

# Small dams for aquaculture negatively impact fish diversity in Amazonian streams

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ABSTRACT: Much has been written about the negative impacts of large hydroelectric dams on fish species diversity in the Amazon River Basin; however, less is known about the impacts of small dams in streams that are created for fish aquaculture. Our study of fish assemblages upstream and downstream of fish farm dams in Rondônia State, Brazil, revealed that the dams act as physical barriers to fish movement and that upstream assemblages showed lower measures of diversity and abundance compared to downstream. The greatest impact was the obstruction of upstream movement of a number of fish groups, coupled with isolation and disappearance of relatively rare fish species living upstream. The fish species most affected were from frugivore, herbivore and detritivore trophic levels that are associated with migration and the forming of schools (potamodromous species), although the impact was also evident in piscivorous fish commonly found in lentic habitats. Although stream dams may cause small negative effects relative to huge hydroelectric barriers, the cumulative impact of hundreds of fish farms in stream channels could be considerable. Amelioration of the damage caused by fish farm impoundments will require (1) design of effective fish passage systems around dams to reduce impact on fish diversity and (2) prohibition of the complete stream blocking to build these fish farms, which will require derivative channels to their water supply.

KEY WORDS: Fish assemblages  $\cdot$  Dams  $\cdot$  Stream basin  $\cdot$  Tributaries

# INTRODUCTION

There are >154 large hydroelectric dams in operation in the Brazilian Amazon, with 21 dams under construction and 277 more planned over the next few decades (Finer & Jenkins 2012, Castello & Macedo 2015) in order to supply the Brazilian demand for power (Agostinho et al. 2008). It is well known that these obstructions greatly alter the landscape and negatively affect aquatic ecosystems, including fragmentation and isolation of fish communities (Girard 2002, Khan et al. 2014, Hurd et al. 2016, Pereira et al. 2016, Winemiller et al. 2016). Dams interrupt the tim-

ing and intensity of the annual hydrological cycle in the Amazon River Basin, which largely determines important life cycle characteristics of native fish such as dispersal during breeding seasons (Maltchik & Medeiros 2006) and movement related to feeding opportunities (Hahn & Fugi 2007). In particular, dams prevent migratory fish species from using river channels for reproductive movements (Ribeiro et al. 1995, Cox-Fernandes 1997, Freitas & Garcez 2004, Sousa & Freitas 2008, Miranda 2012). Fish ladders in this region have proven to be either ineffective or detrimental to fish survival (Pelicice & Agostinho 2008, Agostinho et al. 2012, Pelicice et al. 2015). Both

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upstream and downstream dispersal remains disrupted, and mortality of fish that are able to traverse the fish ladders tends to be high (Pelicice et al. 2015).

Although most research to date has focused on the impacts caused by large-scale hydroelectric barriers in major rivers (Winemiller et al. 2016), there are also many smaller dams built in streams for fish aquaculture (Neto et al. 2015, Lima et al. 2016). The impact of individual dams would likely be small, but the cumulative negative effects from multiple impoundments over an entire sub-basin could cause irreversible damage to the aquatic environment (Albanez & Albanez 2000) and specifically to fish assemblages (Agostinho et al. 2007). To determine the number of aquaculture farms that a given watershed can support, it is essential to verify the impacts associated with the construction of small dams for fish farm impoundments (Agostinho et al. 2007). Apparently, almost all of the fish farms in Brazil already in operation are not up to code and have contributed to deforestation of riparian areas, fragmentation of river habitats, blockage of migratory routes and degradation of nursery areas (Barletta et al. 2010).

Rondônia State is located in the southern part of the Brazilian Amazon and currently has >4000 licensed fishing farms, mainly in the Machado River basin (Ostrensky et al. 2008, Rondônia 2015). These farms specialize in the production of tambaqui Colossoma macropomum (Cuvier 1818), a large-sized characiform species that is endemic to the Amazon basin (MPA 2010). Studies of the effects of aquaculture on native fish assemblages are very scarce in Amazonia and completely nonexistent in the Machado River basin. The present research aimed to identify the impacts of fish aquaculture farms on the wild fish fauna of the streams in the headwaters of the Machado River by testing the following null hypotheses: (1) that small aquaculture dams have no effect on the structure of fish communities upstream or downstream; and (2) that there are no environmental changes in water quality associated with these fish farms.

