



Habitat and community structure modulate fish interactions in a neotropical clearwater river

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Species interactions can modulate the diversity and enhance the stability of biological communities in aquatic ecosystems. Despite previous efforts to describe fish interactions in tropical rivers, the role of habitat characteristics, community structure, and trophic traits over these interactions is still poorly understood. To investigate among-habitat variation in substratum feeding pressure and agonistic interactions between fishes, we used remote underwater videos in three habitats of a clearwater river in the Central Western, Brazil. We also performed visual surveys to estimate the abundance and biomass of fishes and proposed a trophic classification to understand how these variables can affect fish interactions. Community structure was the main factor affecting the variation in the interactions among the habitats. Biomass was the main variable determining which habitat a fish will feed on, while species abundance determined with how many other species it will interact in the agonistic interaction networks for each habitat. Specific habitats are not only occupied, but also used in distinct ways by the fish community. Overall, our results demonstrate the importance of the heterogeneity of habitats in tropical rivers for the interactions performed by the fishes and how the intensity of these interactions is affected by community structure.

Keywords: Bodoquena plateau, Centrality, Characidae, Feeding pressure, Habitat heterogeneity.

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Interações realizadas por peixes podem modular a diversidade e assegurar a estabilidade de comunidades em rios tropicais. Apesar dessa importância, poucos estudos relacionam as interações ecológicas com as características do habitat, estrutura da comunidade e atributos das espécies de peixes. Por meio de filmagens remotas subaquáticas nós verificamos como a pressão alimentar dos peixes sobre a comunidade bentônica e as interações agonísticas entre peixes são influenciadas por essas características do habitat e da comunidade em um rio tropical de água clara na região Centro-Oeste do Brasil. Também realizamos censos visuais para estimar a abundância e a biomassa dos peixes e propusemos uma classificação funcional para entender como essas variáveis podem afetar as interações dos peixes. A estrutura da comunidade foi o principal fator que afetou a variação nas interações entre os habitats. A biomassa dos peixes determinou em qual habitat um peixe se alimentará, enquanto a abundância das espécies determinou com quantas outras espécies elas interagem nas redes de interações agonísticas de cada habitat. Habitats específicos não são apenas ocupados, mas também utilizados de maneiras distintas pela comunidade de peixes. Nossos resultados demonstram a importância da heterogeneidade de habitats para as interações realizadas pelos peixes em rios tropicais e como a intensidade dessas interações é afetada pela estrutura da comunidade.

Palavras-chave: Centralidade, Characidae, Heterogeneidade de habitats, Pressão alimentar, Serra da Bodoquena.

INTRODUCTION

Tropical rivers often encompass high habitat-heterogeneity along their course (Vannote *et al.*, 1980). These habitats are characterised by physical and biological features that promote distinct structural complexity (Bell *et al.*, 1991), which can explain gradients of species diversity for freshwater organisms. As a result, the distribution of many organisms within a river can closely reflect habitats characteristics (Bell *et al.*, 1991; Petry *et al.*, 2003). For instance, small invertebrates and fishes that would otherwise be exposed to predation in low complexity habitats can find refuge in highly complex habitats, such as those formed by aquatic plants (Gorman, Karr, 1978; Coull, Wells, 1983; Savino, Stein, 1989; Sabino, Zuanon, 1998; Smith *et al.*, 2014). Indeed, impaired visual contact between individuals in structurally complex habitats might reduce detectability (Bell *et al.*, 1991), thus reducing the frequency of visually oriented interactions in general, not only during predation. These visually-mediated interactions are thought to be particularly common in clear water rivers and lakes (Bergman, Moore, 2003; Ranåker *et al.*, 2014).

Habitat characteristics, such as three dimensionality and food resource availability, and species traits, such as morphological and behaviour adaptations, can directly affect the intensity and outcomes of biological interactions (Crowder, Cooper, 1982; Baber, Babbitt, 2004). For instance, prochilodontid fishes use their thick, fleshy and often

suctorial lips to scrape the substratum, feeding on detritus and periphyton (Bowen, 1983; Power, 1983; Taylor *et al.*, 2006). As a result, these fishes would be expected to be particularly abundant on habitats that offer such conditions, such as those with rocky and sand bottoms instead of macrophyte banks. In addition to habitat and species traits, species abundance can also play an important role on species interactions because abundant species tend to interact more intensely and with more components than rare ones (Vázquez *et al.*, 2007).

Freshwater fishes are conspicuous components of tropical rivers, where they perform a variety of interactions (*e.g.*, Sabino, Sazima, 1999; Taylor *et al.*, 2006). The structure of their interaction networks is, however, not well understood, particularly because of limitations in water transparency that are critical to *in situ* observation of species interactions (Moss, 2010). When these conditions are met, observational studies have revealed a myriad of behaviours that are analogous to marine reef systems (*e.g.*, Sazima, 1986). Many of these newly described behaviours and interactions, have important energetic consequences for the ecosystems in which they take place (*e.g.*, Sazima, 1983; Sazima, 1986; Sazima, 1988; Sabino, Zuanon, 1998; Lima *et al.*, 2012). More recently, technological advances (*i.e.*, remote filming) have helped scientist to better understand the structure of freshwater fish assemblages and the interactions in which they engage (Ebner, Morgan, 2013; King *et al.*, 2018).

In this study, we used remote underwater videos (RUVs) to quantify trophic and agonistic interactions of fish species in a highly diverse clearwater neotropical river. Specifically, we evaluated how these interactions are dependent on fish community structure (*i.e.*, species-level density and biomass), habitat characteristics and species traits. We hypothesized that species traits and abundance, as well as habitat particularities, will modulate differences in trophic and agonistic interactions among habitats. We also hypothesized higher interaction intensity in visually low complexity habitats. Studies in these systems can help us to understand the importance of biological interactions in shaping species distributions and their energetic links in tropical freshwater river systems.

