FRANCISCO RICARDO DE ANDRADE NETO

ESTUDOS ECOLÓGICOS DOS PEIXES DA BACIA DO RIO JEQUITINHONHA

LAVRAS - MG

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> Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração em Ecologia e Conservação de Recursos Naturais em Ecossistemas Fragmentados e Agrossistemas, para a obtenção do título de Doutor.

Prof. Dr. Paulo dos Santos Pompeu

Orientador

Prof. Dr. José Luis Birindelli

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ECOLOGICAL STUDIES OF THE FISHES FROM THE JEQUITINHONHA RIVER BASIN

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RESUMO GERAL

Esta tese lida com a ecologia de peixes da bacia do rio Jequitinhonha. Ela foi escrita por mim e nove coautores. E a dividi em três capítulos que foram formatados de acordo com os periódicos para os quais foram ou serão submetidos. No primeiro capítulo investigamou-se a distribuição da riqueza de espécies de peixes ao longo do gradiente altitudinal. Os dados revelaram um pico de riqueza em altitudes intermediárias o que sugeria os efeitos do domínio médio como uma explicação. Entretanto, há evidência de que as espécies não se distribuem ao acaso e assim refutou-se essa teoria, bem como a regra de Rapoport. No segundo capítulo avaliou-se, pela primeira vez o pastejo de *Serrasalmus brandtii* em peixes emalhados, fora de sua área de distribuição natural. Observou-se maiores proporções de pastejo em amostras onde *S. brandtii* era a espécie dominante em relação aos locais onde ela é classificada como presente ou onde ela está ausente. *S. brandtii* pastou preferencialmente em nadadeiras caudais de peixes maiores e evitou o canibalismo. O número de espécies que são preferencialmente pastadas aumentou à medida em que a abundância de *S. brandtii* aumentava. O capítulo três lidou com a movimentação de peixes. Foram marcados e rastreados peixes de três espécies de Loricaiideos de um tributário do rio Jequitinhonha. Esses peixes tiveram pequenas áreas de vida (menores que 700 m) e requeriram hábitats específicos. O rio estudado parou de fluir em duas ocasiões durante a realização do estudo o que é preocupante em relação ao futuro de uma das espécies, *Delturus brevis*. Esses peixes dependem de matacões e águas correntes, duas características hidráulicas típicas das áreas do rio que foram as primeiras a secar. A recorrência de secas severas nas próximas décadas pode levar a extinção dessa espécie nos tributários de maior ordem do rio Jequitinhonha.

Palavras-chave: Gradiente altitudinal de riqueza de espécies. Efeitos do domínio médio. Regra de Rapoport. *Serrasalmus brandtii*. Pastejo. Loricariidae. Rádio telemetria. Hábitat hidráulico.

ABSTRACT

This thesis deals with the ecology of freshwater fishes from the Jequitinhonha river basin. It was written by me and nine co-authors. I have divided it into three independent chapters, written and formatted according to the journals for which they were or will be submitted. In the first chapter we've investigated the distribution of freshwater fish richness along the elevational gradient in the upper Jequitinhonha river basin. Data revealed a mid-elevational peak in richness, which suggested the mid domain effect as an explanation. However, we saw evidence that species were not randomly distributed and therefore refuted this theory as well as the Rapoport's rule. In the second chapter we've assessed for the first time, grazing by *Serrasalmus brandtii* upon netted fishes outside its natural range. We observed higher grazing proportions in samples from sites where *S. brandtii* was the dominant species in relation to sites where it was recorded as present and sites where it was absent. *S. brandtii* grazed preferentially on caudal fins from larger fish and avoided mutilating conspecifics. The number of species being preferentially grazed increased as the abundance of *S. brandtii* also increases. Chapter three deals with fish movement. We tagged and tracked three species of Loricariid fishes in a tributary from the Jequitinhonha river. Fishes exhibited small home range sizes (less than 700 m) and showed specific habitat requirements. The study river ceased flowing at least twice during the study, which concerned us about the future of the species *Delturus brevis*. These fishes relied on cobbles and fast flowing waters, two hydraulic features typical from the riverine areas that dried first. The recurrence of severe draughts in the next decades can lead to the extinction of this species in higher order tributaries from the Jequitinhonha river.

Keywords: Elevational gradient in species richness. Mid-domain effect. Rapoport's Rule. *Serrasalmus brandtii. G*razing. Loricariidae. Radiotelemetry. Hydraulic habitat.

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PRIMEIRA PARTE

INTRODUÇÃO GERAL

A bacia do Jequi abrange uma área de cerca de 77 mil km², dos quais quase 94% estão situados no estado de Minas Gerais (Vieira, 2005). De acordo com o Mapa das Áreas Prioritárias para Conservação de Peixes de Minas Gerais (Vieira, 2005), a bacia apresenta três áreas de importância para a conservação de peixes: Alto rio Jequitinhonha e rio Itacambiruçu, a montante do reservatório da Usina Hidrelétrica de Irapé (UHIR); Médio Jequitinhonha, a jusante da UHIR até o município de Jequitinhonha; e alto rio Araçuaí, principalmente seu tributário Rio Preto, que possui alto grau de conservação (indicações na Figura 1). Além dessas, consta na Lei dos rios de preservação permanente (lei estadual n° 15082) o trecho da bacia do Jequi que vai das nascentes até a confluência com o ribeirão Tabatinga (Pompeu, 2012).

As primeiras contribuições ao estudo dos peixes do Jequi foram amealhadas pelos naturalistas viajantes Auguste Saint-Hilaire (1817), Johann Spix (1818) e Johann Emanuel Pohl (1819) (M. L. Martins, 2008; Andrade, 2010). Anos mais tarde, a grande expedição Thayer (Agassiz & Agassiz, 1868), que se propagou pelo interior do Brasil, trouxe ao Jequi os grandes naturalistas Charles Frederick Hartt e Edward Copeland (Higuchi, 1996). O material coletado entre 1865-66 serviu para as primeiras descrições de espécies da bacia.

No século XX merece destaque a descrição de *Nematocharax venustus* (Weitzman, Menezes, & Britski, 1986), que levou ao Jequi os professores Heraldo Britski e Naércio Menezes da USP, e Stanley Weitzman do Smithsonian Institution, nas décadas de 1960 e 80. A partir do final da década de 1980 até o início do século atual, outros pesquisadores, como Alexandre e Hugo Godinho, Volney Vono (H. P. Godinho, Godinho, & Vono, 1999), Gilmar Bastos Santos, Júlio Garavello, Osvaldo Oyakawa (Oyakawa, 1993), Mauro Triques (Mauro L Triques, Vono, & Caiafa, 2003; Mauro Luis Triques & Vono, 2004), retomaram não só as descrições de espécies, mas também trouxeram uma abordagem ecológica ao estudo dos peixes da bacia (H. P. Godinho, Godinho, & Vono, 1999).

No início dos anos 2000, intensificaram-se os impactos advindos do barramento do rio Jequi. Em 2002 entrou em operação a Usina Hidrelétrica de Itapebi na divisa de Minas Gerais e Bahia. Em 2006 foi a vez da UHIR no alto Jequi. Segundo a Agência Nacional de Energia Elétrica (ANEEL), outras oito barragens podem ser construídas só na calha principal do rio Jequi.

As pesquisas mais recentes estão partindo para avaliações de impactos ambientais decorrentes da introdução de espécies não-nativas (Capítulo 2 desta tese , Sales et al., 2017). Outras técnicas de estudo estão sendo utilizadas, como a rádio telemetria (Capítulo 3 desta tese) e telemetria acústica, que vem sendo abordada na pesquisa da bióloga Fernanda Silva (aluna de doutorado em Ecologia Conservação e Manejo de Vida Silvestre na UFMG) sobre transposição de peixes na UHE Irapé. Além

dessas, a biologia molecular tem ajudado na identificação de espécies crípticas (Pugedo et al., 2016), e até mesmo na identificação de híbridos de curimbas nativas e não-nativas (Sales et al., 2017).

Em meio a esse avanço nas pesquisas, as descrições de espécies também cresceram, seja de cascudinhos de riachos (F. O. Martins et al., 2014; F. O. Martins, Rosa, & Langeani, 2014; E. H. L. Pereira et al., 2017), espécie de distribuição restrita (*Cyphocharax jagunco*) (Dutra et al., 2016), espécie de maior porte e ameaçada de extinção (piabanha do Jequi, *Brycon howesi*) (Lima, 2017) até ao cascudo de maior porte (*Hypostomus nigrolineatus*) e amplamente distribuído na bacia (Zawadzki et al., 2016). Nesse contexto se destaca o pesquisador Tiago Pessali (Puc Minas) e seu empenho em ampliar a rede de amostras ao longo da bacia e fornecer material para novas descrições e estudos moleculares.

Mesmo com o esforço intensificado nos últimos anos, uma grande parte da diversidade de peixes do Jequi ainda é bastante desconhecida, assim como era na década passada (Vieira, 2005; Vieira, Alves, & Pompeu, 2009), pois ainda há muitas espécies a se descrever. Apesar do alto ritmo de descrições de novas espécies ser uma tendência atual global (Pelayo-Villamil et al., 2015), outros aspectos biológicos também estão bastante defasados em relação aos peixes da bacia do Jequi.

Também global é a incompletude da informação sobre a biodiversidade nos mais variados grupos taxonômicos (Hortal et al., 2015). Efeitos dessas lacunas são o comprometimento e a não generalização de teorias ecológicas, além da proposição de medidas de conservação e manejo errôneas ou limitadas. Tentei reproduzir na Tabela 1 os principais limitadores apontados em escala global por Hortal et al. (2015) que bloqueiam o conhecimento sobre os peixes da bacia do Jequi, com alguns exemplos.

Com o objetivo de reduzir as lacunas no conhecimento, produzi, junto com meus coautores, três contribuições independentes ao estudo ecológico dos peixes da bacia do rio Jequi. No primeiro capítulo abordamos o gradiente altitudinal de riqueza na região de maior prioridade para a conservação da bacia (Vieira, 2005; Pompeu, 2012), o Alto Jequi. Este capítulo foi submetido ao periódico Ecology of Freshwater Fish. Ele se encaixa nos limitadores Wallaceano e Hutchinsoniano de Hortal et al. (2015). No segundo capítulo avaliamos a predação de nadadeiras por pirambebas não-nativas (*Serrasalmus brandtii*) sobre peixes nativos e não-nativos emalhados em vários trechos da bacia do Jequi. Este manuscrito foi recentemente aceito para publicação no periódico Marine and Freshwater Research e fornece informações relacionadas aos limitadores Prestoniano e Eltoniano. No terceiro e derradeiro capítulo investigamos a área de vida linear e as especificidades de habitat de três espécies de Loricariideos da bacia. Este capítulo foi escrito no formato do periódico Journal of Applied Ichthyology e ainda não foi submetido. Seus objetivos estão relacionados aos limitadores Hutchinsoniano e Prestoniano. A todos que se dispuserem a ler este documento, eu vos saúdo.

Tabela 1- Principais limitadores do conhecimento indicados em escala global por Hortal et al. (2015), sua breve definição e exemplos aplicados à realidade da bacia do Jequitinhonha. Quando possível, são fornecidas as referências que abordam indiretamente o limitador.

Limitador	Definição	Exemplo da bacia do Jequitinhonha	Referências
Linneano	Muitas espécies ainda não descritas	- Espécies de ampla distribuição ainda não descritas (*Hypostomus* sp.) ou descritas recentemente (*Brycon howesi*, *Hypostomus nigrolineatus*). - Espécies crípticas	- (Zawadzki et al., 2016; Lima, 2017) - (Pugedo et al., 2016)
Wallaceano	Área de distribuição da maior parte das espécies desconhecida	- Espécies com ocorrência no rio Jequitinhonha e Pardo (*Astyanax pelecus*, *Wertheimeria maculata*, *Megaleporinus garmani*, *Oligosarcus macrolepis*, etc). - *Pareiorhaphis stephanus* descrito com base em um indivíduo (como determinar a área de ocorrência?)	- (Bertaco & Lucena, 2006; Camelier & Zanata, 2014) - (J. C. Oliveira & Oyakawa, 1999)
Prestoniano	Dados populacionais (abundância) escassos	- Espécie considerada ameaçada de extinção, sem que dados populacionais estivessem disponíveis: *Rhamdia jequitinhonha*	(Rosa & Lima, 2008)
Darwiniano	Falta de conhecimento evolutivo	Hipótese da atuação das bacias costeiras do leste brasileiro como áreas de ocorrência relictual para alguns grupos, como Delturinae e Doraridae basais	(Ribeiro, 2006)
Raunkiaeriano	Falta de conhecimento sobre características e funções ecológicas	Não se sabe quais são as espécies migratórias reprodutivas da bacia. Assume-se algumas espécies devido ao seu comportamento em outras bacias.	(H. P. Godinho, Godinho, & Vono, 1999)
Hutchinsoniano	Falta de conhecimento sobre os limites de tolerância e as respostas das espécies	Espécies que colonizarão ou não os ambientes lênticos proporcionados pelos reservatórios já formados e que ainda serão construídos.	
Eltoniano	Falta de conhecimento sobre as interações entre as espécies e suas consequências	Não se conhece os efeitos tróficos da introdução de *Serrasalmus brandtii* nas comunidades de peixes do rio Jequitinhonha	

FONTE: Do autor (2018)

Figura 1: Mapa das áreas prioritárias para a conservação de peixes no estado de Minas Gerais. Correspondem à bacia do rio Jequitinhonha os números 6- Alto Jequitinhonha e rio Itacambiruçú, 7- Médio Jequitinhonha e 11- Rio Preto (Alto rio Araçuaí).
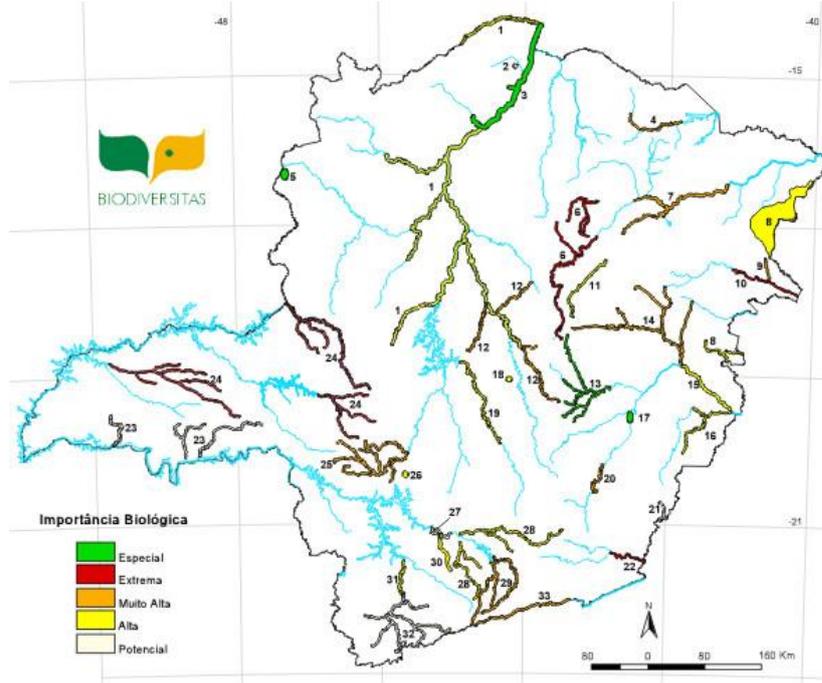
FONTE: Fundação Biodiversitas (2005)

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SEGUNDA PARTE: ARTIGOS

Capítulo 1: Analysis of freshwater fish elevational diversity pattern in a Neotropical watershed.