#### MATERIALS AND METHODS

### Study area

The study area was located in the Machado River basin (Rondônia State, Brazil), where 5 streams were dammed to impound water for aquaculture farms (Fig. 1). All of the studied streams are shallow, low-order tributaries of the Machado River with sandy and rocky substrates. Grasslands are typically found

on the margins of these streams, as well as some stretches of preserved primary and secondary forests, including in the riparian zone. The status of the selected environmental variables was assessed in the field, using notes and a metric rule. The aquaculture impoundments ranged in size from 1.03 to 17.14 ha (10 300 to 171 400 m², Table 1), with no treatment systems in place to purify water before returning it to the stream. These aquaculture impoundments allowed us to investigate the effects of semi-intensive fish production since it is a system that directly interacts with the stream's main channel.

# Sample collections

Fish were sampled in 2 consecutive years, during 2 periods of the annual hydrological cycle: low water (September 2014 and June 2015) and rising water (December 2014 and March 2015). Fish sampling was performed in 150 m long-sections upstream and downstream of fish farming impoundments at 5 small streams, giving a total of 10 sampling locations (1 upstream and 1 downstream of each fish farm). Fish were captured using 3 different types of apparatus that were employed at every sampling site: (1) 2 gill nets 2 m high and 5 m long with 20 mm mesh, applied transversally or on the border of the river channel; (2) 1 ring net trap with a diameter of 2 m and 10 mm mesh size between opposite knots, moving continuously for 2 h, with 15 min intervals within long-sections (from one end to the other) of the stream; (3) 1 dip net with 2 mm mesh and 1 m diameter, also employed at the streams margins for a period of 2 h. Both trap types were set for a period of 2 h at night (18:00 to 20:00 h) and during the day (06:00 to 08:00 h) and were inspected every 20 min. At the same time, physical-chemical parameters were measured, including water temperature, dissolved oxygen, pH and electrical conductivity. The sampled fish were euthanized in cold shock (ice-water solution), labeled, stored in plastic bags and saved in an isothermal box for posterior taxonomic identification in the Aquaculture and Fisheries Laboratory at Rondônia Federal University.

## Data analysis

Fish community composition values were initially subjected to descriptive analysis to determine frequencies, means and standard deviations. The following ecological parameters were also calculated:

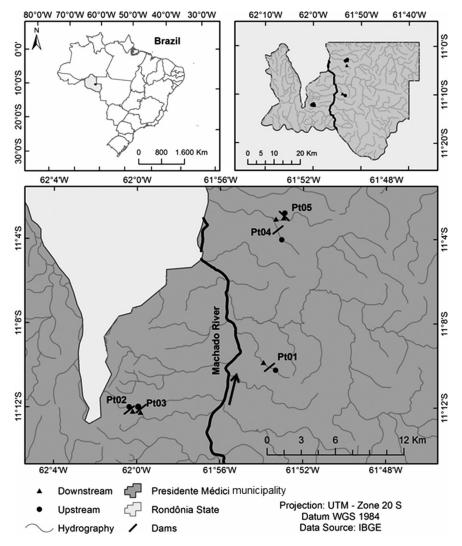


Fig. 1. Sampling sites and aquaculture dam locations in headwater streams of the Machado River basin, Rondônia State,
Brazil. Arrow indicates the direction of flow of the Machado River

species richness (S), Shannon's index of diversity (H'), Berger-Parker index of dominance (D) and Evenness (E) for both upstream and downstream data sets. Differences in water quality measurements between upstream and downstream data were tested with Student's t-test, when the data met the assumptions for normality and homoscedasticity. To test the null hypotheses that fish species composition is similar between upstream and downstream samples and between the low and high water seasons, a 2-way PERMANOVA was employed with 5000 permutations (Anderson 2001), based on a matrix of Canberra distance measures. The assumption of multivariate homogeneity of groups was tested before performing PERMANOVA. The Canberra distance was used to estimate the distance between sampling sites because this metric excludes double zeros and increases the effect of differences between variables with low values and many zeros (Buttigieg & Ramette 2014).

