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# Factors determining the structure of fish assemblages in Tarumã River, Jaru Biological Reserve, Machado River drainage, northern Brazil

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Few studies on fish assemblages and relations with environmental factors in aquatic systems in southeastern Amazonia have been carried out when compared to other areas in the Amazon. Therefore, which are the main environmental variables and processes responsible for structuring them remains unknown. We hypothesized that fish assemblages respond the variation in the physical-chemistry variables between seasons of the hydrological cycle in a pristine river in the Amazon. The study was performed on fish assemblages of the Tarumã River, Jaru Biological Reserve, Rondônia. Samplings were carried out in five sites along the river in March and September, 2015, which included fish collection and environmental data measurements. Principal component analysis was performed to ordinate the sites in high water and low water seasons, according to environmental variables. We used a similarity analysis in order to identify the individual contribution of species in hydrological period and a partial redundancy analysis for quantify the relative importance of environmental variables in the species composition. As predicted by our hypothesis, the species composition was influenced by dissolved oxygen and temperature. *Myloplus rubripinnis*, *Serrasalmus compressus*, and *S. rhombeus* were the most abundant during high water, while *S. rhombeus*, *Myloplus lobatus*, *Prochilodus nigricans*, and *Hydrolycus armatus* were the dominant species during the low water.

Keywords: Amazon, Environmental variables, Hydrological cycle, Madeira River basin, Protected area.

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Poucos estudos sobre assembleias de peixes de sistemas aquáticos do sudeste da Amazônia foram realizados quando comparado a outras áreas na Amazônia. As principais variáveis ambientais e processos responsáveis por sua estruturação permanecem desconhecidas. Nossa hipótese é que as assembleias de peixes respondem as variações das variáveis físico-químicas entre as estações do ciclo hidrológico em um rio preservado na Amazônia. O estudo analisou as assembleias de peixes do rio Tarumã, na Reserva Biológica do Jaru, Rondônia. As amostragens foram realizadas em cinco pontos amostrais ao longo do rio, em março e setembro de 2015, que incluiu coleta de peixes e medições de dados ambientais. A Análise de Componentes Principais ordenou os pontos amostrais nos períodos de cheia e seca, de acordo com as variáveis ambientais. Utilizamos uma análise de similaridade afim de identificar a contribuição individual de cada espécie em cada período hidrológico e uma análise de redundância parcial com o objetivo de quantificar a importância relativa das variáveis ambientais na composição das espécies. Conforme previsto por nossa hipótese, a composição de espécies do rio Tarumã é influenciada pelo oxigênio dissolvido e temperatura. *Myloplus rubripinnis*, *Serrasalmus compressus* e *S. rhombeus* foram mais abundantes durante o período de cheia, enquanto *S. rhombeus*, *Myloplus lobatus*, *Prochilodus nigricans* e *Hydrolycus armatus* foram as espécies dominantes no período de seca.

Palavras-chave: Amazônia, Área protegida, Bacia do rio Madeira, Ciclo hidrológico, Variáveis ambientais.

## INTRODUCTION

The Amazon basin is the largest ecosystem of the Neotropical region in the northern South America with an area of over 8 million km$^2$ (Sioli, 1984). The basin is distributed between the Brazilian and Guiana shield, from the pre-Andean areas as far as the Atlantic Ocean (Gibbs, 1967; Leite, Rogers, 2013). The flood pulse is the phenomenon that drives the fluvial dynamic of this ecosystem (Junk *et al*., 2011). It is characterized by a monomodal flood with an annual cycle of rising, high, receding and low water seasons, resulting in variation up to 10 m in the central portion of the Basin (Junk *et al*., 2011). Annually, the flooding could inundate more than 750,000 km$^2$ of the floodplain (Wittmann *et al*., 2017). Nevertheless, the lateral extension and duration of the flooding is dependent of the annual precipitation and local geomorphology (Junk *et al*., 2011). The annual flooding promotes lateral connectivity that influences life cycles of many organisms within floodplain aquatic habitats (Arrington *et al*., 2006; Neves dos Santos *et al*., 2008; Hurd *et al*., 2016). Lateral migrations performed by small (<15 cm as adults) and larger species (Fernandes, 1997) are primary causes of seasonal changes in the fish assemblages structure (Röpke *et al*., 2016).

The ichthyofauna of larger rivers and their adjacent floodplains of the Amazon basin has been studied for a long time (Freitas, Garcez, 2004; Junk *et al*., 2007; Röpke *et al*., 2016; Jézéquel *et al*., 2020; Duponchelle *et al*., 2021). Recently, as a result of environmental studies associated with large hydroelectric projects, the fish diversity of southeastern basins has been relatively well-studied. Specifically, studies that have been carried out, include those related to the trophic structure, composition and distribution of the fishes of the Madeira River (Araújo *et al*., 2009; Torrente-Vilara *et al*., 2011), fish taxonomic inventories and studies of fish communities living in rapids of the Middle and Lower Xingu River basin (Barbosa *et al*., 2015; Zuluaga-Gómez *et al*., 2016) and studies about the influence of protected areas on fish assemblages and fisheries of the Tapajós River (Keppeler *et al*., 2017). Nevertheless, the fish fauna of the rivers that drain the western portion of the Brazilian Shield have received little attention. In general, depth, water clarity, water temperature, dissolved oxygen and total suspended matter are among the environmental variables with the greatest influence on fish assemblage structures and species distribution (Peláez, Pavanelli, 2019). In addition, the presence of rapids and waterfalls increases the level of endemism (Oberdorff *et al*., 2019). Therefore, factors structuring the fish assemblages in the western portion of the Brazilian could be different than those observed in larger rivers and adjacent floodplains.

Several studies have shown that protecting forests is important for conserving the aquatic environment and fish fauna (Bruner *et al*., 2001; Azevedo-Santos *et al*., 2018; Frederico *et al*., 2018). However, although 43% of the Brazilian Amazon is classified as protected areas, most of the protected areas extension was established to protect terrestrial rather than aquatic components (Veríssimo *et al*., 2011). Among the few that include aquatic systems, the Jaru Biological Reserve (Rebio Jaru) was established on July 11th, 1979, under Federal Decree-law Nº. 83,716, and is managed by the Instituto Chico Mendes Conservação da Biodiversidade /Ministério do Meio Ambiente – ICMBio/MMA (Justina, 2009). This protected unit was created to reduce the changes in ecosystems and habitat degradation, which have been growing in Rondônia state (ICMBio, 2010). The Rebio Jaru is located in the area between the Madeira and Tapajós rivers and it is considered one the most important area of endemism of the southern Amazon (Haffer, 1997; ICMBio, 2010).

