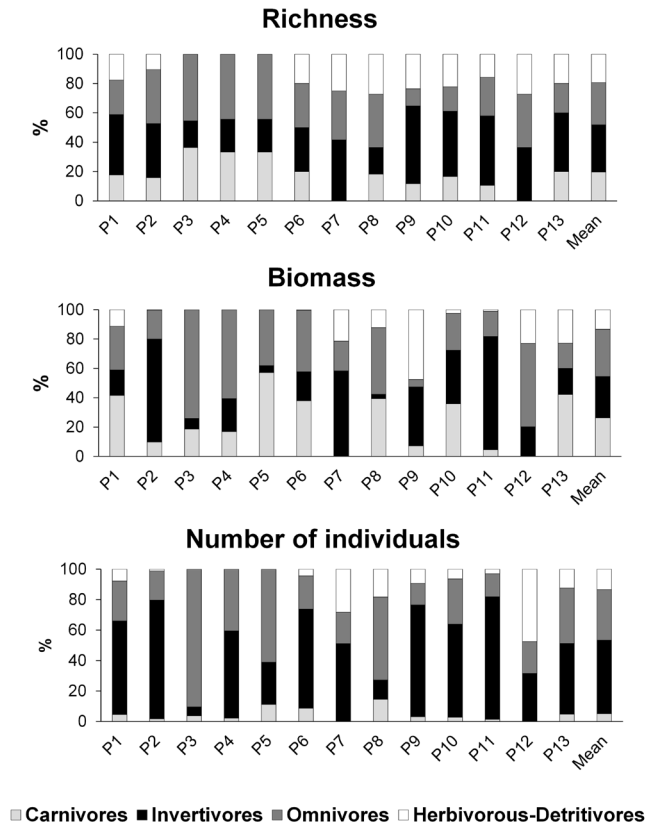


FIGURE 2 | Proportion of fish species richness, biomass, and number of individuals in each trophic group for each sampling point in the Paranapanema river basin, São Paulo state, Brazil.

The measured habitat characteristics were significantly related with trophic group richness. The CCorA analysis for richness yielded three functions (F1, F2, and F3) (r^2 : F1 = 0.885; F2 = 0.678; F3 = 0.048) and the full model across all functions was statistically significant according to Wilks's ($\lambda = 0.035$) or F (12, 16.16) (= 3.4204, $p = 0.012$) criteria. Thus, for the set of three canonical functions, the r^2 type effect size is 0.965, which indicates that the full model explained a substantial proportion (96.5%) of the variance shared between the variables. The first two functions (F1 and F2) were retained because they explained most of the variability in the data. In F1, the MH variable was the primary contributor to the predictor synthetic variable. Considering the F1 coefficients, the relevant criterion variables were richness of omnivores (SOmn) and invertivores (SInv), which reverse signs. This indicates that an increase of meso-habitat diversity was followed by an increase in the omnivores richness and a decrease in the invertivores richness. As for F2, all habitat parameters were positively related to SInv and negatively related to carnivore richness (SCar). This suggests that streams with heterogeneous substrate (with boulders, rocks, trunks, and leaves), high meso-habitat diversity, and stable banks (with rocks, vegetation, and roots) present more invertivores species and less carnivores species (Tab. 4, Fig. 3). Since higher scores for habitat parameters indicate more pristine streams, these results suggest that physical habitat degradation due to human activities (land use change) can lead to a decrease in

invertivores species.

Habitat parameters were not related with trophic group biomass (Wilks's $1-\lambda = 0.85$; $p = 0.069$) but were significantly related with trophic group number of individuals. When analysing the number of individuals, the full model across all functions was significant (Wilks's $1-\lambda = 0.94$; $p = 0.034$). The SC and BS variables were the main contributors to the F1 function. The number of individuals for both omnivores (NOmn) and invertivores (NInv) varied significantly with the variables. However, these two trophic groups presented a contrasting relationship, indicating that streams with high SC scores (*i.e.*, substrate that includes boulders, rocks, wood and leaves) and high BS scores (river banks that consist of rocks, wood and roots etc.) contain less omnivores and more invertivores, in number of individuals (Tab. 4, Fig. 4).

TABLE 4 | Canonical solution for habitat characteristics predicting richness, biomass and number of individuals in each trophic group for Functions 1 and 2. Structure coefficients (r_s) greater than $|\cdot 45|$ are in bold. Community coefficients (h^2) greater than 45% are also in bold. Symbols: Coef = standardized canonical function coefficient; r_s = structure coefficient; r_c^2 = squared structure coefficient. Functions 1 and 2 explained, respectively, 78.07% and 21.41% of the shared variance for richness, 57.08% and 38.31% for biomass, and 90.79% and 6.07% for number of individuals.

