



Damming in the Madeira River modifies the food spectrum of piscivorous and affects their resource partitioning

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Phylogenetic proximity suggests some degree of diet similarity among species. Usually, studies of diet show that species coexistence is allowed by partitioning food resources. We evaluate how visually oriented piscivorous fishes (Characiformes) share prey before and after building the Santo Antônio Hydroelectric Power Plant (HPP) in the Madeira River (Brazil), the largest muddy-water tributary of the Amazon River. Piscivorous species (*Acestrorhynchus falcirostris*, *Acestrorhynchus heterolepis*, *Hydrolycus scomberoides*, and *Rhaphiodon vulpinus*) were sampled under pristine (pre-HPP) and disturbed (post-HPP) environmental conditions. We analyzed species abundance and stomach contents for stomach fullness and prey composition to check variations between congeneric and non-congeneric species. The percent volume of prey taxa was normalized by stomach fullness and grouped into the taxonomic family level to determine diet, niche breadth, and overlap. Only *R. vulpinus* abundance increased in post-HPP. There was no significant variation in niche breadth between the periods, while niche overlap decreased in congeneric and non-congeneric species. Our results indicate that river impoundment affected piscivorous fishes in distinct ways and modified their resource partitioning. Therefore, evaluate interspecific interactions is a required tool to understand how fishes respond to river damming.

Keywords: Amazon, Dietary overlap, Hydroelectric Power Plants, Interspecific Relationships, Trophic niche breadth.

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A proximidade filogenética pode indicar similaridade da dieta entre espécies e a partilha de recursos alimentares é um mecanismo que possibilita a coexistência. Neste trabalho, avaliamos como peixes piscívoros compartilham presas antes e depois da construção da Usina Hidrelétrica (UHE) Santo Antônio no rio Madeira (Brasil), o maior afluente de águas brancas do rio Amazonas. Espécies piscívoras (*Acestrorhynchus falcirostris*, *Acestrorhynchus heterolepis*, *Hydrolycus scomberoides* e *Rhaphiodon vulpinus*) foram coletadas em condições ambientais pristinas (pré-HPP) e impactadas (pós-HPP). Nós avaliamos as abundâncias e as dietas para identificar variações entre as espécies congênicas e não-congênicas. O percentual de volume de cada presa foi corrigido pelo grau de repleção estomacal e os itens agrupados ao nível taxonômico de família para determinar dieta, amplitude e sobreposição alimentar. Apenas a abundância de *R. vulpinus* aumentou no pós-HPP. Não houve diferença na amplitude alimentar das espécies após o represamento, contudo a sobreposição de nicho diminuiu para as espécies congênicas e não congênicas. Nossos resultados indicam que o represamento do rio afetou os peixes piscívoros modificando sua partilha de recursos. Avaliar as interações interespecíficas, portanto, é uma ferramenta necessária para entender como os peixes respondem ao represamento de rios.

Palavras-chave: Amazônia, Amplitude de nicho alimentar, Hidrelétricas, Interações Interespecíficas, Sobreposição alimentar.

INTRODUCTION

Interspecific interactions are fundamental drivers of distribution patterns, local community assemblies, and evolutionary changes. Competition for food resources has been postulated as a key driving factor in the evolution and diversification of species (Hutchinson, 1957; MacArthur, Levins, 1967) and is known as a process that influences fish populations and community structure (Matthews, 1998). In contrast, resource partitioning is an essential mechanism for species coexistence and population structure (Agostinho *et al.*, 2003; Correa, Winemiller, 2014) that may arise from similar ecological requirements or facilitation interactions between species pairs (Robertson *et al.*, 2014).

Phylogenetically close species can share morphological attributes that allow them to explore similar resources. Because of this, they may experience stronger competition than phylogenetically distant species (Darwin, 1859; Webb *et al.*, 2002). Interspecific competition can reduce niche breadth by evolutionary processes, resulting in intraspecific optimization (Polechová, Storch, 2018). For example, usually, the ghost of the competition's past is stated as a historical process that explains contemporary patterns of niche partitioning among species (Connell, 1980). In other words, the niche differentiation observed today would be the result of competition between species in the past, selected for divergent characteristics (Losos, 2008; Cavender-Bares *et al.*, 2009). The environment species skills offer a valuable role in resource partitioning and, the maintenance of competitive interactions depends on ecological stability and predictability (Cavin *et al.*, 2013).

Neotropical freshwater ecosystems are associated with the seasonality of annual variation of rainfall, especially droughts and floods. This seasonality strongly affects the structure and functioning of aquatic communities (Junk *et al.*, 1989), including the influence on trophic interactions and food web structure (Winemiller, 1989; Mérona, Rankin-de-Mérona, 2004; Pool *et al.*, 2017). The historical predictability in resource supply is altered by hydroelectric projects, indirectly affecting interspecific interactions.

Fish assemblage responds to the flood-fueled upsurge in detritus, plants, and animal prey, subsequent changes in community structure reflect the uptake and transfer of diverse food web resources (Monaghan *et al.*, 2020). In this sense, an increase in zooplankton may lead increasing in zooplankton eating fish. In addition, the rapid growth in the population of small prey fishes (r-strategists) in reservoirs may directly benefit piscivores (Hahn, Fugi, 2007; Agostinho *et al.*, 2008; Luz-Agostinho *et al.*, 2009; Sá-Oliveira *et al.*, 2014; Pereira *et al.*, 2016; Dias *et al.*, 2019).