MATERIAL AND METHODS

Study area. Sampling was carried out in May 2011 at the Olho d'Água River, a tributary of the Miranda River in the upper Paraguay basin, state of Mato Grosso do Sul, Brazil (Fig. 1). Located in a Private Reserve of Natural Heritage (fishing is not allowed), this river is directly affected by the karstic geomorphology of the Bodoquena Plateau and the horizontal water transparency is often greater than 40 metres. Along its two kilometres of extension, the Olho d'Água River comprises habitats that vary in their physical features and biological components, but that are subject to near constant temperatures (23–25 °C) and water volume throughout the year (Manço, Pivatto, 2007; Teresa *et al.*, 2014). In this river, we sampled three habitats that differed in substratum physiognomy (see Fig. 1, <https://www.youtube.com/watch?v=RN5ohX7inME>): the “Riverine lake” (further referred as “Lake”), which is a 600 m² and 3m deep lentic habitat located in the upper portion of the river, with a substratum covered by filamentous cyanobacteria, gravel and sand; the “Plant habitat”, a lotic and shallow (~1m deep) habitat presenting medium water flow where the substratum is covered by patches of

macrophytes, mostly *Heteranthera zosterifolia* (Mart.) and *Myriophyllum aquaticum* (Vell.) Verdc., filamentous cyanobacteria, and sand; and the “Rock habitat”, which is also lotic with slow-to-medium water flow and substratum mainly covered by stones, gravel, sand and twigs.

Sampling procedure and analyses. To assess fish abundance and biomass we performed 10 underwater visual censuses (UVCs) in each habitat, with no overlap among sampled areas. This method consisted of a belt transect in which a free diver

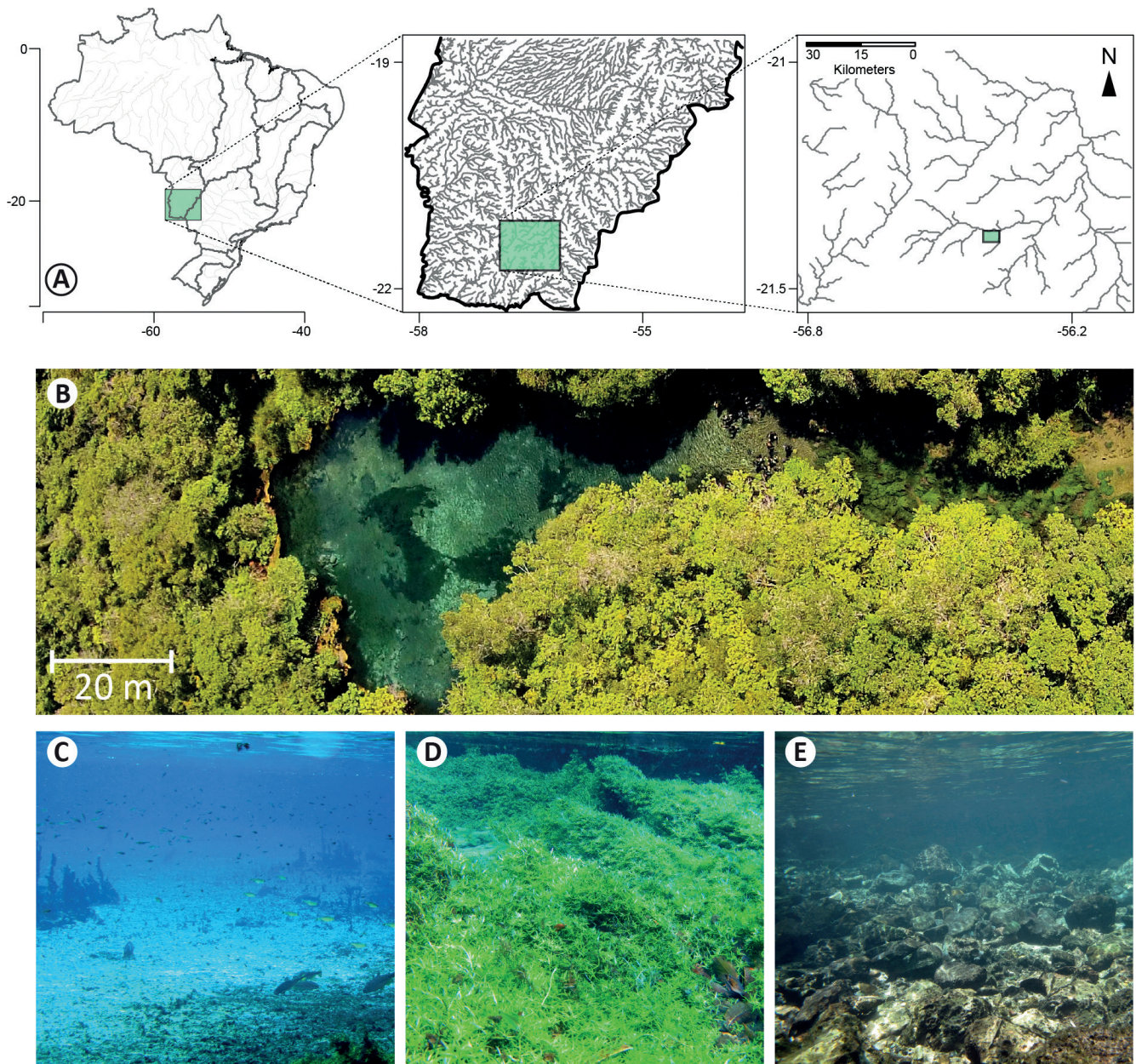


FIGURE 1 | A. Olho d'Água River located in the upper Paraguay River basin, Central Western Brazil. B. Note that clear water allows observation of the underwater vegetation even in aerial photographs. Three sampled habitats are: C. Lake; D. Plant; and E. Rock.

swam in a constant velocity and identified, counted, and estimated the total length of fishes within a 40m² area (20 x 2 m). To assess fish feeding and agonistic interactions, we recorded 14 diurnal Remote Underwater Videos (RUVs) in each habitat, between 0900 and 1600 hours, totalling 42 videos. Videos were recorded with a digital camera on a weighted tripod focused on 2 m² areas of the substratum established with a measuring tape that was then removed before each recording. The minimum distance among recorded areas was three meters. Each 2 m² area was recorded for 15 min and the central 10 min of each video was analysed in laboratory. Both visual surveys and RUVs methods were adapted from previous studies in reef systems (*i.e.*, Longo *et al.*, 2014, 2015; Morais *et al.*, 2017) and demonstrated to be effective to record the community structure and feeding rates of fish assemblages, respectively. Furthermore, both methods are non-lethal for fishes and RUVs have the advantage of keeping the record for the confirmation of species identification and accurately quantifying interactions that may be difficult to count in the field (Longo, Floeter, 2012; Ebner, Morgan, 2013; Ebner *et al.*, 2015).