We classified fish species according to 3 life history strategies adapted from Winemiller & Rose (1992) and Winemiller (2005) based on their bioecologic characteristics (following Carvalho & Tejerina-Garro 2015, Röpke et al. 2017 and Arantes et al. 2017): (1) equilibrium strategists: species with moderate to long generation time, low reproductive effort, variable body size, low batch fecundity, high investment per offspring and, in general, no migratory behavior (24 species); (2) periodic strategists: species with long generation time, moderate reproductive effort, medium to large body size, high batch fecundity, low investment per offspring and migratory behavior (14 species); and (3) opportunistic strategists: species with short generation

Parameter	Pt01	Pt02	Pt03	Pt04	Pt05
Downstream average channel width (m)	$2.75 \pm 0.65$	1.78 ± 1.28	$1.20 \pm 0.81$	$1.99 \pm 0.27$	$1.09 \pm 0.14$
Upstream average channel width (m)	$2.01 \pm 0.30$	$2.45 \pm 0.37$	$2.25 \pm 0.78$	$4.73 \pm 1.01$	$1.09 \pm 0.14$
Downstream average depth (m)	$0.85 \pm 0.49$	$0.25 \pm 0.03$	$0.20 \pm 0.07$	$0.17 \pm 0.05$	$0.18 \pm 0.05$
Upstream average depth (m)	$0.29 \pm 0.08$	$0.36 \pm 0.12$	$0.50 \pm 0.23$	$0.52 \pm 0.23$	$0.18 \pm 0.05$
Area of the impoundment (Ha)	17.14	3.08	1.96	1.77	1.03
Environmental status <b>Downstream</b>					
Riparian condition	Grass land	Grass land, riparian forest	Grass land, riparian forest	Secondary forest	Primary and secondary forest
Benthic condition	Sand ground	Rock and sand ground macrophyte presence	Sand ground, and macrophyte presence	Sand ground, and macrophyte presence	Sand ground, and macrophyte presence
Flow status	lotic water	Lotic water	Lotic water	Lentic water	Lotic water
Upstream					
Riparian condition	Grass land	Secondary forest	Grass land, riparian forest	Grass land	Grass land, riparian forest
Benthic condition	Rock and sand ground	Sand ground, and macrophyte presence	Sand ground, and macrophyte presence	Rock, sand ground, and macrophyte presence	Sand ground, and macrophyte presence
Flow status	Lotic water	Lentic water	Lentic water	Lentic water	Lentic water

Table 1. Environmental characteristics of sampling sites (Pt01-05, see Fig. 1). Mean  $\pm$  SD

time, high reproductive effort, small body size, low batch fecundity, low investment per offspring and no migratory behavior (15 species) (Table 2). We also performed paired *t*-tests, using species richness per life strategy as response variables. Sampling site position related to the farms, upriver and downriver, were used as factors aiming to test the hypothesis that the impacts of the aquaculture farms were the same for fish species of different life strategies. We found 2 species, *Parodon buckleyi* and *Phenacorhamdia* spp., without enough biologic information for a confident classification and an exotic species *Oreochromis niloticus* that were not included in the analysis.

The distance matrix and the PerMANOVA were performed using the Vegan package (Oksanen et al. 2015), and also the t-tests were performed on the R v.2.14.2 statistical software (R Development Core Team 2012, Urbanek et al. 2012).

## **RESULTS**

A total of 6432 individuals was sampled in the study area, distributed among 4 orders, 20 families

and 56 species. Characiformes was the most abundant order with 3987 individuals (61.99%), followed by Perciformes (29.60%), Siluriformes (4.99%) and Gymnotiformes (3.42%). Characiformes was also the most diverse group with 30 species, corresponding to 51% of the total (Table 2).

The highest number of fish was captured at sampling site Pt01, while the lowest occurred at Pt05 (Fig. 2). There was no clear pattern for the number of fish caught between upstream and downstream sites. More fish were caught upstream than downstream at sampling sites Pt01 and Pt02, whereas more fish were caught downstream than upstream at sampling sites Pt03, Pt04 and Pt05 (Fig. 2).

