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**O efeito da heterogeneidade de habitats nas interações alimentares e agonísticas da ictiofauna**

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"...Try not. Do or do not. There is no try."  
Master Yoda





## RESUMO

As interações ecológicas de peixes podem modular a diversidade e assegurar a estabilidade de comunidades biológicas em rios tropicais. Apesar dessa importância, pouco se sabe sobre como essas interações ecológicas estão relacionadas com o ambiente em que ocorrem, e como a heterogeneidade de habitats pode afetar essas interações. Visto isso, o presente estudo pretendeu investigar a variação na estrutura das interações alimentares e agonísticas que peixes realizam em um rio tropical de águas claras, através de filmagens remotas subaquáticas em três habitats (Lago, Planta e Rocha), com diferentes características ambientais, do rio Olho d'água, localizado no município de Jardim, MS. Cada amostra consistiu na filmagem por 15 min de uma área de 2 m<sup>2</sup>, previamente delimitada com trena. Em laboratório, foram analisados os 10 min centrais contínuos de cada vídeo, onde foi registrado o número de mordidas de cada peixe no substrato e coluna d'água, estimado o tamanho de cada indivíduo de peixe que interagiu e o número de perseguições realizadas por cada indivíduo. O número de mordidas no substrato e o tamanho do indivíduo foram utilizados para calcular a pressão alimentar que cada peixe exerceu no substrato. Para verificar como diferiu a estrutura da pressão alimentar entre os habitats, foi utilizado um escalonamento multidimensional não-métrico (nMDS) e uma análise de similaridade (ANOSIM). Também foi investigado o papel da biomassa e abundância das espécies (obtidos através de censos visuais) na pressão alimentar e interações agonísticas (respectivamente) através de uma regressão linear. Os resultados demonstram haver diferenças na estrutura de ambas as interações entre os habitats. A pressão alimentar foi maior no habitat de Rocha, se comparado com os outros dois habitats, isso se deve especialmente a pressão alimentar exercida por peixes pastejadores que raspam o perifíton e detritos nesse habitat. O maior número de perseguições foi realizado no habitat de Lago, sendo o número de perseguições intraespecíficas maior que interespecíficas em todos os habitats, e essas perseguições foram realizadas, principalmente, pelas espécies mais abundantes em cada habitat. Este estudo mostra a importância de se entender interações de peixes em rios tropicais considerando a heterogeneidade desse ecossistema juntamente aos aspectos biológicos das espécies.

**Palavras-chave:** Heterogeneidade ambiental, ecologia de peixes, interações ecológicas, micro-habitat, serra da Bodoquena, pressão alimentar



## ABSTRACT

Ecological interactions of fishes can modulate the diversity and enhance the stability of biological communities in tropical rivers. Despite previous efforts to describe among-habitat variation in freshwater fish diversity and abundance, the relation between ecological interactions and habitat heterogeneity remains poorly understood. To investigate the among-habitat variation in fish feeding pressure on the benthos and agonistic interactions between fishes, we recorded remote underwater videos in three habitats (Lake, Plant and Rock), with different environmental characteristics, on the Olho d'água river, Jardim city, MS - Brazil. Each sample consisted in a recording of a 2m<sup>2</sup> area during 15 minutes with the central 10 minutes of each video analyzed in the laboratory. For each individual fish in each video, we recorded the number of bites taken in the water column and on the substrate, the number of chases given and received, and its total body length (estimated visually). The number of bites and the size of each individual was used to calculate the feeding pressure on the substratum. We performed a non-metric Multidimensional Scaling (nMDS) and similarity analyses (ANOSIM) to test how feeding pressure changes according to the habitat. We also investigated the relationship between these ecological interactions and fish abundance/biomass obtained in each habitat through underwater visual surveys. We found differences in the structure of both interactions among habitats. Fish feeding pressure was higher in the Rock habitat, mostly due to the presence of grazer fishes that scrape this substratum in search of periphyton and detritus. The intensity of chases was higher in the Lake habitat and the intensity of intraspecific chases higher than interspecific in all the habitats and mostly performed by the most abundant species. With this study we show the importance of understanding interactions in tropical rivers according to different aspects such as habitat complexity, biotic traits and species life-history.

**Keywords:** Bodoquena plateau, feeding pressure, fish ecology, fish interaction, habitat heterogeneity, micro-habitats



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## 1. INTRODUÇÃO

### **Interações ecológicas**

Interações ecológicas podem ser definidas como relações harmônicas e desarmônicas que ocorrem entre indivíduos pertencentes a uma mesma comunidade biológica. Interações harmônicas são aqueles na qual pelo menos um dos indivíduos envolvidos é beneficiado da interação sem causar prejuízos ao outro indivíduo (+/0 ou +/+). Como exemplo dessa relação, podemos citar as interações mutualísticas de limpeza em que peixes e invertebrados estão envolvidos em ambientes recifais (FLOETER; VÁZQUEZ; GRUTTER, 2007; QUIMBAYO et al., 2016). Interações desarmônicas, por sua vez, são aquelas em que pelo menos um dos indivíduos é beneficiado da relação em detrimento do outro indivíduo (+/-). Como exemplo dessa interação, pode-se citar a competição por recursos alimentares, abrigos e parceiros sexuais, e a predação em comunidades biológicas.

Estudos prévios demonstram a importância tanto de interações harmônicas e desarmônicas, principalmente, em modular e estruturar comunidades biológicas. Em seu estudo, Stachowicz (2001) revisa a importância que as interações positivas possuem em reduzir o estresse físico e biótico de um determinado ambiente e criar habitats nos quais outras espécies dependeram para seu crescimento e desenvolvimento, dessa forma influenciando na estruturação de comunidades biológicas. Estes *et al.* (2011) demonstraram a importância de interações de predação na estruturação de comunidades e até mesmo na regulação do ecossistema. Nesse estudo os autores demonstram como o efeito das ações antropogênicas (como remoção de predadores de topo através da caça), podem modificar a cascata trófica de uma comunidade biológica e mudar a fisionomia do ambiente.

### **Interações tróficas e agonísticas de peixes**

Em rios tropicais, peixes são elementos conspícuos conhecidos pela variedade de interações nas quais estão envolvidos, tanto com elementos autóctones (e.g. macrófitas aquáticas, outros peixes) quanto com alóctones (e.g. folhas, sementes e frutos; SABINO; SAZIMA, 1999). Dentre essas muitas interações, possíveis de ocorrerem nos ambientes aquáticos, as relações tróficas e agonísticas podem ser consideradas como duas das mais importantes interações nas quais peixes estão envolvidos, devido, principalmente, a sua capacidade de

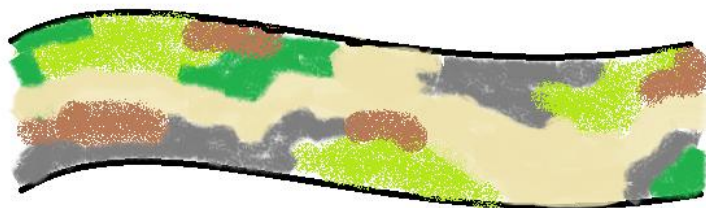
moldar a comunidade local, atuando nas teias tróficas através de efeitos de predação e competição.

Apesar dessa importância, estudos que quantificam essas interações tendem a focar em relações de predação entre peixes (JACKSON; PERES-NETO; OLDEN, 2001; SAVINO; STEIN, 1989). Poucos trabalhos relatam a interação trófica entre peixes e a comunidade bentônica (e.g. detrito, macrófitas, algas, invertebrados) em termos de grupos funcionais, sendo a maioria focado em uma única espécie (LODGE, 1991; POWER, 1983; TAYLOR; FLECKER; HALL JR., 2006). Interações agonísticas, além de predação, podem ocorrer devido a diversos comportamentos animais, como predação de escamas (SAZIMA, 1983), territorialidade (GERKING, 1959) ou competição por recursos como comida, abrigo ou companheiros sexuais (BONIN et al., 2015).

Estudos prévios em ambientes dulcícolas demonstram a importância de compreender o papel dessas interações na ciclagem de nutrientes e estruturação da comunidade, e como elas são dependentes de características intrínsecas à espécie como morfologia e tamanho (POWER, 1983; TAYLOR; FLECKER; HALL JR., 2006; WINEMILLER et al., 2006). Apesar dessa importância, poucos estudos demonstram como essas interações são dependentes do contexto em que ocorrem (CHAMBERLAIN; BRONSTEIN; RUDGERS, 2014; THOMPSON, 1988), ou seja, como são estruturadas de acordo com a heterogeneidade ambiental presente em sistemas aquáticos como rios tropicais.

### **Heterogeneidade de habitats e fatores que afetam interações em rios tropicais**

A maioria dos rios tropicais apresentam um mosaico de habitats ao longo de seu percurso (**Figura 1**), esses habitats podem ser definidos através da composição do substrato, fluxo da água, profundidade, entre outros fatores físicos do ambiente, que conferem uma estrutura tridimensional ao sistema. Essa estrutura tridimensional do habitat pode influenciar diretamente na comunidade de peixes, determinando de que forma e quais espécies de peixes utilizaram esse habitat (BELL; MCCOY; MUSHINSKY, 1991; GORMAN; KARR, 1978; WILLIS; WINEMILLER; LOPEZ-FERNANDEZ, 2005).



**Figura 1.1** - Exemplificação teórica do mosaico de substratos em um rio tropical. Cores representam tipos de habitats, que diferem quanto ao seu substrato e podem estar distribuídos em manchas ou serem contínuos ao longo do rio.

Mesmo pertencentes a uma mesma comunidade, diferentes espécies tendem a utilizar esses habitats de forma diferenciada, justamente, para evitar uma sobreposição de nichos que poderia resultar em uma exclusão da espécie do ambiente. Essas características do habitat, somadas as características intrínsecas a espécie, como tamanho corporal, posição da boca e preferência alimentar, vão determinar como e qual habitat será o preferencial para uma determinada espécie interagir (WERNER et al., 1977).