In the video analyses, we identified each individual fish that bit the substratum or chased another fish inside the RUVs' focal area. The number of bites in the substratum of each fish individual was counted and its total length (cm) estimated based on the measuring tape that was initially deployed. A bite was defined as the moment when a fish hits the substratum with its jaw open, with or without intake (Longo *et al.*, 2014). We used the number of bites on the substratum and the total length of each individual to calculate their feeding pressure (FP) following the equation: $FP = (\text{bites} * \text{biomass}) / (2\text{m}^2 * 10\text{min})$ (Longo *et al.*, 2014). For each video (*i.e.*, sample) we obtained the feeding pressure of each fish species from the sum of the feeding pressure of all individuals of each species. The individual biomass (B) was calculated based on the equation: $B = a * (TL * CF)^b$, where *TL* is the total length (centimetres), *a* and *b* are parameters of length-weight relationships and *CF* is a correction factor that rescales length-weight parameters obtained for standard length to the working measure total length (Tab. 1).

Fish species were assigned into trophic groups based on their feeding mode/behaviour, obtained from *in situ* observations and RUVS, and diet obtained from the literature (Tab. 1). When data for a given species was not available, we used the trait of a congeneric species that had similar morphology and likely similar feeding behaviour. This classification resulted in eight trophic groups:

Grazing detritivores: Bottom-dwelling fishes that forage mostly on sand and rock substrate and have morphological adaptations to scrape the substratum (*e.g.*, labial teeth). These fish sort the sediment in their oral cavity, retain organic detritus and eliminate inorganic matter such as sand (Bowen, 1983). They can ingest a large amount of detritus and sediment, and small portions of plant material and benthic invertebrates.

Grazing periphytivores: Bottom-dwelling fishes that forage over hard substratum such as rocks, fallen trees and twigs, and have morphological adaptations to scrape periphyton (Power, 1983). A small portion of detritus and plant material can also be part of the diet of this group.

TABLE 1 | Parameters of length-weight relationship (a and b), coefficient of determination (r^2) and trophic guild (based on species diet) for species recorded in the visual surveys and remote underwater videos in the Olho d'água River. TL/SL is the relation between Total length (TL) and Standard length (SL). When data for a given species was not available, we considered the traits of a congeneric species (see observation column).

Species	Code	TL/SL	a	b	r ²	Reference for a, b and r ²	Guild	Reference for guild	Observation
Anostomidae									
<i>Leporinus friderici</i>	Lep fri	1.19	0.0272	2.98	0.99	Batista-Silva <i>et al.</i> (2015)	Omnivore	Albrecht, Caramaschi (2003)	
<i>Megalopterius macrocephalus</i>	Meg mac	1.23	0.0171	3.12	0.98	Benedicto-Cecilio <i>et al.</i> (1997)	Omnivore	Balassa <i>et al.</i> (2004)	<i>M. obtusidens</i>
<i>Leporinus striatus</i>	Lep str	1.00	0.0100	2.95	0.94	Nuner, Zaniboni-Filho (2009)	Omnivore	Balassa <i>et al.</i> (2004)	
<i>Leptorellus vittatus</i>	Lep vit	1.23	0.0243	2.92	0.92	Benedicto-Cecilio <i>et al.</i> (1997)	Invertivore	Gandini <i>et al.</i> (2012)	
Bryconidae									
<i>Brycon hilarii</i>	Bry hil	1.25	0.0129	3.14	0.99	Benedicto-Cecilio <i>et al.</i> (1997)	Herbivore	Zuntini <i>et al.</i> (2004)	
Characidae									
<i>Aspvarax lacustris</i>	Asl lac	1.33	0.0593	2.65	0.96	Oliveira <i>et al.</i> (2014)	Omnivore	Corrêa, Silva (2010)	
<i>Aspvarax lineatus</i>	Asl lin	1.26	0.0618	2.65	0.96	Oliveira <i>et al.</i> (2014)	Omnivore	Santos <i>et al.</i> (2009)	
<i>Aspvarax marionae</i>	Asl mar	1.26	0.0530	2.63	0.97	Oliveira <i>et al.</i> (2014)	Omnivore	Cameira <i>et al.</i> (2014)	
<i>Bryconops melanurus</i>	Bry mel	1.29	0.0509	2.50	0.98	Oliveira <i>et al.</i> (2014)	Invertivore	Godoi (2004)	
<i>Hyphessobrycon eques</i>	Hyp equ	1.27	0.0216	3.39	0.98	Batista-Silva <i>et al.</i> (2015)	Invertivore	Casatti <i>et al.</i> (2003)	
<i>Jupiaha acanthogaster</i>	Jup aca	1.24	0.0131	3.33	-	pers. commu. Fabrício Teresa	Omnivore	Souza <i>et al.</i> (2013)	
<i>Moenkhausia bonita</i>	Moe bon	1.26	0.0347	2.51	-	pers. commu. Fabrício Teresa	Invertivore	Carniatto <i>et al.</i> (2016)	
<i>Odontostilbe pequira</i>	Odo peg	1.32	0.0449	2.92	0.79	Oliveira <i>et al.</i> (2014)	Omnivore	Lima <i>et al.</i> (2012)	
<i>Phenacogaster tegatus</i>	Phe teg	1.25	0.0080	3.08	0.91	Terra <i>et al.</i> (2017)	Invertivore	Ibañez <i>et al.</i> (2007)	<i>P. calverti</i> and <i>P. pectinatus</i>
<i>Salminus brasiliensis</i>	Sal bra	1.20	0.0113	3.14	0.98	Batista-Silva <i>et al.</i> (2015)	Piscivore	Novakowski <i>et al.</i> (2008)	
<i>Serrapinnus calliurus</i>	Ser cal	1.32	0.0194	3.31	0.97	Batista-Silva <i>et al.</i> (2015)	Herbivore	Flori <i>et al.</i> (2016)	<i>S. notomelas</i>
Cichlidae									
<i>Cichlasoma dimerus</i>	Cic dim	1.38	0.0470	3.14	0.98	Batista-Silva <i>et al.</i> (2015)	Omnivore	Casatti <i>et al.</i> (2009)	<i>C. paranaense</i>
<i>Crenicichla lepidota</i>	Cre lep	1.21	0.0370	2.71	0.93	Benedicto-Cecilio <i>et al.</i> (1997)	Invertivore	Gibran <i>et al.</i> (2001)	<i>C. haroldoi</i> and <i>C. britskii</i>
<i>Crenicichla vitata</i>	Cre vit	1.00	0.0030	3.37	0.99	Nuner, Zaniboni-Filho (2009)	Invertivore	Gibran <i>et al.</i> (2001)	<i>C. britskii</i>
Creomichidae									
<i>Characidium spp.</i>	Cha spp	1.25	0.0466	2.33	0.84	Oliveira <i>et al.</i> (2014)	Invertivore	Cetra <i>et al.</i> (2011)	<i>C. zebra</i>
Curimatidae									
<i>Cyphocharax gyllii</i>	Cyp gyl	1.26	0.0353	2.90	0.96	Benedicto-Cecilio <i>et al.</i> (1997)	Herbivore	Vari (1992)	<i>C. modestus</i>
Loricariidae									
<i>Ancistrus spp.</i>	Anc spp	1.34	0.0377	2.83	-	pers. commu. Fabrício Teresa	Periphytivore	Roa-Tuentes (2011)	
<i>Hypostomus spp.</i>	Hyp spp	1.35	0.0290	2.99	0.97	Benedicto-Cecilio <i>et al.</i> (1997)	Detritivore	Novakowski <i>et al.</i> (2008)	
Parodontidae									
<i>Parodon nasus</i>	Par nas	1.17	0.0602	2.50	0.98	Oliveira <i>et al.</i> (2014)	Periphytivore	Silva <i>et al.</i> (2009)	
Prochilodontidae									
<i>Prochilodus lineatus</i>	Pro lin	1.00	0.0110	3.06	0.89	Nuner, Zaniboni-Filho (2009)	Detritivore	Smolders <i>et al.</i> (2002)	
Serrasalminidae									
<i>Piaractus mesopotamicus</i>	Pia mes	1.25	0.0540	2.88	0.98	Gubiani <i>et al.</i> (2009)	Herbivore	Paula <i>et al.</i> (1989)	
<i>Serrasalminus maculatus</i>	Ser mac	1.22	0.0162	3.23	0.98	Benedicto-Cecilio <i>et al.</i> (1997)	Piscivore	Novakowski <i>et al.</i> (2008)	<i>S. marginatus</i>