This study evaluated the influence of environmental variables on the structure of fish assemblages in the Tarumã River, a pristine river in the southwestern Amazon that is partially located inside the Rebio Jaru, while also taking into account the changes between high and low water seasons. The contribution of species in each season to the fish assemblage, as well as the description trophic categorization based on the literature, in high and low water seasons were investigated. Our hypothesis is that the fish assemblages respond closely to physicochemical variables that vary between seasons of the hydrological cycle (high and low water seasons). Our results elucidated the influence of environmental variables on the fish diversity for a little studied a conservation area of the Amazon basin.

## MATERIAL AND METHODS

**Sampling sites.** The Jaru Biological Reserve (Rebio Jaru) has a total area of 47,733 $km^2$ (Brasil, 2010), with a high level of conservation and pristine forests. The protected area this localized in an area which has a humid, tropical climate with temperatures varying between 23 °C and 26 °C. The average annual rainfall ranges from 1,700 to 2,400 mm and the dry season occurs between May and October (Justina, 2009). The Rebio Jaru's hydrographic network is part of the Machado River Basin and is located in eastern

Rondônia State, northern Brazil. The Tarumã River, the main sub-basin of the Rebio Jaru, is almost entirely (99%) within the Rebio Jaru and thus extremely well preserved (Fig. 1). The Tarumã River has many rapids and flows across the granitic formation of the Serra da Providência and Jamari complex (Justina, 2009).

**Sampling.** We collected fish in the main channel of the Tarumã River in March (high water season) and September (low water seasons) in 2015 five sites (R1 – 09°27'19"S 61°40'43"W; R2 – 09°32'15"S 61°40'13"W; R3 – 09°42'46"S 61°39'42"W; R4 – 09°46'23"S 61°38'45"W; R5 – 09°47'04"S 61°40'19"W) (Fig. 1), totaling 10 samples. The average distance between the sites was 48 km ($\text{distance}_{\text{Min}}$ = 10 km and $\text{distance}_{\text{Max}}$ = 100 km). Samplings were performed in the river channel using eight gillnets of standard size of 2 m in height and 20 m in length, and mesh sizes varied from 30 to 100 mm between opposite knots. A single sampling was performed at each site in high and low water season. At each sampling site, the fishing nets were set during the morning, from 8:00 am to 12:00 pm, and at night, from 8:00 pm to 5:00 am. For the same period, we used a trotline with four 5/0 hooks with ends tied either to the vegetation on the riverbank or to mooring spikes. We used pieces of piranha, *Serrasalmus rhombeus* (Linnaeus, 1766), as bait on the trotline hooks.

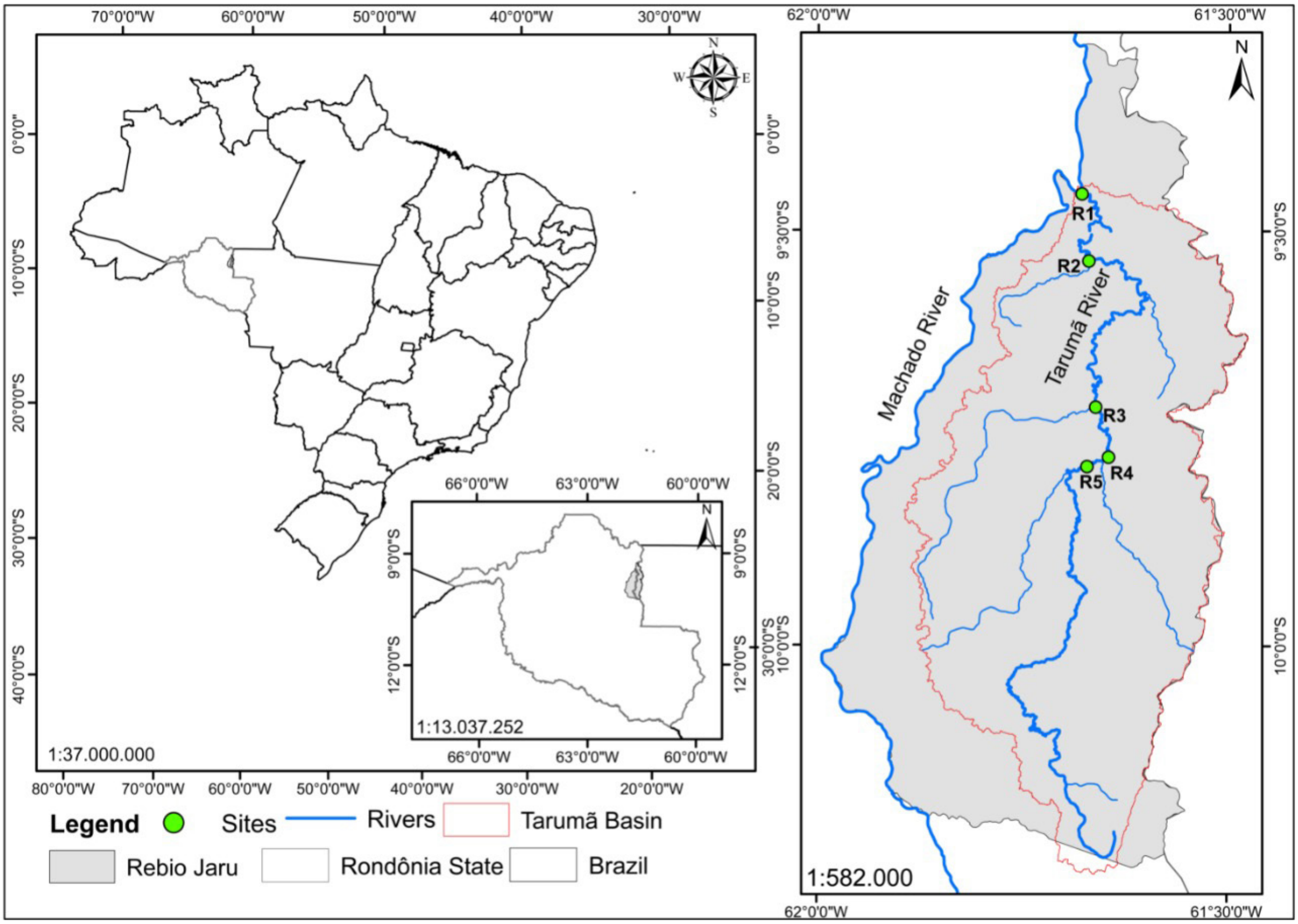

**FIGURE 1** | Map of the study area showing the collection stations in the drainage systems in the Jaru Biological Reserve (shaded area), Rondônia, Brazil. Circles represent collection points in the river channels of the Tarumã River.