Variable	Function 1			Function 2			$h^2(\%)$
	Coef	r_s	$r_c^2(\%)$	Coef	r_s	$r_c^2(\%)$	
Richness							
Carnivores	23.33	0.02	0.04	-51.27	0.67	44.89	44.93
Invertivores	23.38	-0.49	24.01	-51.38	-0.67	44.89	68.90
Omnivores	23.48	0.83	68.89	-51.36	0.38	14.44	83.33
Herbivorous-detritivores	23.36	-0.35	12.25	-51.31	-0.41	16.81	29.06
r_c^2			88.48			67.80	
Substrate composition	-0.15	-0.43	18.49	-0.15	-0.90	81.00	99.49
Meso-habitat variability	0.14	0.67	44.89	-0.06	-0.54	29.16	74.05
Bank stability	0.07	0.22	4.84	-0.04	-0.46	21.16	26.00
Biomass							
Carnivores	-2.68	-0.25	6.25	32.32	0.65	42.25	48.50
Invertivores	-2.67	0.63	39.69	32.28	-0.51	26.01	65.70
Omnivores	-2.72	-0.83	68.89	32.28	-0.15	2.25	71.14
Herbivorous-detritivores	-2.67	0.44	19.36	32.32	0.22	4.84	24.20
r_c^2			73.34			64.86	
Substrate composition	0.21	0.98	96.04	0.04	-0.16	2.56	98.60
Meso-habitat variability	-0.03	0.08	0.64	-0.16	-0.88	77.44	78.08
Bank stability	-0.01	0.22	4.84	-0.08	-0.40	16.00	20.84
Number of individuals							
Carnivores	15.47	-0.42	17.64	-9.65	0.47	22.09	39.73
Invertivores	15.50	0.92	84.64	-9.84	0.04	0.16	84.80
Omnivores	15.46	-0.88	77.44	-9.86	0.11	1.21	78.65
Herbivorous-detritivores	15.47	-0.05	0.25	-9.89	-0.41	16.81	17.06
r_c^2			89.05			35.23	
Substrate composition	0.19	0.87	75.69	0.01	-0.30	9.00	84.69
Meso-habitat variability	0.04	0.49	24.01	-0.07	-0.37	13.69	37.70
Bank stability	-0.07	-0.17	2.89	-0.16	-0.91	82.81	85.70

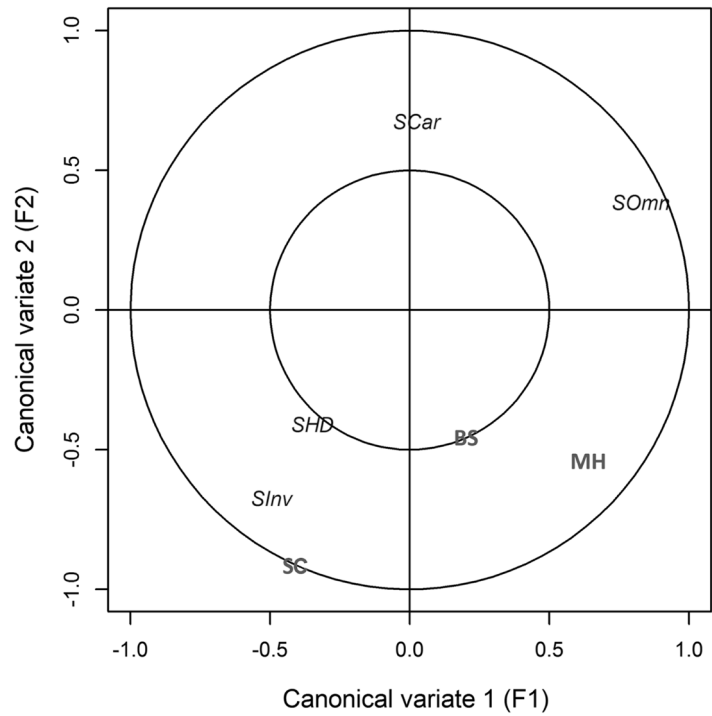


FIGURE 3 | Biplot of the first two canonical functions showing how substrate composition (SC), meso-habitat variability (MH), and bank stability (BS) correlate with richness of carnivores (SCar), invertivores (SInv), omnivores (SOMn), and herbivorous-detritivores (SHD).