Browsing herbivores: Fishes that browse pieces of macrophytes and macroalgae (Sazima, 1986), as well as allochthonous material such as leaves, seeds and fruits.

Digging omnivores: Bottom-dwelling fishes that excavate the sandy substrate ingesting plant parts (including roots) and buried invertebrates, commonly attracting follower fishes by revolving the sediment (Sazima, 1986).

Nibbling omnivores: Bottom-dwelling fishes that ingest both animal (*e.g.*, invertebrates) and vegetable items (*e.g.*, seeds and macrophytes), taking small bites on the substratum (Sazima, 1986). They commonly bury a part of their snouts in the substratum but causing minimum bottom disturbance (Teresa *et al.*, 2014).

Nibbling invertivores: Bottom-dwelling fishes that behave similarly to nibbling omnivores but rarely, if ever, ingest vegetable matter.

Picking omnivores: Water column fishes that pick items on the surface, water column, commonly ingesting leaves, seeds, other plant fragments and small invertebrates (Sazima, 1986).

Picking invertivores: Water column fishes that behave similarly to picking omnivores but rarely, if ever, ingest vegetable matter.

We considered as agonistic interactions, both intra and interspecific events in which a fish chased another one without any obvious feature that could be associated to predation. Predation features could be 1) large size disparities, with the chaser fish much larger than the chased one, or 2) a deliberate bite was observed, such as when mucus or scales are targeted (Curio, 1976; Sazima, 1983; Lima *et al.*, 2012). This last interaction, also called mutilating predation, can be easily distinguished because the chased fish appears unaware, fleeing only after physical contact (Lima *et al.*, 2012), while in an agonistic interaction the chased fish flees as a response to the chaser's movement.

Statistical analyses. To assess whether our categorical classification of habitat was able to capture environmental heterogeneity, we used a principal coordinate analyses (PCoA) and a permutation analysis of variance (PERMANOVA), with Euclidean distance matrix obtained from nine environmental variables (response variables) visually estimated from the videos (samples) and subsequently transformed by standardization. These were: 1–5) percent cover of cyanobacteria, macrophytes, rock, gravel and sand; 6–7) height of macrophytes and height of the filamentous cyanobacteria; 8) presence or absence of twigs near or inside the RUVs area; and 9) maximum depth of each habitat. To check if habitats differed according to fish abundance or biomass (*i.e.*, parameters of community structure) we used the UVCs as samples and performed a PCoA and a PERMANOVA analysis with Bray–Curtis similarity. The null hypothesis for this analysis was that habitats are not different in terms of fish community structure.

To check for differences in the feeding pressure (response variable) of fish species and trophic groups among the habitats (factor), we used the RUVs as samples to

perform a PCoA and a PERMANOVA analysis with Bray–Curtis similarity. This was used to test the null hypothesis that habitats are not different regarding this feeding interaction. To relate the degree of centrality of a species in the agonistic interaction network to its average abundance (ind. / 40m²) we performed a linear regression model for each habitat. Species centrality was obtained through the “degree centrality”, which indicates the central node (*i.e.*, species) in the networks accounting for the number of connections (*i.e.*, agonistic interactions) with other species. The degree centrality of a given species (sample) in each habitat was obtained by summing the number of species that were chased and number of chaser species in the habitat.

To test the influence of species (sample) average biomass (kg / 2m²), average abundance (ind. / 40m²), habitat and trophic group on the average feeding pressure and centrality in the agonistic interactions, we performed a generalized linear model with Gaussian distribution. A F test through the function `drop1` of the package “car” (Fox, Weisberg, 2011) was used to evaluate significance. Abundance/biomass, feeding pressure and centrality were natural log transformed to decrease data dispersion. All the analyses and graphics were performed using “ggplot2” (Wickham, 2016), “gridExtra” (Baptiste, 2017), “plotrix” (Lemon, 2006), “reshape” (Wickham, 2007), “scales” (Wickham, 2017) and “vegan” (Oksanen *et al.*, 2018) packages of R software version 3.4.3 (R Core Team, 2019). All data and R code can be downloaded from the Zenodo Digital Repository: <http://doi.org/10.5281/zenodo.3587961>.

RESULTS

We recorded 27 different fish species in the visual surveys (Tab. 1), of which 21 in the Lake, 25 in the Plant and 20 in the Rock habitat. In the RUVs, we recorded 23 fish species encompassing 85% of the richness found in the visual surveys. These habitats also differed considerably in their benthic composition, with habitat alone explaining over 58% of the benthic variability observed among samples (Permanova $F = 27$; $R^2 = 0.58$; $p < 0.01$; Fig. 2A).