Environmental variables were measured between 8:00 am and 9:00 am at the center of the river channel. We recorded four physical-chemical variables immediately before the fish samplings: dissolved oxygen (mg/l), electrical conductivity ($mS/cm^2$), temperature (°C) and pH with an YSI-85 data logger. Four physical variables were also measured: depth (m) with the aid of a measuring tape with a weight; transparency (cm) with a Secchi disk; width (m) of the river using a GPS device and water velocity (Wv) with a flow meter (General Oceanics model 2030 R mechanical) that has a six digit odometer style counter and can indicate a minimum velocity of 10 cm/s. We calculated the average of four measurements of depth, water transparency, width and water velocity to standardize the measurement of environmental variables.

The specimens captured with the nets and trotline were sacrificed in a solution of clove oil (Eugenol, 2 drops per liter; cf. AVMA, 2001) and subsequently fixed in a 10% formalin solution and preserved in 70% ethanol. For species identifications, we consulted the most currently accepted taxonomic literature and identification keys (Queiroz *et al*., 2013). The classifications followed Nelson *et al.* (2016). Specimens were deposited in the Fish Collection of the Universidade Federal do Mato Grosso, Cuiabá (CPUFMT), Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP), Ichthyology collection at the Universidade Federal de Rondônia (UFRO-I), and Laboratório de Ictiologia de Ribeirão Preto da Universidade de São Paulo, Ribeirão Preto (LIRP).

Aiming to describe the trophic categories of species in each period of the hydrological cycle, the trophic categorization of the sampled species was described through the use of the literature (evisceration and analysis of gut contents were not performed). Species were classified and described as detritivores, herbivores (more than 60% of the diet consists of Phanerogam plant structures); omnivores (when no feature of animal or vegetable origin alone reaches more than 60% of the diet), insectivores (over 60% of the diet consists of aquatic and terrestrial insects); invertivores (more than 60% of the diet is generally comprised of invertebrates, including insects, but with no preference for the latter), carnivores (over 60% of the diet comprises various types of animal resources, such as vertebrates and invertebrates), piscivorous (more than 60% of the diet is composed by fish, fish larvae or fins and scales) (Röpke, 2008), iliophagous (ingest silt or sand substrate looking for food of animal, plant or detritus origins) planktivores (predominantly feed on plankton) (Zavala-Camin, 1996).

**Statistical analyses.** The water physical-chemical variables, used to characterize each site in Tarumã River, were summarized in a matrix, which was the basis for a principal component analysis (PCA). The PCA was performed to ordinate the sites in high water and low water seasons according to their environmental similarity, while preserving the Euclidean distance among sites based on eigenvectors (Borcard *et al*., 2018). A similarity percentage analysis (SIMPER) then determined the individual contribution of each species (Oksanen *et al*., 2017), thus clarifying those that exerted the strongest influence in high water and low water seasons. As a potential source of collinearity between abiotic variables could be the spatial distance between sampling sites, we used Moran's I statistic (Fortin *et al*., 1989) to test for spatial autocorrelation. As width, Wv, conductivity and altitude showed spatial autocorrelation (as shown in the Tab. **S1**), a partial redundancy analysis (pRDA) with a variation partitioning method (Borcard, Legendre, 2002) was used to quantify the relative importance of environmental variables and spatial distances (positive eigenvectors of a principal coordinates of neighborhood matrix – PCNM) to the variation in species composition. We prepared two matrices for the analysis: a matrix of fish species abundances after performing a Hellinger transformation, which makes community composition data reliable for linear modeling (Legendre, Gallagher, 2001) and a matrix of environmental factors (dissolved oxygen, electrical conductivity, temperature, hydrogen potential, transparency, depth, width and water velocity). The pRDA is similar to multiple regression models, except that it allows for the analysis of multiple response variables. Previously, to remove collinearity among variables, a forward selection ($\alpha = 0.05$) procedure was applied to select and evaluate sets of environmental variables that each explained significant additional variation in river assemblage composition and abundance (Ter Braak, Smilauer, 1998). Significance of canonical axes and variation explained by environmental variables were based on 10,000 Monte Carlo permutations. The VEGAN package (Oksanen *et al*., 2017) was used to run pRDA and PCNM analyses; the function "princomp" in the "vegan" package was used for the PCA and the APE Package (Paradis *et al*., 2004) was used to run MORAN I. All analyses were performed in R 3.5.0 (R Development Core Team, 2018). The results were considered significant when $P \leq 0.05$.

## RESULTS

The average depth of the Tarumã River during the low water season was 2.8 ± 0.9 m; the average width was 32.8 ± 7.8 m; and the average water velocity 0.4 $m.s^{-1}$. During the wet season, the average depth, width, and water velocity values were 5.6 ± 1.2 m; 41.9 ± 4.0 m; and 0.3 ± 0.1 $ms^{-1}$, respectively. The average transparency in the low water season was 1.2 ± 2.1 cm and the average transparency in the high water seasons 1.1 ± 0.4 cm. The first two axes of the PCA summarized 61.8% of the variation in the environmental matrix (PC1 = 41.6% and PC2 = 20.2%; Tab. 1). The ordination of the samples in the space formed by these axes evidenced that sampling sites in the high water period are more similar than sampling sites in low water, and that the depth, temperature, dissolved oxygen and electrical conductivity were the most important variables for explaining these differences (Fig. 2).