Manuscrito submetido ao periódico Ecology of Freshwater Fish

Freshwater fish elevational diversity pattern in a Neotropical basin.

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Running title: Elevational diversity pattern of fish

Keywords: Jequitinhonha river basin, Brazil, additive partitioning of diversity, Rapoport's rule, Mid Domain Effect, species richness estimation

Abstract

Along the elevational gradient, species richness more often peak at lower or middle areas. Interpretations for these patterns usually rely on the Rapoport's rule and the Mid Domain Effect (MDE), two conflicting approaches seldom addressed to freshwater fishes. We used data from Jequitinhonha river basin (southeast of Brazil) to test the distribution of fish richness in relation to Rapoport's rule and MDE. We rejected the Rapoport's rule due to the absence of a positive correlation between species elevational range and its mid-point. Data revealed a mid-elevational peak in richness, endorsed by gamma and beta diversity, but not for alpha diversity. Beta diversity contributed most for gamma, and its values are supposedly related to the inverse of mean range values of fish species distribution. Despite the mid-elevational peak, we also refute MDE. If fishes were distributed by chance, only wide-ranged species would be expected to occur in mid-elevations. However, short-ranged species preferably occurred in such areas. Furthermore, temperature at the time of sampling also displays a mid-elevational distribution, suggesting collinearity between fish richness and temperature "richness". We hope these findings can help the conservation of the most preserved stretch of Jequitinhonha river basin.

Introduction

The most common relationships between species richness and elevation are the monotonic decrease and the hump-shaped pattern (Rahbek, 1995; Nogués-Bravo et al., 2008). The first, once treated as a dogma (Colwell & Lees, 2000) or an intuitive relation (Rahbek, 1995) predicts the reduction in species richness with increasing elevation. To explain this, Stevens (1992) stated that elevation mirrors latitude when it comes to patterns of species richness, and extended Rapoport's rule to the elevational domain. According to this rule, species ranges are expected to increase with elevation, so the higher its location in the vertical gradient, the greater its range. This would restrict short- ranged species to the lower elevations, where richness would be inflated. Hence, higher elevations would contain only wide-ranged species. The difference in richness between higher and lower areas would be associated to climatic conditions (e.g., temperature and precipitation) at different elevations. Latter, Stevens (1996) extended the same rule to the bathymetrical domain.

The second pattern, the hump-shaped, appears when richness peaks at mid-elevations. Ecologists evoke the Mid Domain Effect (MDE) as a possible explanation for this pattern in the elevational (McCain, 2004; Kumar et al., 2009; Hsu, Wolf, & Tamis, 2014; Miyamoto et al., 2014) and other domains (Colwell, Rahbek, & Gotelli, 2004; Morales, Dodge, & Inouye, 2005; Dunn, Mccain, & Sanders, 2007) . The MDE is a null and non-biological model in which species are constrained by the geographical boundaries of the domain. In the absence of environmental gradients, the random placement of each species ranges in the elevational domain produces mid-elevational peaks (Colwell & Lees, 2000). The major criticism to this model is the collinearity of MDE predictions and environmental gradients, mainly temperature (Currie & Kerr, 2008).

The Rapoport's rule and the MDE explain different patterns of species richness in a given domain, but over the last three decades much of the acquired knowledge on species distribution has grown upon their rivalry (Colwell & Hurtt, 1994; Colwell & Lees, 2000). Many studies accessed species richness patterns by testing simultaneously for Rapoport's rule and MDE predictions, with different results (Sanders, 2002; Moreno et al., 2008; Fattorini, 2014). But despite being tested elsewhere, across many taxonomic groups and domains, together or independently, the Rapoport's rule and MDE have rarely been addressed for freshwater fishes (see the absence of examples in the reviews from Rahbek 1995; Dunn *et al.* 2007; Currie & Kerr 2008). Furthermore, what literature is available for this group, often deals with large elevational gradients such as the Andes (Carvajal-Quintero et al., 2015) and Tibetan Plateaus (Li et al., 2009).

Nevertheless, elevation is one of the most influential factors shaping freshwater fish assemblages. Variation in elevation alters topography and climate, which in turn affect stream geomorphology and discharge (Winemiller, Agostinho, & Caramaschi, 2008). and the general pattern of vertical distribution seems to follow the monotonic decrease at least for tropical watersheds (Pouilly, Barrera, & Rosales, 2006; Ibanez et al., 2007; Santos & Caramaschi, 2007; Albert, Petry, & Reis, 2011; Bhatt,

Manish, & Pandit, 2012; Carvajal-Quintero et al., 2015) . According to Ibanez (2007), elevation, position within the watershed and physical-chemical characteristics should be considered in conservation planning and river management. However, only recently protected areas are been established primarily to protect freshwater resources in the Neotropical region (Anderson & Maldonado-Ocampo, 2011). In Brazil, protected areas are mainly created for terrestrial organisms or environments (A. A. Agostinho, Thomaz, & Gomes, 2005), and the establishment of aquatic protected areas is not yet a reality (Barletta et al., 2010). So, for Brazilian ecologists and ichthyologists the elevational distribution of freshwater fishes and its application to conservation biology are challenging tasks. In this paper we used, for the first time, the two competing hypothesis of Rapoport's rule and MDE to assess how freshwater fish species richness changes with elevation.

Materials and methods

Study Area

The Jequitinhonha river basin (JRB hereafter) drains an area of approximately 70,000 km² (Fig. 1) of the east of Brazil and belongs to the Northeastern Mata Atlântica Freshwater Ecoregion , whose levels of freshwater fish endemism exceeds 70% (Abell et al., 2008). The Mata Atlântica or Atlantic Forest biome itself is not the dominant physiognomy in this basin, with the Cerrado (Savanna) being the main biome, with some overlap with semi-arid areas (Costa, Ribeiro, & Castro, 2010).

Our study was conducted in the upper JRB (S18°1' W43°3', S17°0 W42°0; Fig. 1) within an area of approximately 15,000 km^2. In the upper JRB elevation varies from 1,400 to 300 m asl. The rainy season lasts from November to March (Costa, Ribeiro, & Castro, 2010), and annual rainfall averages from 600 to 1,300 mm (V. D. O. Ferreira & Silva, 2012). Mean monthly temperature ranges from 16 to 27 °C (M. M. Silva & Ferreira, 2011). All field work was carried during the dry season in September 2013 and June 2014.

Fish sampling and identification

We sampled fishes from 1st to 5th orders streams in the upper JRB, following Strahler's classification (Allan & Castillo, 2007). In each sample we used sieves and trawls for approximately 40 minutes. We took the geographical coordinates and the water temperature. Captured fishes were fixed in formalin 10%, separated by sample, transported, identified and deposited in the Museum of Zoology at the Universidade Estadual de Londrina or in the Museum of Natural Sciences of Puc Minas.

Analysis

A total of 119 samples comprised our data set, all of them from an elevational gradient of 475 m from 516 to 991 m asl. We categorized data by three elevational belts as follows: Belt A from 516 to 681 m (165 m wide) with 31 samples, belt B from 686 to 813 m (133 m wide) with 51 samples and belt C from 814 to 991 (177 m wide) with 37 samples. For each belt we used species richness to calculate alpha (α - mean species richness, beta (β - species turnover) and gamma (γ - regional richness) diversities. We considered the relation between these three components to be additive, that is: regional

= alpha + beta (Gering, Crist, & Veech, 2003). By doing so, one can figure how much beta and alpha contributes individually to the regional diversity (Gering, Crist, & Veech, 2003), since all the components have the same units (Lande, 1996). The additive partition of diversity also makes comparisons between the three components more natural (Lande, 1996).

We estimated species richness through the classic routine of Estimates 9.1 (a single set of samples on abundance data), with 500 randomizations (Colwell, 2013). Since the number of samples varied among belts, we used the extrapolation routine of this software to check if overall tendencies in belt richness would be the same if more samples were added. According to Colwell et al. (2012) long-range extrapolations (> 3x the original sample size) leads to wide confidence intervals. So we limited extrapolation to the 90th sample, once it almost triples our smallest sample (belt A).

Rarity can be defined in many ways in ecology (Pritt & Frimpong, 2014). Here, we adopted an "absolute" classification (Magurran, 2004), on which frequent and infrequent are species present >10 or ≤10 samples, respectively (Colwell, 2013). Within infrequent, the uniques and duplicates are the basis for the incidence based richness estimators: Jackknife 1, Jackknife 2, Chao 2, ICE (incidence-based coverage estimator), the Jackknives also considering the number of samples (Magurran, 2004). We obtained richness estimates from these estimators and also from Bootstrap.

We calculated for each belt the sampling efficiency from the number of observed species (S_{obs}) as a mean percentage of the five estimators: [$S_{obs} \bullet 100/((Jack\ 1 + Jack\ 2 + Chao\ 2 + ICE + Boot)/5)$], equation modified from Puker et al. (2014). Due to the low numbers of singletons and doubletons, abundance based estimators were excluded, otherwise sampling efficiency would be nearly 100% for all belts.

Next, we calculated the elevational range of each species by subtracting the highest from the lowest elevation at which it was collected (Sanders, 2002). By doing this, we assumed range continuity, that is, the species was present in its entire range even if not sampled in all points within its endpoints. This assumption does not seem to bring significant bias for most studied taxa, and according to Colwell *et al.* (2004), "at any spatial scale recorded occurrences of a species are more likely to be close together than far apart". We arbitrarily added half meter above the highest and below the lowest elevations of each species, so that minimum range size was one meter.

We tested data for Rapoport's rule by Spearman's correlation (α=0.05). We used elevational range against species elevational mid-point, obtained as the average of lowest and highest elevations observed (Moreno et al., 2008; Fattorini, 2014). Rapoport's rule applies if mid-point and range are positively correlated (Moreno et al., 2008). We also correlated range against inferior and superior endpoints, following Fattorini (2014).

We verified if species range sizes fitted the MDE using Mid-Domain Null, a Monte Carlo based simulation program (McCain, 2004). We applied 50,000 simulations without replacement, based on empirical range sizes, following McCain (2004) and Moreno *et al.* (2008). If our 119 samples were uniformly distributed along the gradient, we'd expect one sample at each 3.99 m. We confirmed that by correlating (Spearman's correlation: $rs = 0.99$; $P < 0.01$) the empirical elevations of each sample with the uniformly distributed elevations (one sample at each 3.99 m). So, we considered the total number of samples (119) equal to the number of divisions of the domain, and set the number of Bins to 118. We regressed empirical species richness data against simulated richness data (based on average values for each bin after 50,000 simulations), to estimate the fit to the null model (McCain, 2004).

In order to seek for the causes of a possible mid-elevational peak in species richness, we considered that MDE is more likely to occur, the more wide-ranged species in the domain (Colwell, Rahbek, & Gotelli, 2004; Dunn, Mccain, & Sanders, 2007). So we ran Mid-domain Null with the same settings described above for short ($\leq 50\%$ of the domain) and wide - ranged ($>50\%$) species.

We also ran the former analysis considering temperatures instead of species. So we had for each Celsius degree, the corresponding elevational range of occurrence, as a measure of the "richness" of temperatures available at each elevation.

Results
We captured 7,115 fishes from 40 species that presented a diverse altitudinal range (Fig 2). Rarefied species richness estimates for the whole data set were ICE = 43.09 ± 0.00; Chao 2 = 47.44 ± 8.12; Jack 1 = 45.95 ± 2.38; Jack 2 = 50.87 ± 0.00; Bootstrap = 42.65 ± 0.00. Richness estimations for each belt were summarized in Table 1. The overall sampling efficiency was $86.95\% \pm 7.33$ for the Upper JRB.

Sampling efficiency varied with the number of samples for the three belts (Fig. 3). It always increased for belt C, reaching 90%, the highest percentage for the three belts. For belts A and B we observed a slight decrease in sampling efficiency after peaking at the 19th and 33th sample, respectively (Fig. 3). For both, final sampling efficiencies were 78% (belt A) and 73% (belt B).

Richness of the three belts increased after extrapolation (Fig. 4). Belts A, B and C are expected to present respectively 37.16 ± 7.06, 42.30 ± 5.36, 28.30 ± 2.72 species with 90 samples, each. Extrapolation did not change the order previously observed for empirical data, so that richness remained higher in belt B, followed by belt A and then belt C (Fig. 4). Confidence interval was higher for belt A, as expected (Colwell et al., 2012), but belt C had the lower value instead of belt B, which had more samples (Fig. 4).

Alpha, beta and gamma diversities data are summarized in Fig. 5. Mean alpha diversity significantly differed only from belt A to belt C (Anova: $F_{(2, 116)}= 3.99$, $P < 0.02$, Post-hoc HSD test for unequal

N: $P < 0.03$). For beta diversity, belt B significantly differed from belts A and C (Anova: $F_{(2, 116)}=$ 180.62, $P < 0.01$, Post-hoc HSD test for unequal N: $P < 0.01$).

Data did not fit the monotonic decrease, or Rapoport's rule. Mid-point and range had no significant correlation (Spearman's correlation: $rs = 0.20$; $P > 0.20$). There was a strong positive correlation between range and upper endpoint (Spearman's correlation: $rs = 0.83$; $P < 0.01$) and a strong negative correlation of range and inferior endpoint (Spearman's correlation: $rs = -0.77$; $P < 0.01$). Interestingly wide ranged species seemed to be limited by lower elevations, but no the short-ranged ones.

Species richness peaked at mid-elevations for the upper JRB fishes (Fig. 6), and the corresponding peak values were 26 - 27 species at 680 - 708 m. Empirical species richness data strictly fitted the null model predictions ($y = 3.86 + 0.79x$; $R^2 = 0.89$; $P < 0.01$). Only sixteen points (13%) from the empirical richness values deviated from the 95% prediction curves obtained after 50,000 simulations, mostly (8%) values above the predicted at mid-elevations.

Within the 23 short-ranged species, range occupied 0.21 to 40.23% of the evaluated domain. The remaining 17 wide-ranged species distributed themselves from 57.56 to 100% of the evaluated domain. For both, data fitted well the null model predictions (Fig. 7), with lower R^2 values for short-ranged species ($y = 1.98 + 0.45x$; $R^2 = 0.74$; $P < 0.01$) when compared to wide-ranged ones ($y = 1.61 + 0.88x$; $R^2 = 0.91$; $P < 0.01$).

Temperature ranged 11.1 degrees from 17.2 to 28.1°C. A strict fit to the null model was also observed for this variable ($y = 0.89 + 0.82x$; $R^2 = 0.91$; $P < 0.01$). In this case, all points were inside the 95% prediction curves (Fig. 8).

Discussion

Our analyses converge to support mid-elevational peak of freshwater fish in the upper JRB. Intermediary elevational belt B had higher richness values than marginal ones, A and C. For belt B sampling efficiency was the lowest and richness is expected to increase according to richness rarefaction and extrapolation. The same is expected for belt A. However, belt A shows no tendency to surpass belt B's richness, if its sampling efficiency was slightly higher and the observed richness is already lower than belt B. Thus, with more samples, we could expect changes in curves of Fig. 6, but not enough to turn a hump-shaped pattern into a monotonic decrease.