The most frequent species were *Serrapinnus* aff. *microdon*, with 15.57 % (n = 908) and *Serrapinnus* aff. *notomelas* with 15.29 % (n = 892). Many species were considered rare, with  $\leq 5$  individuals collected per species, including *Paradon bucleyi*, *Curimata inornata*, *Curimata ocellata*, *Cyphocharax notatus*, *Hemiodus unimaculatus*, *Hyphessobrycon agulha*, *Jupiaba anteroides*, *Jupiaba* cf. *apenima*, *Moenkhausia cotinho*, *Phenacogaster* cf. *beni*, *Roeboides affinis*, *Ituglanis* cf. *amazonicus*, *Corydoras* cf. *trilineatus*,

Table 2. Fish species, the number of individuals sampled in each location (Pt01–05, see Fig. 1) and their life history strategy (LHS). Up: upstream; Dn: down-stream of the fish farm plant

Taxon	Pt	Pt01		02	Pt03		Pt	t04	Pt	05	LHS	
	Up	Dn	Up	Dn	Up	Dn	Up	Dn	Up	Dn		
CHARACIFORMES												
Parodontidae												
Parodon buckleyi Boulenger, 1887				2		1					Unknown	
Curimatidae												
Curimata inornata Vari, 1989								1			Periodic	
Curimata ocellata Eigenmann & Eigenmann, 1889								2			Periodic	
Curimatella dorsalis (Eigenmann & Eigenmann, 1889)	35	34						20	6		Periodic	
Cyphocharax notatus (Steindachner, 1908)			0.5					_		1	Periodic	
Steindachnerina fasciata (Vari & Géry, 1985)	112	220	25	34	19	101		5		8	Periodic	
Prochilodontidae				_		0		4.0		_	D . 11	
Prochilodus nigricans Spix & Agassiz, 1829		1		7		3		10		7	Periodic	
Anostomidae												
Leporinus friderici (Bloch, 1794)		39		4		1		3		1	Periodic	
Crenuchidae	_	_										
Characidium aff. zebra Eigenmann, 1909	7	1									Opportunistic	
Hemiodontidae											D : 11	
Hemiodus unimaculatus (Block, 1794)								1			Periodic	
Characidae												
Astyanax aff. bimaculatus (Linnaeus, 1758)	4	68	11	54	110	119		38	1	3	Periodic	
Astyanax cf. maximus (Steindachner, 1876) Brachychalcinus copei (Steindachner, 1882)		1	1	27 17		1		3 4	1	11		
Hyphessobrycon agulha Fowler, 1913			1	17		1		4	1		Opportunistic Periodic	
Jupiaba anteroides (Géry, 1965)									1	5	Opportunistic	
Jupiaba cf. apenima Zanata, 1997										5	Opportunistic	
Knodus cf. heteresthes (Eigenmann, 1908)		1	14	25	10	46					Opportunistic	
Moenkhausia cf. pankilopteryx Bertaco & Lucinda, 2006			1	19						4	Opportunistic	
Moenkhausia cotinho Eigenmann, 1908								5			Periodic	
Moenkhausia oligolepis (Günther, 1864)		1	26	11	2	2			3	19	Opportunistic	
Phenacogaster cf. beni Eigenmann, 1911					1						Opportunistic	
Poptella compressa (Günther, 1864)								9		_	Opportunistic	
Roeboides affinis (Günther, 1868)	4.04	000	4.04	0	C.4	400		4.5	0	2	Opportunistic	
Serrapinnus aff. microdon (Eigenmann, 1915) Serrapinnus aff. notomelas (Eigenmann, 1915)	181 217	296 54	161 185	9 31	64 14	138 103		15 172	3 108	41 8	Opportunistic	
	217	34	100	31	14	103		172	100	0	Opportunistic	
Serrasalmidae  Mylophys actorics (Müller & Treashel, 1944)				7				1			Egyilibrium	
Myloplus asterias (Müller & Troschel, 1844) Serrasalmus altispinis Merckx, Jégu & Santos, 2000	40	65		7				1 8			Equilibrium Opportunistic	
	-10	00						O			Opportunistic	
Iguanodectidae  Bryconops cf. giacopinii (Fernández-Yépez, 1950)	1	11	2	29		20		67	5	15	Periodic	
	1		2	20		20		07	0	10	remodie	
Acestrorhynchidae Acestrorhynchus falcatus (Bloch, 1794)										6	Periodic	
Erythrinidae										3	_ 0110 010	
Hoplias malabaricus (Bloch, 1794)	27	4	20	2	16	4	6	9	4	1	Opportunistic	
	**	=		_		-	-	-	=	-	T. T.	
SILURIFORMES Trichomycteridae												
Ituglanis cf. amazonicus (Steindachner, 1882)										1	Equilibrium	
Callichthyidae										1	_4	
Callichthys callichthys (Linnaeus, 1758)				2		9		16			Equilibrium	
Corydoras aeneus (Gill, 1858)			5	4	35	9		10			Equilibrium	
Corydoras cf. trilineatus Cope, 1872			5	1	50						Equilibrium	
Hoplosternun littorale (Hancock, 1828)		3	14	1		10					Equilibrium	
											1.	