Por exemplo, é esperado que um peixe com um tamanho corporal grande e uma boca propícia para raspar o substrato de forma grosseira, evite uma interação alimentar em habitats tridimensionalmente mais complexos, como habitats cobertos por plantas. Da mesma forma, peixes com tamanho corporal pequeno (e.g. lambaris e piavas), tendem a utilizar mais esses habitats de plantas como abrigos contra a predação. Cascudos tendem a evitar substratos arenosos e utilizar substratos consolidados para se alimentar, como troncos de árvores e rochas, isso se deve, principalmente, ao seu hábito alimentar e sua morfologia bucal adaptada a raspar o substrato em busca de alimento.

Além das condições abióticas do ambiente e as características das espécies, a abundância de indivíduos é outro fator que pode afetar e ser afetada pelas interações que as espécies realizam. Por exemplo, a predação pode atuar diretamente na distribuição e abundância da presa, podendo levar, inclusive a extinção da presa, caso a abundância do predador seja maior que o suportado pelo ambiente. Em interações interespecíficas de competição, a agressividade proporcionada por espécies raras (baixa abundância) terá baixo efeito sobre a população de uma espécie com elevada abundância, porém, o contrário, espécies

abundantes podem levar a extinção de espécies raras no local, caso haja uma competição por um determinado recurso (BEGON; TOWNSEND; HARPER, 2006).

### **Olho d'água e Filmagens remotas**

Localizado no município de Jardim e pertencente a bacia hidrográfica do Paraguay, o rio Olho d'água está contido na Reserva Particular do Patrimônio Natural Cabeceiras do Prata, sendo utilizado como atrativo turístico para a prática de flutuações. Devido estar sob influência da Serra da Bodoquena esse rio possui alta transparência horizontal da água, comumente maior que 30 metros, e uma heterogeneidade de habitats ao longo de seu percurso de aproximadamente 2 quilômetros (MORAIS, 2011).

Essas características físicas, como a alta transparência da água e a diversidade de habitats, somadas a uma elevada diversidade de espécies, possibilitam estudos dos mais diversos propósitos, o que torna o local um “laboratório natural” principalmente para estudos que abordam o comportamento das espécies de peixes desse local. Nesse contexto, a utilização de filmagens remotas subaquáticas, ou seja, filmagens sem a presença do pesquisador, representam um avanço na ciência da história natural e ecologia já que permitem o registro de interações sem uma possível influência, do pesquisador, no comportamento e interações dos peixes.

O uso desse método, para quantificar interações de peixes, ocorreu primeiramente em ambientes marinhos, mais especificamente em recifes rochosos e de corais, e permitiu aos pesquisadores entender melhor a relação entre a assembleia de peixes e a comunidade bentônica (substrato do recife composto por diversos invertebrados e algas). Especificamente, permitiu aos pesquisadores saber a real importância das funções exercidas pelos peixes no sistemas, como por exemplo, a importância e os padrões de herbivoria exercida pelos peixes (ver mais detalhes em LONGO; FERREIRA; FLOETER, 2014).

### **Objetivo, perguntas e hipóteses**

Visto que interações podem variar em intensidade e estrutura de acordo com parâmetros abióticos e bióticos e a possibilidade de entender interações visualmente orientadas em um rio de águas claras, o objetivo desta dissertação é compreender como as interações que os

peixes desempenham são relacionadas (quali e quantitativamente) à heterogeneidade ambiental de um rio tropical.

Especificamente, pretendeu-se responder às seguintes questões: [1] Como a estrutura das interações alimentares (peixe-bentos) e agonísticas (peixe-peixe) diferem entre habitats? Como hipótese, considera-se que tanto as características dos peixes quanto as particularidades do habitat vão determinar a estrutura e força das interações que os peixes realizam. [2] A pressão alimentar e as interações agonísticas são dependentes da biomassa e abundância dos peixes (respectivamente)? Como hipótese, considera-se que a biomassa e a abundância de uma espécie exercem um importante papel em explicar a pressão alimentar no substrato e as interações agonísticas em que a espécie está envolvida.

## 2. CAPÍTULO

Formatado para ser submetido ao periódico *Freshwater Biology*

### **Among-habitat variation in fish feeding and agonistic interactions in a tropical clearwater river**

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**Abbreviated title:** Among-habitat variation in fish interactions

**Keywords:** Bodoquena plateau, feeding pressure, fish behavior, habitat heterogeneity



## Summary

1 - Ecological interactions of fishes can modulate the diversity and enhance the stability of biological communities in freshwater ecosystems. Despite previous efforts to describe fish interactions in tropical rivers, how fish ecological interactions vary in heterogeneous tropical rivers, is still poorly understood.

2 - To investigate the among-habitat variation in fish feeding pressure on the benthos and agonistic interactions between fishes, we used remote underwater videos in three different habitats (lake, plant and rock) in a clearwater river in Central Western, Brazil. We also investigated the relationship between ecological interactions and fish abundance/biomass quantified in each habitat through underwater visual census.

3 - We found differences in the structure of both feeding and agonistic interactions among habitats. Fish feeding pressure was higher in the rocky habitat, mostly due to the presence of grazer fishes that scrape this substratum probably targeting periphyton and detritus. Intraspecific dominated over interspecific agonistic interactions in all the habitats, and were mostly performed by small characins. More species interacted agonistically in the plant habitat, but more interactions were recorded in the lake.

4 – Species' biomass and abundance explained respectively 46% and 63% of the variation in the number of feeding and agonistic interactions, performed by species across habitats. Species' traits, such as food preferences or territoriality, could be influencing why a species interact more or less than expected by their biomass and abundance.

5 – We showed how the intensity and species composition of feeding and agonistic interactions change according to habitat heterogeneity, fish biomass and abundance. Because the effects of these interactions can scale-up and affect the ecosystem functioning, this study highlights the importance of understanding among-habitat variation in species interactions in tropical rivers.

## Introduction

Studies addressing species interactions has shown that biological interactions per se and its combination with abiotic components can determine the community structure in freshwater systems at a local scale (Winemiller 1991; Jackson, Peres-Neto & Olden 2001; Montaña & Winemiller 2010; Brown & Lawson 2010). However, researchers are still building knowledge of ecological interactions performed by the entire fish assemblage in the highly heterogeneous and often complex tropical freshwater systems (Thompson 1988). In these systems, previous studies have demonstrated the importance of interactions and how it are dependent of habitat particularities and animal traits (Power 1983; Bergman and Moore 2003; Winemiller et al. 2006). Both habitat particularities (e.g. substrate type and complexity) and animal traits (e.g. mouth morphology) can determine to which extent and how a fish will use a certain habitat on heterogeneous environments such as tropical rivers.

Although freshwater fishes are known to perform a variety of interactions with autochthonous and allochthonous components in tropical rivers, studies that quantify trophic interactions in a community perspective tend to focus only on predation events between fishes (Savino & Stein 1989; Jackson *et al.* 2001). Despite the importance to the energy flow and nutrient cycle in aquatic ecosystems, few studies have quantified fish feeding on the benthos from the perspective of different fish functional groups (i.e. invertivores, herbivores and omnivores) and how it relates to fish abundance and biomass (but see Longo, Ferreira & Floeter 2014; Longo *et al.* 2015 for marine systems; and Power 1983; Lodge 1991 for freshwater systems). By grouping species into functional groups according to similar traits, we assume that those species have the same role in the environment and, by consequence, we can better understand the importance for their function in an ecosystem perspective (Halpern & Floeter 2008).

Agonistic interactions in freshwater systems could be motivated by different reasons such as resource acquisition (Sazima 1983), territorial defense (Gerking 1959) and sexual selection (Bergman & Moore 2003). Although the exact cause of agonistic interactions is hardly identifiable in field studies, intrinsic and extrinsic aspects (i.e. species abundance, habitat structure) can affect interaction intensity in a community (Bergman & Moore 2003; Brown & Lawson 2010). Despite being poorly studied on freshwater systems, studies addressing principally territorial defense on coral and rock reefs showed the

importance of agonistic interactions for community structure (see Bonin *et al.* 2015 for a review on competition).

Species abundance can contribute substantially to the asymmetry in the structure of interactions network, for instance they can explain why the strength of the interactions are disproportional among species, being less abundant species asymmetrically affected by abundant partners, while high abundant species tended to interact symmetrically (Vázquez *et al.* 2007). Habitat structure may also affect species interactions. For example, increased habitat complexity generated by three-dimensional biotic and abiotic elements (Savino & Stein 1989; Bell, McCoy & Mushinsky 1991; Petry, Bayley & Markle 2003), can be used differentially by fishes as a refuge, to avoid predation, and as a foraging site (Coull & Wells 1983; Savino & Stein 1989; Smith, Johnston & Clark 2014). Besides that, impaired visual contact between individuals in structurally complex habitats might reduce detectability. This would be more important in clear water environments that favor visually oriented interactions (Bergman & Moore 2003; Ranåker *et al.* 2014).

Since species interactions, especially feeding and agonistic, are so understudied in heterogeneous tropical rivers, our main goal is to understand how fish interactions are related (qualitatively and quantitatively) to habitats with structural differences. Specifically, we addressed the following questions: [1] How does the structure of fish feeding and agonistic interactions differ among habitats? We hypothesized that species traits, such as feeding mode, and habitat characteristics, such as structural complexity, could determine variations in the structure and strength of interactions among habitats. [2] Do species' feeding and agonistic interactions vary according to species' biomass and abundance, respectively? We hypothesized that the intensity of the feeding pressure of a particular species is positively related to this species' biomass; and that the intensity of agonistic interactions is dependent on species abundance.