A total of 223 fish belonging to five orders, fourteen families and twenty-eight species were sampled (see Tab. **S2**). Characiformes was the most abundant and diverse of the orders in both seasons of the hydrological cycle, followed by Siluriformes and Cichliformes. In the high water season, the most abundant species were *Myloplus rubripinnis* (Müller & Troschel, 1844), *Serrasalmus compressus* Jégu, Leão & Santos, 1991, and *Serrasalmus rhombeus*. In the low water season, the piranha *S. rhombeus* was the most abundant, followed by *Myloplus lobatus* (Valenciennes, 1850) and *Prochilodus nigricans* Spix & Agassiz, 1829. Piscivorous were the most abundant trophic category in both seasons ($n_{\text{Low-water (Lw)}} = 73.58\%$; $n_{\text{High-water (Hw)}} = 53.54\%$), followed by herbivores ($n_{Lw} = 21.17\%$; $n_{Hw} = 29.29\%$), detritivores ($n_{Lw} = 20.16\%$) and omnivores ($n_{Hw} = 12.12\%$) (Tab. 2).

**TABLE 1** | Descriptors of the fish assemblages, environmental variables (mean ± SD), and scores on the first two axes of the principal components (PCA) in the high water and low water seasons of the Tarumã River.

| | Seasons | | PCA | |
|---|---|---|---|---|
| | **High water** | **Low water** | **PC 1** | **PC2** |
| Fish species richness | 18 | 24 | | |
| Fish numerical abundance | 97 | 128 | | |
| **Physical and chemical variables** | | | | |
| Dissolved oxygen (mg.L$^{-1}$) | 7.5 ± 0.5 | 5.8 ± 1.0 | 0.41 | 0.45 |
| Electrical conductivity (µS.cm$^{-1}$) | 7.1 ± 1.0 | 7.1 ± 0.5 | 0.37 | -0.38 |
| Temperature (°C) | 27.6 ± 1.4 | 25.0 ± 0.9 | 0.37 | 0.32 |
| Hydrogen potential (pH) | 6.2 ± 0.3 | 6.4 ± 0.5 | -0.34 | 0.26 |
| Transparency (cm) | 127.4 ± 21.1 | 114.2 ± 42.7 | 0.26 | |
| Depth (m) | 5.62 ± 1.24 | 2.86 ± 0.99 | -0.39 | -0.39 |
| Width (m) | 41.9 ± 43.90 | 32.8 ± 7.8 | -0.41 | 0.28 |
| Water velocity (m.s$^{-1}$) | 0.4 ± 0.0 | 0.3 ± 0.1 | -0.29 | 0.48 |
| Eigenvalue | | | 2.99 | 1.50 |
| Proportion of variance explained (%) | | | 41.6 | 20.2 |
| Cumulative proportion (%) | | | 41.6 | 61.8 |

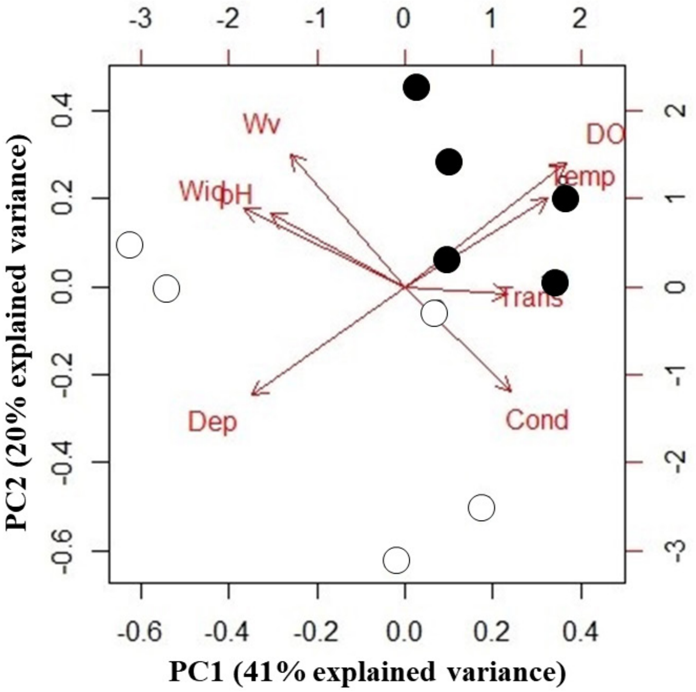

**FIGURE 2** | Ordination of sampling sites in the Tarumã River basin studied during the high water (black circle) and low water (white circle) season, along the first two axes of the Principal Component Analysis (PCA).

**TABLE 2** | Taxons, species code, numerical abundance of the species sampled during the high water (Hw) and low water (Lw) seasons, trophic categorization (TC) (CAR = Carnivores, DET = Detritivores, HER = Herbivores, ILI = Iliophagous, INS = Insectivores, INV = Invertivores, ONI = omnivores, PIS = piscivorous, PLA = planktivores, LEP = lepidophagous) and references of the species collected in the Tarumã River, Jaru Biological Reserve, Machado River basin, northern Brazil. * = in process of deposit in Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP). ** = specimens not listed in collection.