Mean alpha diversity alone provides an idea of a monotonic decrease in species richness from belt A to C (Fig. 5), for this measure of diversity doesn't consider range continuity. Gamma diversity, on the other hand, is consistent with the mid-elevational peak in richness, once intermediary belt had higher values. If we decompose gamma diversity into alpha and beta components, we can have a clue of how important is beta diversity in enhancing overall species richness in each belt. In fact, beta diversity increases as mean range declines. There are cases in which beta diversity can be measured simply by

obtaining the inverse of the mean range distribution (Arita & Rodríguez, 2002). When exploring the longitudinal scale of the São Francisco and Upper Paraná river basins, Leal et al. (2014) had results very similar to ours, with beta diversity contributing most for gamma. On the other hand, alpha and beta diversities played a meaningful role in determining overall diversity in the Missouri and Illinois rivers (Pegg & Taylor, 2007). Whether a lower contribution of alpha is a characteristic pattern of Neotropical rivers is still unknown, since there's no comprehensive paradigm applied to all systems when it comes to spatial diversity patterns (Pegg & Taylor, 2007).

The absence of a positive correlation between range and mid-point is enough to refute the monotonic decrease and the Rapoport's rule. However, range strongly and positively correlated with upper endpoint is a characteristic of this rule, as wide-ranged species were found at higher elevations. Yet, the feature that corroborated most for the absence of a Rapoport effect and the observed mid-elevational peak in richness is the placement of short-ranged species in the mid-elevations. That explains why lower endpoints and range had negative correlations. In a Rapoport scenario, those species should be in lower elevations, whereas in our data, lower areas are inhabited by wide-ranged species. So, the way Rapoport's rule was refuted also corroborates with mid-elevational peak in richness.

We have two reasons to refute the MDE and believe that the mid-elevational peak observed was not caused by chance. First, wide-ranged species can't avoid occurring in the middle of the domain, while the short-ranged ones are free to be placed anywhere within it in the absence of environmental gradients (Colwell & Lees, 2000). In our data, wide-ranged species do occur in the middle of the domain, as expected. However, short-ranged species also occurred in the middle of the domain, increasing richness in this area, especially by increasing beta diversity.

Our second reason is temperature. Studies often treat temperature as an independent variable that is regressed against species richness (McCain, 2004; Brehm, Colwell, & Kluge, 2007). In our study we didn't relate these variables. Instead, we treated temperature as a dependent variable in relation to elevation, the same way as species richness. Mid-elevations from upper JRB provides more temperature options than the extremes, which reminds us the "middle is good" hypothesis (Sanders, 2002).

We only recorded water temperature once and this could be a source of error if we claimed richness to be strictly dependent from temperature. Instead, our aim here was to present arguments to avoid unsubstantiated conclusions about the MDE predictions, even if the richness data points to this direction. When reviewing the evidence for the MDE in several studies, Currie & Kerr (2008) found that nearly all occurred when MDE predictions were strongly collinear with environment gradients, mostly temperature. This seems to be our case, although we do not exclude other variables (e.g.

history, precipitation, biotic interactions, anthropogenic impacts) from being shaping freshwater fish richness in the upper JRB.

Our study focused a 500 - 1,000 m asl elevational gradient and we're aware of the controversy regarding the omission of segments (Nogués-Bravo et al., 2008) as well as the difficulty in finding transects with natural environments along the entire gradient (Rahbek, 1995; Brehm, Colwell, & Kluge, 2007; Nogués-Bravo et al., 2008). According to Carvajal-Quintero et al. (2015), this omission may lead to spurious conclusions. However, from 0 - 500 m asl the JRB harbors streams that suffer most from draught and anthropogenic impacts, such as sewage discharge and removal of riparian vegetation (Andrade & Pompeu unpublished data). We believe that spurious or biased conclusions could emerge if these reaches were included, so we kept only the upper JRB in the analysis once it is closer to reference conditions. We also consider that missing segments favors the monotonic decrease instead of the hump shaped pattern, especially when it's the lower part of the gradient (our case) that is omitted (Nogués-Bravo et al., 2008). Besides, even incomplete sampling could successfully reveal mid-elevational peak in fish richness in the Tibetan Plateau (Li et al., 2009).

Implications for conservation

Part of the upper JRB is protected by the Minas Gerais state Law n° 15,082. In addition to JRB, reaches of São Francisco and Upper Paraná river basins enjoy the benefits of this Law. This is an important step towards the protection of aquatic organisms in Brazil and even without technical support (Pompeu, 2012), these areas are free from mining and modification of the riverbed and its margins. In the context of this Law, our results provide technical support for the conservation of freshwater fish from the upper JRB, regarding the elevational domain. Short-ranged species are less likely to be protected than wide-ranged ones (Lawler et al., 2003) and thus should be targets for conservation (Nogueira et al., 2010). An advantage of the pattern observed for this area is that short-ranged species are concentrated in the mid-elevations. Such distribution can reflect localized biotas (Nogueira et al., 2010) and make conservation efforts simpler.

Acknowledgments

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Authorship

Conceived and designed the investigation: F.A. Performed field and/or laboratory work: F.A; T.A.B.; I.G.P.; J.B. Analyzed the data: F.A. Contributed materials, reagents, and/or analysis tools: L.Z. Wrote the paper: F.A.; T.A.B; I.G.P.; P.S.P.; J.B.; L.Z.; A.M.

Table 1: Rarefied species richness estimates and standard deviations for belts A, B and C for the estimators ICE (incidence-based coverage estimator), Chao 2, Jackknife 1, Jackknife 2 and Bootstrap.

Belt	ICE	Chao 2	Jack 1	Jack 2	Bootstrap
A	32.88 ± 0.01	37.16 ± 10.26	33.77 ± 2.68	39.42 ± 0.00	29.85 ± 0.00
B	46.67 ± 0.01	52.97 ± 14.81	45.78 ± 3.23	54.47 ± 0.00	39.50 ± 0.00
C	28.04 ± 0.00	27.46 ± 2.18	29.89 ± 3.05	30.92 ± 0.00	28.03 ± 0.00

Figures
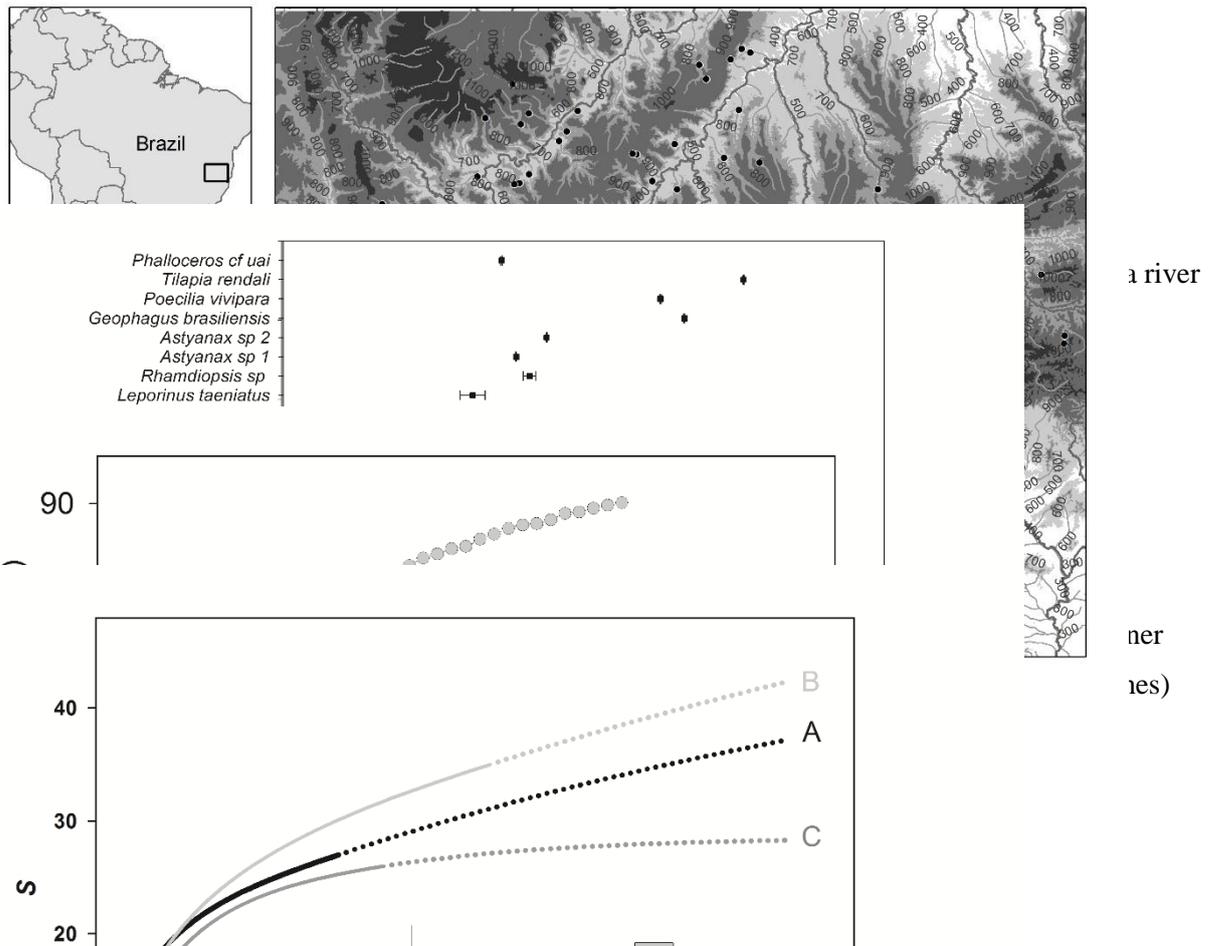
for elevational belts A (black), B (light grey) and C (dark grey). Boxes A, B and C refers to rarefied richness estimation and boxes A exp, B exp and C exp reffers to extrapolated richness.

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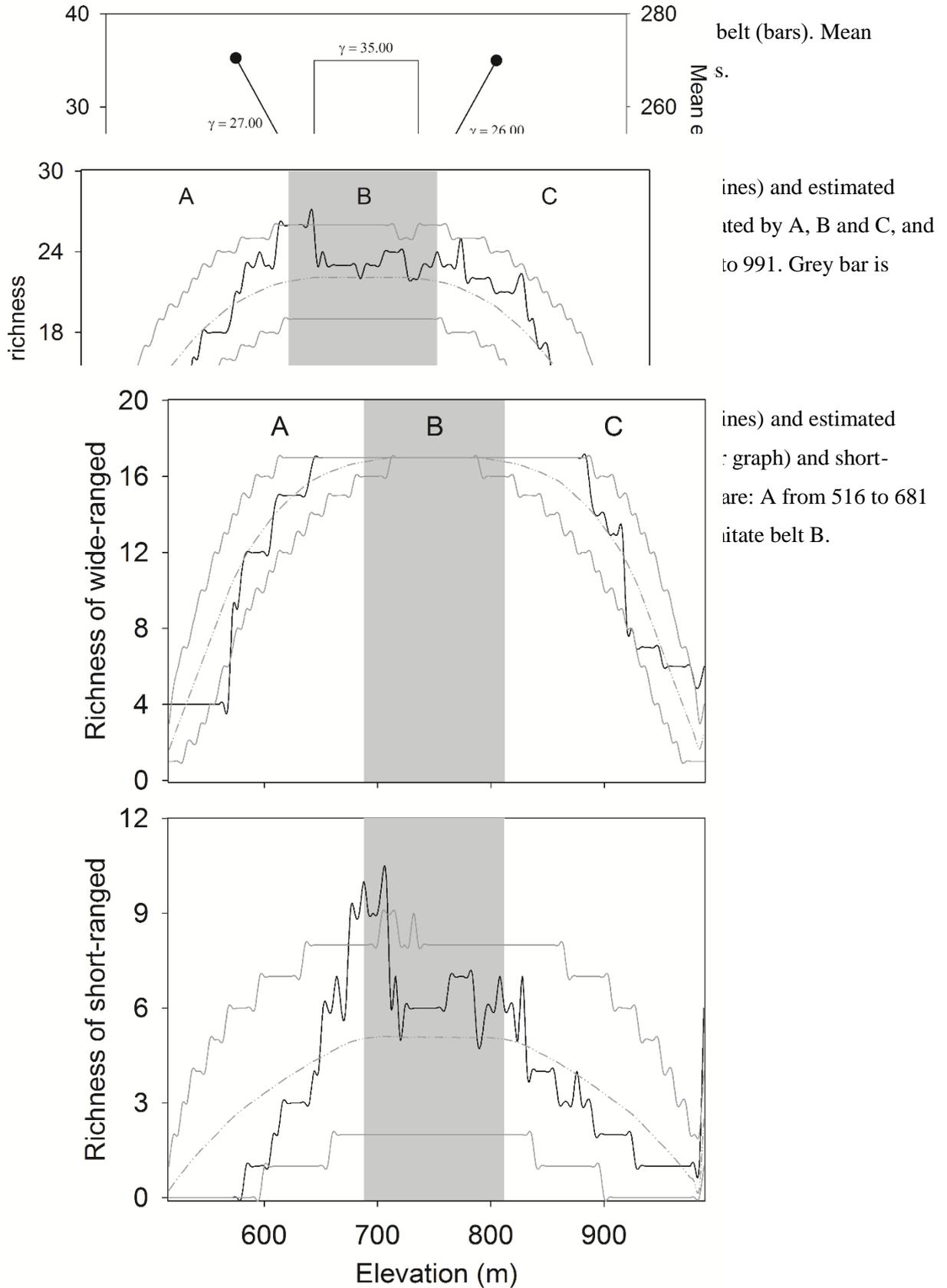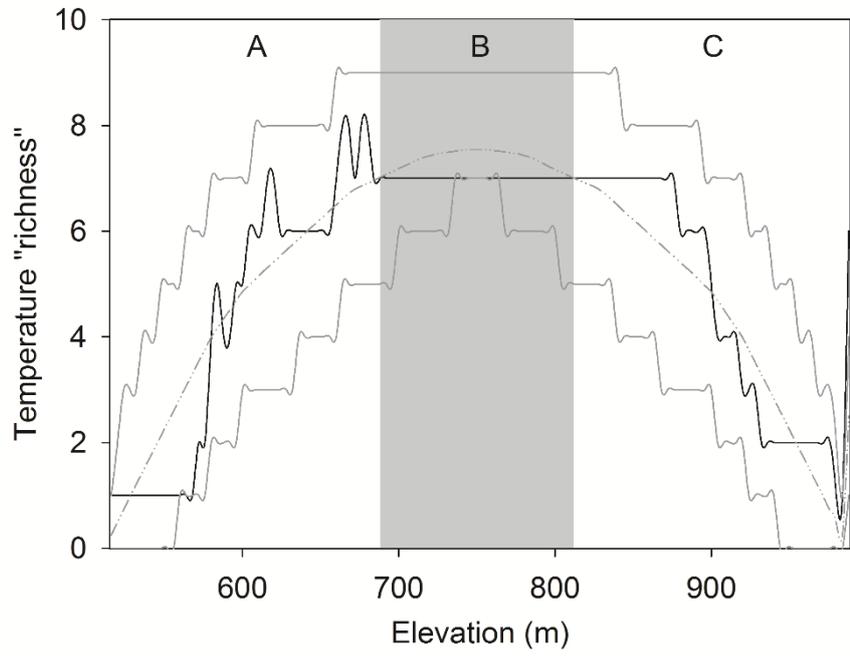
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Capítulo 2: Non-native white piranhas graze preferentially on caudal fins from large netted fishes in Brazil

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Non-native white piranhas graze preferentially on caudal fins from large netted fishes in Brazil

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Abstract

We assessed, for the first time, grazing by *Serrasalmus brandtii* outside its natural range. We observed higher grazing proportions in samples from sites where *S. brandtii* is the dominant species in relation to sites where it is recorded as present and sites where it is absent. *S. brandtii* grazed preferentially on caudal fins in relation to all other fins alone or combined. It also preferred to mutilate fins instead of flesh. Larger fishes had a higher probability of being mutilated and had a higher number of mutilated fins in relation to smaller ones, which is expected as large fish represent a larger resource to their consumers. *S. brandtii* avoided mutilating conspecifics, and as its abundance increased, so does the number of species being preferentially grazed.