## **Methods**

### *Study area*

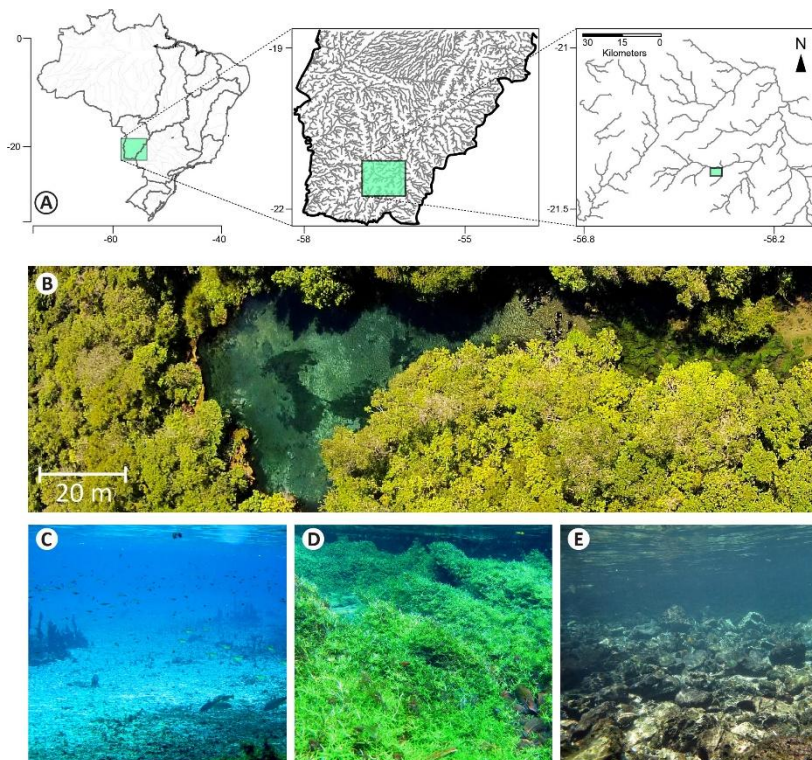
Sampling was carried during four consecutive days of May 2011 in the Olho d'Água river, a tributary of the Miranda River in the upper Paraguay basin, in the state of Mato Grosso do Sul, Central Western Brazil (Fig 1). Located in a Private Reserve of Natural Heritage, this

river is directly affected by the karstic geomorphology of the Bodoquena Plateau and has, as a consequence, high horizontal water transparency (often greater than 30 m). Along its two kilometer course, this river have a great variety of habitats (here defined according to their substrate type) and is subject to constant environmental conditions such as temperature (23 – 25°C) and water volume (Manço & Pivatto 2007; Teresa *et al.* 2014).

We sampled three habitats (Lake, Plant and Rock) in the first kilometer of the river (Fig 1) that differed in substratum physiognomy and heterogeneity. The "Lake" is a 600 m<sup>2</sup> and three-meter-deep lentic habitat located in the upper portion of the river, with a substratum covered by filamentous cyanobacteria, gravel and sand. The "Plant" habitat occurs in patches along the river; it is a lotic and shallow (about one-meter-deep) habitat with a slow water flow where the substrate is covered by macrophytes, mostly *Myriophyllum aquaticum* (Haloragaceae; A. Vaill 1719) and *Heteranthera zosterifolia* (Pontederiaceae; Mart. 1885) (Manço and Pivatto 2007), filamentous cyanobacteria, and sand. The "Rock" is also a lotic habitat that occurs in patches along the river and has a slow-to-medium water flow and substratum covered by macrophytes, stones, gravel, sand and twigs.

### *Underwater remote videos*

In each habitat, we recorded 14 underwater remote videos during the day (from 0900 to 1600 hours) to assess the fish feeding and agonistic interactions. Videos were recorded with a digital camera, on a tripod with lead weights, focused on areas of the river bottom. A measuring tape was set to establish focal areas of 2 m<sup>2</sup>. After the demarcation, the tape was removed and these focal areas were recorded over 15 minutes, with the central 10 minutes of each video analyzed in the laboratory (Longo *et al.* 2014). Care was taken so that the area of the plots did not overlap, with a minimum distance of three meters between plots. This method was adapted from previous studies in the marine system (Longo *et al.* 2014, 2015).



**Fig 1** - Olho D'Água river located in the upper Paraguay River basin, Central Western Brazil (A). The clear water allows observation of the underwater vegetation even in aerial photographs (B). Three sampled habitats are Lake (C), Plant (D) and Rock (E).

### *Underwater visual surveys*

To assess the mean species biomass and abundance in the habitat we performed 10 underwater visual surveys in each habitat. This method, adapted from previous works conducted in marine systems, consisted of a belt transect in which a researcher, in free diver, swim in a constant velocity and identified, counted and estimated the total length of fish species inside an area of 40 m<sup>2</sup> (20 x 2 m; Floeter *et al.* 2007). These surveys were performed in the same habitats and at the same moment where the videos were recording, but care was taken to avoid that the surveys areas overlap de plot areas.

### *Feeding interactions*

Individual fish that bit the substrate and floating material on the water column inside the focal area were identified and assigned to a functional group; the number of bites was counted, and individual total length was estimated based on the measuring tape initially deployed. A bite was considered when a fish hit the substratum with its jaw open, with or without further 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:  $FP = (\text{bites} \cdot \text{biomass}) / (2\text{m}^2 \cdot 10\text{min})$  (Longo *et al.* 2014). For each video (sample) we had the feeding pressure of each fish species and functional group, this was obtained by the sum of the feeding pressure of all individuals that belong to the same species and functional group. For further simplicity, we employ the unity "FP" as equivalent to the outcome of the feeding pressure equation.

The biomass (B) of each individual that bit the substrate was calculated based on the equation:  $B = a \cdot (TL \cdot CF)^b$ , where TL represents the total length (cm) visually estimated from the videos, a and b are parameters of length-weight relationships for each species obtained from the literature (e.g. Benedito-Cecilio & Agostinho 1997; Batista-Silva *et al.* 2015; Oliveira *et al.* 2015), and CF is the correction factor between total length and standard length, used depending on whether a and b were derived from individuals measured in total or standard length. In the case of species for which a and b parameters were not found, we used parameters of a congeneric species (Supplementary material Table 2).

### *Functional groups*

To better understand the relationship between fishes and benthic communities, we used two traits to classify all fishes into functional groups depending on their food capture behavior and diet. Species' food capture mode were obtained through the videos analyses and literature and species diet according to the literature. When data for a given species were not available, we considered a congeneric species on our search. Fish species were classified as:

**Grazing detritivore:** Bottom-dwelling fishes that forage mostly on sand and rock substrata. They have morphological adaptations such as labial teeth to scrape the substrate and sort the sediment in their oral

cavity to retain organic detritus and eliminate inorganic matter such as sand (Bowen 1983). They can ingest a large amount of detritus and sediment, but can also eat a small portion of plant material and benthic invertebrates.

**Grazing periphytivore:** Bottom-dwelling fishes that forage over hard substrata such as rocks, fallen trees and twigs. They have also morphological adaptations to scrape periphyton that covers this substrate. A small portion of detritus and plant material might also be ingested.

**Browsing herbivore:** Fishes that browse pieces of macrophytes and algae. They can also eat allochthonous material such as leaves, seeds, fruits and in a smaller scale invertebrates.

**Digging omnivore:** Bottom-dwelling fishes that excavate the sandy substrate or among plants while biting, ingesting plant parts (including roots) and buried invertebrates. They commonly stir the sediment up, attracting follower fishes.

**Nibbling omnivore:** Bottom-dwelling fishes that ingest both animal (e.g. invertebrates) and vegetable (e.g. seeds and macrophytes) items taking small bites on the substratum. They commonly bury a part of their snouts in the substratum, but without causing sediment clouds that attract followers.

**Picking omnivores:** Water column fishes that pick loose items at the surface, water column or bottom, commonly ingesting leaves, seeds, other plant fragments and small invertebrates.

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

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

### *Agonistic interactions*

We considered as agonistic interactions all events in which a fish chased another without any obvious feature that could be associated to predation. We defined as a chase an event, generally no longer than three seconds, when a given individual fish swam rapidly towards another fish with subsequent escape of the latter, with or without contact between them. Features that could be associated to predation would usually include large size disparities, with the chaser fish much larger than the chased one, or when a fish deliberately bit another one in pursuit of mucus or scales (Sazima 1983; Lima *et al.* 2012). This last interaction, also called mutilating predation, could be easily

distinguished because the chased fish would flee only after physical contact (Lima *et al.* 2012), while in an agonistic interaction the chased fish would flee as a response to the chaser's movement, with or without physical contact.

### *Data analysis*

To assess whether our categorical classification of habitat was able to capture the main features of environmental heterogeneity, we used a non-metric Multidimensional Scaling and Similarity Analyses (nMDS and ANOSIM), both made with Euclidean distance matrix, among habitats. Both analyses were performed with nine environmental variables visually estimated from the videos and subsequently transformed by their “range”. The variables were: percent cover of cyanobacteria, macrophytes, rock, gravel and sand; height of macrophytes and height of the filamentous cyanobacteria; presence or absence of twigs near or inside the plot; and maximum depth of each habitat (Supplementary Material Fig 1). We also performed a nMDS and an ANOSIM (both made with Bray-Curtis distance matrix) to visualize and test how feeding pressure of species and functional groups differed among habitats.

We used simple linear regression models to assess the influence of: 1) the mean biomass of each fish species at a determined habitat (obtained through visual surveys) on its corresponding feeding pressure; and 2) the mean abundance of each fish species at a determined habitat (also obtained through visual surveys) on the corresponding number of agonistic interactions in which it was involved, including chases performed and received. Both response and explanatory variables were logarithmic (ln) transformed to decrease data dispersion. For significant correlations, 95% confidence intervals were generated, species that are not included inside this interval are considered to feed/chase disproportionately to its biomass/abundance in the habitat. All analyses were performed using the packages “Scales” and “Vegan” from R software version 3.2.4 (R Core Team 2016).

## **Results**

In 420 minutes of video we counted a total of 12489 fishes' bites on the substrate (87% on the Rock, 9% Lake and 4% on the Plant habitat) performed by 18 species; and 1322 chases between fishes (59%



on the Lake, 27% Plant and 14% Rock habitat) performed by 14 species.