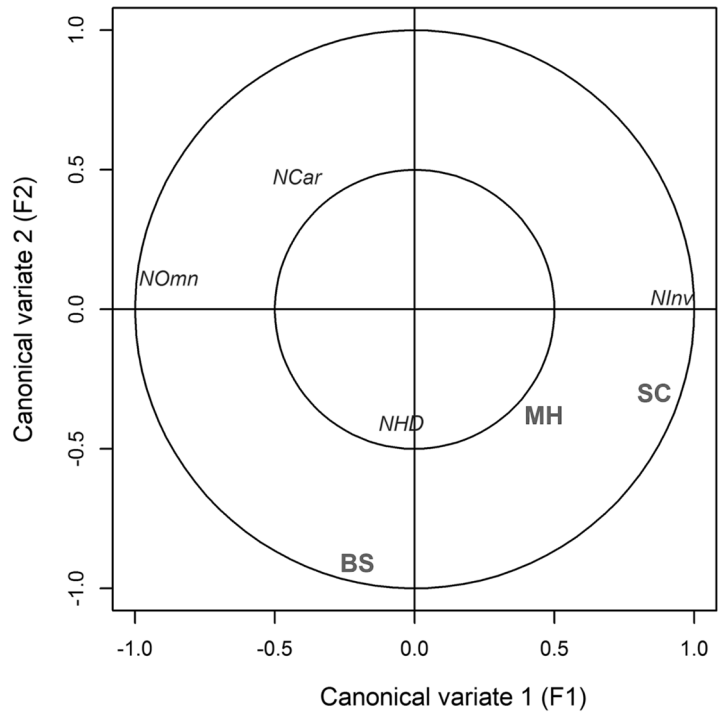


FIGURE 4 | Biplot of the first two canonical functions showing how substrate composition (SC), meso-habitat variability (MH), and bank stability (BS) correlate with number of individuals of carnivores (NCar), invertivores (NInv), omnivores (NOMn), and herbivorous-detritivores (NHD).

DISCUSSION

Our study results demonstrated that SC, MH, and BS influence trophic structure of fish assemblages, considering both richness and number of individuals. Invertivorous and omnivorous fish exhibit contrasting responses to habitat structure in terms of richness and number of individuals. Richness and number of individuals of invertivores increased in streams with larger substrate particles, meso-habitat variability, and bank stability, while the opposite was true of omnivorous fish. Similarly, opposite response patterns were revealed between invertivorous and carnivorous fish, but only for species richness. Although the results of the biomass model were not significant, the same pattern was observed for the three trophic groups. Herbivorous-detritivores, on the other hand, presented no significant response to any of the habitat characteristics.

In stream habitats, changes in the banks can result in changes in flow (Vietz *et al.*, 2018) which, in turn, can alter substrate composition (Shields *et al.*, 1994), the latter being a key aspect for changes in fish assemblages (Hortle, Lake, 1983). Higher scores for SC, MH, and BS were generally associated with more intact environments since lower scores indicated a predominance of smaller particles in the substrate, such as sand and silt, more homogeneous flow, and exposed margins – all characteristics typical of more degraded environments (Kemp *et al.*, 2011; Leal *et al.*, 2016). Consequently, our results indicate a higher number of species and number of individuals of invertivorous fish in more pristine environments.

We found that the number of invertivore individuals increased with higher SC and BS scores, and that invertivore species richness was positively correlated to all measured habitat characteristics. Despite some nektonic species such as *Piabina argentea* and *Piabarchus stramineus* (Ferreira, 2007), invertivores in our study comprised mainly species associated with fast water and substrates composed of larger diameter particles. These include the nectobenthic *Characidium* spp. (Sabino, Castro, 1990) and heptapterid catfishes (Siluriformes: Heptapteridae) that practice substrate speculation (Casatti *et al.*, 2009b). Benthic invertivores have often been associated with preserved streams (Teresa, Casatti, 2012; Krause *et al.*, 2013). Furthermore, their feeding habits are frequently correlated with morphological characteristics, leading to dependence on substrate type (Ribeiro *et al.*, 2016). Most invertivore species in our study had large pectoral fins, flattened dorsal-ventral bodies and wide mouths (Ribeiro *et al.*, 2016). Such species tend to be benthic, rheophilic, and are sensitive to changes in substrate composition – especially siltation which, in turn, leads to changes in flow; these species are generally associated with structurally complex and pristine environments (Teresa, Casatti, 2012; Cruz *et al.*, 2013).