Keywords: Jequitinhonha River basin; Biological invasions; predation; piscivory; invasive species; fin and flesh mutilation.

Running title: Fin grazing by non-native *Serrasalmus*

Introduction

Fishes from the genus *Serrasalmus* (i.e. piranhas) feed mainly on fish scales, fins and flesh (Pompeu, 1999; A. K. Oliveira et al., 2004; Junior, Gomiero, & Goitein, 2008; F. S. Ferreira et al., 2014; A. T. da Silva et al., 2015). Throughout their growth these fishes undergo ontogenetic diet shifts with invertebrate feeding by juvenile followed by fish feeding in subadults and adults (Winemiller, 1989) *Serrasalmus* are common to lentic environments, display parental care and are multiple spawners,

which allows them to successfully colonize natural or man-made reservoirs (A. R. M. Silva, Santos, & Ratton, 2006; A. A. Agostinho, Gomes, & Pelicice, 2007; Honorato-Sampaio et al., 2009).

The presence of *Serrasalmus* in basins or reaches outside its natural range has been reported and is related to river damming. In the Paraná River basin, the filling of Itaipu dam reservoir eliminated natural barriers and promoted the spread of the spotted piranha *S. marginatus* to the upper reaches of that river (Júlio-Júnior et al., 2009), where it depleted its native congener, the ruby red piranha *S. maculatus* (Alves et al., 2017). The rupture of tanks during floods led to the introduction of *S. brandtii* in the Contas River and its subsequent establishment in the Barra Bonita dam reservoir (Trindade & Jucá-Chagas, 2008).

The Jequitinhonha River basin exhibits a similar situation to that of the Contas River: recent damming and appearance of *S. brandtii* in lentic environments, followed by its rapid population increase. Whatever the range, native or non-native, *S. brandtii* damages fishing gears and captured fishes, impairing fisheries and fisherman (Teles & Godinho, 1997; Trindade & Jucá-Chagas, 2008). Although this species is sometimes referred to as the white piranha in the literature, from now on we use its common name *pirambeba*, which means flattened piranha in the indigenous language Tupi (i.e. native Tupi indians).

Due to their feeding habits *Serrasalmus* are known as "mutilating predators" (Pompeu, 1999; C. S. Agostinho & Marques, 2001; A. K. Oliveira et al., 2004; Junior, Gomiero, & Goitein, 2008; Trindade & Jucá-Chagas, 2008), "mutilators" (Sazima & Machado, 1990; Carvalho, Zuanon, & Sazima, 2007), "fin specialists" (Winemiller, 1989) or even "grazers" (Goulding, 1980). The term grazer more often refers to species that feed on periphyton from the surface of stones (Flecker, 1992) or on "plants growing very close to the substrate" (Gerking, 1994) when applied to freshwater fish trophic classification. However, grazing activity is also valid for the cropping of fish fins, if "not grazed to down" and allowing regeneration (Winemiller & Kelso-Winemiller, 1993; A. K. Oliveira et al., 2004).

In this paper we investigate the mutilations of non-native pirambebas upon netted fishes from the Jequitinhonha River basin, by addressing two questions: 1- Are netted fish more mutilated in the presence of pirambebas? 2- Do pirambebas show apparent feeding preference for specific body parts, body sizes or fish species? We hypothesised an increase in mutilation related to the presence of pirambebas, and an apparent preference for caudal fins of larger fishes, since these individuals are more exposed to fin predation (Winemiller, 1990; Winemiller & Kelso-Winemiller, 1993).

Methods
Study area and the introduction of pirambeba in the Jequitinhonha River basin

The Jequitinhonha River basin covers an approximate 70 000 km^2 of the east coast of Brazil (Andrade, 2010; Pugedo et al., 2016). Native and non-native fish richness surpasses a hundred species (Pugedo et

al., 2016). Many of the non-native fish species are native to the neighbouring São Francisco River basin, e.g. blackline tail tetra *Moenkhausia costae*, piau jeju *Leporinus taeniatus*, curimatá pacu *Prochilodus argenteus*, curimatá pioa *P. costatus* (H. P. Godinho, Godinho, & Vono, 1999; Pugedo et al., 2016; Sales et al., 2017) and *S. brandtii*.

Pirambebas were first reported in the Jequitinhonha River in 2006 by Godinho (2008), during the fish monitoring immediately downstream the Irapé Dam (same location as site 4 in Fig. 1). By this time, Irapé Dam construction had just been finished and the reservoir was on the filling stage. After that, only in 2009 were pirambebas reported again, this time in the reservoir (authors' personal communication). Since then, its' populations have increased rapidly in the immediate vicinity of the reservoir and it is now found hundreds of km downstream from Irapé dam (Fernanda Oliveira Silva, Universidade Federal de Minas Gerais, personal communication, 2015).

Sampling

We analysed netted fish data from experimental fisheries from 2011 to 2016. We did not assess all 2014 fishes for mutilation, so we decided to exclude this year from the analysis. Fishes were captured in nine sites grouped into three classes according to the presence and abundance of pirambebas, namely pirambeba classes: Absent: no pirambeba sampled throughout the entire period. Present: pirambebas were present in less than 50% of all samples of these sites, and never exceeded 50% of all fishes from a single sample. Dominant: pirambebas were present in more than 80% of all samples and reached up to 83% of all fishes from a single sample.

Mutilation assessment

We evaluated all netted fish for mutilation at harvest, by accounting for each fin individually, and flesh mutilations separately. We define flesh mutilation as an injure that led (or would lead) to the victim's death as it extends to vital parts of the body (e.g. viscera, head). Whenever encountering a flesh- mutilated fish we did not assess fins.

Data analysis

First we verified if pirambebas' presence and dominance were related to an increase in netted fish mutilation. For each sample, we calculated the proportion of mutilated fish (*pmf*). As these were mostly non-parametric data we ran a Kruskal-Wallis to test the null hypothesis that the *pmf* is the same for each pirambeba class (group). Subsequently we proceeded with a Nemenyi's *post-hoc* test (method= Tukey) from the R-studio (R Development Core Team, 2016) package 'desctools'.

Apparent preference for fins

In our study a fish (with seven fins) could exhibit one of 129 conditions when netted: 127 possible combinations of fin mutilation ($\sum_{p=1}^{7} C_n^p = \frac{n!}{p!(n-p)!}$), flesh mutilation, or no signs of mutilation at all (integer). We checked the combinations observed for all species in each pirambeba class, to verify if our data corroborates the hypothesis that the caudal fin is be the most frequently mutilated (Northcote, Northcote, & Arcifa, 1986; Winemiller & Kelso-Winemiller, 1993; C. S. Agostinho, Hahn, & Marques, 2003; A. T. da Silva et al., 2015).

Netted fish were divided into one of three categories *Integer*, *Fin* and *Flesh*, to assess whether there were differences in their relative abundance (proportion) in each pirambeba class. Our alternative hypothesis was that these proportions would differ between pirambeba classes. In this case, each species comprised a sample. We used a one-way Kruskal-Wallis followed by Nemenyi's *post-hoc* tests.

Apparent preference for size

We used generalized linear models (GLM) to verify if mutilations were related to netted fish size. The distribution of the dependent variable was chosen after fitting with the 'fitdistrplus' package. We assumed a binomial distribution (Zuur, Hilbe, & Ieno, 2013) for a binary dependent variable (*fish condition:* no mutilated fin = 0, mutilated fin = 1) regressed against the log - transformed standard length (*logsl*) in a binomial GLM with (link= logit). We did this for all data (Model 1) and separately for each pirambeba class (Model 2 - Absent, Model 3 - Present and Model 4 - Dominant). We used the logi.hist.plot function from the package 'popbio' (Stubben & Milligan, 2007) to plot these four models regressions.

To investigate effects of body size on the number of mutilated fins, we used *logsl* in a Poisson GLM (link= log). Again, we ran four separate models (Model 5 - All data, Model 6 - Absent, Model 7 - Present and Model 8 - Dominant). We calculated all GLMs pseudo - R^2 and checked for overdispersion. No correction on model structure was needed, since the dispersion parameter never exceeded 1.5 (Zuur et al., 2009).

Regarding flesh mutilation, we used the median standard length for each species in each pirambeba class to answer if larger individuals are more prone to flesh mutilation. The dependent variable was the proportion of flesh mutilated fishes (*pflesh*) which fitted a beta distribution after a transformation needed to include all data within the (0, 1) interval. We regressed *pflesh* against the median of the standard length in a beta regression (link.phi = identity) from the 'betareg' package (Zeileis et al., 2016). Again, we considered all data and each pirambeba class.

Apparent preference for species

We attempted to quantify the apparent preference for species in each pirambeba class by calculating Manly's alpha preference index (Chesson, 1978) for each sample. It accounts for the abundance of

each prey (species) but doesn't require a specific number of prey types (Chesson, 1978), an important feature for us, since the number of species varies among samples and pirambeba classes.

In the absence of preference each species should account for an equal share of the total mutilations. So, the more species, the smaller is that share. Following Wallinger et al. (2014) we established a threshold above which apparent preference may be indicated, by dividing total mutilation by richness ($1/S$). Richness varied among pirambeba classes and within samples from each pirambeba class. To cope with this variation, we set a threshold band to the $1/S$'s 1st and 3rd quartiles for each pirambeba class. Adjustments were needed to avoid total preference in a sample, so we excluded samples in which $S = 1$, and species with less than 10 individuals in each pirambeba class. We excluded two samples from Absent class with zero mutilation, since one cannot measure mutilation preference in the total absence of mutilation.

Results

We analysed 3 900 fishes from 16 species from 2011 to 2016. Abundance varied among pirambeba classes ($N_{absent}= 501$, $N_{present}= 1\ 452$ and $N_{dominant}= 1\ 947$ fishes) and species, with the non-natives pirambeba and *M. costae* being the most abundant (Fig. 2). We found that *pmf* varied significantly among pirambeba classes (Kruskal-Wallis chi-squared = 40.422, df = 2, $p<< 0.00001$), and differences were detected for all pairwise comparisons (*p*-values of Nemenyi's *post-hoc* test never exceeding 0.023). Accordingly, the null hypothesis that *pmf* does not vary among pirambeba classes was rejected. We found an inverse relationship between median *pmf* values and variance between pirambeba classes with sites included in the Absent class having the lowest median values for *pmf* (Fig. 3) and the largest variance ($\sigma^2_{Absent}= 0.1057$), whereas the Dominant class had the highest median and lowest variance ($\sigma^2_{Dominant}= 0.0288$).

Apparent preference for fins

We observed 79 (62.2%) of 127 possible combinations of fin mutilation. The caudal fin appeared in 55 combinations (69.6%) and on 1468 individuals (93.14% of fin mutilated fishes). Caudal fin mutilation alone represented 52.4% of fin mutilated fish. These results corroborate the hypothesis that the caudal fin is the most mutilated.

For all pirambeba classes proportion of fish included in the categories *Integer*, *Fin* and *Flesh* varied significantly (Kruskal-Wallis chi-squared $_{Absent}$ = 18.55, df = 2, $p< 0.0001$; Kruskal-Wallis chi-squared $_{Present}$ = 16.69, df = 2, $p< 0.0003$; Kruskal-Wallis chi-squared $_{Dominant}$ = 17.97, df = 2, $p< 0.0002$). We also found significant differences in proportions of *Fin* and *Integer* fish among pirambeba classes (Kruskal-Wallis chi-squared $_{Integer}$ = 21.18, df = 2, $p< 0.0001$; Kruskal-Wallis chi-squared $_{Fin}$ = 8.58, df = 2, $p< 0.0138$), but not the proportion of fish with *Flesh* damage (Kruskal-Wallis chi-squared $_{Flesh}$ =2.59, df = 2, $p> 0.273$). Pairwise differences between groups for the two tests are highlighted in Fig. 4.

Apparent preference for size

A total of 2 542 fishes had their standard length measured. All species captured and its standard length ranges for each pirambeba class are available as Supplementary Material. Standard length ranged from 33 to 595 mm (mean= 140, 1st quartile= 85, median= 123, 3rd quartile= 189). Binomial GLMs (Models 1 to 4) showed that larger fish had a higher probability of being fin mutilated when netted (Table 1, Fig. 5). Although highly significant, pseudo-R^2 values were extremely low, indicating a weak relationship (Table 1). We had similar results with the Poisson GLM (Table 2) with significance for all models (Models 5 to 8). In this case the larger the netted fish, the higher the number of mutilated fins. Pseudo-R^2 values were higher than those for binomial GLM, but the relationships remained weak. In both kinds of regressions, Absent (Models 2 and 6) is the class where this relationship was weakest (Tables 1 and 2). There was no relationship between species median size and the proportion of flesh mutilation (*pflesh*), even considering all data or each pirambeba class separately. Beta regression resulted in *p*-values ranging from 0.16 to 0.98.

Apparent preference for species

We detected an apparent preference for specific species in all pirambeba classes. Threshold bands harbouring 50% of the 1/S's possible results provides a means to identify preferred/non-preferred species (Fig. 6). In the Absent class, median values inside or above the threshold band were observed for *Oligosarcus macrolepis* and *Astyanax brevirhynus* respectively (Fig. 6). In the Present class, median values below the threshold band were observed for four species: *Hypostomus* sp., *Trachelyopterus galeatus*, *M. costae* and pirambeba (Fig. 6). An even reduced number of species (two) had median values placed below the threshold band in Dominant class, pirambeba and *T. galeatus* (Fig. 6).

Discussion

This is neither a pirambeba diet study, nor a presentation of the feeding habits of this species. Instead, this is an attempt to investigate its apparent preference for different resources in the presence of choice. As shown by the results, we confirmed our hypotheses that pirambebas are related to an increase in the proportion of mutilated fish and that they apparently prefer caudal fins from large netted fishes because fins provide an abundant and easy food resource for pirambebas.

At least to a certain size, *Serrasalmus* (i.e. juvenile and sub-adults) are fin specialists (Nico & Taphorn, 1988; Winemiller, 1989). For instance, the only fin specialist fish in our dataset belongs to this genus (*S. brandtii*). So, even without direct observations of netted fish mutilation, it is extremely likely that the damage can be attributed to pirambebas. Other authors link the shape of the mutilation to (Winemiller & Kelso-Winemiller, 1993; C. S. Agostinho & Marques, 2001), or assume mutilations were from *Serrasalmus* species (A. T. da Silva et al., 2015). We believe mutilations were made by pirambebas due to striking differences in data collected in the Absent class, that acts as a control in our study. A control that is often lacking in field studies where *Serrasalmus* is native. We also found that

not just its presence, but also its abundance was related do the proportion of mutilation observed, as we detected a clear increase in the proportion of mutilated fish (*pmf*) between Present and Dominant classes.

Samples taken in the absence of pirambebas ranged from 0 to 100% mutilations, a scenario never observed when it is present/dominant. In the other two pirambeba classes it is increasingly easier to predict the *pmf* in a random sample, since data varies less among extremes.