### *Feeding interactions*

The structure of feeding interactions by species (ANOSIM R = 0.68, p = 0.001) and functional group (ANOSIM R = 0.48, p = 0.001) varied among habitats (Table 1), with higher similarity within the habitat' samples than with others habitats. The functional structure of the feeding pressure did not vary between the Lake and Plant habitat (Fig. 2). The highest total feeding pressure was found in the Rock habitat (Mean  $\pm$  SE = 57.5  $\pm$  19.4 fp), followed by Lake (13.6  $\pm$  8.3 fp) and Plant (5.4  $\pm$  4.16 fp). Species with the highest feeding pressure tended to only feed or feed predominantly in just one habitat (Fig 3).

**Table 1** - Pairwise comparison of the feeding pressure between habitats in the Olho d'Água river, through similarity analyses (Anosim) by species and functional groups.

	Specie		Functional group	
	R	P-value	R	P-value
Lake – Plant	0.33	0.001	-0.03	0.73
Plant – Rock	0.77	0.001	0.83	0.001
Rock – Lake	0.88	0.001	0.59	0.001

In the Rock habitat, grazer fishes were the main group responsible for the feeding pressure, especially the Prochilodontidae *Prochilodus lineatus* (Fig 3), which was responsible for 58% of the total feeding pressure on this habitat. *Parodon nasus* (Parodontidae), *Jupiaba acanthogaster* (Characidae) and *Leporellus vittatus* (Anostomidae) were the most representative species of grazing periphytivore, picking omnivore and nibbling invertivore groups (respectively) and fed in almost all plots. The functional groups browsing herbivore, digging omnivore and Picking invertivore were not recorded feeding in this habitat.

In the Lake habitat, seven species distributed into five functional groups were recorded feeding on the substratum (Fig 3). The picking omnivore *Odontostilbe pequirá* (Characidae), fed at the benthos in all plots and had the highest feeding pressure of all species. The digging omnivore *Leporinus macrocephalus* (Anostomidae) and the grazing detritivore *P. lineatus* had the second and third highest feeding pressure

at this habitat, but were recorded feeding only in a few plots. The functional groups grazing periphytivore, browsing herbivore and nibbling omnivore were not observed feeding in this habitat.

Most of the eleven species feeding on the substratum in the Plant habitat had small feeding pressure and two of the 14 plots had no species feeding on the benthos. The highest feeding pressure was observed for the browsing herbivore *Brycon hilarii* (Bryconidae), followed by the digging omnivore *L. macrocephalus* and the picking omnivore *J. acanthogaster*. No grazers were detected feeding on the substratum in this habitat.

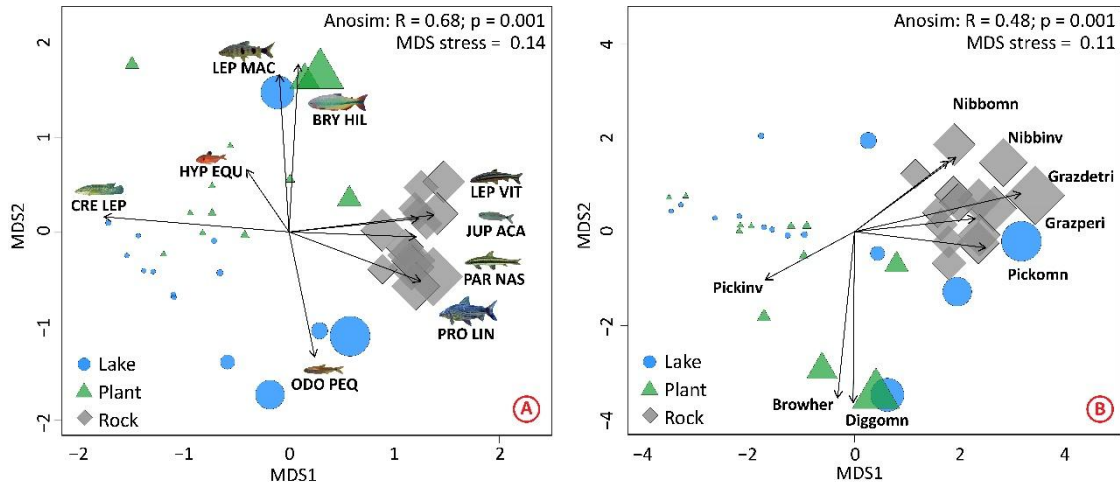
Fish biomass explained 46% of the feeding pressure variation (Fig 4) among habitats. In the Rock habitat, *P. lineatus*, *P. nasus*, *J. acanthogaster* and *L. vittatus* fed on the benthos disproportionately for their biomass in the habitat, while in the Plant habitat most of the species fed less than or equally to the expected. In the Lake habitat, *P. lineatus* fed as expected for its biomass, while *O. pequirá* and *L. macrocephalus* fed more than expected.

### *Agonistic interactions*

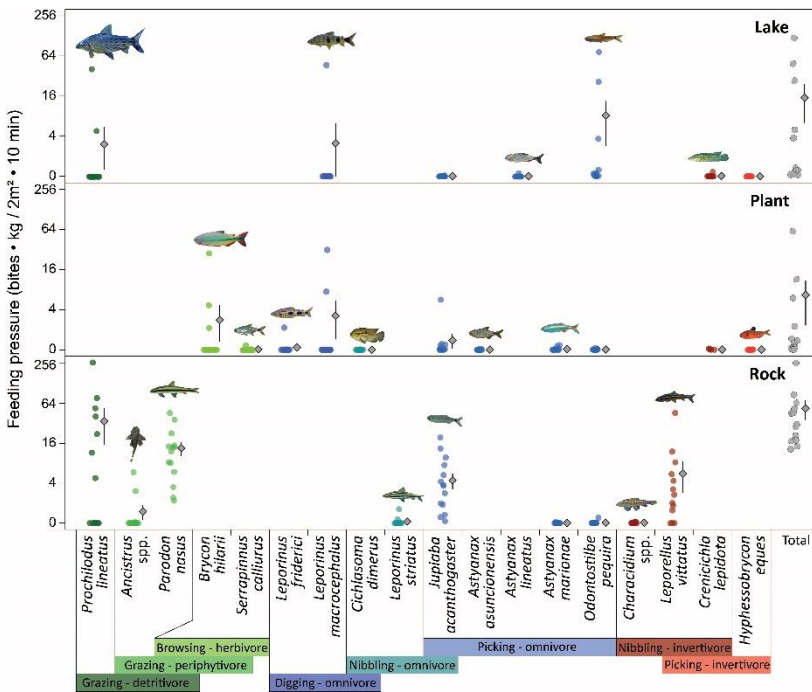
The structure of agonistic interactions changed according to habitat (Fig 5), with ten species interacting in the Plant habitat, nine species in Rock and six in Lake. In all habitats, intraspecific interactions were more intense than interspecific interactions, especially for the most abundant species (Fig 5; e.g. *O. pequirá* in the Lake and Plant habitats, and *J. acanthogaster* in the Rock habitat).

Interspecific interactions generally involved two small specimens (total length < 10cm), mainly characins. For example, *O. pequirá* chased almost all the species in the Lake and Plant habitats and was also responsible for the highest number of intraspecific interactions in these habitats (81% of the total of agonistic interactions in the Lake and 53% in the Plant, Fig 5). In the Rock habitat, *J. acanthogaster* was responsible for 50% of the total of agonistic interactions.

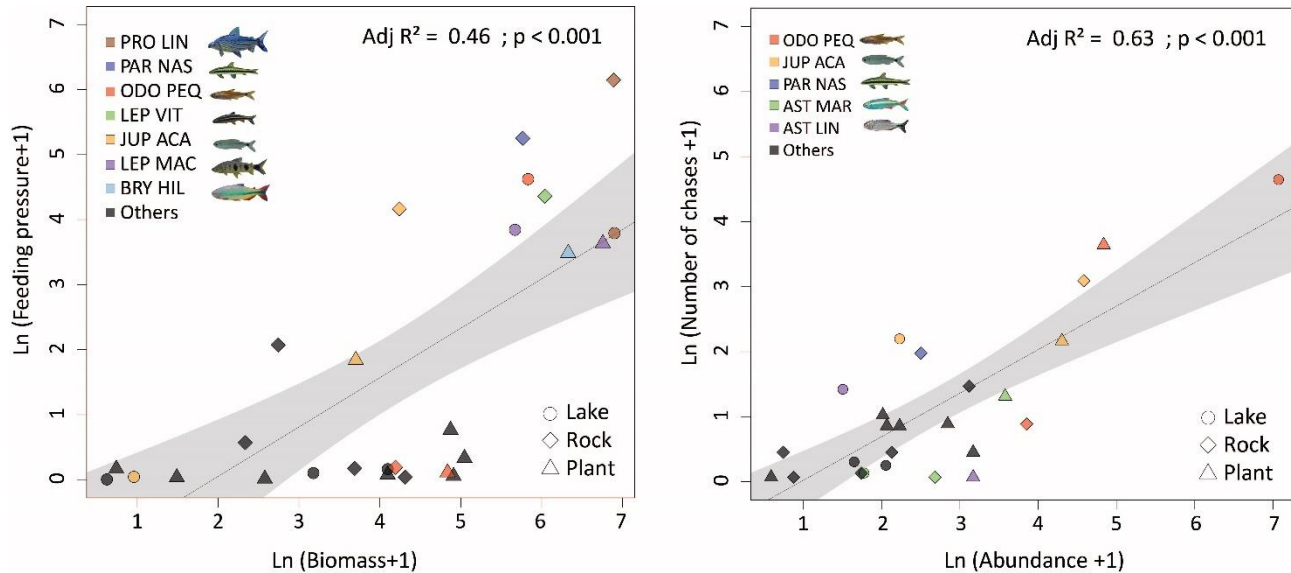
Species abundance explained 63% of the variation in the number of agonistic interactions across habitats (Fig 4). In the Lake habitat, *O. pequirá* interacted as expected by its abundance in the habitat, in the Plant habitat more than the expected and in the Rock habitat, less. In the Lake and Rock habitats, *J. acanthogaster* performed agonistic interactions disproportionately less than their abundance, while in Plant it interacted according to its abundance. *P. nasus* also interacted disproportionately more than its abundance in the Rock habitat.