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Table 2 (continued)

Taxon	Pto	Pt01		Pt02		Pt03		Pt04		05	LHS	
	Up	Dn	Up	Dn	Up	Dn	Up	Dn	Up	Dn		
Loricariidae												
Ancistrus cf. dubius Eigenmann & Eigenmann, 1889	1	3	9	11		6		3		1	Equilibrium	
Farlowella oxyrrhyncha (Kner, 1853)			1	6			1	2			Equilibrium	
Hypostomus pyrineusi (Miranda Ribeiro, 1920)	1	5	6	11	3	16		30		1	Equilibrium	
Hypostomus spp.				2				3			Equilibrium	
Pterygoplichthys lituratus (Kner, 1854)		2						1	2	2	Equilibrium	
Rineloricaria lanceolata (Günther, 1868)				7	1	13		1			Equilibrium	
Rineloricaria spp. 'Juruema'		20		1	2	14		6			Equilibrium	
Heptapteridae												
Phenacorhamdia spp.										1	Unknown	
Pimelodella serrata Eigenmann, 1917			7	6		3					Equilibrium	
Rhamdia quelen (Quoy & Gaimard, 1824)		3			8	1					Equilibrium	
Auchenipteridae												
Trachelyopterus galeatus (Linnaeus, 1766)								1			Equilibrium	
GYMNOTIFORMES												
Gymnotidae												
<i>Gymnotus carapo</i> Linnaeus, 1758		21	10	4	33	28	9	4	2	4	Equilibrium	
Sternopygidae												
Eigenmannia sp. nov.		17		9	5	15		9		8	Opportunistic	
Sternopygus macrurus (Bloch & Schneider, 1801)	6	2		5	6	14		3		2	Equilibrium	
Apteronotidae												
Apteronotus albifrons (Linnaeus, 1766)				1				1		2	Equilibrium	
PERCIFORMES												
Cichlidae												
Aequidens tetramerus (Heckel, 1840)	113	72	118	81	151	104	86	6	22	14	Equilibrium	
Cichla monoculus Agassiz, 1831	3			3				9			Equilibrium	
Crenicichla lepidota Heckel, 1840	6	23	4	2	8	2		6	4	2	Equilibrium	
Crenicichla spp.				5	27	14		12		8	Equilibrium	
Oreochromis niloticus (Linnaeus, 1758)					8	1		1			Not classified	
Satanoperca jurupari (Heckel, 1840)	282	228	1	13	23	47		48	64	33	Equilibrium	

Hypostomus spp., Phenacorhamdia spp., Trachely-opterus galeatus, and Apteronotus albifrons. In addition, 10 individuals of the exotic species Oreochromis niloticus were collected.

A clearer pattern was observed for ecological measures. All sampling sites showed lower richness (S) at locations upstream of the dams (Table 3, Fig. 3). Shannon's (H') index was also lower in the upstream areas, indicating that overall diversity was higher downstream than upstream. Evenness (E) also showed more equitability downstream than upstream, with the exception of Pt03, which exhibited similar values of evenness for both areas. With exception of Pt01, the Berger-Parker (D) index shows that species dominance was highest in upstream locations (Table 3).

The test for homogeneity of multivariate dispersions did not reveal negative eigenvalues, indicating that there is multivariate homogeneity between

groups. PERMANOVA rejected the null hypothesis for similarity between upstream and downstream locations at each site (Pseudo-F = 1.373; df = 1, 16; p = 0.036), indicating that species composition was not the same between the sampling points upstream and downstream of the aquaculture dams. We detected no differences between seasons of the hydrologic cycle (Pseudo-F = 0.312; df = 1, 16; p = 0.909) and no interaction effects (Pseudo-F = 0.335; df = 1, 16; p = 0.887). However, water quality parameters did not show significant differences between upstream and downstream locations when submitted to the paired t-test presenting p > 0.05 (Table 4).