Apparent preference for fins

It was expected that *Integer* and *Fin* mutilated fish varied between pirambeba classes, especially after rejecting the null hypothesis for *pmf* along pirambeba classes. However, the proportion of *Flesh* mutilated fish did not increase in response to pirambebas. Even in areas dominated by pirambebas, few fish are mutilated to point where death is the likely consequence of such feeding activity. Moreover, we expect proportions of flesh-mutilated fish to be even lower in natural conditions (non-netted fish), as fish are better able to hide, escape or defend against pirambebas and other threats in open water.

A small proportion of flesh mutilation occurs even in Absent class. This may be due to the predation by turtles, otters or piscivorous fishes. Although we never bycaught a turtle in our nets, it was commonly observed basking on stones in lotic river stretches and are known agents of mutilation in netted fishes (C. S. Agostinho et al., 1997). We didn't directly observed predation by otters in the Absent class, but it happened twice in site 4 (Present class) throughout the study period. In these cases, otters moved the whole nets out of the water and ate parts of the fish on the ground. Other piscivorous fishes can be responsible for the mutilations observed in the three classes, such as the trahiras *Hoplias malabaricus* and *H. brasiliensis*. Even with other organisms from different taxonomic groups being able to predate netted fishes, its proportion remained low for all pirambeba classes.

Apparent preference for sizes

Larger fish were more frequently mutilated than smaller, and that was the observed pattern for all pirambeba classes when either considered separately or together. Although, this relationship was barely perceptible in the Absent class, it became more evident in the presence/dominance of pirambebas, which thus demonstrates their apparent preference for larger fish.

We consider that large fish provide more resource than small fish to its predators. However, small fish comprise the vast majority of individuals in an assemblage, especially in man-made reservoirs (A. A. Agostinho et al., 1999). This is the case for Irapé dam reservoir (Dominant class), where non-native pirambebas graze more often on large netted fish. This probably reflects preference rather than reality.

Not only did the probability of a fish being mutilated increase with netted fish size, but also the number of mutilated fins per fish. This relationship was more evident in the Dominant class. It is probably more difficult for large fish to hide or escape from pirambebas than smaller ones, as

hypothesized by Winemiller and Kelso-Winemiller (1993). Fish rely on body integrity to escape from predators. Thus, as more fins are damaged, swimming capacity is thought to decrease and consequently a fishes' ability to avoid predation or grazing (Fu, Cao, & Fu, 2013). Large fish are also preferred by fisherman, because they provide more revenue. This can lead to conflict between fisheries and pirambebas both inside (Teles & Godinho, 1997) and outside (Trindade & Jucá-Chagas, 2008) its natural range. However, as flesh mutilation was rare, and did not increase with body size, we expect that financial impacts of pirambebas on fisheries are minimal.

Apparent preference for species

We found a clear decrease in the number of species below the preference threshold when pirambebas were either present or dominant. The only species with a median placed below the threshold in all pirambeba classes was the auchenipterid *T. galeatus*. Members of this family often present the first ray of dorsal and pectoral fins modified as piercing spines that may deter mutilations, as these structures are recognized as antipredation defences (Lowe-McConnell, 1975). Unfortunately, this and *Wertheimeria maculata* are the only species with such characteristics in our dataset. The doradid *W. maculata* possesses similar spines, but its median value was inside the threshold and we had no samples outside the Dominant class. Therefore, we cannot test if these spines were effectively preventing mutilation by pirambebas.

Our data also suggest that pirambebas avoid mutilating themselves. Maybe by using a broader array of prey species (Northcote, Northcote, & Arcifa, 1986; A. T. da Silva et al., 2015), pirambebas reduce the frequency of attacks on conspecifics and consequently the incidence of cannibalism. Scarcity of alternative prey and predator density are related to increases in cannibalism in *Gobiomorus dormitor* introduced in Nicaraguan lakes (Bedarf et al., 2001). Gomiero and Braga (2004) discuss the same results soon and after the introduction of *Cichla* species in a Venezuelan lake and also reports high levels of cannibalism for two *Cichla* species in a Brazilian reservoir. Although cannibalism is a well debated issue for the *Cichla* genus (L. S. Pereira, Agostinho, & Winemiller, 2017), it is scarcely documented for *Serrasalmus*, maybe because it is indeed undocumented, or in fact rarely occurs. Or, a third option is the difficulty in identifying fish remains to the species level in *Serrasalmus* stomach analysis. Unlike *Serrasalmus*, most piscivores ingests the whole prey (Juanes, Buckel, & Scharf, 2002), which facilitates further identification by researchers.

Manly's index of preference takes into account both the richness and abundance of species within a sample. So, at higher abundances, pirambebas exploit a higher number of different species to avoid cannibalism. This explains why most species are within and above the threshold in the Present and Dominant classes, whilst only two are in this position in the Absent class. Still, growing populations of pirambebas in the Dominant class (density-dependent mechanism) may lead to increased number of cannibalistic interactions if fins on other species are grazed to exhaustion.

A recent study from Sales et al. (2017) revealed a threat to *P. hartii* via genetic admixture with non-native *Prochilodus* species in the Jequitinhonha river basin. This study identifies the reach upstream of the Irapé Dam as the least threatened by non-native haplotypes. Within this reach are all Dominant class sample sites, where netted *P. hartii* was highly mutilated. Furthermore, *P. hartii* and *Megaleporinus elongatus* are migratory Characiformes (H. P. Godinho, Godinho, & Vono, 1999). Mutilations from non-native grazing pirambebas upon these fishes may impact reproductive and juvenile migrations if swimming performance is compromised. However, we must remember that our results do not necessarily reflect an ecologically important effect, but rather the preference of pirambebas.

Netted fish mutilation by Serrasalmus has been debated in the literature for over thirty years, and according to Winemiller (1990), fin damage inflicted by piranhas is undoubtedly a major selective pressure on large native fishes that inhabit rivers of South America. Nevertheless, it has never been addressed in the context of biological invasions, nor with a control in a natural experiment (Absent class). Here, we provide conclusive evidence that pirambebas more often graze on fins from netted fishes. Pirambebas apparently prefer some native species such as *O. macrolepis*, *P. hartii* and *M. elongatus*. Pirambebas also avoid cannibalism no matter its abundance (so far) and they achieve this by broadening their feeding preferences under higher population densities.

Acknowledgments

Conflicts of interest

The authors certify that they have no affiliations with or involvement in any organization or entity with or without financial interest in the subject matter or materials discussed in this manuscript. The authors also declare that they have no conflict of interest.

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Tables

Table 1: Summarized results of the binomial GLM for the four models regressing fin mutilation/no fin mutilation against log scaled standard length.

Model	pseudo-R^2	Coefficient	Estimate	SE	Z	p
1- all data	6.89	Intercept	-6.677	0.47	-14.22	<<<0.0001
		log(sl)	1.419	0.097	14.58	<<<0.0001
2- Absent	2.15	Intercept	-5.065	1.216	-4.164	<<0.0001
		log(sl)	0.796	0.256	3.113	<0.0019
3- Present	6.52	Intercept	-6.867	0.871	-7.883	<<<0.0001
		log(sl)	1.345	0.178	7.577	<<<0.0001
4- Dominant	6.35	Intercept	-6.009	0.712	-8.442	<<<0.0001
		log(sl)	1.43	0.148	9.642	<<<0.0001

Table 2: Summarized results of the Poisson GLM for the four models regressing the number of mutilated fins against log (standard length).

Model	pseudo-R^2	Coefficient	Estimate	SE	Z	p
5- all data	17.92	Intercept	-5.904	0.207	-28.43	<<<0.0001
		log(sl)	1.228	0.041	30.25	<<<0.0001
6- Absent	3.62	Intercept	-4.75	0.906	-5.24	<<0.0001
		log(sl)	0.731	0.187	3.901	<0.0019
7- Present	11.3	Intercept	-5.421	0.486	-11.14	<<<0.0001
		log(sl)	1.011	0.095	10.61	<<<0.0001
8- Dominant	21.51	Intercept	-5.399	0.254	-21.21	<<<0.0001
		log(sl)	1.197	0.049	24.14	<<<0.0001