| Taxon | Codes | Hw | Lw | TC | References | Vouchers |
|---|---|---|---|---|---|---|
| **CLASS CHONDRICHTHYES** | | | | | | |
| MYLIOBATIFORMES | | | | | | |
| **Potamotrygonidae** | | | | | | |
| *Potamotrygon falkneri* Castex & Maciel, 1963 | Potfal | 0 | 1 | CAR | Lonardoni *et al.* (2006) | * |
| **CLASS OSTEICHTHYES** | | | | | | |
| CHARACIFORMES | | | | | | |
| **Acestrorhynchidae** | | | | | | |
| *Acestrorhynchus falcirostris* (Cuvier, 1819) | Acefal | 2 | 0 | PIS | Santos *et al.* (2004) | UFRO-I 5523, UFRO-I 18313 |
| **Chalceidae** | | | | | | |
| *Chalceus guaporensis* Zanata & Toledo-Piza, 2004 | Chagua | 1 | 0 | INV | Torrente-Vilara *et al.* (2018) | UFRO-I 4321, UFRO-I 17473 |
| **Bryconidae** | | | | | | |
| *Brycon amazonicus* (Agassiz, 1829) | Bryama | 0 | 1 | ONI | Anjos *et al.* (2019) | MZUSP 14017 |
| *Brycon* cf. *pesu* Müller & Troschel, 1845 | Brypes | 3 | 0 | ONI | Anjos *et al.* (2019) | LIRP 11773 |
| *Brycon falcatus* Müller & Troschel, 1844 | Bryfal | 1 | 1 | ONI | Anjos *et al.* (2019) | LIRP 13045, 10269 |
| **Characidae** | | | | | | |
| *Moenkhausia* sp. | Moesp | 0 | 2 | INS | Moura *et al.* (2010) | |
| *Roeboides affinis* (Günther, 1868) | Roeaff | 0 | 4 | LEP | Peterson, McIntyre (1998) | CPUFMT 3393 |
| **Ctenoluciidae** | | | | | | |
| *Boulengerella cuvieri* (Spix & Agassiz, 1829) | Boucuv | 6 | 10 | PIS | Duarte *et al.* (2010) | CPUFMT 3392 |
| **Hemiodontidae** | | | | | | |
| *Hemiodus unimaculatus* (Bloch, 1794) | Hemuni | 2 | 0 | HER | Dary *et al.* (2017) | UFRO-I 12750, UFRO-I 14109 |
| **Anostomidae** | | | | | | |
| *Leporinus friderici* (Bloch, 1794) | Lepfri | 4 | 0 | ONI | Santos *et al.* (2006) | CPUFMT 3400 |
| *Leporinus* sp. | Lepsp | 1 | 0 | ONI | Santos *et al.* (2006) | ** |
| **Cynodontidae** | | | | | | |
| *Hydrolycus armatus* (Jardine, 1841) | Hydarm | 4 | 12 | PIS | Dary *et al.* (2017) | CPUFMT 3390 |
| *Hydrolycus tatauaia* Toledo-Piza, Menezes & Santos, 1999 | Hydtat | 6 | 0 | PIS | Dary *et al.* (2017) | LIRP 10293, 10298 |
| **Serrasalmidae** | | | | | | |
| *Myloplus lobatus* (Valenciennes, 1850) | Myllob | 4 | 20 | HER | Anjos *et al.* (2019) | CPUFMT 3394 |
| *Myloplus rubripinnis* (Müller & Troschel, 1844) | Mylrub | 23 | 1 | HER | Reis *et al.* (2003) | CPUFMT 3397 |
| *Pygocentrus nattereri* Kner, 1858 | Pygnat | 3 | 1 | PIS | Mérona, Rankin-de-Mérona (2004) | CPUFMT 3401 |
| *Serrasalmus compressus* Jégu, Leão & Santos, 1991 | Sercomp | 16 | 14 | PIS | Anjos *et al.* (2019) | CPUFMT 3399 |

➡

**TABLE 2** | (Continued)

| Taxon | Codes | Hw | Lw | TC | References | Vouchers |
|---|---|---|---|---|---|---|
| *Serrasalmus rhombeus* (Linnaeus, 1766) | Serrho | 15 | 30 | PIS | Santos *et al.* (2004) | CPUFMT 3391 |
| *Serrasalmus* sp. | Sersp | 0 | 2 | PIS | Reis *et al.* (2003) | ** |
| **Prochilodontidae** | | | | | | |
| *Prochilodus nigricans* Spix & Agassiz, 1829 | Pronig | 2 | 19 | DET | Dary *et al.* (2017) | CPUFMT 3396 |
| **Triportheidae** | | | | | | |
| *Triportheus albus* Cope, 1872 | Trialb | 4 | 0 | ONI | Pouilly *et al.* (2003) | CPUFMT 3398 |
| SILURIFORMES | | | | | | |
| **Pimelodidae** | | | | | | |
| *Pimelodus ornatus* Kner, 1858 | Pimorn | 0 | 2 | INV | Dary *et al.* (2017) | LIRP 11969, 12177 |
| *Platynematichthys notatus* (Jardine, 1841) | Planot | 0 | 1 | PIS | Santos *et al.* (2006) | UFRO-I 3835 |
| Pimelodidae (undetermined) | Pimsp | 0 | 1 | PIS | Santos *et al.* (2006) | ** |
| CICHLIFORMES | | | | | | |
| **Cichlidae** | | | | | | |
| *Cichla pleiozona* Kullander & Ferreira, 2006 | Cicple | 0 | 2 | PIS | Santos *et al.* (2006) | CPUFMT 3395 |
| *Satanoperca jurupari* (Heckel, 1840) | Satjur | 0 | 1 | DET | Anjos *et al.* (2019) | UFRO-I 16652, UFRO-I 17429 |
| PERCIFORMES | | | | | | |
| **Sciaenidae** | | | | | | |
| *Petilipinnis grunniens* (Jardine & Schomburgk, 1843) | Petgru | 1 | 0 | PIS | Anjos *et al.* (2019) | UFRO-I 4883, LIRP 10405 |

Seven species contributed to 72% of the dissimilarity of the fish assemblages between the hydrological seasons. *M. rubripinnis* (4.6%), *S. compressus* (3.2%), *S. rhombeus* (3.0%), *B. cuvieri* (1.2%), *M. lobatus* (0.8%), *Hydrolycus armatus* (Jardine, 1841) (0.8%) and *P. nigricans* (0.4%) showed the highest abundance during the high water season. However, *S. rhombeus* (6.0%), *M. lobatus* (4.0%), *P. nigricans* (3.8%), *S. compressus* (2.8%), *H. armatus* (2.4%), *Boulengerella cuvieri* (Spix & Agassiz, 1829) (2.0%) and *M. rubripinnis* (0.2%) were the dominant species during the low water seasons (Fig. 3; Tab. 3).