The paired *t*-test performed using species richness clustered by life history strategies showed significant differences between up- and downstream locations for equilibrium (t = -3.428, df = 4, p = 0.026) and periodic (t = -2.954, df = 4, p = 0.042), with species rich-

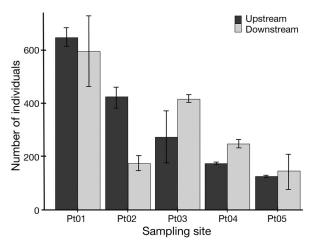


Fig. 2. Number of fish (mean ± SD) caught both upstream and downstream of aquaculture dams at the sampling sites

ness higher at the sampling sites located down-river for both fish groups. No difference was observed for opportunistic species (t = -1.856, df = 4, p = 0.137).

#### **DISCUSSION**

Pelicice et al. (2015) hypothesized that reservoirs of large dams act as ecologic barriers for downstream fish movements due to the presence of a gradient of hydraulic and limnological features. However,

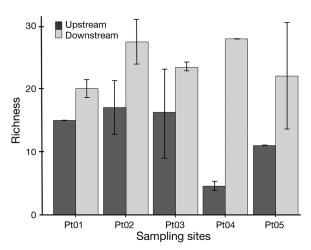


Fig. 3. Fish species richness distribution (mean  $\pm$  SD) both upstream and downstream of aquaculture dams at the sampling sites

whether they are small or large, dams primarily impede upstream fish movements, especially if they do not have effective accommodations for fish to bypass these barriers. Allowing for fish to bypass dam barriers is likely to be easier in small streams where the slope is shallower.

Our study focused on small dams and detected similar effects to the ones reported for larger dams. Indeed, most of the studies on river regulation at large hydroelectric developments report an alteration in species richness and diversity, and consequently in

Table 3. Estimates of fish richness (S), abundance (N), diversity index (H'), dominance index (D), and evenness (E) from upstream (up) and downstream (down) of each sampling site (Pt01-05, see Fig. 1)

Fish assem- Pt01		)1	Pt02		Pt(	)3	Pt0	04	Pt05		
blage attribute	Up	Down									
$\overline{S}$	18	25	20	34	21	28	5	36	15	29	
N	1,299	1,194	841	349	546	836	340	497	248	282	
H'	1.981	2.269	2.048	3.100	2.316	2.562	0.574	2.532	1.711	2.617	
D	0.2402	0.2479	0.2592	0.0974	0.2766	0.1651	0.8412	0.3461	0.4355	0.2553	
E	0.6853	0.7050	0.6835	0.8792	0.7606	0.7689	0.3572	0.7067	0.6317	0.7772	

Table 4. Water quality parameters (mean  $\pm$  SD) measured at sampling sites (Pt01–05, see Fig. 1), during the years 2014 and 2015 considering 2 seasons including day and night samples from upstream and downstream locations (n = 8). EC: electrical conductivity

Location	Limnological parameter	Pt01	Pt02	Pt03	Pt04	Pt05
Upstream	Dissolved oxygen (mg $l^{-1}$ ) pH Temperature (°C) EC ( $\mu$ S cm <sup>-1</sup> )	$3.65 \pm 1.32$ $6.02 \pm 0.87$ $27.50 \pm 1.58$ $55.60 \pm 12.97$	$2.07 \pm 0.79$ $6.37 \pm 0.66$ $26.67 \pm 2.49$ $97.00 \pm 17.32$	$3.47 \pm 1.23$ $5.97 \pm 1.18$ $25.31 \pm 0.76$ $103.07 \pm 14.85$	$4.85 \pm 0.61$ $5.47 \pm 0.83$ $24.85 \pm 0.61$ $60.17 \pm 15.36$	$4.67 \pm 1.45$ $6.02 \pm 0.44$ $26.42 \pm 3.46$ $13.50 \pm 2.69$
Downstream	Dissolved oxygen (mg $l^{-1}$ ) pH Temperature (°C) EC ( $\mu$ S cm $^{-1}$ )	$4.60 \pm 2.99$ $6.17 \pm 1.32$ $28.30 \pm 0.94$ $59.52 \pm 9.73$	$3.65 \pm 2.08$ $6.64 \pm 0.79$ $26.92 \pm 0.89$ $119.80 \pm 24.80$	$4.75 \pm 0.66$ $6.26 \pm 1.08$ $26.30 \pm 1.14$ $112.20 \pm 14.07$	$5.72 \pm 2.19$ $5.73 \pm 1.31$ $27.72 \pm 2.19$ $51.15 \pm 32.62$	$5.31 \pm 0.78$ $6.00 \pm 0.17$ $27.98 \pm 1.80$ $13.60 \pm 2.77$