Figures
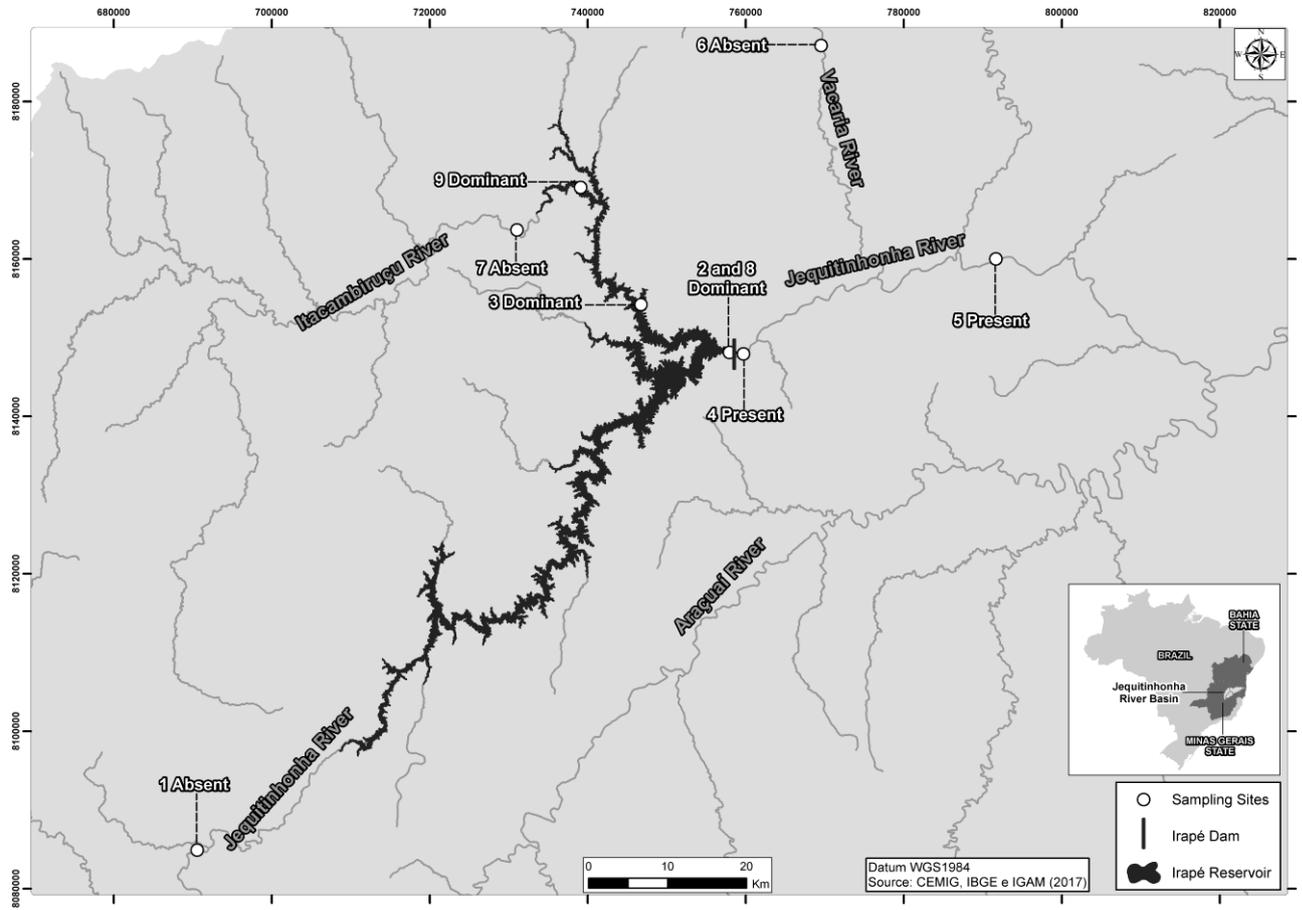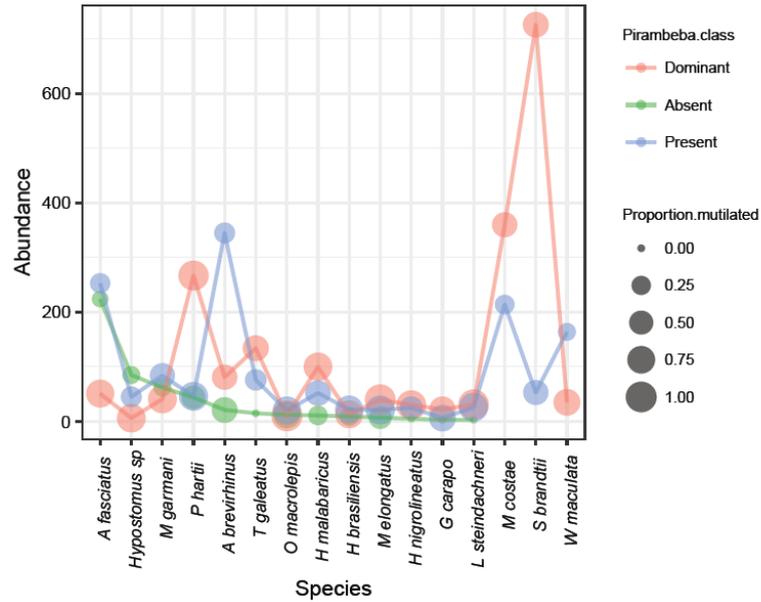
Figure 2: Rank-abundance curves for on each pirambeba class (differentiable by colours). Rank order followed Absent class (green) species abundance once it represents the natural environment without non-native species (*S. brandtii* and *M. costae*) and flow regulation by Irapé Dam. Dot size represents the species proportion of mutilated fish at each pirambeba class.
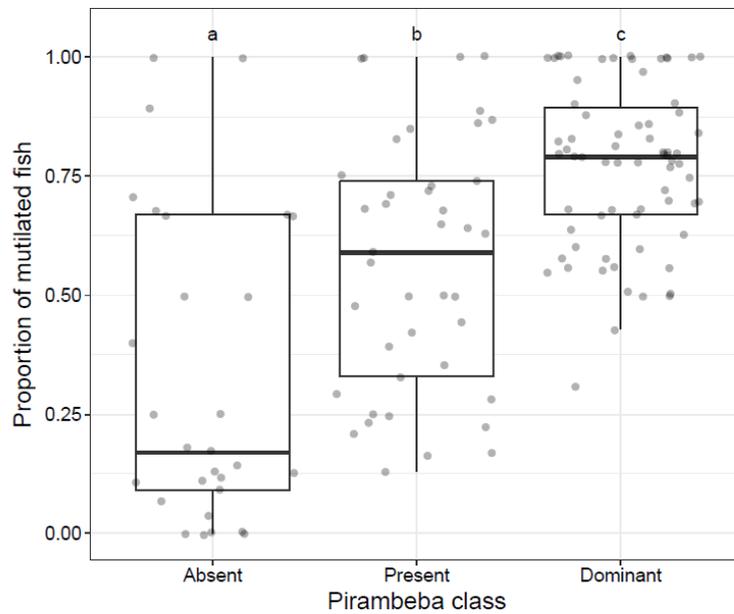
Figure 3: Proportion of mutilated fish for each pirambeba class. Each dot indicates a sample, boxplots provide position of the central value (median),1st and 3rd quartiles (boxes) and the non-outlier range (whiskers). Dots outside the boxplot limits are outliers.
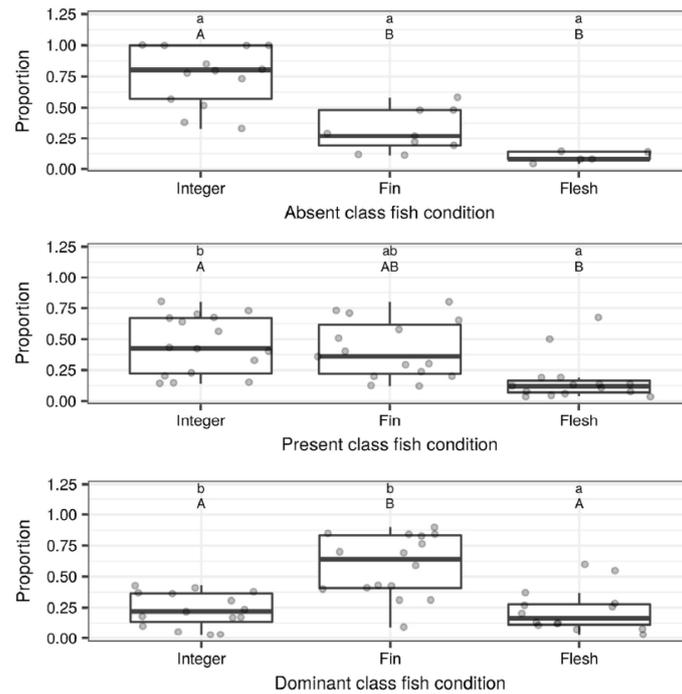
Figure 4: Proportion of *Integer*, *Fin* mutilated and *Flesh* mutilated fish for each pirambeba class. Each dot indicates a sample, boxplots provide position of the central value (median),1st and 3rd quartiles (boxes) and the non-outlier range (whiskers). Dots outside the boxplot limits are outliers. This figure also brings the pairwise results of Nemenyi's post hoc tests, by means of the letters above boxplots. Uppercase A, B or AB indicate if *Integer*, *Fin* and *Flesh* are significantly different from each other in each pirambeba class (must be compared horizontally). Lowercase a, b or ab refer to comparisons within a condition indicating significant differences. So, comparisons are vertically oriented (e.g. *Fin* from Absent (a) and *Fin* from Dominant (b) are significantly different, while *Fin* from Present (ab) is not different from the other classes).
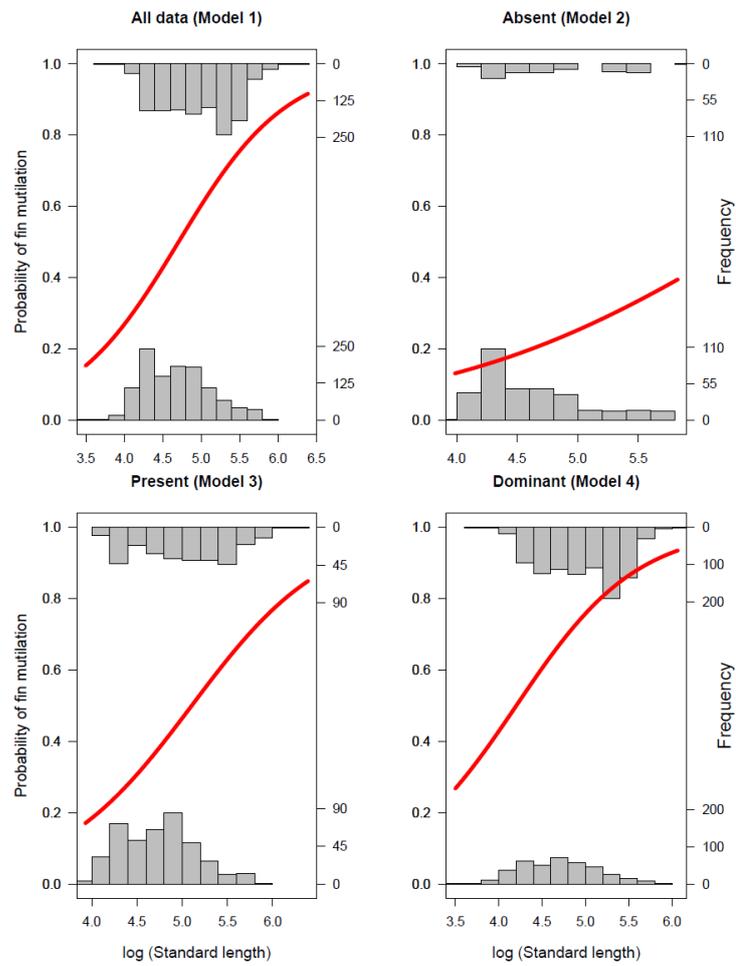
Figure 5: Predicted probabilities of fin mutilation in relation to fish log scaled standard length (red lines), for each pirambeba class (Models 1- 4). Histograms (grey bars) on each plot represent de log scaled standard length distribution for no fin mutilated (lower) and mutilated (upper) fish.
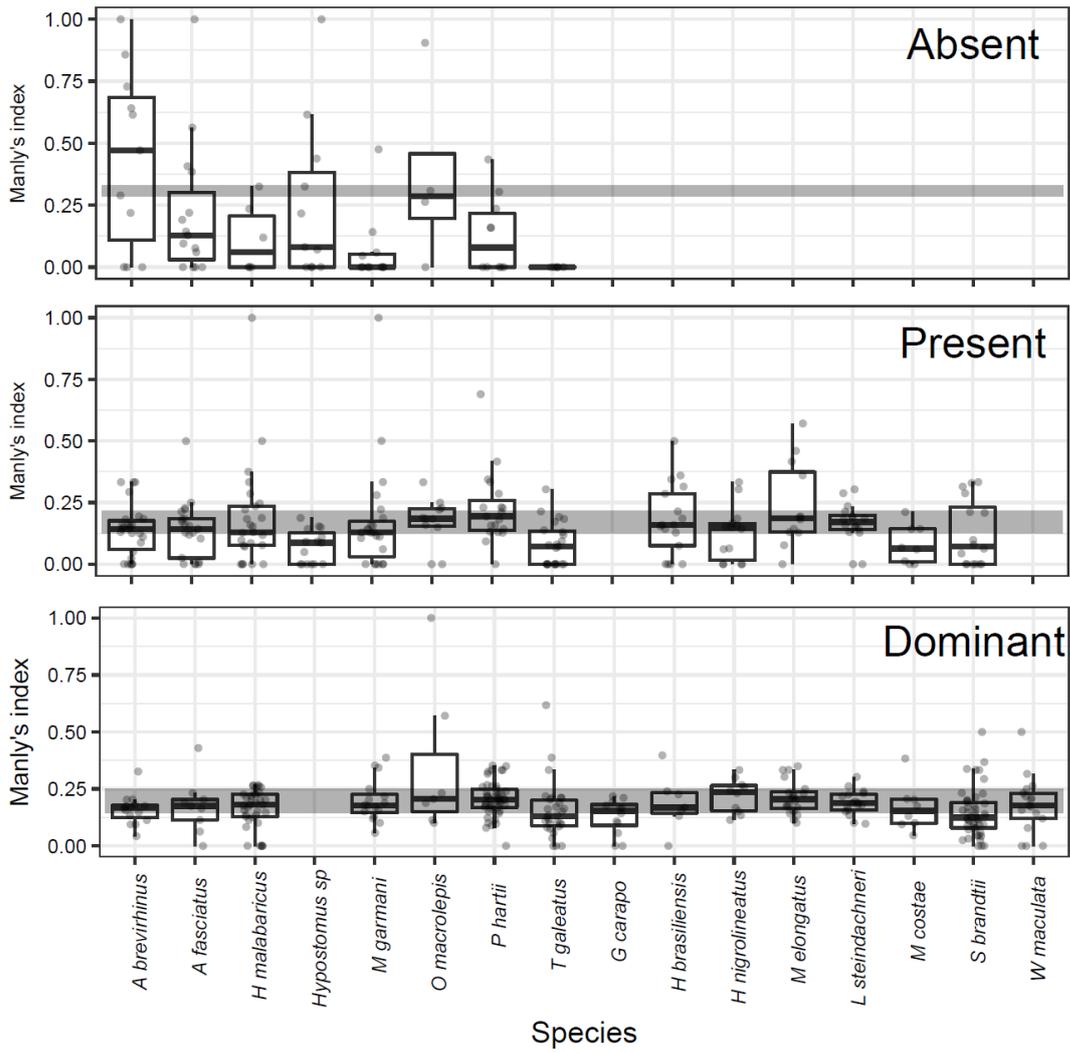
Figure 6: Manly's index for each pirambeba class (Absent, Present and Dominant). Each dot indicates a sample, boxplots provide position of the central value (median),1st and 3rd quartiles (boxes) and the non-outlier range (whiskers). Dots outside the boxplot limits are outliers. The horizontal bands represent apparent preference threshold (1/richness's 1st to 3rd quartiles).

Capítulo 3: Small home ranges, different habitat requirements and for three Loricariidae species inhabiting a Brazilian river

Manuscrito a ser submetido ao periódico Journal of Applied Ichthyology

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Small home ranges, different habitat requirements and its possible long-term consequences for three Loricariidae species inhabiting a drying Brazilian river

Running title: Loricariidae home ranges and habitats

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Acknowledgements

Introduction

The ability to disperse across the riverscape allows freshwater fishes to mix up their genes and to colonize new areas (Radinger & Wolter, 2014). At the community level, moving fishes conduct matter and energy through the ecosystems (Winemiller & Jepsen, 1998), and create seasonal differences in species turnover (FitzGerald et al., 2017).

In order to move fishes need free stretches, and these are increasingly being reduced by river damming (Pelicice et al., 2017). Not only higher order rivers are threatened, but the growing expansion of small hydropower plants (Couto & Olden, 2018), which usually demands damming, also affects non-migratory and short distance migratory fishes moving between habitats or during the course of their development, heading to upstream areas (Menezes & Caramaschi, 2000).

Combined with other human activities, such as water diversion or even climatic changes, damming can change the hydrological regime, reduce the water supply and promote the dewatering of river stretches. The most severe consequence of river flow reduction are fish kills, but also dispersal is thought to be affected whether by restricting higher densities of individuals to ponds or by promoting evasion to perennial stretches (Davey & Kelly, 2007).

The idea that stream fishes are sedentary has been under debate for decades and currently, ecologists recognise that fish populations are heterogeneous (Rodríguez, 2002; Radinger & Wolter, 2014): part of the individuals are stationary and the other part are mobile. Radinger & Wolter (2014) provided a meta-analysis on 62 species and concluded that in most of the studies the stationary individuals comprised 2/3 of the population, and their median displacement was 36.4 m.

Knowing the share of mobile individuals, the home range sizes and habitat requirements can help ecologists to propose conservation and management actions in polluted, dammed or drying rivers. These can be the minimum effective size of founder populations (Radinger & Wolter, 2014), the sizes of river stretches that allow species to complete their life cycle (Godinho & Kynard, 2006) and the habitats they tolerate or not.

In this contribution, we combined radio telemetry and traditional external tagging to investigate the movements of three species of Loricariidae from the Jequitinhonha river basin. This family went through a spectacular diversification in Neotropical region (Reis, Kullander, & Ferraris, 2003) but are mainly comprised by sedentary species (Celestino et al., 2017; FitzGerald et al., 2017). Based on the literature we hypothesised small home range sizes (Mazzoni et al., 2018) and habitat specificity (Cecília Gontijo Leal, Junqueira, & Pompeu, 2011). The recent droughts in this basin and the future perspectives of even more severe droughts encouraged us to make predictions about the persistence of such species in the light of our results.

Materials and methods

Study area

The Vacaria river is a 5th order, perennial, left margin tributary from the Jequitinhonha river (Almeida, Borges, & Rodrigues, 2017). The cerrado *strictu-sensu* is the main phytophysiognomy in this sub-basin (21% coverage), but more than 30% of its total area is already compromised by urbanization, pasture, *Eucalyptus* and *Pinus* monocultures (Almeida, Borges, & Rodrigues, 2017).

Flow data are available for the Vacaria river from 1976 to 2015 at http://www.snirh.gov.br/hidroweb (daily maxima= 446.3, minima= 0.1, mean= 8.1 and median= 3.5 m^3/s). River flow rises from September to February, peaking at November (mean= 16.1 m^3/s), and decreases from March to August, when it reaches the lowest levels (mean= 2.5 m^3/s). We conducted our study in the low water period, from April to October 2016. This was an extremely low flow year, on which at least two occasions (August and October) the Vacaria river ceased flowing.

We delimited a study region approximately 0.75 km long in the Vacaria river, between the coordinates S16°23'1.47" W42°28'32.16" and S16°22'40.06" W42°28'40.06" (Figure 1). This region is 43 km away from the Vacaria river mouth in the Jequitinhonha river.
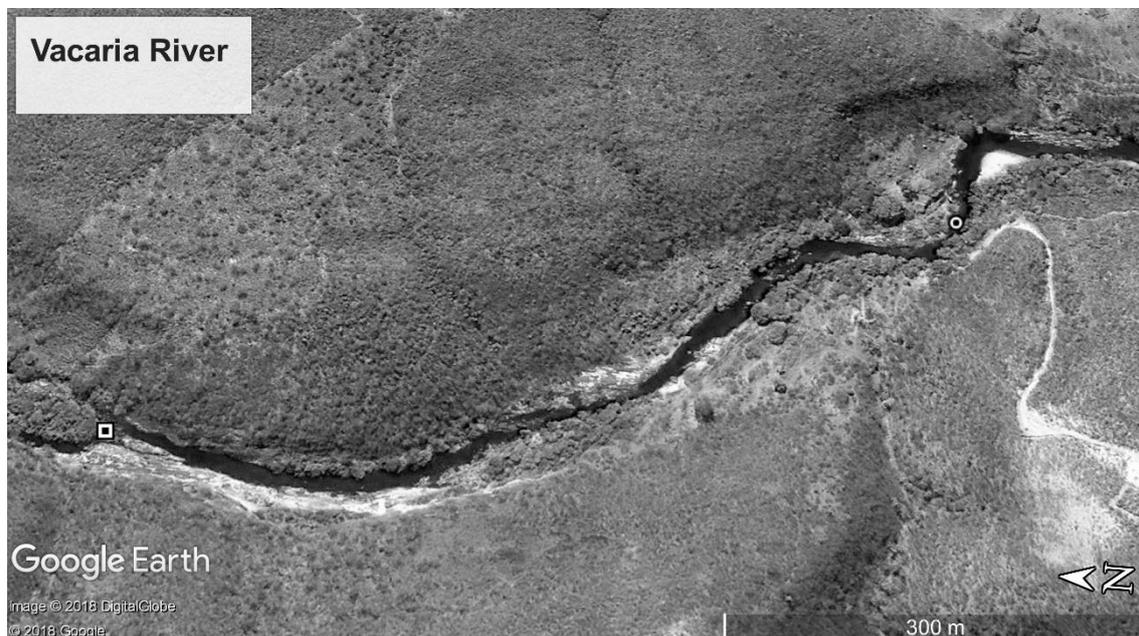
Figure 1: Vacaria river in the study section. Square in the left and circle in the right sides indicates the most upstream and downstream boundaries, respectively.