**TABLE 3** | Results of SIMPER analysis of the fish assemblage between high (H) and low (L) water seasons.

| Species | Contribution (%) | Cumulative contribution (%) | Mean abundance (%) | |
|---|---|---|---|---|
| *Serrasalmus rhombeus* (Linnaeus, 1766) | 15.61 | 15.61 | 3.00 | 6.00 |
| *Myloplus rubripinnis* (Müller & Troschel, 1844) | 13.08 | 28.69 | 4.60 | 0.20 |
| *Myloplus lobatus* (Valenciennes, 1850) | 11.48 | 40.17 | 0.80 | 4.00 |
| *Prochilodus nigricans* Spix & Agassiz, 1829 | 11.02 | 51.19 | 0.40 | 3.80 |
| *Serrasalmus compressus* Jégu, Leão & Santos, 1991 | 7.273 | 58.46 | 3.20 | 2.80 |
| *Boulengerella cuvieri* (Spix & Agassiz, 1829) | 7.016 | 65.48 | 1.20 | 2.00 |
| *Hydrolycus armatus* (Jardine, 1841) | 6.171 | 71.65 | 0.80 | 2.40 |
| *Hydrolycus tatauaia* Toledo-Piza, Menezes & Santos, 1999 | 3.03 | 74.68 | 1.20 | 0.00 |

**TABLE 3** | (Continued)

| Species | Contribution (%) | Cumulative contribution (%) | Mean abundance (%) | |
|---|---|---|---|---|
| *Triportheus albus* Cope, 1872 | 2.778 | 77.46 | 0.80 | 0.00 |
| *Roeboides affinis* (Günther, 1868) | 2.735 | 80.19 | 0.00 | 0.80 |
| *Pygocentrus nattereri* Kner, 1858 | 2.172 | 82.36 | 0.60 | 0.20 |
| *Leporinus friderici* (Bloch, 1794) | 2.096 | 84.46 | 0.80 | 0.00 |
| *Hemiodus unimaculatus* (Bloch, 1794) | 1.749 | 86.21 | 0.40 | 0.00 |
| *Brycon* cf. *pesu* Müller & Troschel, 1845 | 1.633 | 87.84 | 0.60 | 0.00 |
| *Pimelodus ornatus* Kner, 1858 | 1.519 | 89.36 | 0.00 | 0.40 |
| *Cichla pleiozona* Kullander & Ferreira, 2006 | 1.367 | 90.73 | 0.00 | 0.40 |
| *Moenkhausia* sp. | 1.279 | 92.01 | 0.00 | 0.40 |
| *Serrasalmus* sp. | 1.128 | 93.14 | 0.00 | 0.40 |
| *Brycon falcatus* Müller & Troschel, 1844 | 1.08 | 94.22 | 0.20 | 0.20 |
| *Acestrorhynchus falcirostris* (Cuvier, 1819) | 1.01 | 95.23 | 0.40 | 0.00 |
| *Brycon amazonicus* (Agassiz, 1829) | 0.7154 | 95.94 | 0.00 | 0.20 |
| *Platynematichthys notatus* (Jardine, 1841) | 0.7154 | 96.66 | 0.00 | 0.20 |
| *Leporinus* sp. | 0.6043 | 97.26 | 0.20 | 0.00 |
| *Satanoperca jurupari* (Heckel, 1840) | 0.5638 | 97.82 | 0.00 | 0.20 |
| *Potamotrygon falkneri* Castex & Maciel, 1963 | 0.5638 | 98.39 | 0.00 | 0.20 |
| Pimelodidae (undetermined) | 0.5638 | 98.95 | 0.00 | 0.20 |
| *Chalceus guaporensis* Zanata & Toledo-Piza, 2004 | 0.524 | 99.48 | 0.20 | 0.00 |
| *Petilipinnis grunniens* (Jardine & Schomburgk, 1843) | 0.524 | 100.00 | 0.20 | 0.00 |

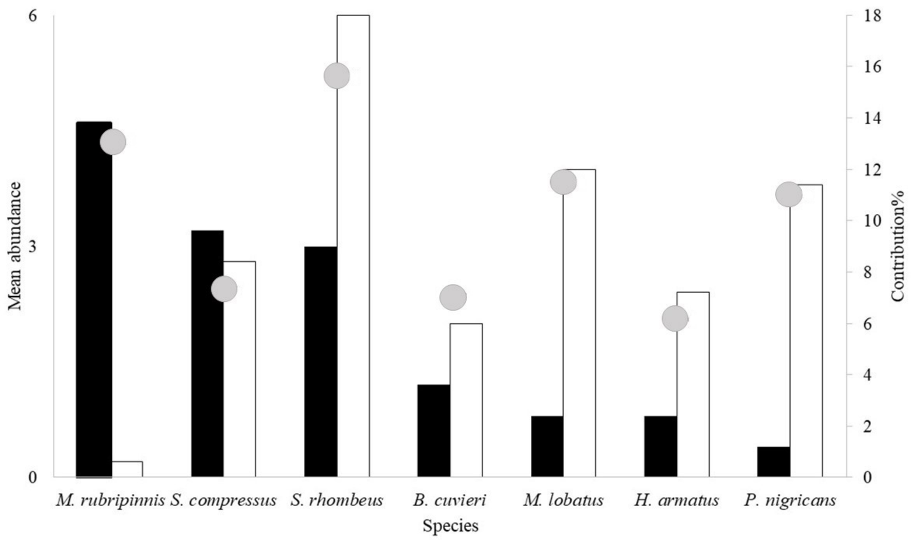

**FIGURE 3** | Mean abundance and relative contribution of the most important species accounted by SIMPER analysis for both seasons of the hydrological cycle. Black and white bars represent the mean abundance of each species ate high water and low water season, respectively. The gray circles are the relative contribution estimated by the SIMPER Analysis.

The association of the composition of fish species and the seasons, environmental variables and spatial distances explained 33 % (pRDA1 = 21%; pRDA2 = 12%) of the assemblage composition variation ($Radj^2 = 0.23$; F = 1.90; p = 0.03). Assemblage composition was significantly influenced by environmental variables and accounted for 26% (pRDA1 = 18%; pRDA2 = 8%) ($Radj^2 = 0.43$; F = 1.21; p = 0.02), but none of the spatial predictors presented significant effects ($Radj^2 = 0$; F = 0.69; p = 0.79). The pRDA indicated that six variables were redundant, therefore these variables were excluded from the environmental data set. The forward selection procedure showed that depth, water velocity and pH were the environmental variables that accounted for significant ($P < 0.05$) portions of the total variance in fish species composition. The pRDA with these three environmental variables produced an ordination in which all canonical axes were significant (Monte Carlo test; $P < 0.05$). The first axis of pRDA separated the low water season sampling points with predominance of *M. rubripinnis*, *Hydrolycus tatauaia* Toledo-Piza, Menezes & Santos, 1999 and *S. compressus* from high water season with predominance of *M. lobatus* and *P. nigricans*. The most important abiotic variables for species composition, positively related to the first axis of analysis were depth (F = 2.20; p = 0.05) and pH (F = 2.69; p = 0.03), associated with *H. tatauaia*, *M. rubripinnis*, and *S. compressus*; and water velocity, that presented negative values in axis 1 of the pRDA (F = 2.56; p = 0.03), associated with *B. cuvieri*, *S. rhombeus*, and *P. nigricans* (Fig. 4).