Fish community structure varied among habitats both in terms of abundance ($F = 26.44$; $R^2 = 0.66$; $p < 0.01$; Fig. 2B) and biomass ($F = 3.07$; $R^2 = 0.18$; $p < 0.01$; Fig. 2C). Samples from the Lake habitat tended to group in the PCoA, mainly due to patterns of abundance and particularly driven by large numbers of *Odontostilbe pequirá* (Steindachner, 1882). This species dominated species abundance in the Lake, but not in the other two habitats (Fig. 2B). Conversely, the biomass structure was not clearly distinct among habitats (Fig. 2C). Fish abundance and biomass were the variables that better explained the variation of agonistic and feeding interactions, respectively, among habitats (Tab. 2).

In 420 min of video, we counted a total of 12,364 bites on the substratum (approximately 87% on the Rock, 10% Lake and 3% on the Plant habitat), performed by 18 species (Fig. 3). In the Rock habitat, nine species were recorded feeding on the substratum. *Prochilodus lineatus* (Valenciennes, 1837) alone was responsible for ~ 58% of the total feeding pressure (Fig. 3). The grazing periphytivores *Ancistrus* spp. and *Parodon nasus* Kner, 1859 were only recorded feeding in this habitat. In the Lake

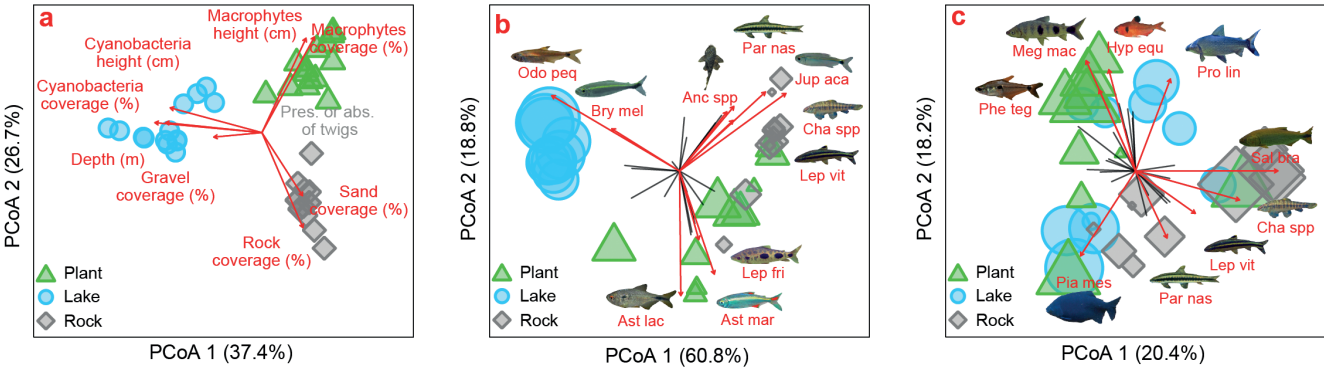


FIGURE 2 | A. Principal coordinate analysis (PCoA) showing ordination of samples according to substratum composition (i.e., habitat categorization); **B.** PCoA performed with the abundance of fishes, points sized according to the sum of the abundance in the sample (logarithm scaled for better visualization); **C.** PCoA performed with the biomass of fishes, points sized according to the sum of the biomass in the sample (logarithm scaled for better visualization). Red lines indicate significant variables ($p < 0.05$) while black lines non-significant. Anc spp = *Ancistrus* spp., Ast lac = *Astyanax lacustris*, Ast mar = *Astyanax marionae*, Bry mel = *Bryconops melanurus*, Cha spp = *Characidium* spp., Hyp equ = *Hyphessobrycon eques*, Jup aca = *Jupiaba acanthogaster*, Lep vit = *Leporellus vittatus*, Lep fri = *Leporinus friderici*, Meg mac = *Megaleporinus macrocephalus*, Odo peq = *Odontostilbe pequirá*, Par nas = *Parodon nasus*, Phe teg = *Phenacogaster tegatus*, Pia mes = *Piaractus mesopotamicus*, Pro lin = *Prochilodus lineatus*, Sal bra = *Salminus brasiliensis*.

TABLE 2 | Output of GLM evaluating the influence of habitat, trophic group and abundance/biomass over the feeding pressure performed by the fishes on the benthic substratum and agonistic interactions among fishes.

Feeding pressure	df	F	p value
Habitat	2	3.917	0.027
Functional group	7	2.001	0.076
Biomass	1	30.503	<0.001
Agonistic interactions	df	F	p value
Habitat	2	0.668	0.519
Functional group	5	0.191	0.964
Abundance	1	44.785	<0.001

habitat, seven species were recorded feeding on the substratum, with the picking omnivore *Odontostilbe pequirá* feeding in all the samples and responsible for ~53% of the total feeding pressure. In the Plant habitat, 11 species were detected feeding on the substratum, with the highest feeding pressure performed by two species: the digging omnivore, *Megaleporinus macrocephalus* (Garavello, Britski, 1988), responsible for ~51% of the total feeding pressure; and the browsing herbivore, *Brycon hilarii* (Valenciennes, 1850), responsible for ~44% (Fig. 3). The structure of feeding pressure varied among habitats in terms of both species ($F = 4.88$; $R^2 = 0.21$; $p < 0.01$) and trophic groups ($F = 4.74$; $R^2 = 0.20$; $p < 0.01$). There was higher similarity among samples from the same habitat than between samples from different habitats, particularly in the Rock habitat (Fig. 4).