Target species

At least nine Loricariidae species occur in the JRB: *Delturus brevis* (Reis, Pereira, & Armbruster, 2006), *Hypostomus nigrolineatus* (Zawadzki et al., 2016), *Hypostomus* sp. (Zawadzki et al., 2016), *Harttia garavelloi* (Oyakawa, 1993), *Microlepidogaster discus* (F. O. Martins, Rosa, & Langeani, 2014), *Chauliocheilos saxatilis* (F. O. Martins et al., 2014), *Pareiorhaphis stephanus* (J. C. Oliveira & Oyakawa, 1999), *Pareiorhaphis lineata* (E. H. L. Pereira et al., 2017) and *Parotocinclus jequi* (Lehmann et al., 2013). We studied the three largest species: *Hypostomus nigrolineatus*, *Hypostomus* sp.*,* and *D. brevis*. Standard length ranges are available for *H. nigrolineatus* (5.5 - 21.2 cm) and *D. brevis* (7.7 - 18.6 cm) (Salvador et al., 2017), and are consistent with our data.

Hypostomus nigrolineatus, the last described Loricariidae from the basin, frequently presents conspicuous horizontal stripes on the posterior portion of the flanks, an unusual pattern among its congeners (Zawadzki et al., 2016). Although Godinho et al. (1999) reports four *Hypostomus* species to the JRB, there may be only two as pointed out by other studies (Bizerril & Lima, 2005; Zawadzki et al., 2016; E. H. L. Pereira et al., 2017). The second and still undescribed *Hypostomus* (*Hypostomus* sp.) differs from *H. nigrolineatus* by the color pattern and by the incomplete abdominal coverage with minute scutelets, even in adults (versus complete abdominal coverage in adults). Unpublished data from ichthyological inventories on low order streams showed that *Hypostomus* sp. are widespread throughout the basin and one of the most abundant species (personal communication). Conversely, *H. nigrolineatus* has never been captured in such streams, and appears to be more common to higher order rivers. The presence of two species with such distribution pattern was also observed in the lower Paraíba do Sul basin (Mazzoni, Caramaschi, & Weber, 1994).

Delturus is a four species genus restricted to the Jequitinhonha (*D. brevis*), Paraíba do Sul (*D. parahybae*), Mucuri (*D. angulicauda*) and Doce (*D. carinotus*) river basins (Reis, Pereira, & Armbruster, 2006; Buckup, 2011). *Delturus* have a strong and massive body and display marked sexual dimorphism: mature males develop patches of thin hypertrophied odontodes in the lateral margins of head and in the first thickened pectoral fin ray (Reis, Pereira, & Armbruster, 2006). *D. brevis* is distinguished from its congeners by having a concave caudal fin. Males are larger than females (personal communication).

Capture, tagging and tracking

We ran all fieldwork from April to October 2016. We captured fish with gillnets (stretched size mash= 5 cm), placed randomly overnight. We applied a daily effort of 100 linear meters (usually 10 units of 10 m nets). Captured fish were identified and weighted. If weight was above 50g fish was eligible for radio tagging. Most of the remaining fish were tagged with T-shaped anchor tags on the dorsal fin base.

We used Lotek Wireless radio telemetry equipment. Fishes were tagged with MST 820 radio tags (weigh in air= 2.1 g, estimated operational life = 180 days). Prior to radio tagging, fishes were anesthetized with eugenol (concentration= 2 drops/ liter of water). Then, radio tags were inserted surgically inside body cavity after a tiny incision in the abdomen. Incision was sutured with non-absorbable monofilament, and fish were kept in a small tank immersed in the river for a recovery period of 1-2 hours. All recovered fish were released in the same location of the river.

Since the Vacaria river is wadeable in most of the study region, we tracked fish manually with a SRX800-MD2 mobile receiver and an omni-directional antenna. Whenever we locate a tagged fish or captured a still non-tagged one on nets, we determined its geographical position with a GPS and measured the water depth and water velocity (with a flowmeter) at that location. The same procedure was applied to most netted fishes by the time nets were checked. In most cases we determined the exact location of fish by reducing receiver gain below 10 and assuring a power higher than 200.

Substrate size classification

On November 2016, a month after fieldwork, Vacaria river ceased flowing and we returned to the study area to measure substrate size. Along the area we set a hundred evenly spaced cross-sections upon which we estimated substrate size in five channel locations (from one margin to the other), according to Peck et al. (2006). As most of the riverbed was exposed, substrate size ranges (SSR) were visually classified as silt (SSR< 0.06 mm), sand (SSR from 0.06 to 2 mm), fine gravel (SSR from 2 to 16 mm), coarse gravel (SSR from 16 to 64 mm), cobble (SSR from 64 to 250 mm), small boulder (SSR from 250 to 1000 mm) and rough bedrock (SSR > 4000 mm) (Peck et al., 2006). We determined the percent coverage of each substrate for every cross section and associated it to each fish record.

Data analysis

All analyses were performed in R-Studio (R Development Core Team, 2016). First we calculated linear home range as the distance from the most upstream to the most downstream locations (Godinho & Kynard, 2006), for each individual with at least two records. For instance, here we use the term recapture to designate fish exclusively externally tagged and location when referring to radio-tagged fish. When the type of tagging is not of concern, we use record. We tested for differences in linear home range size for each species and, whenever possible, for the type of tagging by applying a Kruskal Wallis test.

We considered linear home range a discrete variable to be regressed against the number of days since tagging and the number of records an individual had during the study. To cope with overdispersion and non-normality of residuals we applied a negative binomial GLM with a log link function (Zuur et al., 2009).

Based on linear home range sizes we analyzed the heterogeneity of movements (Rodríguez, 2002) performed by *Hypostomus* sp. individuals. We used the 'fishmove' package (Radinger & Wolter,

2014) to estimate movement parameters. From the fishmove.estimate function we obtained the mean linear home range of the stationary (σ stat) and mobile (σ mob) components, and the share of stationary component (P= the proportion of stationary individuals). We also used the fishmove and fishmove.query functions to predict the cumulative kernel probability for the segment corresponding to the stationary and mobile components. The fishmove function uses four variables to calculate the parameters: fish length (*Hypostomus* sp. mean total length= 159 mm), Strahler stream order (Vacaria river = 5), time duration of the study (t= 180 days) and the aspect ratio of the caudal fin as a proxy for the species type of locomotion (*Hypostomus* sp. = 1.4) (Radinger & Wolter, 2014).

We tested the relationship between fish total length and linear home range with negative binomial regression and with a Kruskal- Wallis test, using the mobile and stationary fishes as the grouping variable and fish total length as the response variable.

Regarding physical habitat, we verified if the presence of the three species was associated with hydraulic characteristics: water depth and velocity at which the fish was recorded, eight substrate size classes (percent coverage on each cross-section) and the number of substrates classes *per* section (substrate richness). As we had multiple variables and produced sets of competing models, we used the multimodel inference approach (Burnham & Anderson, 2002; Symonds & Moussalli, 2011). First, we checked for collinearity among predictors with Spearman's correlation. Values ranged from -0.48 to 0.47, which indicate low to moderate collinearity ($-0.6 < r_{Spearman} < 0.6$) and thus produce no bias on the parameters estimates (Freckleton, 2011). So, we included all predictors in the initial global models. Second, all possible models were produced with the dredge function from the package 'MuMIn'. Each species required a different number of dredges as we eliminated non-significant variables from the global model and reduced the number of candidate models. At the last dredge, we kept those models within ΔAIC < 4 interval from the best model, since at this distance, the models are considered to be as good as the best model (Symonds & Moussalli, 2011). At this step, we proceeded with model selection including the evidence ratio (w_1/w_i), which is a comparison of the evidence for the best model (w_1) versus the w_i[th] best model (Burnham & Anderson, 2002). The higher the evidence ratio, the stronger the support for w_1 to be the best over w_i. We also accounted for the number of times a predictor appeared in the final set of models and their averaged pseudo R^2 as useful tools for inference (Burnham & Anderson, 2002; Solar et al., 2016).

We also related fish presence to water flow and depth with multiple logistic regression. Dispersion parameter varied from 0.43 (*D. brevis*), 0.61 (*H. nigrolineatus*) to 0.92 (*Hypostomus* sp.), never matching 1. So, to deal with underdispersion (response variable with a variance smaller than the mean) we used a quasibinomial correction for logistic regression models and a logit link function (Stokland, Halvorsen, & Støa, 2011).

Results

We captured 380 loricariids: 34 *D. brevis* (due to mortality soon after radio-tagging, 26 individuals provided information), 24 *H. nigrolineatus* and 322 *Hypostomus* sp. Highest proportion of records were observed for *H. nigrolineatus* = 45.8%, followed by *D. brevis* = 38.4%, and then by *Hypostomus* sp. = 25.1%. The number of records for a single individual varied from one to seven (Table 1). Considering the river flowing period, water depth varied from 8-200 cm and velocity from 0.0022 – 0.9271 m/s. Fish occurrence in relation to water depth and velocity are available in Figure 2

Table 1: Number of individuals from each species recorded from one to seven times during the study.

Number of records	*Delturus brevis*	*Hypostomus nigrolineatus*	**Hypostomus** sp.
1	16	13	241
2	2	1	65
3	3	3	7
4	1	1	5
5	3	4	2
6	0	0	2
7	1	2	0
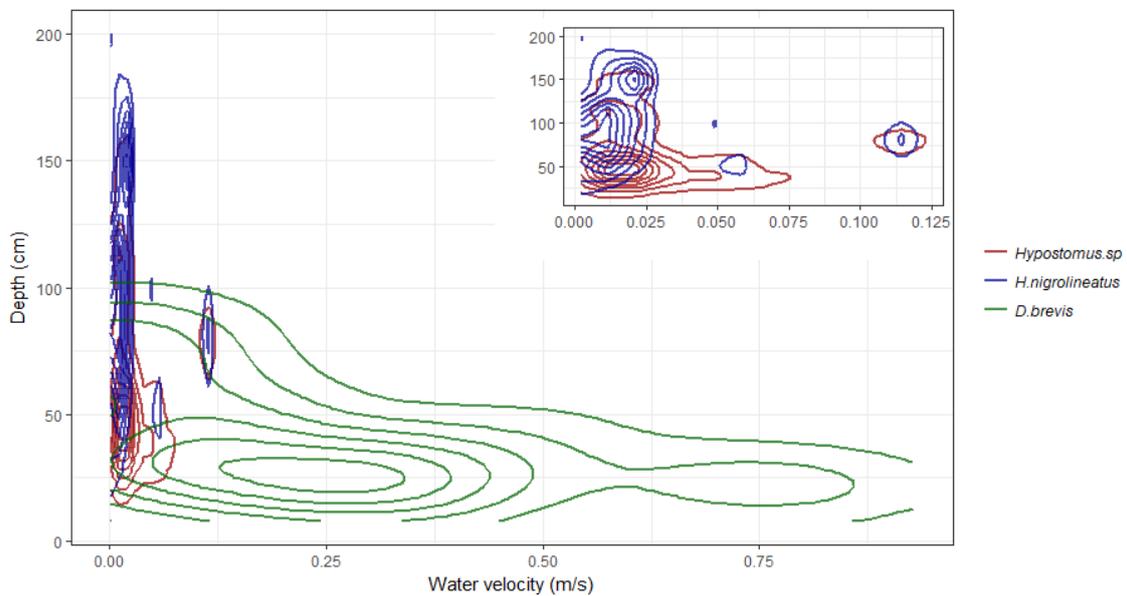
Figure 2: Two dimensional density plot for water velocity and depth used by the tree species of Loricariidae in the Vacaria river. The inner plot restricts to the two *Hypostomus* in the velocity range of 0 to 0.125 m/s. This plot was meant to help visualization of the most used depths and velocities for each species, not to provide cause and effect relationships.

Linear home range

Linear home range sizes varied from 2.01 - 19.85 m (mean= 9.75 ± 5.65) for *D. brevis*, 3.53 - 627.66 m (mean= 226.70 ± 255.91) for *H. nigrolineatus* and 0.88 - 496.39 m (mean= 40.62 ± 83.09) for *Hypostomus* sp. We observed specific differences in linear home range size (Kruskal-Wallis chi-squared = 6.577, df = 2, p < 0.038). However, pairwise comparisons are significant to *H. nigrolineatus* and *Hypostomus* sp., only. The lack of significance between *H. nigrolineatus* and *D. brevis* is clearly related to the small number of replicates for the latter (Figure 3).
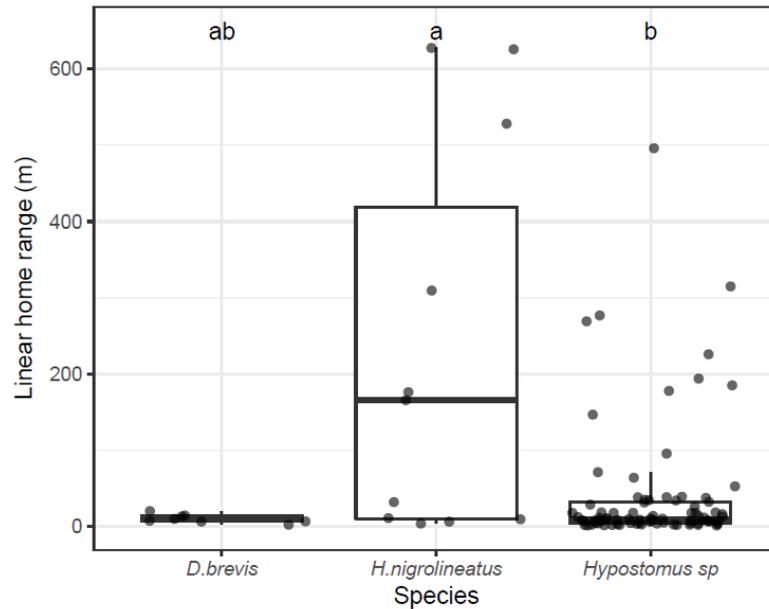
Figure 3: Linear home range sizes comparisons for the targeted species. Letters above the boxes refer to post-hoc pairwise differences between species. Each dot is an individuals linear home range size. Boxplots provide position of the central value (median) and the spread of the data (boxes and whiskers).

Only three *D. brevis* and *H. nigrolineatus* tagged exclusively with external tags were recaptured, which precluded us from making comparisons among linear home range sizes from radio-tagged and externally only tagged fishes. As for *Hypostomus* sp., we observed no significant differences in linear home range size related to the type of tagging (Kruskal-Wallis chi-squared = 1.23, df = 1, p > 0.25). Linear home ranges from externally only tagged *Hypostomus* sp. were positively related to the number of records and to the number of days since tagging (Table 2). Although significant, both relationships were weak.

Table 2: Negative binomial GLM results for the two models regressing *Hypostomus* sp. linear home range against the number of days since tagging and the number of records a fish had during the study.