assemblage composition (Pusey et al. 1995, Reyes-Gavilán et al. 1996, Gehrke et al. 2002). However, we hypothesized that there are different causal mechanisms. We believe that the short distance between sampling points located up- and downstream of these small dams, not large enough to be linked to environmental/landscape differences between these sampling points, which supports the hypothesis that a physical barrier is the main factor to explain the observed differences. It appears that dams in smaller streams block upstream movements of resident fish, probably associated with reproductive and feeding strategies, thereby reducing fish diversity in the headwater areas. The results here suggest that dams separated these fish assemblages, leading to the isolation of certain fish groups in upstream areas. In comparison, fish in downstream areas have free movement to access the Machado River and its other tributaries. The fish remaining upstream effectively become trapped in a smaller area and face increasing competition and predation pressures that may eliminate some species, especially if they are rare or require downstream access as part of their life cycles.

The magnitude of the dams' effect is associated with fish life strategy. Some of the most abundant periodic species, such as *Steindachnerina fasciata*, *Astyanax* aff. *bimaculatus* and *Bryconops* cf. *giacopinii*, showed reduced abundance in upstream areas and were dominant in downstream areas. In the sense of Winemiller & Rose (1992), this group includes mostly migratory species and therefore should be particularly sensitive to the connectivity loss resulting from physical barriers imposed by aquaculture farms in the river channel.

Equilibrium species includes most groups belonging to Siluriformes, Gymnotiformes and Perciformes. We hypothesized that the unclear pattern observed for equilibrium species could be explained by the different level of demographic compensation via dispersal exhibited by these species (Rose et al. 2001). Two equilibrium species were very abundant up- and downstream—Aequidens tetramerus and Satanoperca jurupari—without a clear pattern of dominance associated with the position related to the aquaculture farm. Both are small-size fish and exhibit life history traits that could permit survival even with the loss of connectivity.

Finally, opportunistic species showed no effect of dams' presence. The high abundance of sedentary and opportunistic species in upstream areas could be associated with the new environment, predominantly lentic, caused by the stream impoundment (Loureiro & Hahn 1996, Hoshino et al. 2016, Oliveira et al.

2016). These slow-moving environments are favorable for these species to complete their life cycle because they do not rely on seasonal variations in water level to reproduce (Graça & Pavanelli 2007, Queiroz et al. 2013, Zuanon et al. 2015). They are predominantly small-sized species (e.g. small pelagic forage fish species), which exhibit high abundance and fecundity (Hahn & Fugi 2007).

A critical threat associated with upstream isolation is that it could end up causing localized extinction of rare and endemic species, but in our study, we were not able to sample these sites before the streams were dammed. Comparisons with such areas as controls would be important to determine if species suffer declines or extinctions as a result of impoundments of fish farms. Headwater areas of Amazonian streams, regionally called igarapés, host several rare and endemic species adapted to these environments, as small streams (Mendonça et al. 2005, Espírito-Santo et al. 2009). One of the consequences of permanent flooding due to dam impoundment is the elimination of temporary pools adjacent to the stream channels that form after heavy rains, which are known to be important to the stability of fish assemblages in headwater areas of Amazonian streams (Espírito-Santo & Zuanon 2016). However, these newly flooded environments could create further niches for species that require more slow-moving habitats for feeding or reproduction.

A final consideration related to impacts caused by fish farming activity of tambaqui in the Machado River basin is the presence of an introduced invasive species, the tilapia *Oreochromis niloticus*, which is another common aquaculture species (Zambrano et al. 2006). Tilapia has been spreading invasively throughout Brazilian waterways due to escapes from aquaculture pens, causing competition with native species for space and food. Furthermore, tilapia has been disseminating parasites and diseases among native fish (Fernandes et al. 2008, Miranda et al. 2010, Miranda 2012), putting in peril native fish communities (Agostinho et al. 1999, Dias 2016).

We conclude that there are 2 important agendas to follow: (1) create and test more natural fish passage systems (FAO/DVWK 2002) as alternatives to fish ladders to reduce the impact of impoundments on aquatic biodiversity; (2) prevent introductions of nonnative fish to the Amazon Basin, substituting native species to tilapia in fish farming. Given the high rate at which anthropogenic changes are occurring in the Amazonian environment (Hurd et al. 2016), the urgency for research aimed at preserving the diversity of these fish communities could hardly be greater.

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