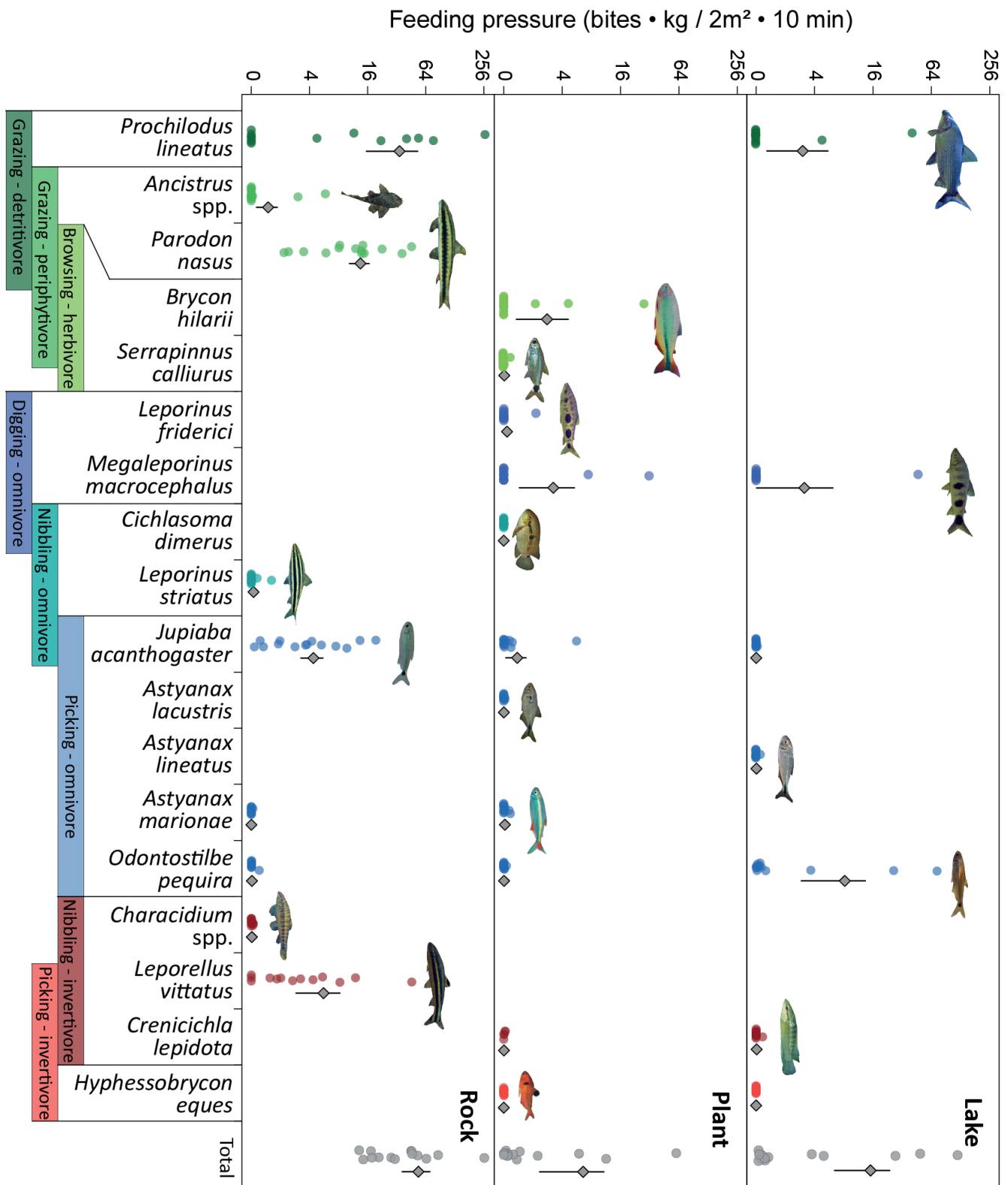


FIGURE 3 | Feeding pressure of the 18 fishes that bit the substratum, and their respective trophic groups (colours) at the Olho d'Água River. Black diamonds and lines represent the mean \pm standard error, respectively. Habitats in which certain species did not fed on the substratum (zero values) are not represented in the graph. The Y-axis scale is log₁₀-transformed to better show data dispersion.

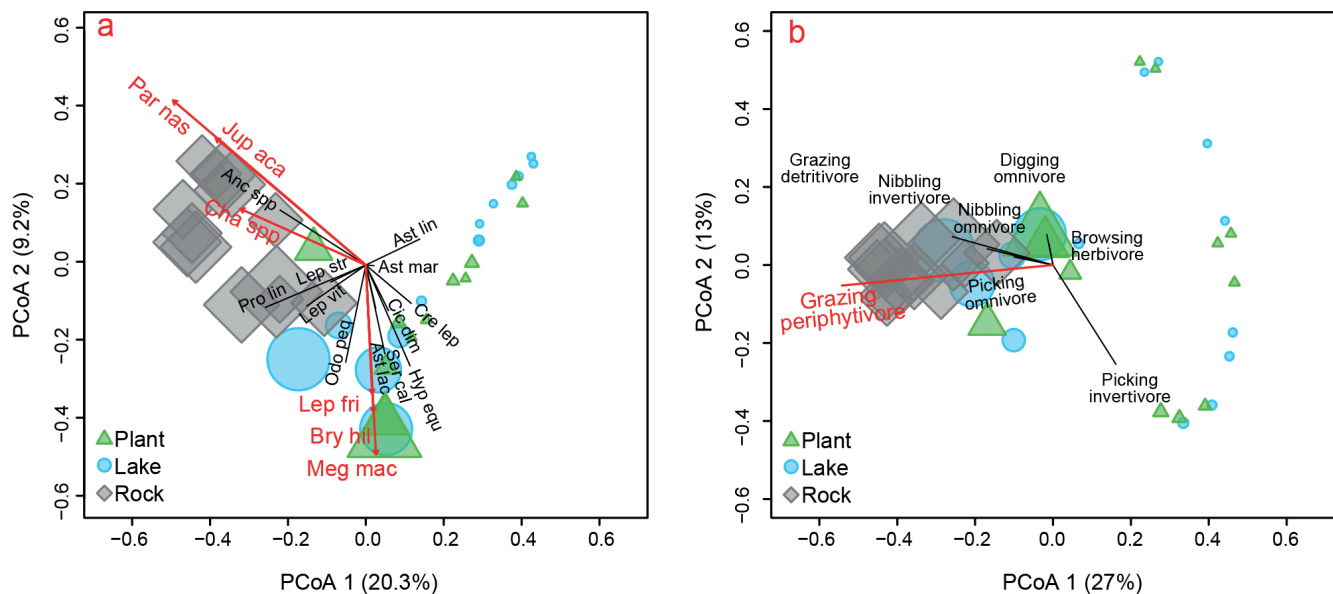


FIGURE 4 | Principal coordinate analysis (PCoA) and permutational analysis of variance (PERMANOVA) to demonstrate feeding pressure variation among habitats accounting for **A.** species and **B.** trophic groups, points sized according to the sum of the feeding pressure in the sample (logarithm scaled for better visualization). Red lines indicate significant variables ($p < 0.05$) while black lines non-significant. Anc spp = *Ancistrus* spp., Ast lac = *Astyanax lacustris*, Ast lin = *Astyanax lineatus*, Ast mar = *Astyanax marionae*, Bry hil = *Brycon hilarii*, Cha spp = *Characidium* spp., Cic dim = *Cichlasoma dimerus*, Cre lep = *Crenicichla lepidota*, Hyp equ = *Hyphessobrycon eques*, Jup aca = *Jupiaba acanthogaster*, Lep fri = *Leporinus friderici*, Meg mac = *Megaleporinus macrocephalus*, Lep str = *Leporinus striatus*, Lep vit = *Leporellus vittatus*, Odo peq = *Odontostilbe pequiri*, Par nas = *Parodon nasus*, Pro lin = *Prochilodus lineatus*, Ser cal = *Serrapinnus calliurus*.