Parameter	Estimate	Std.Error	z	p-value	pseudo-R^2
Intercept	2.63715	0.237624	11.098	2.00E-16	
n_days	0.02427	0.004767	5.092	3.55E-07	0.17
Intercept	1.9558	0.7106	2.752	0.00592	
n_records	0.7939	0.3158	2.514	0.01193	0.06

Mean linear home ranges for stationary and mobile *Hypostomus* sp. were 15.33 ± 1.29 and 206.60 ± 27.91, respectively. The percentage of stationary individuals was 79.9% and the corresponding linear home range size that harbors these individuals was 37 m. The mobile share (20.1%) is mostly represented by outliers (Figure 3). The largest predicted linear home range size was 5,009 m. The predicted kernel probability for the stationary fish was 0.442 (from 0 to 37 m) and 0.558 for mobile fish (from 37.1 to 5,009 m) (Figure 4). Most of the cumulative probability (0.95) was predicted for linear home ranges from 0 to 1,174 m. Linear home range increased in size as the total length of *Hypostomus* sp. decreased (negative binomial regression results: Intercept: Estimate= 8.06, SE= 1.78, z= 4.52, p< 0.001; Total length: Estimate= -0.03, SE= 0.01, z= -2.54, p< 0.012).
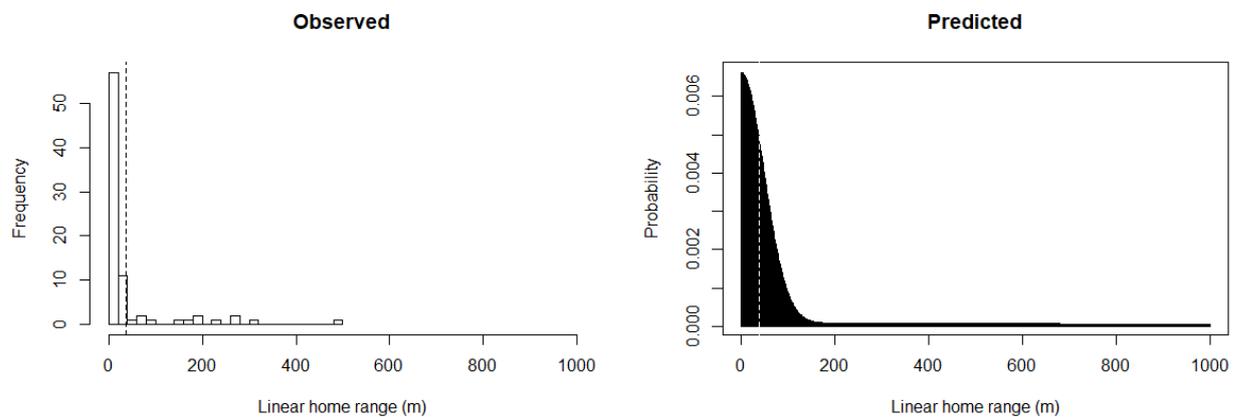
Figure 4: Observed frequency distribution (left) and predicted probability distribution (right) for linear home ranges of *Hypostomus* sp. X-axis is limited to 0-1000 m, to improve visualization, but predicted probabilities extend to 5,009 m. Dotted vertical lines at 37 m indicate the linear home range size that divides the stationary from mobile components, according to the share of stationary compartment = 0.799.

Physical habitat

The 10 physical habitat predictors initially provided 2^{10}= 1024 models for each species. Early explanatory dredges allowed us to exclude Fine Grain and Coarse Grain from the analysis. Although present in the final set of models of all species, substrate richness had no significance at all. The same was observed for Small Boulder in the *D. brevis* models. The remaining six predictors were significant for at least one, but never for the three species (Figure 5). Cumulative Akaike weights were almost the

desired by Burnham & Anderson (2002) (≥0.95) for *D. brevis* and below for both *Hypostomus* (Table 3). Evidence ratio was greater than 14 for the first model out of the ΔAICc < 4 interval, for the *Hypostomus* species. For *D. brevis* we opted to extend the ΔAICc inverval to 4.28 and included another model. This more than doubled the evidence ratio for the first excluded model in relation to the best model (Table 3).
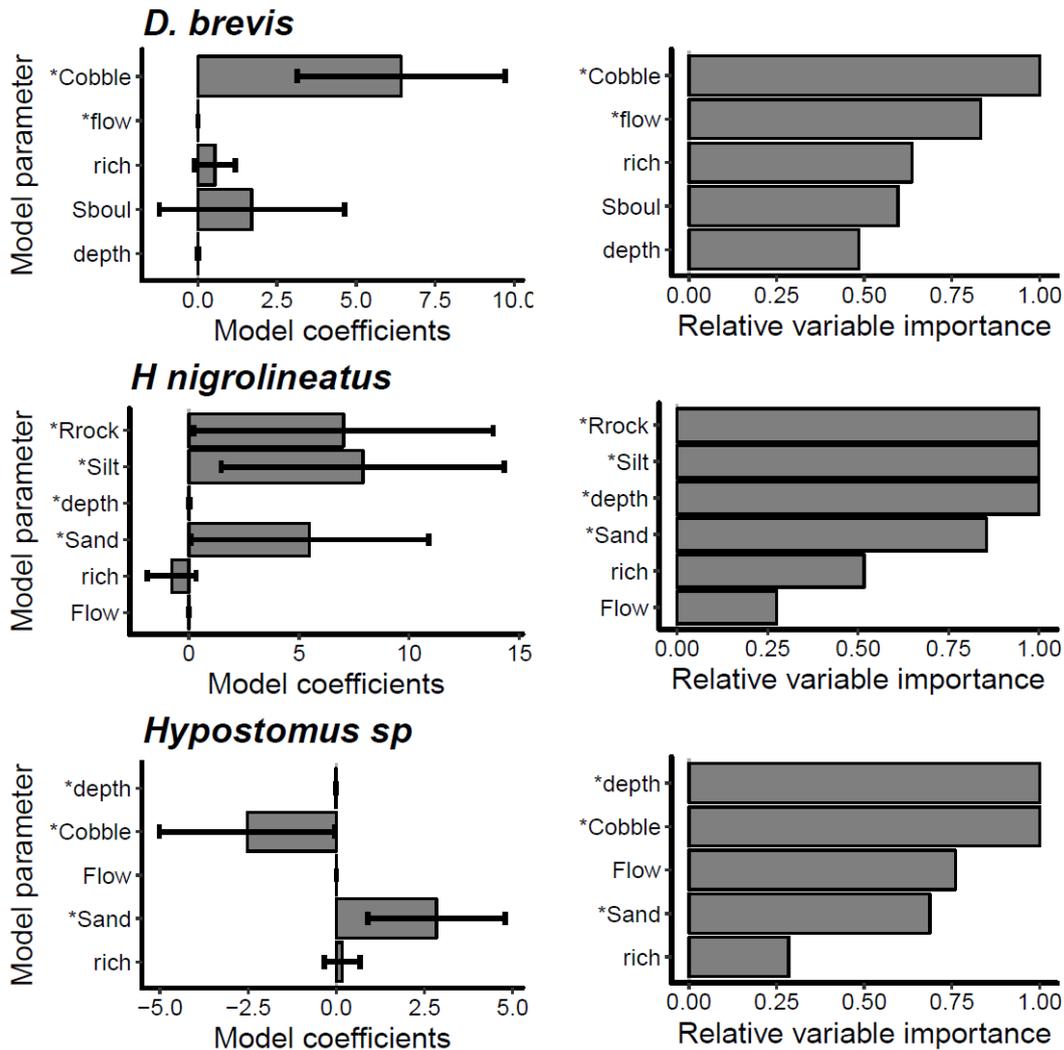
Figure 5: Left: Model averaging of candidate models within ΔAICc < 4 (or ΔAICc= 4.28 for *Delturus brevis*) interval for fish presence according to substrate percentual coverage, water depth and velocity. Right: Relative importance of each variable measured as the proportion of models on which it was included. * indicates significant variables. Rrock = Rough bedrock, Sboul = Small boulder, rich = substrate richness, Flow = water velocity (m/s).

Table 3: Final numbers of models for the three targeted species, their cumulative Akaike weights, weight of evidence for the first model outside the ΔAICc<4 interval (For *Delturus brevis* ΔAICc= 4.28) and the mean Pseudo R^2 with standard deviations.

Species	n models	cumulative AICc	Evidence ratio	Pseudo R^2
D brevis	11	0.94	16.0	0.21 ± 0.010
H nigrolineatus	6	0.89	18.6	0.29 ± 0.007
Hypostomus sp.	7	0.85	14.6	0.13 ± 0.013

Discussion

We provide the first evidence for small home ranges associated to specific habitat requirements in Loricariidae. As an extremely diverse group these fishes explore the full variety of hydraulic conditions of benthic habitats from Neotropical streams (Langeani et al., 2005; Casatti & Castro, 2006; Cecília Gontijo Leal, Junqueira, & Pompeu, 2011). The same, though, is not observed for dispersal. These catfishes are frequently described as sedentary or non-migratory (Celestino et al., 2017), and only one species (*Rhinelepis aspera*) is currently reported as migratory (Carosfeld et al., 2003).

The most sedentary of the three species, *D. brevis* had the smallest home range sizes and its presence is highly related to cobble, a more stable substrate class in relation to sand, which was important to the *Hypostomus* species. These traits coupled with marked sexual dimorphism, namely (i) the hypertrophied odontodes possibly acting as weapons for males (Reis, Pereira, & Armbruster, 2006); (ii) the fact that males are larger than females (authors personal communication), and that male-male contest can push males size beyond females (Parker, 1992); suggests that *D. brevis* may be territorial fishes. Territories or defended home ranges may demand higher energy costs, and thus optimal smaller areas may be preferred to larger home ranges (Grant, Chapman, & Richardson, 1992; Slavík, Horký, & Závorka, 2014).

Most *Hypostomus* sp. were stationary, but the population seems to be heterogeneous as proposed by Rodríguez (2002). Even in smaller proportion, mobile individuals are crucial for colonization, especially in drying environments, such as the Vacaria river by the end of our study. This species is the most successful Loricariidae colonizing the Jequitinhonha river basin. It occurs from the upper to lower stretches (H. P. Godinho, Godinho, & Vono, 1999; Bizerril & Lima, 2005; Andrade, 2010) and from lower to higher order rivers (personal communication).

The predicted proportion of stationary fishes is way above the observed (almost half), but the pattern is the same, if we consider the presence of stationary and mobile components. Besides, the movement

heterogeneity has been tested for at least 62 species from 12 families over five continents (Rodríguez, 2002; Radinger & Wolter, 2014; Wells et al., 2017), but this is the first attempt to use it with a Neotropical species, from a group notably comprised of sedentary fishes.

The increase in linear home range in relation to *Hypostomus* sp. length may indicate that home ranges (and even habitat requirements) vary as individuals grow. In this case, smaller (not necessarily juvenile) fish are the main drivers for colonization of new areas. This pattern is similar for *Hypostomus punctatus*: in a 15 km stream, Menezes & Caramaschi (2000) collected juvenile fish along the entire longitudinal gradient, whereas adults were caught in more restricted ranges from the upper to middle reaches.

We must, however, be cautious with this result for two reasons. (i) Although male and female fish often have similar sizes (Parker, 1992), length is commonly related to sex among *Hypostomus* (Suzuki, Agostinho, & Winemiller, 2000). As we have no information on reproductive strategies, length at maturity or length differences between sexes, it is possible that sex instead of size be the reason for the observed pattern. (ii) We have only used one mash size to capture fish. Had we used a wider range of mashes, we would have a better picture of the *Hypostomus* sp. size classes inhabiting the Vacaria river and its movement patterns.

The largest linear home range sizes observed for *H. nigrolineatus* may be explained by the arrangement of pools near the ends of the study area. To move among habitats individuals must cross a large stretch of the river. On the other hand, fishes located at the extremes of the study area have lower probability of being recorded than those in the middle (Rodríguez, 2002). That was not observed in our study, since the proportion of records for *H. nigrolineatus* was the highest for the three species.

Interestingly, *H. nigrolineatus* was associated to the most unstable (silt and sand) and stable (Rough Redrock) substrate classes, which co-occurred only in pools with higher depths (> 1m). It also explains the significance of depth as a predictor in our model selection. These stretches were characterized by rough bedrock over one or both marginal banks with sand or silt in the middle and did not dried out during the study.

Deeper stretches associated to both *Hypostomus* will possibly increase their probability of survival on episodes of severe drought. The dependence on cobbles and fast flowing waters may be risky for *D. brevis* and maybe other Loricariidae from this basin with similar habitat requirements, like *Pareiorhaphis lineata* and *P. stephanus* (E. H. L. Pereira et al., 2017). River stretches with these characteristics were the first to dry out during our study. Specificity for such habitats combined with low mobility are a threat to *D. brevis* in drying rivers. When the Vacaria river ceased flowing, most of the cobble substrate went exposed, water was retained only in pools, and resident people reported many fish dying below cobbles and rocky substrates. In this situation, we succeeded to capture a single

D. brevis in a pool, which indicates that at least some individuals resort to lentic soft-sedimented habitats in extreme situations.

Our target species are phylogenetically close and occur syntopically along the basin, including the Jequitinhonha river, itself (personal communication). In this case, some morphological differentiation and specialization is expected, in order to improve coexistence (Delariva & Agostinho, 2001; Cecília Gontijo Leal, Junqueira, & Pompeu, 2011). For example, the current distribution of the basal group Delturinae, bounded to the Southeastern Brazil, may be a result of past competition. Reis et al. (2006) hypothesized that more recent Loricariidae groups with similar life histories, but less diversified in Southeastern Brazil (*e.g.* Ancistrini) out-competed the Delturinae from other Brazilian regions.

Hypothesis aside, *D. brevis* clearly explores different habitats in relation to the other studied species. The *Hypostomus*, on the other hand, overlapped their habitats to some extent. The presence of rough bedrock (for *H. nigrolineatus*) and the absence of cobble (for *Hypostomus* sp.) seem to segregate these species spatially.

Lower Akaike weights (less than 0.9 for a single model) and large numbers of competing models set the scene for inference based on model selection, since the best model has no credibility alone (Burnham & Anderson, 2002). The low standard deviations observed for the Pseudo R^2 values showed that based on this parameter (explained variance) the remaining models are as good as the best. However, as the number of models increases, so does uncertainty (Burnham & Anderson, 2002). To cope with this issue we reduced the number of non-significant variables and relied on the evidence ratio. For both *Hypostomus* the models within the ΔAICc<4 interval were close to the best model (low evidence ratio) and the first model outside this interval was at least 14 times away from the best (higher weight of evidence values). For the *D. brevis*, we included one more model out of the ΔAICc>4 interval (evidence ratio= 8.5 and ΔAICc= 4.28, for instance) so that the best model had 16 times more weight of evidence than the first excluded model.

Flow and depth separately were important and significant variables for the occurrence of the *D. brevis* and both *Hypostomus*, respectively. However, the low coefficients may be related to the measurement of these variables, instead of low influence upon the occurrence of these fishes. Flow and depth were taken for individual fish, while substrate classes were defined for the whole study section. We only know *D. brevis* is not related to higher depths or lentic waters due to the measures taken from recorded *H. nigrolineatus*, and vice versa. This may have underestimated the influence of these variables. Moreover, flow and depth vary seasonally while substrate classes are more stable through the time scale of our study. A given section in the Vacaria river may have had multiple depths and water velocities during the study period, but always the same substrate classes at such time scale.

Among the three species, we are more concerned with the future of *D. brevis*. One of its congeners *D. parahybae* is already endangered and the causes are the lack of suitable habitats and vulnerability to environmental degradation (Pompeu & Vieira, 2003). It's being predicted for the end of this century a reduction in precipitation ranging from 10-15% in the Jequitinhonha river basin (IPCC, 2007). These will certainly reduce the availability of the habitats required for *D. brevis* possibly leading to a shrinkage of its original range of distribution. Water shortage will certainly increase efforts to regulate the Jequitinhonha river (there are currently two dams in the mainstem) and its tributaries (at least one dam is planned for the Vacaria river), to ensure human water supply. Although *D. brevis* uses small areas, damming will decrease lotic stretches, increase depth and promote sedimentation over cobbles, thus destroying the hydraulic habitat of this species. Based on that information we predict a significant reduction in *D. brevis* populations and its subsequent inclusion in the endangered species lists within the next few decades.

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