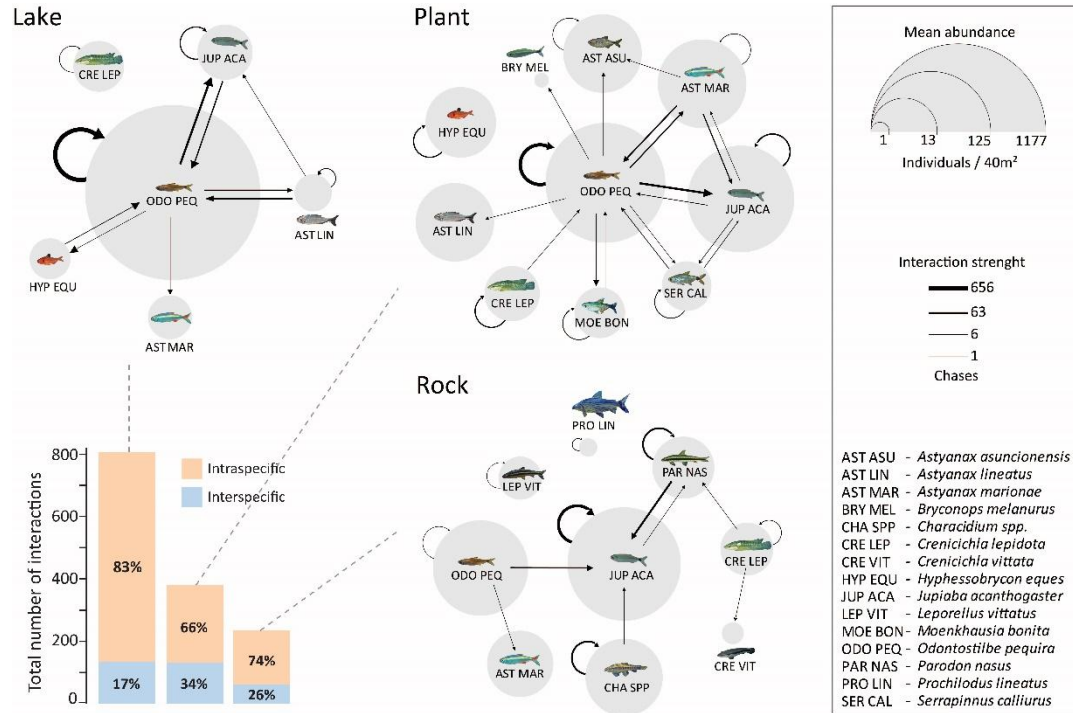
**Fig 2** - Non-metric Multidimensional scaling (nMDS) and similarity analyses (ANOSIM) of fish feeding interactions, as measured by feeding pressure among habitats of the Olho d'Água river, upper Paraguay river basin, Brazil. Symbols' sizes are proportional to the total feeding pressure in each video. (A) vectors represent species: BRY HIL = *Brycon hilarii*; CRE LEP = *Crenicichla lepidota*; HYP EQU = *Hyphessobrycon eques*; JUP ACA = *Jupiaba acanthogaster*; LEP MAC = *Leporinus macrocephalus*; LEP VIT = *Leporellus vittatus*; ODO PEQ = *Odontostilbe pequirá*; PAR NAS = *Parodon nasus*; PRO LIN = *Prochilodus lineatus*. (B) vectors represents the eight functional groups: Browher = Browsing herbivore, Diggomn = Digging omnivore, Grazdetri = Grazing detritivore, Grazperi = Grazing periphytivore, Nibbomn = Nibbling omnivore, Nibbinv = Nibbling invertivore, Pickinv = Picking invertivore, Pickomn = Picking omnivore.



**Fig 3** - Feeding pressure of the 18 fishes that interact with the substratum, and their respective functional groups (colors) at the Olho d'Água river, upper Paraguay river basin, Brazil. Gray diamonds and lines represent the mean  $\pm$  standard error, respectively. Habitats in which certain species did not feed on the substratum (zero values) are not represented in the graph. The Y-axis is log<sub>2</sub>-transformed to better show data dispersion.



**Fig 4** - Relationship between feeding pressure and biomass; and between agonistic interactions (number of chases) and biomass of fishes in the Olho d'Água river, upper Paraguay river basin, Brazil. Colors represent species with the highest interaction intensity in each case. AST LIN = *Astyanax lineatus*; AST MAR = *Astyanax marionae*; BRY HIL = *Brycon hilarii*; JUP ACA = *Jupiaba acanthogaster*; LEP MAC = *Leporinus macrocephalus*; LEP VIT = *Leporellus vittatus*; ODO PEQ = *Odontostilbe pequirá*; PAR NAS = *Parodon nasus*; PRO LIN = *Prochilodus lineatus*.



**Fig 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; gray circles are proportional to the mean abundance of each species.

## Discussion

Our study evidences the variance of feeding and agonistic interactions with habitat heterogeneity in tropical clearwater rivers. We particularly draw attention to the interplay between species' functional traits, abundance/biomass and environmental characteristics leading to habitat-specific sets of species interactions in these systems. Both types of interaction varied largely in intensity and species structure among habitats. The Rock habitat concentrated most of the fish feeding interactions on the benthic community, especially due to grazer fishes. In the Lake habitat, abundant small characins were the major players of agonistic interactions. In the Plant habitat, both the feeding and agonistic interactions were less intense, but involved more species.

The results support that species' biomass and abundance explained a good portion of the variance in the feeding and agonistic interactions (respectively) across habitats. For example, the higher the species' body-size (e.g. *P. lineatus*), the higher will be its gross energetic consumption (Brown *et al.* 2004; Taylor, Flecker & Hall Jr. 2006) and so, we expect, its feeding pressure. All else being equal, the more abundant a species is, the greater will be the probability of it encountering other species that share the same microhabitat, and, therefore, interacting with them.

However, in many cases, fishes interacted disproportionately to their biomass or abundance in a habitat. In these cases, species traits such as body-size, swimming capacity, food preferences and morphological adaptations of the mouth and eyes, might determine its preference for a substratum type to be exploited or the species with which to interact (Douglas & Matthews 1992; Gerking 1994; Wainwright & Bellwood 2002). The interaction between these functional traits and environmental features, such as substratum type, water flow, depth, and coverage of riparian vegetation results in distinct behaviors, and therefore interactions, associated with distinct habitats of the river (Power 1983).

### *Feeding interactions*

Grazer herbivores and grazer detritivores are critical in freshwater ecosystems (Power 1983; Bowen 1983; Prejs 1984; Lodge 1991; Taylor *et al.* 2006), in this study, higher feeding pressure was observed in the Rock habitat, justified by these grazer fishes that fed almost exclusively in this habitat. The grazer periphytivore (*Ancistrus*

spp. and *P. nasus*) were recorded scraping on hard substratum such as trunks and rocks, probably to feed on periphyton. This is a food resource with a high nutritional value mostly composed of microalgae, specially diatoms and cyanobacteria (Power 1983). More than the simple availability of periphyton, which tends to concentrate over hard structures, its algal composition and proportion of associated detritus may vary according to habitat features leading to differences in nutritional quality and, therefore, determining the selection by a fish to feed (Power 1983).

Detritivory by fishes, as well as herbivory, contribute to the control of carbon organic flow, energy flux and material cycling in tropical rivers (Bowen 1983; Winemiller *et al.* 2006; Taylor *et al.* 2006). In this study, the grazer detritivore *P. lineatus* fed more than was expected based on its biomass in the Rock habitat. This species is capable of feeding over both consolidated and unconsolidated, ingesting deposited material, sorting it through its gills and retaining only preferential food items such as algae and detritus (Bowen 1983; Fugi, Hahn & Agostinho 1996). Contrarily, the association of its morphological features (e.g. labial teeth) and habitat characteristics, such as inaccessibility to sand patches due to the high canopy of macrophytes might explain why this fish was not observed feeding on the Plant habitat.

The browsing herbivore *B. hilarii* fed exclusively on the Plant habitat. This fish is known to consume, besides of aquatic plants, also fallen fruits and insects from riparian vegetation, as well as aquatic snails (Sabino & Sazima 1999). Its frontal mouth might difficult or even prevent it from relying on other food sources, such as detritus or periphyton. Similar situation might be faced by the digging omnivores, such as *L. macrocephalus* and *L. friderici*. Their frontal, small-gaped mouth might prevent them from relying on particles (such as detritus) scattered over hard substrate (Albrecht & Caramaschi 2003). These are normally exploited resources in both soft substrate or among macrophytes by digging through it (Sazima 1986; Albrecht & Caramaschi 2003). Also during their feeding activities they usually created clouds of particles that attract a large number of follower fishes in search for food (Teresa *et al.* 2014).

In the Lake habitat, although *P. lineatus* and *L. macrocephalus* performed two of the largest feeding pressure at this habitat, they fed in just a few videos. We hypothesize that this was due to the high abundance of the small characin *O. pequirá* and the overspread occurrence of mutilating predation (Lima *et al.* 2012). In these



occasions, we observed that when these fishes approximated the bottom to feed on cyanobacteria or even in the sand spots, they were quickly targeted by small groups of *O. pequirá*. After being "attacked", these fish frequently gave up their feeding activity and rapidly swam away from the bottom to flee their attackers. This interaction was described by Lima *et al.* (2012) that suggested that *O. pequirá* targets large fishes to feed from their mucus and skin. Thus, the high abundance of *O. pequirá* in this habitat and the frequency of mutilating predation by this species might be also indirectly affecting the feeding behavior of larger bottom-feeding fishes.

Small size fishes, especially those belonging to the family Characidae, are conspicuous components from neotropical rivers and streams and are essentially known for their versatility in feeding behavior, feeding over the bottom, water column, surface and even other fishes (Sazima 1984; Lima *et al.* 2012). This versatility associated with their feeding behavior and omnivorous diet hampers the identification of feeding patterns that cannot be explained by their biomass. The feeding pressure exerted by *J. acanthogaster* was higher than expected by its biomass in the Rock habitat, as was that of *O. pequirá* in the Lake. Both species are morphologically similar (e.g. size, mouth), both are present in all three habitats (although in different abundances) and both also feed frequently on the water column (Supplementary Material Fig 2). Thus, the preference for feeding in a certain habitat could be associated with dietary preferences. In the Rock habitat, we saw small shoals (between four and 15 individuals) of *J. acanthogaster* constantly taking bites on the rocky surface, probably eating periphyton or even aquatic invertebrates due to the omnivorous character of this species (Souza, Silva & Bilce 2013).