We counted 1,420 agonistic interactions involving 15 species (approximately 57% occurred in the Lake, 27% in the Plant and 16% in the Rock habitat). The structure of these interactions varied among habitats, with ten species interacting in the Plant habitat, nine species in Rock and six in Lake (Fig. 5). Intraspecific interactions were more frequent than interspecific interactions, especially for the most abundant species (Fig. 5). In the Lake and Plant habitats, *O. pequiri* was responsible for most of the agonistic interactions, targeting almost all the species observed (approximately 93% of the total of agonistic interactions in the Lake and 77% in the Plant, Fig. 5). This species was, thus, central to the species interaction network of these two habitats. In the Rock habitat, however, *Jupiaba acanthogaster* (Eigenmann, 1911) was responsible for approximately 51% of the agonistic interactions. This species was chased by *Parodon nasus* with high frequency.

DISCUSSION

To our knowledge, our study is the first to quantify the degree of variability in fish interactions among different habitats in a tropical clearwater river. Moreover, it also emphasizes the overwhelming role of community structure and habitat variability in defining the intensity, species and trophic composition of feeding and agonistic

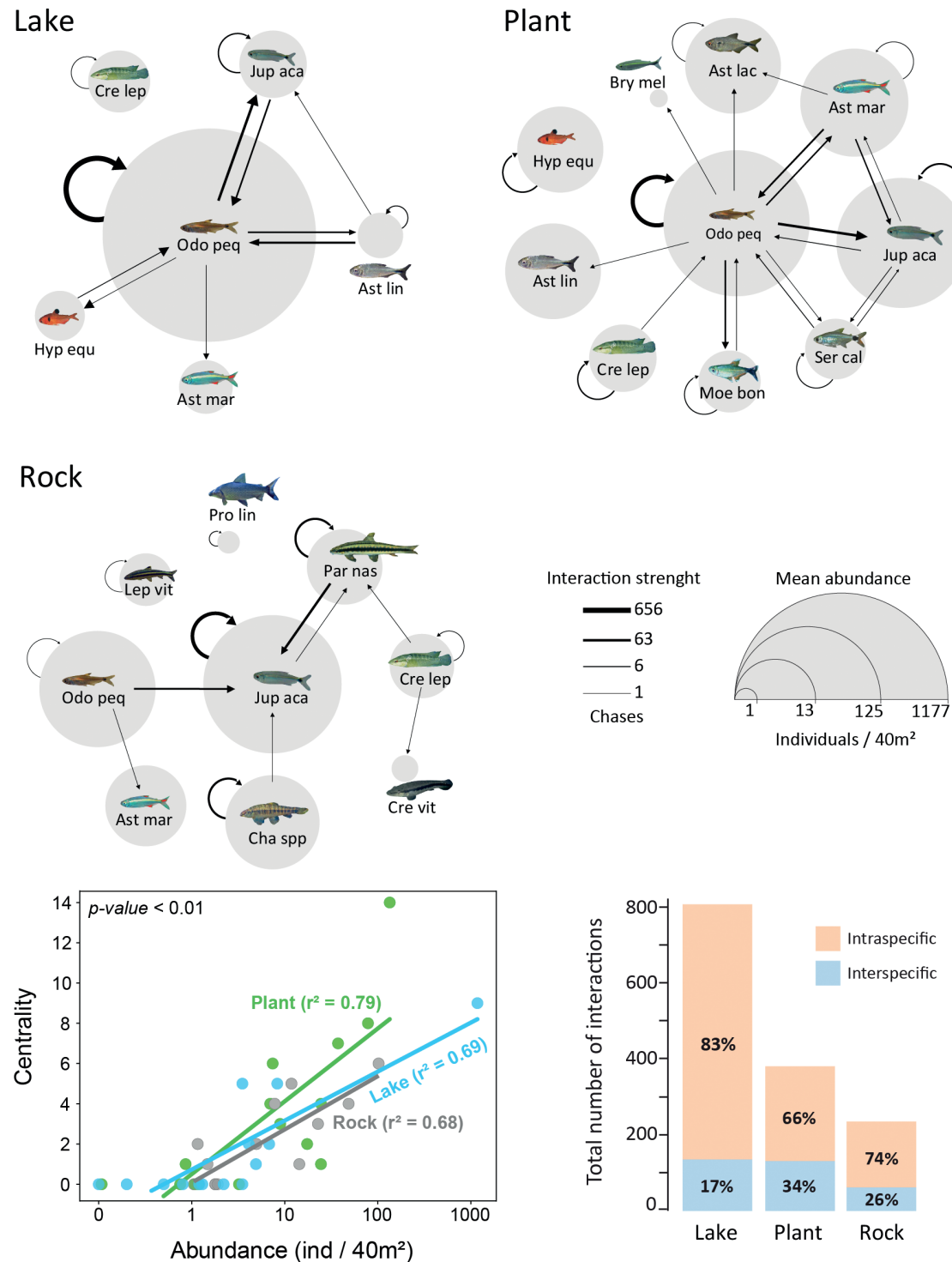


FIGURE 5 | Agonistic interactions between fishes in three habitats of the Olho d'Água River, upper Paraguay River basin, Brazil. Arrow thickness is proportional to agonistic interaction intensity in all three habitats; grey circles are proportional to the mean abundance of each species. Ast lac = *Astyanax lacustris*, Ast lin = *Astyanax lineatus*, Ast mar = *Astyanax marionae*, Bry mel = *Bryconops melanurus*, Cha spp = *Characidium* spp., Cre lep = *Crenicichla lepidota*, Cre vit = *Crenicichla vittata*, Hyp equ = *Hypessobrycon eques*, Jup aca = *Jupiaba acanthogaster*, Lep vit = *Leporellus vittatus*, Moe bon = *Moenkhausia bonita*, Odo peq = *Odontostilbe pequirá*, Par nas = *Parodon nasus*, Pro lin = *Prochilodus lineatus*, Ser cal = *Serrapinnus calliurus*.

interactions. While the Rock habitat concentrated most of the feeding interactions with the substratum, particularly due to periphytivorous fishes, most of the agonistic interactions occurred in the Lake habitat, led by abundant small characins. The Plant habitat, which has a higher structural complexity compared to the two other habitats, hosted substantially less feeding and agonistic interactions, although these interactions involved more species (especially small characins fishes). Altogether, these findings suggest that these habitats deliver different functions for the local fish community.