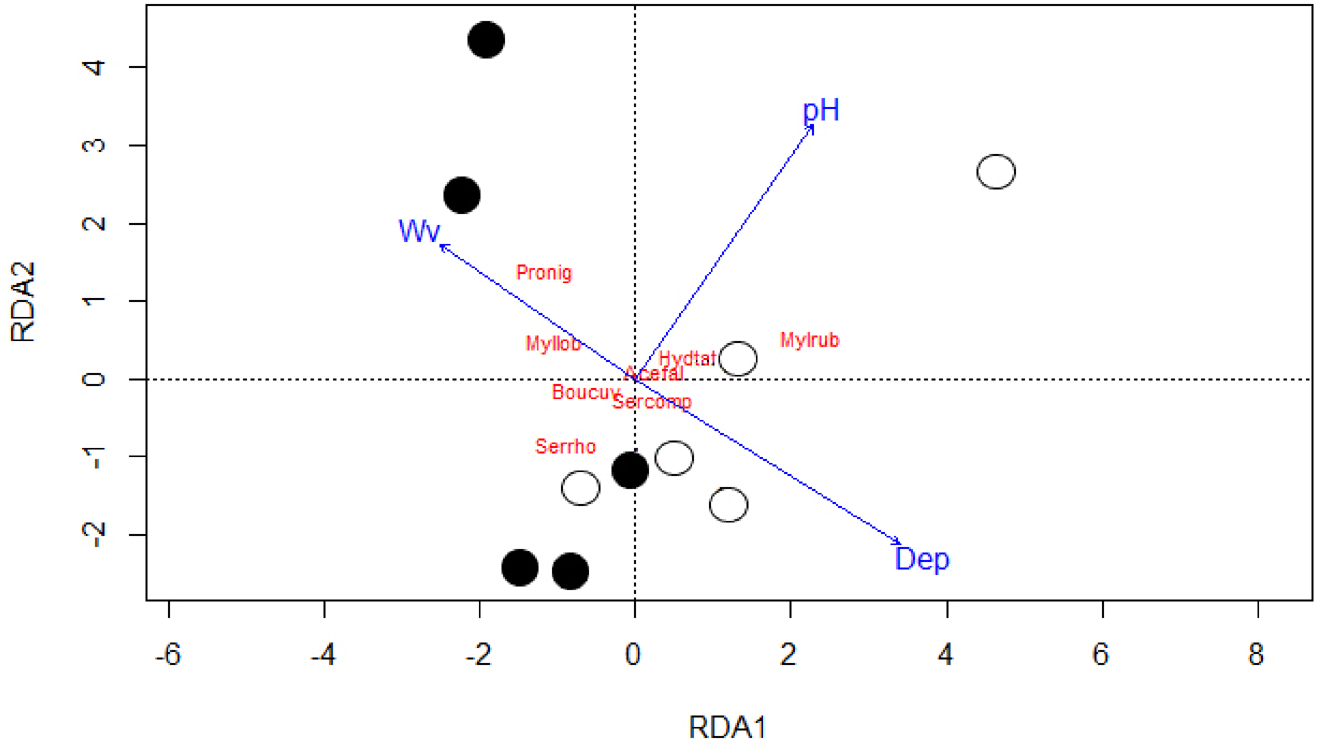

**FIGURE 4** | Ordination of the Partial Redundancy Analysis (pRDA) on fish species composition (see codes on Tab. 2) with sites in high water (black circle) low water (white circle) season and abiotic variables relationships (arrows). Dep = Depth; Wv = Water velocity; pH = Hydrogen potential.

## DISCUSSION

The species composition of the Tarumã River basin was influenced by environmental variables as predicted by our hypothesis, however, this composition differed seasonally. As indicated by pRDA, the fish assemblages sampled during high water were positively associated with chemical variables: dissolved oxygen and temperature. During the low water season, the reduction of the water body was determinant for the negative association the fish assemblages and the physical variables of depth and width.

Our pRDA results demonstrated that, depth and dissolved oxygen were significant determinants of the structure of fish assemblages as found in other studies conducted in Neotropical rivers (Tejerina-Garro *et al*., 1998; Petry *et al*., 2003; Arantes *et al*., 2013; Arantes *et al*., 2018). Deeper aquatic habitats in the floodplain support greater abundance of fish species, as they are more stable during periods of extreme drought (Arantes *et al*., 2013). Previous studies showed that the lateral flooding changes the proportion of suspended and dissolved substances in the water, with consequent alterations of the physicochemical variables of lotic systems (Melack, Forsberg, 2001). Nevertheless, Bayley (1995) indicates that when the water level increases in high water seasons the decomposition rates of organic matter also increases, resulting increased levels of dissolved oxygen. In general, floodplain water bodies have lower concentrations of dissolved oxygen, probably as a result of the combination of elevated amounts of organic matter and the inhibiting effects of the vegetation cover in the aquatic photosynthesis process (Arantes *et al*., 2018).

Most rivers in the Amazon basin are extremely poor in carbonate buffering capacity (Sioli, 1984), while pH is controlled predominantly by the concentration of these organic acids (Belger, Forsberg, 2006). Although pH was an important variable in fish assemblage structure in our analysis, it did not show much variation between the low and high water seasons. However, we highlight that the pH values of the Tarumã River ($\overline{X}_{(Lw)} = 6.4$; $\overline{X}_{(Hw)} = 6.2$) were similar to those found for other tributaries in the Amazon region. Barbosa *et al*. (2010) describe that the pH in the Amazon River was nearly constant (~6.5), whereas on the floodplain it increased from an average of 6.7 during low water to 7.7 at receding state. The pH promotes physiological constraints upon aquatic organisms, this influences ionic balance (Matsuo, Val, 2002) and a host of other physiological processes in fishes, including oxygen affinity of hemoglobin, digestion, and osmotic balance (Val, Almeida-Val, 1995). Clearwaters of the Upper Orinoco River, Upper Casiquiare River, Upper Siapa River, as well as the Tarumã River, are associated with more moderate pH, but also with higher levels of suspended particulate matter, including clay, particularly during periods of high flow (Winemiller *et al*., 2008). Most of the clearwater rivers have high water transparency during periods of base-flow conditions, but many of these rivers may become slightly to moderately turbid during periods of high water (Winemiller *et al*., 2008). In clearwater rivers, sustained low water conditions result in lower water transparency owing to higher concentrations of phytoplankton (Cotner *et al*., 2006).