In the Lake habitat, we observed a type of "feeding frenzy" when masses of cyanophycaea that grow attached to the bottom detached from it and floated in the water column and were immediately attacked by groups of many individuals of *O. pequirá*. These blue green algae seem to detach from the bottom due to oxygen bubbles formed by photosynthetic activity. Since we did not observe these "frenzies" happening to cyanophycaea still attached to the bottom, we suspect that *O. pequirá* could be targeting small invertebrates associated to the algae that becomes accessible only when it is detached (Dias 2007).

### *Agonistic interactions*

Although we were unable to identify the proximate reason for the chases in the video analyses, intra- and interspecific interactions that were not explained density-dependence effect may be mostly caused by competition for resources. Thus, differences in the structure and intensity of these agonistic interactions among habitats could be attributed to multiple factors, such as environmental features (e.g. substratum type, food availability, habitat structure), body-size or even by population density-dependence (Byström & Garcia-Berthou 1999; Bergman & Moore 2003; Ranåker *et al.* 2014).

Agonistic interactions were primarily intraspecific, although interspecific interactions were far from negligible in proportion (between 17 and 36% depending on habitat). Across all studied habitats, interspecific agonistic interactions were mostly associated to small-sized characin fishes and the territorial *P. nasus*. Particularly, two small characins, *O. pequirá* and *J. acanthogaster* were central to agonistic interactions: the former in both Lake and Plant habitats and the later in the Rock habitat. This centrality involved not only interacting with most of the species in each network, but also by performing and/or receiving the largest number of chases. Despite the fact that these two species interacted much more intraspecifically than interspecifically, they differ in that while *O. pequirá* chased and was chased interspecifically, *J. acanthogaster* was mostly chased by other fish.

Some species that interacted agonistically disproportionately to their abundance did that not by chasing, but by being chased by an “aggressive” species. This is the case, for example, of *J. acanthogaster* and *Astyanax lineatus* in the Lake habitat. These species were chased frequently by *O. pequirá*, the most abundant species in this habitat. The high abundance of this species, associated with high water transparency and a low substrate complexity, could lead the fishes to encounter each other more frequently and, thus, this high intensity of agonistic intraspecific interactions might simply be density-dependent (Forrester *et al.* 2006; Bonin *et al.* 2015). This is supported by the fact that this species interacted exactly as expected by its abundance on this habitat.

In the Plant habitat, most of the agonistic interactions were proportional to fish’s abundance. Since feeding pressure was generally low in this habitat, we believe that competition for shelter rather than competition for food could explain the observed pattern (Johnson 2006; Bonin *et al.* 2015). The high structural complexity proportionate by the macrophytes banks on the riverbed of this habitat might allow fishes to

shelter from predators among leaves and branches (Werner *et al.* 1977; Savino & Stein 1989; Suarez, Ferreira & Tondato 2013).

Most of the interspecific agonistic interactions in the Rock habitat involved *P. nasus* and *J. acanthogaster*, the only two species of this habitat whose number of interactions was not as explained by their abundance. In fact, *P. nasus* chased *J. acanthogaster* with high frequency, likely as a result of defense of feeding territories. Although feeding territories in freshwater fishes have rarely been documented (Sazima 1988; Barlow 1993; Silva *et al.* 2009), this species might be establishing feeding territories because: 1) it has small home ranges, spending much time on patrol, chasing and feeding as observed by Silva *et al.* (2009); 2) we observed this fish to feed on the bottom with high frequency and intensity in the Rock habitat, where this fish is abundant, and to remain in the same area during complete footages frequently; 3) it chased mostly *J. acanthogaster*, an abundant species that also bit frequently over the same set of resources, namely periphyton and detritus over the rocks, than *P. nasus*.

The trophic interaction between fish and benthos (feeding pressure), and agonistic interactions between fishes can be influenced by many environment features such as habitat structure and substrate type, as well as biotic elements such as density-dependence and fish species traits. All these aspects seem to be decisive in the outcomes and intensity of both interactions analyzed, and by consequence could give us a better idea of factors that can drive patterns of distribution and abundance of fishes in tropical rivers. Thus, we demonstrate the importance of quantitatively understanding fish intra- and interspecific interactions while considering the heterogeneity of the environment. We also highlight the strong dependence of fishes on the substrate for feeding interactions, thus reinforces, the importance of keeping habitat heterogeneity by preserving the riparian forest to avoid silting, and, its negative consequences on the structure of fish assemblage, their interactions and ecosystemic functions.

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## References

- Albrecht M.P. & Caramaschi E.P. (2003) Feeding Ecology of *Leporinus friderici* (Teleostei; Anostomidae) in the Upper Tocantins River, Central Brazil, before and after Installation of a Hydroelectric Plant. *Studies on Neotropical Fauna and Environment* 38, 33–40.
- Barlow G.W. (1993) The puzzling paucity of feeding territories among freshwater fishes. *Marine Behaviour and Physiology* 23, 155–174.
- Batista-Silva V.F., Bailly D., Kashiwaqui E.A.L., Abelha M.C.F. & Graça W.J. da (2015) Length-weight relationships for 55 freshwater fish species from the Iguatemi River, Upper Paraná River basin, Brazil. *Journal of Applied Ichthyology* 31, 257–260.
- Bell S.S., McCoy E.D. & Mushinsky H.R. (1991) Habitat Structure: The physical arrangement of objects in space. (Eds M.B. Usher, M.L. Rosenzweig & R.L. Kitching), St Edmundsbury Press Ltd.
- Benedito-Cecilio E. & Agostinho A.A. (1997) Length-weight relationship of fishes caught in the Itaipu Reservoir, Parana, Brazil. *The ICLARM Quarterly, Naga*, 57–61.
- Bergman D.A. & Moore P.A. (2003) Field Observations of Intraspecific Agonistic Behavior of Two Crayfish Species, *Orconectes rusticus* and *Orconectes virilis*, in Different Habitats. *Biological Bulletin* 205, 26–35.
- Bonin M.C., Boström-Einarsson L., Munday P.L. & Jones G.P. (2015) The Prevalence and Importance of Competition Among Coral Reef Fishes. *Annual Review of Ecology, Evolution, and Systematics* 46, 169–190.
- Bowen S.H. (1983) Detritivory in neotropical fish communities. *Environmental Biology of Fishes* 9, 137–144.

- Brown B.L. & Lawson R.L. (2010) Habitat heterogeneity and activity of an omnivorous ecosystem engineer control stream community dynamics. *Ecology* 91, 1799–1810.
- Brown J.H., Gillooly J.F., Allen A.P., Savage V.M. & West G.B. (2004) Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789.
- Byström P. & Garcia-Berthou E. (1999) Density dependent growth and size specific competitive interactions in young fish. *Oikos* 86, 217–232.
- Coull B.C. & Wells J.B.J. (1983) Refuges from Fish Predation: Experiments with Phytal Meiofauna from the New Zealand Rocky Intertidal. *Ecological Society of America* 64, 1599–1609.
- Dias T.S. (2007) Estudo da dieta de oito espécies da Subfamília Cheirodontinae (Characiformes: Characidae) em diferentes sistemas lacustres nos estados do RN e RS. Universidade Federal do Rio Grande do Sul.
- Douglas M.E. & Matthews W.J. (1992) Does Morphology Predict Ecology? Hypothesis Testing within a Freshwater Stream Fish Assemblage. *Oikos* 65, 213–224.
- Floeter S.R., Krohling W., Gasparini J.L., Ferreira C.E.L. & Zalmon I.R. (2007) Reef fish community structure on coastal islands of the southeastern Brazil: the influence of exposure and benthic cover. *Environmental Biology of Fishes* 78, 147–160.
- Forrester G.E., Evans B., Steele M.A. & Vance R.R. (2006) Assessing the magnitude of intra- and interspecific competition in two coral reef fishes. *Oecologia* 148, 632–640.
- Fugi R., Hahn N.S. & Agostinho A.A. (1996) Feeding styles of five species of bottom-feeding fishes of the high Parana river. *Environmental Biology of Fishes* 46, 297–307.
- Gerking S.D. (1994) Feeding ecology of fish. Academic Press, Inc., San Diego.
- Gerking S.D. (1959) The restricted movement of fish populations. *Biological Reviews* 34, 221–242.

- Halpern B.S. & Floeter S.R. (2008) Functional diversity responses to changing species richness in reef fish communities. *Marine Ecology Progress Series* 364, 147–156.
- Jackson D.A., Peres-Neto P.R. & Olden J.D. (2001) What controls who is where in freshwater fish communities - the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* 58, 157–170.
- Johnson D.W. (2006) Predation, habitat complexity, and variation in density-dependent mortality of temperate reef fishes. *Ecology* 87, 1179–1188.
- Lima M.R.L., Bessa E., Krinski D. & Carvalho L.N. (2012) Mutilating predation in the Cheirodontinae *Odontostilbe pequirá* (Characiformes: Characidae). *Neotropical Ichthyology* 10, 361–368.
- Lodge D.M. (1991) Herbivory on freshwater macrophytes. *Aquatic Botany* 41, 195–224.
- Longo G.O., Ferreira C.E.L. & Floeter S.R. (2014) Herbivory drives large-scale spatial variation in reef fish trophic interactions. *Ecology and Evolution* 4, 4553–4566.
- Longo G.O., Morais R.A., Martins C.D.L., Mendes T.C., Aued A.W., Cândido D. V., et al. (2015) Between-Habitat Variation of Benthic Cover, Reef Fish Assemblage and Feeding Pressure on the Benthos at the Only Atoll in South Atlantic: Rocas Atoll, NE Brazil. *PLOS ONE* 10, e0127176.
- Maço D.G. & Pivatto M.A.C. (2007) Diagnóstico e Plano de Manejo da Reserva Particular do Patrimônio Natural (RPPN) da Fazenda Cabeceira do Prata. Programa de Incentivo às Reservas Particulares do Patrimônio Natural do Pantanal.
- Montaña C.G. & Winemiller K.O. (2010) Local-scale habitat influences morphological diversity of species assemblages of cichlid fishes in a tropical floodplain river. *Ecology of Freshwater Fish* 19, 216–227.