In more simplified environments, generalist species tend to prevail (Bozzeti, Schulz, 2004; Casatti *et al.*, 2015). In our study, omnivorous fish decreased in richness, responding to an increase in SC, MH, and BS. However, since we used the proportion of trophic groups to represent trophic structure, an increase in the values of richness and number of individuals for invertivores can result in an apparent reduction in the participation of omnivores in the trophic structure, even though the latter does not present an actual reduction in the number of individuals. The omnivore group was mainly represented by species that present nektonic foraging habits and are able to forage in different environments (Sabino, Castro, 1990; Gomiero, Braga, 2008). Moreover, omnivore

species richness responded positively to MH. This group also included species with diverse habits, such as *Astyanax* spp. and *Geophagus brasiliensis*, with deep, laterally-compressed bodies and terminal mouths; the genus *Phalloceros*, whose representative species are commonly observed in pools and slow waters and feed on the surface of shallow waters (Casatti, 2002); and *Pimelodus maculatus*, species associated with deeper parts of the water column (Lobon Cerviá, Bennemann, 2000).

The richness of carnivorous species decreased in streams with higher substrate diversity, mesohabitat diversity, and bank stability, *i.e.*, more pristine streams. In our study, carnivores were represented predominantly by *H. malabaricus* and *Rhamdia quellen*, two of the largest species collected. Both are found mainly in waters with greater depth and slower water velocity, if compared with other stream species (Daga *et al.*, 2012; Teresa, Casatti, 2012; Peressin, Cetra, 2014). As this meso-habitat generally has smaller substrate particles than high velocity meso-habitats, these species tends to occur in restricted conditions of SC and MH. For herbivorous-detritivores, on the other hand, a positive relationship with SC was expected, since many species from this group have specialized buccal morphology for grazing which allows the consumption of periphyton on hard substrates (Lujan *et al.*, 2012). However, we did not detect a significant relationship between any of the trophic structure predictors of herbivorous-detritivores and the habitat characteristics measured. This may be explained by the fact that fish species in this group also consume detritus, which commonly occurs in almost all types of habitat, and it is therefore a food resource that is not restrictive (Peressin *et al.*, 2018). Furthermore, the species with the highest number of individuals in this group was *H. ancistroides*, a species tolerant to reductions in environmental quality due to pollution (Smith *et al.*, 1997), and it has been also considered a reliable indicator of anthropogenically altered environments (Oliveira, Bennemann, 2005).

The CCorA for richness explained greater amounts of variance in trophic groups than CCorA for biomass and number of individuals. Diversity indices generally ignore fish species identity and their roles in the community (Green, 1979). Consequently, species replacement may keep richness unchanged, preventing the detection of alterations and impacts on the fish assemblage (Scott, Helfmann, 2001). Trophic structure, on the other hand, incorporates species feeding habits, providing insights into ecological function and reflecting the role of species within an assemblage as well as their relationships with the environment. According to Teresa *et al.* (2016), in similar environmental conditions, different species of the same trophic group may replace each other. As a result, trophic structure would remain unchanged. On the other hand, as observed in this study, under physical environmental changes, species can be replaced by others with different feeding habits.

Invertivores species richness varied in response to all habitat parameters analysed in this study. In addition, invertivores richness and number of individuals were greater in more pristine streams, which had substrate composed by larger substrate particles, more variations between depth and shallow waters, more variations between high and low velocities, and more rocks and trunks along river banks. Furthermore, invertivore richness presented changes related to all measured habitat characteristics, and the richness canonical correlation explained a greater amount of variance in this data. Thus, we conclude that trophic structure can be a good indicator of environmental alteration,

and, more specifically, species richness of invertivores offers the best indicator of trophic structure responses to physical environmental changes in streams, and should be considered in further studies.

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AUTHOR'S CONTRIBUTION

Alexandre Peressin: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing-original draft, Writing-review & editing.

Ruanny Casarim: Data curation, Investigation, Writing-original draft, Writing-review & editing.

Ivo Gavião Prado: Investigation, Writing-original draft, Writing-review & editing.

Maurício Cetra: Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Writing-original draft, Writing-review & editing.

ETHICAL STATEMENT

The fishes was collected under the License n° 13352-1 SISBIO/IBAMA/MMA.

COMPETING INTERESTS

The authors declare no competing interests.

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