Fluctuations in the water-level strongly influence the water velocity of rivers, which in turn change limnological variables and assemblage composition (Affonso *et al*., 2015). Corroborating with previous studies (Willis *et al*., 2015) our results show that water velocity negatively influences the fish assemblage structure. In the Tarumã River the composition of fish species, in more complex habitats in the low water period, possibly was associated with the greater production of peripheral algae, favoring the occurrence of algivores such as *P. nigricans*. The occurrence of structurally more complex habitat within the river during low waters, provides refuge and food for species of low trophic fish (prey), thus favoring an increase in the abundance of piscivorous fish such as *B. cuvieri* and *S. rhombeus*. In fast-flowing environments, which is common in periods of high water, the current velocity introduces an element of physical complexity that influences the use of horizontal and vertical aquatic habitats by fishes (Wood, Bain, 1995).

In both hydrological periods, piscivorous, followed by herbivores, were the most representative group in abundance. Many studies on trophic ecology in clear water basins, including in the Trombetas, Mucajaí and Teles Pires rivers, have analyzed the trophic structure of the fish assemblage pointing out the greater representativeness of piscivorous and herbivore fish in the samples (Dary *et al*., 2017). However, the greater representativeness of piscivorous in fish assemblages was also pointed out by Ferreira *et al*. (1988), Ferreira (1993), Zuanon (1999), Dary *et al*. (2017), Araújo *et al.* (2009), and Lima *et al.* (2020) for the Mucajaí, Trombetas, Xingu, Teles Pires and Madeira rivers, respectively, with their drainage basins located in the Guiana and Brazilian shields, which have geomorphologies similar to the Tarumã River. Similar to our study, herbivorous fish also constituted a large part of the biomass and abundance of these clear water rivers (Zuanon, 1999; Dary *et al*., 2017). This fact indicates that clear water rivers with low primary production (compared to white water rivers, see Melack, Forsberg, 2001) can sustain high fish abundance and biomass, probably due to the rapid assimilation of local productivity in the biomass of fish (Dary *et al*., 2017). Due to the seasons of the hydrological cycle, and the trophic ecology of the fish, a classic pattern of species distribution (predominance of frugivorous/omnivorous species in high water and piscivorous/carnivorous in low water seasons) has been observed in the Amazonian rivers in several studies (Costa, Freitas, 2015; Castello *et al*., 2015; Duarte *et al*., 2019). During rising and high water seasons, expansions in the aquatic environment toward the forest favors the exploration of various habitats and broadens the food spectrum of fishes (Noveras *et al*., 2012; Loebens *et al*., 2020). In these seasons, fishes inhabit river channels and floodplain lakes in order to spawn and migrate laterally on to the advancing littoral zone (Fernandes, 1997). The advancing littoral zone allows fish of all ages to feed on abundant food sources (*i.e*., detritus, insects, fruits and seeds) found in vegetated floodplain habitats (Goulding, 1980). During low water season, the reduction of the aquatic environment area leads to food scarcity for most fish species (Resende *et al*., 1996).

For carnivorous/piscivorous fishes this pattern may be inverted. During the high water season, fish species disperse over the floodplain in search of different food sources and shelter, which decreases their accessibility to predators. During the low water season, prey species are more concentrated in the restricted water bodies and become more available to potential predators, such as *S. rhombeus*, *H. tatauaia*, and *S. compressus* (Ferreira *et al*., 2014). This season can be characterized as a "biological interaction phase", since space (*i.e*., size and number of habitats) decreases while density of individuals and species increases (Ward *et al*., 1999), thus increasing biotic interactions (Espínola *et al*., 2017).

Ecological dynamics in rivers with tropical floodplains are governed by deterministic and stochastic mechanisms (Hurd *et al*., 2016). Improved understanding of the mechanisms that regulate the dynamic structure of fish assemblages is extremally needed. As previously proposed by several studies (Junk *et al*., 1983; Saint-Paul *et al*., 2000; Hoeinghaus *et al*., 2003; Siqueira-Souza, Freitas, 2004; Freitas, Garcez, 2004; Torrente-Vilara *et al*., 2011; Freitas *et al*., 2013; Costa, Freitas, 2015; Cella-Ribeiro *et al*., 2017; Arantes *et al*., 2018; Costa *et al*., 2020), our results have also shown the importance of environmental variables as drivers of fish assemblages. In particular, our results reveal the great importance of the flood pulse, as a key environmental factor to the assemblage structure in the western portion of the Amazon basin. Our recommendation is to increase efforts, by the public and private sector, towards the protection of Amazonian hydrographic basins in order to guarantee functionality (ecosystem services) and connectivity between aquatic environments. We emphasize that greater financial support and the implementation of adequate infrastructure to carry out studies in protected areas, are needed for understanding its environmental dynamics, as well as for decision-making in the reassessment of the limits of part of the existing reserves. There is a great concern for the future of these areas, especially when we considering the current environmental policies in progress in Brazilian territory. Rivers constitute the main axes of PAs in the Amazon and must be conserved to promote the adequate preservation of headwaters and hydrological connectivity. This understanding further serves as a baseline in order to support the efficient management of exploited species, as well as aiding in the development of conservation strategies against anthropic and natural environmental changes.

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## AUTHORS' CONTRIBUTION

**Igor David Costa:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing-original draft, Writing-review and editing.

**Natalia Neto dos Santos Nunes:** Formal analysis, Supervision, Visualization.

**Carlos Edwar de Carvalho Freitas:** Formal analysis, Methodology, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

## ETHICAL STATEMENT

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## COMPETING INTERESTS

The authors declare no competing interests.

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