Oliveira V.A., Loverde-Oliveira S.M., Mateus L.A. & Teixeira-de Mello F. (2015) Length-weight relationships of 26 fish species from the streams of the upper section of the Paraguay River basin (Mato Grosso, Brazil). *Journal of Applied Ichthyology* 31, 225–227.

Petry P., Bayley P.B. & Markle D.F. (2003) Relationships between fish assemblages, macrophytes and environmental gradients in the Amazon River floodplain. *Journal of Fish Biology* 63, 547–579.

Power M.E. (1983) Grazing responses of tropical freshwater fishes to different scales of variation in their food. In: *Environmental Biology of Fishes* 9, 25–38.

Prejs A. (1984) Herbivory by temperate freshwater fishes and its consequences. *Environmental Biology of Fishes* 10, 281–296.

R Core Team (2016) R: A language and environment for statistical computing.

Ranåker L., Persson J., Jönsson M., Nilsson P.A. & Brönmark C. (2014) Piscivore-Prey Fish Interactions: Mechanisms behind Diurnal Patterns in Prey Selectivity in Brown and Clear Water. *PLoS ONE* 9, e102002.

Sabino J. & Sazima I. (1999) Association between fruit-eating fish and foraging monkeys in western Brazil. *Ichthyological Exploration of Freshwaters* 10, 309–312.

Savino J.F. & Stein R. a. (1989) Behavioural interactions between fish predators and their prey: effects of plant density. *Animal Behaviour* 37, 311–321.

Sazima I. (1983) Scale-eating in characoids and other fishes. *Environmental Biology of Fishes* 9, 9–23.

Sazima I. (1986) Similarities in feeding behaviour between some marine and freshwater fishes in two tropical communities. *Journal of Fish Biology* 29, 53–65.

- Sazima I. (1988) Territorial behaviour in a scale-eating and a herbivorous Neotropical characiform fish. *Revista Brasileira de Biologia* 48, 189–194.
- Silva S.E., Assunção W.R.C., Duca C. & Penha J. (2009) Cost of territorial maintenance by *Parodon nasus* (Osteichthyes: Parodontidae) in a Neotropical stream. *Neotropical Ichthyology* 7, 677–682.
- Smith R.S., Johnston E.L. & Clark G.F. (2014) The Role of Habitat Complexity in Community Development Is Mediated by Resource Availability. *PLoS ONE* 9, e102920.
- Souza T.S.S., Silva S.A.A.R. & Bilce J.M.B. (2013) Dieta de *Jupiaba acanthogaster* (Eingenmann, 1911) em duas sub-bacias do sistema de drenagem do alto Tapajós. *Revista de Ciências Agro-Ambientais, Alta Floresta-MT* 11, 33–41.
- Suarez Y., Ferreira F. & Tondato K. (2013) Assemblage of fish species associated with aquatic macrophytes in Porto Murinho Pantanal, Mato Grosso do Sul, Brazil. *Biota Neotropica* 13, 182–189.
- Taylor B.W., Flecker A.S. & Hall Jr. R.O. (2006) Loss of a Harvested Fish Species Disrupts Carbon Flow in a Diverse Tropical River. *Science* 313, 833–836.
- Teresa F.B., Sazima C., Sazima I. & Floeter S.R. (2014) Predictive factors of species composition of follower fishes in nuclear-follower feeding associations: a snapshot study. *Neotropical Ichthyology* 12, 913–919.
- Thompson J.N. (1988) Variation in Interspecific Interactions. *Annual Review of Ecology and Systematics* 19, 65–87.
- Vázquez D., J. Melián C., M. Williams N., Blüthgen N., R. Krasnov B. & Poulin R. (2007) Species abundance and asymmetric interaction strength in ecological networks. *Oikos* 116, 1120–1127.
- Wainwright P.C. & Bellwood D.R. (2002) Ecomorphology of Feeding in Coral Reef Fishes. In: *Coral Reef Fishes*. pp. 33–55.

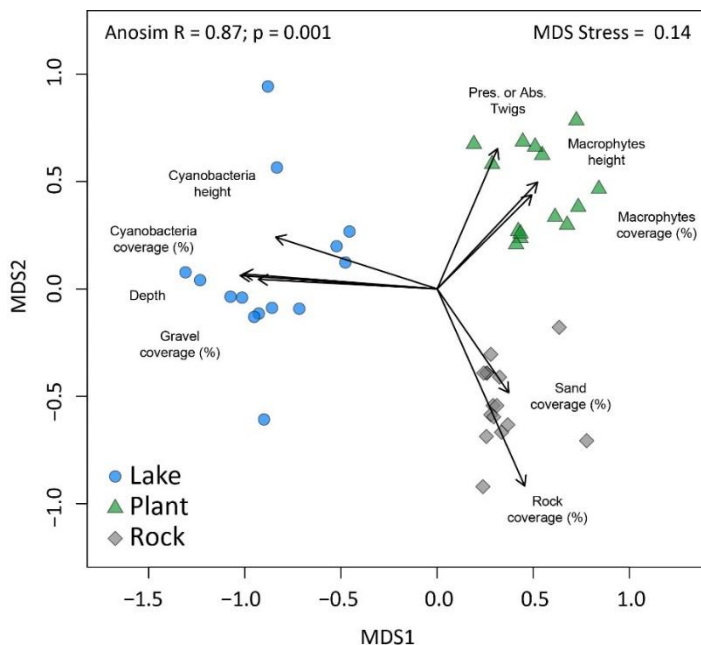


Werner E.E., Hall D.J., Laughlin D.R., Wagner D.J., Wilsmann L.A. & Funk F.C. (1977) Habitat Partitioning in a Freshwater Fish Community. *Journal of the Fisheries Research Board of Canada* 34, 360–370.

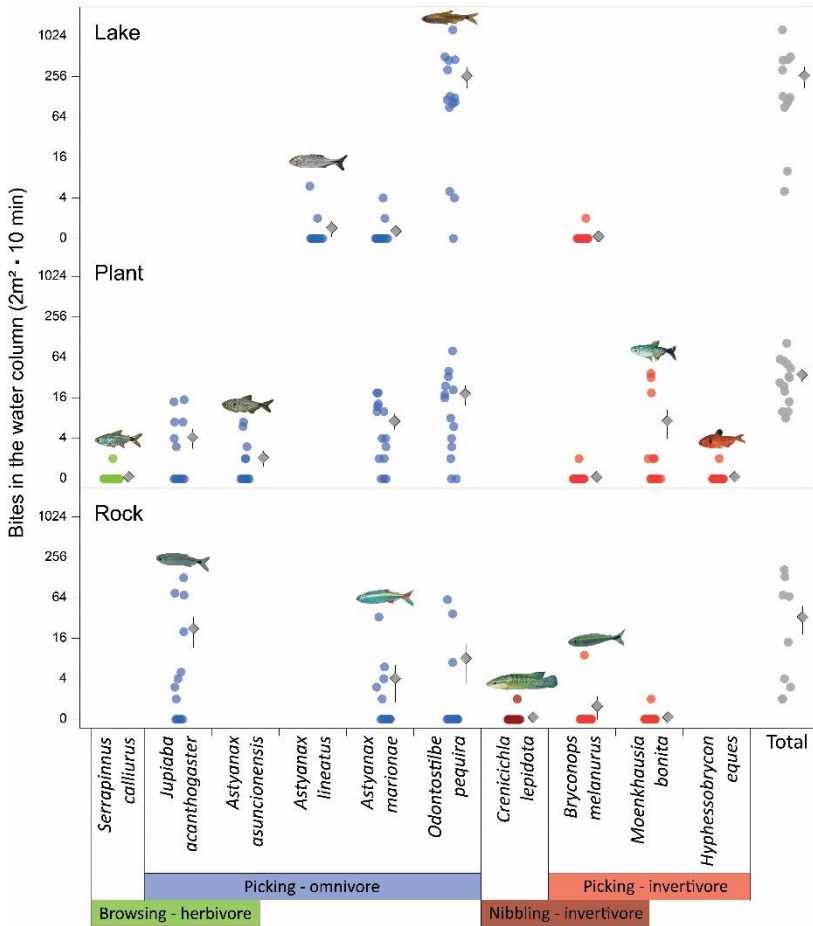
Winemiller K.O. (1991) Ecomorphological Diversification in Lowland Freshwater Fish Assemblages from Five Biotic Regions. *Ecological Monographs* 61, 343.

Winemiller K.O., Montoya J. V., Roelke D.L., Layman C. a. & Cotner J.B. (2006) Seasonally varying impact of detritivorous fishes on the benthic ecology of a tropical floodplain river. *Journal of the North American Benthological Society* 25, 250–262.

### Supplementary material



**Fig 6** - Non-metric Multidimensional scaling (nMDS) and Similarity analyses (Anosim) of nine environmental variables (arrows), visually estimated from the videos, showing that there is heterogeneity among habitats of the Olho d'água river.



**Fig 7** - Scatter plot of the bites in the water column performed by 10 species and their respective functional group. Gray diamond and lines represents the mean  $\pm$  standard error respectively. Species that does not interact on the habitat are not represented. Note that Y-axis are in logarithm scale.