The highest feeding pressure observed in the Rock habitat is likely associated to periphyton that overgrows trunks and rock surfaces in this habitat (Power, 1983). Fishes that fed on the Rock habitat, such as *Prochilodus lineatus* and *Ancistrus* spp. have morphological adaptations that allow them to scrape periphyton and detritus deposited on solid surfaces (Bowen, 1983). They sort materials through their gills, retaining algae and detritus while eliminating the sediments (Bowen, 1983; Fugi *et al.*, 1996). Detritus and periphyton are abundant food resources in tropical freshwater systems, characterized by high turnover rates (Bowen, 1983; Power, 1983). The River Continuum concept predicts that periphyton growing on rocks would be available as a food resource for upstream river communities whereas detritus would be more important for downstream communities (Vannote *et al.*, 1980). However, similarly to other tropical lowland river systems, our system cannot be clearly distinguished in upstream and downstream communities: rocks and trunks occupy patches alongside a sandy matrix along most of the river extension. Thus, rocky habitats provide detritivores and periphytivores with abundant food sources that are likely critical in terms of energy flow and nutrient cycling for the whole system (Bowen, 1983; Power, 1983; Prejs, 1984; Lodge, 1991; Taylor *et al.*, 2006; Winemiller *et al.*, 2006). For instance, it has been shown elsewhere that a related species, *Prochilodus mariae* Eigenmann, 1922, is a keystone species modulating organic carbon transport along with a lowland river system in Venezuela (Taylor *et al.*, 2006).

Contrary to the Rock habitat, the Plant habitat featured a high cover of macrophytes, but not periphyton. In this habitat, aquatic plants are routinely consumed, cropped by the scissor-like teeth of *Brycon hilarii*, which also ingests fruits and insects from the riparian vegetation (Sabino, Sazima, 1999). Additionally, the digging omnivore *M. macrocephalus* feeds largely on invertebrates buried among macrophytes' roots by digging through the soft substrate or among branches with their snout (Sazima, 1986; Albrecht, Caramaschi, 2003). *Brycon hilarii* and *M. macrocephalus*, thus, employ behavioural strategies to exploit resources that are abundant in this habitat. In the Lake habitat, most of the feeding pressure performed by *O. pequirá* occurred in the context of a "feeding frenzy", which consisted in large groups feeding on masses of benthic cyanophytes that become detached from the sand substrate. These blue-green algae seem to be detached during the daylight as a function of oxygen bubbles forming from photosynthetic activity. Since these feeding frenzies did not occur unless the cyanophytes got detached from the substratum, we suspect that *O. pequirá* were targeting small invertebrates that inhabit the meandering structure of cyanophyte filaments (Dias, 2007). Small-sized characins are conspicuous components of Neotropical rivers and are essentially known for their versatility in feeding behaviour. They feed over the bottom, water column, surface, and target mucus and scales of other fishes (Sazima, 1983; Lima *et al.*, 2012; Brejão *et al.*, 2013). As such, they dominate trophic links in Neotropical river food webs, also serving as a primary food for predators (Bozza, Hahn, 2010).

Interspecific agonistic interactions were mostly associated with small-sized characin fishes and the territorial *P. nasus*. Particularly, two characins, *O. pequirá* and *J. acanthogaster*, comprised most of the agonistic interactions. These species not only interacted with most of the species within each network, but also performed or received the largest number of agonistic interactions. The centrality of *O. pequirá* in the networks of the Lake and Plant habitats and *J. acanthogaster* in the Rock habitat was a product of the high abundance of this species in these habitats. Density-dependence leads to intense competitive interactions in many organisms, including reef fishes (Bonin *et al.*, 2015). We believe that competition for shelter could account for the observed pattern, since leaves and branches of the macrophytes banks in tropical rivers attain high structural complexity and are intensely used by small characins to shelter from predators (Werner *et al.*, 1977; Savino, Stein, 1989; Suarez *et al.*, 2013). The main predators to which these fish are exposed in daylight are visually oriented birds and predatory fishes such as *Salminus brasiliensis* (Cuvier, 1816).

Most of the interspecific agonistic interactions in the Rock habitat involved *P. nasus* and *J. acanthogaster*. *Parodon nasus* chased *J. acanthogaster* with high frequency, likely as a result of defence of feeding territories. Feeding territories in tropical freshwater fishes have rarely been detected, particularly in comparison to other systems in which this strategy is common, such as reef systems (Sazima, 1988; Barlow, 1993; Silva *et al.*, 2009). However, there is evidence that this species establishes feeding territories: 1) it has small home ranges, spending much time on patrol, chasing and feeding, as was also observed by Silva *et al.* (2009); 2) this fish feeds on the bottom with high frequency and intensity in the Rock habitat, where it is abundant, and remains in the same area for long periods of time (as revealed by the remote videos); 3) it chased mostly *J. acanthogaster*, an abundant species that also feeds frequently over the same substratum, presumably targeting a similar set of resources (periphyton over the rocks).

In this study, we present evidence that fish interactions in a tropical river depend largely on patterns of fish abundance/biomass, but also, to some extent on particularities of habitat. These factors were decisive in the intensity and structure of feeding and agonistic interactions among the sampled habitats and can also contribute to understanding patterns of fish species distribution in other tropical rivers. We demonstrated the importance of quantitatively understanding fish intra- and interspecific interactions while considering the heterogeneity of the environment. This reinforces the logical conclusion that keeping habitat heterogeneity in tropical rivers, for example by controlling anthropogenic impacts and preserving the riparian forest, is essential to maintaining the structure of species interactions and likely also ecosystem functions.

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