**Table 2** – Parameters of length-weight relationship for species involved on feeding and agonistic interactions in the Olho d'água river. Ref = Reference for a and b parameters

<b>Specie</b>	<b>Code</b>	<b>TL / SL</b>	<b>a</b>	<b>B</b>	<b>r<sup>2</sup></b>	<b>Ref</b>
<b>Anostomidae</b>						
<i>Leporinus friderici</i>	LEP_FRI	1.1888	0.0272	2.98	0.99	Batista-Silva et al. (2015)
<i>Leporinus macrocephalus</i> *	LEP_MAC	1.23	0.0171	3.12	0.98	Benedito-Cecilio et al. (1997)
<i>Leporinus striatus</i>	LEP_STR	1	0.01	2.95	0.94	Nuner & Zaniboni-Filho (2009)
<i>Leporellus vittatus</i>	LEP_VIT	1.23	0.0243	2.92	0.92	Benedito-Cecilio et al. (1997)
<b>Bryconidae</b>						
<i>Brycon hilarii</i>	BRY_HIL	1.2463	0.0129	3.14	0.99	Benedito-Cecilio et al. (1997)
<b>Characidae</b>						
<i>Astyanax asuncionensis</i>	AST_ASU	1.3253	0.0593	2.65	0.96	Oliveira et al. (2014)
<i>Astyanax lineatus</i>	AST_LIN	1.2623	0.0618	2.65	0.96	Oliveira et al. (2014)

<i>Astyanax marionae</i>	AST_MAR	1.2559	0.053	2.63	0.97	Oliveira et al. (2014)		
<i>Bryconops melanurus</i>	BRY_MEL	1.2941	0.0509	2.5	0.98	Oliveira et al. (2014)		
<i>Hyphessobrycon eques</i>	HYP_EQU	1.2744	0.0216	3.39	0.98	Batista-Silva et al. (2015)		
<i>Jupiaba acanthogaster</i>	JUP_ACA	1.2366	0.0131	3.33	-	pers.	communication	Fabrcio Teresa
<i>Moenkhausia bonita</i>	MOE_BON	1.2586	0.0347	2.51	-	pers.	communication	Fabrcio Teresa
<i>Odontostilbe pequirá</i>	ODO_PEQ	1.3214	0.0449	2.92	0.79	Oliveira et al. (2014)		
<i>Serrapinnus calliurus</i> **	SER_CAL	1.3235	0.0194	3.31	0.97	Batista-Silva et al. (2015)		

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**Cichlidae**

<i>Cichlasoma dimerus</i> ***	CIC_DIM	1.3846	0.047	3.14	0.98	Batista-Silva et al. (2015)		
<i>Crenicichla lepidota</i> ****	CRE_LEP	1.21	0.037	2.71	0.93	Benedito-Cecilio et al. (1997)		
<i>Crenicichla vittata</i>	CRE_VIT	1	0.003	3.37	0.99	Nuner & Zaniboni-Filho (2009)		

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<b>Crenuchidae</b>							
<i>Characidium</i> spp. *****	CHA_SPP	1.2464	0.0466	2.33	0.84	Oliveira et al. (2014)	
<b>Loricariidae</b>							
<i>Ancistrus</i> spp	ANC_SPP	1.3361	0.0377	2.83	-	pers. communication	Fabrcio Teresa
<b>Parodontidae</b>							
<i>Parodon nasus</i>	PAR_NAS	1.1709	0.0602	2.5	0.98	Oliveira et al. (2014)	
<b>Prochilodontidae</b>							
<i>Prochilodus lineatus</i>	PRO_LIN	1	0.011	3.06	0.89	Nuner & Zaniboni-Filho (2009)	

\* Data obtained for *Leporinus obtusidens*; \*\* Data obtained for *Serrapinnus notomelas*; \*\*\* Data obtained for *Cichlasoma paranaense*; \*\*\*\* Data obtained for *Crenicichla haroldoi*; \*\*\*\*\* Data obtained for *Characidium zebra*

### 3. CONSIDERAÇÕES FINAIS

Este estudo demonstrou como as interações biológicas que os peixes realizam em ambientes dulcícolas podem ser dependentes das características estruturais dos habitats e de características intrínsecas (como preferência alimentar), abundância e biomassa das espécies no ambiente. Ambas as interações analisadas (pressão alimentar no substrato e agonísticas entre peixes) variaram quanto a sua estrutura e intensidade entre os três habitats analisados. Sendo que, o habitat estruturalmente mais complexo (habitat de macrófitas) abrigou o maior número de espécies que interagem, porém com uma menor intensidade para ambas as interações. No habitat de lago foi observado uma maior intensidade de interações agonísticas desempenhadas, principalmente, por uma espécie abundante nesse habitat. No habitat de rocha foi observado a maior intensidade de interações alimentares com o substrato, isso ocorreu, principalmente, devido aos peixes raspadores que possuem mandíbula adaptada para raspar itens alimentares como detrito e perifiton das rochas.

Além de entender a relação entre interações biológicas e a heterogeneidade ambiental, esse estudo demonstrou a forte relação entre os peixes e o substrato do rio. Esse resultado reforça a necessidade de conservar não apenas algumas espécies, mas sim, conservar todo o ambiente no qual essas espécies estão envolvidas. No caso de rios e riachos, essa conservação deve se estender para a mata ripária, principalmente, devido seu papel em evitar o assoreamento dos cursos d'água. Esse assoreamento pode resultar na descaracterização do substrato, o que pode afetar diretamente nas populações de peixes que dependem do substrato para se alimentar.

Futuros estudos precisam ser realizados nesse rio de águas claras, já que o mesmo pode ser considerado um “laboratório natural”, para teste de hipóteses envolvendo interações entre espécies. Interações de competição, por exemplo, podem ser analisadas para determinar quais espécies exploram o mesmo recurso alimentar e por consequência pode explicar os padrões de interações agonísticas encontradas nesse trabalho. Além de trabalhos de competição, trabalhos que determinem a fonte de produção primária que sustenta a cadeia trófica nesse sistema, poderia explicar os padrões alimentares aqui encontrados.

#### 4. REFERÊNCIAS

BEGON, M.; TOWNSEND, C. R.; HARPER, J. L. *Ecology From Individuals to Ecosystems*. p. 759, 2006.

BELL, S. S.; MCCOY, E. D.; MUSHINSKY, H. R. **Habitat Structure: The physical arrangement of objects in space**. [s.l.] St Edmundsbury Press Ltd, 1991.

BONIN, M. C. et al. The Prevalence and Importance of Competition Among Coral Reef Fishes. **Annual Review of Ecology, Evolution, and Systematics**, v. 46, n. 1, p. 169–190, 4 dez. 2015.

CHAMBERLAIN, S. A.; BRONSTEIN, J. L.; RUDGERS, J. A. How context dependent are species interactions? **Ecology Letters**, v. 17, n. 7, p. 881–890, jul. 2014.

ESTES, J. A et al. Trophic Downgrading of Planet Earth. **Science**, v. 333, n. 6040, p. 301–306, 15 jul. 2011.

FLOETER, S. R.; VÁZQUEZ, D. P.; GRUTTER, A. S. The macroecology of marine cleaning mutualisms. **Journal of Animal Ecology**, v. 76, n. 1, p. 105–111, 2007.

GERKING, S. D. The restricted movement of fish populations. **Biological Reviews**, v. 34, n. 2, p. 221–242, maio 1959.

GORMAN, O. T.; KARR, J. R. Habitat Structure and Stream Fish Communities. **Ecology**, v. 59, n. 3, p. 507, jan. 1978.

JACKSON, D. A.; PERES-NETO, P. R.; OLDEN, J. D. What controls who is where in freshwater fish communities - the roles of biotic, abiotic, and spatial factors. **Canadian Journal of Fisheries and Aquatic Sciences**, v. 58, n. 1, p. 157–170, jan. 2001.

LODGE, D. M. Herbivory on freshwater macrophytes. **Aquatic Botany**, v. 41, n. 1-3, p. 195–224, jan. 1991.

LONGO, G. O.; FERREIRA, C. E. L.; FLOETER, S. R. Herbivory drives large-scale spatial variation in reef fish trophic interactions. **Ecology and Evolution**, v. 4, n. 23, p. 4553–4566, dez. 2014.

MORAIS, R. A. **Diversidade e estrutura da ictiofauna de rios da Serra**

**da Bodoquena, Mato Grosso do Sul.** [s.l.] Universidade Federal de Santa Catarina, 2011.

POWER, M. E. Grazing responses of tropical freshwater fishes to different scales of variation in their food. In: **Environmental Biology of Fishes.** [s.l.: s.n.]. v. 9p. 25–38.

QUIMBAYO, J. P. et al. Fish cleaning interactions on a remote island in the Tropical Eastern Pacific. **Marine Biodiversity**, 23 abr. 2016.

SABINO, J.; SAZIMA, I. **Association between fruit-eating fish and foraging monkeys in western Brazil** Ichthyological Exploration of Freshwaters, 1999.

SAVINO, J. F.; STEIN, R. A. Behavioural interactions between fish predators and their prey: effects of plant density. **Animal Behaviour**, v. 37, p. 311–321, fev. 1989.

SAZIMA, I. Scale-eating in characoids and other fishes. **Evolutionary ecology of neotropical freshwater fishes**, v. 9, n. 2, p. 9–23, 1983.

STACHOWICZ, J. J. Mutualism, Facilitation, and the Structure of Ecological Communities. **BioScience**, v. 51, n. 3, p. 235, 2001.

TAYLOR, B. W.; FLECKER, A. S.; HALL JR., R. O. Loss of a Harvested Fish Species Disrupts Carbon Flow in a Diverse Tropical River. **Science**, v. 313, n. 5788, p. 833–836, 11 ago. 2006.

THOMPSON, J. N. Variation in Interspecific Interactions. **Annual Review of Ecology and Systematics**, v. 19, n. 1, p. 65–87, nov. 1988.

WERNER, E. E. et al. Habitat Partitioning in a Freshwater Fish Community. **Journal of the Fisheries Research Board of Canada**, v. 34, n. 3, p. 360–370, mar. 1977.

WILLIS, S. C.; WINEMILLER, K. O.; LOPEZ-FERNANDEZ, H. Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river. **Oecologia**, v. 142, n. 2, p. 284–95, 2005.

WINEMILLER, K. O. et al. Seasonally varying impact of detritivorous fishes on the benthic ecology of a tropical floodplain river. **Journal of the North American Benthological Society**, v. 25, n. 1, p. 250–262, mar. 2006.