Reservoirs can also promote changes in the trophic interactions (predation and competition) rising in predatory fish (Turgeon *et al.*, 2019). For example, in the Manso Reservoir *Acestrorhynchus pantaneiro* Menezes, 1992 shifted its diet composition, trophic niche breadth, and prey sizes to feed on more abundant and available prey (Cantanhêde *et al.*, 2008); the feeding behavior of *Mylossoma albiscopum* Cope, 1872 (= *Mylossoma duriventre*) changed its herbivorous diet to an insect-based diet right after the construction of Santo Antônio dam in the Madeira River (Melo *et al.*, 2019) and, *Astyanax* spp. that varied their diet but displayed a decreased feeding activity and body condition after the construction of the Salto Caxias dam in the Iguazu River (Pereira, Agostinho, 2019).

Dam construction causes rapid and drastic alterations in riverine environments by changing limnological conditions and spatial heterogeneity (Araújo *et al.*, 2013). The lotic systems previously described by high water velocities are replaced by a lentic environment that attenuates the flood pulse (Junk *et al.*, 1989), eliminates the marginal flooded forest, and reduces the sediment flux (Oliveira *et al.*, 2010; Pelicice *et al.*, 2014; Winemiller *et al.*, 2016; Pokhrel *et al.*, 2018; Wu *et al.*, 2019). These changes promote an almost immediate response by fish populations with rapid modifications in their abundances and assemblage composition (Agostinho *et al.*, 2008).

The sharp, abrupt, and long-lasting environmental changes caused by river damming can create two new scenarios that can mediate resource use and competition among species. First, modified habitats may change community structure without reducing food resources, allowing fishes to feed on alternative items to meet dietary requirements, as predicted by the optimal foraging theory (OFT) and increasing interspecific dietary overlap (Perry, Pianka, 1997). Second, the modified environmental conditions may reduce prey, causing niche narrowing and increasing diet segregation among fishes, affecting closely related species more strongly (Pianka, 1974; Schoener, 1974). Additionally, resource competition theory predicts that species might become specialized and consume fewer alternative resources (*i.e.*, trophic niche contraction), thereby segregating in niche space and reducing interspecific dietary overlap (Pianka, 1974; Schoener, 1974).

Despite some studies that previously assessed responses of piscivorous in reservoirs, as Serra da Mesa dam (Novaes *et al.*, 2004), Corumbá Reservoir (Fugi *et al.*, 2008) and Salto Caxias dam (Pereira *et al.*, 2016), the role of the environmental changes resulting from river damming on piscivores in Neotropics is still scarce, mainly in Amazonian rivers.

Acestrorhynchidae and Cynodontidae were the most abundant piscivorous fish families before and after the Santo Antônio dam construction in Madeira River (Toledo-Piza, 2013; Toledo-Piza *et al.*, 2013). Regarding the fish assemblage in the reservoir area, the species biomass and abundance were higher post-damming, mainly by increase small-sized opportunistic species (Cella-Ribeiro *et al.*, 2017). This scenario presents a unique opportunity for exploring the dietary niche breadth and overlap of phylogenetically related species under disturbances caused by damming in muddy-water river, shedding light on the relevance of interspecific interactions.

Considering that dams strongly disrupt river dynamics, resulting in new ecological conditions and variations in the fish assemblage, alterations in the feeding spectrum of piscivorous fish species are expected (Cantanhêde *et al.*, 2009; Delariva *et al.*, 2013). We hypothesize that those environmental disturbances resulting from river damming in the Madeira River would influence trophic interaction with changes in prey spectrum by the four piscivorous species. This paper evaluated the species abundance, diet composition, dietary niche breadth, and diet overlap of congeneric (*Acestrorhynchus falcistrostris* (Cuvier, 1819) and *Acestrorhynchus heterolepis* (Cope, 1878)) and non-congeneric (*Hydrolycus scomberoides* (Cuvier, 1819) and *Rhaphiodon vulpinus* Spix & Agassiz, 1829) piscivorous species before and after the construction of hydropower plant in the Amazon. We predict that changes in trophic relations may affect (i) species abundances, (ii) changes in diet that lead to (iii) an increase in dietary niche breadth and, (iv) an increase niche overlap for species pairs (congeneric and non-congeneric) after river damming, typically due to increasing prey availability, as predicted by OFT. Moreover, as closely related species can explore similar resources and may experience stronger competition than phylogenetically distant species, we expect prominent alterations in trophic niche breadth and overlap between congeneric than in non-congeneric species after the river damming.

MATERIAL AND METHODS

Study area. Madeira River is one of the largest and most complex tributaries of the Amazon River Basin (Goulding *et al.*, 2003) with an annual average discharge of 31,704 m³·s⁻¹ that corresponds to ~15% of the Amazon River discharge (Siqueira-Júnior *et al.*, 2015). The study area included a river section of approximately 20 km that originally comprised rapids. We established six sampling sites in this segment: three fixed (sampled in both phases) and three sites collected only in the reservoir area, in the post-damming phase (Fig. 1).

Biological data. We examined four piscivorous fishes: *Acestrorhynchus falcistrostris*, *A. heterolepis* (Acestrorhynchidae), *Hydrolycus scomberoides* and *Rhaphiodon vulpinus* (Cynodontidae). These species were abundant in the study area before and after the river damming (Cella-Ribeiro *et al.*, 2016, 2017).

Exemplars were collected in 13 monthly expeditions over one year before the river damming (April/2009 – April/2010) and 13 bi-monthly expeditions over two years after (August /2011 – August /2013). We used standardized sets of 13-gill nets (each gillnet 10 m in length and 1.5–3.5 m in height), making an area of 431m² left in the water for

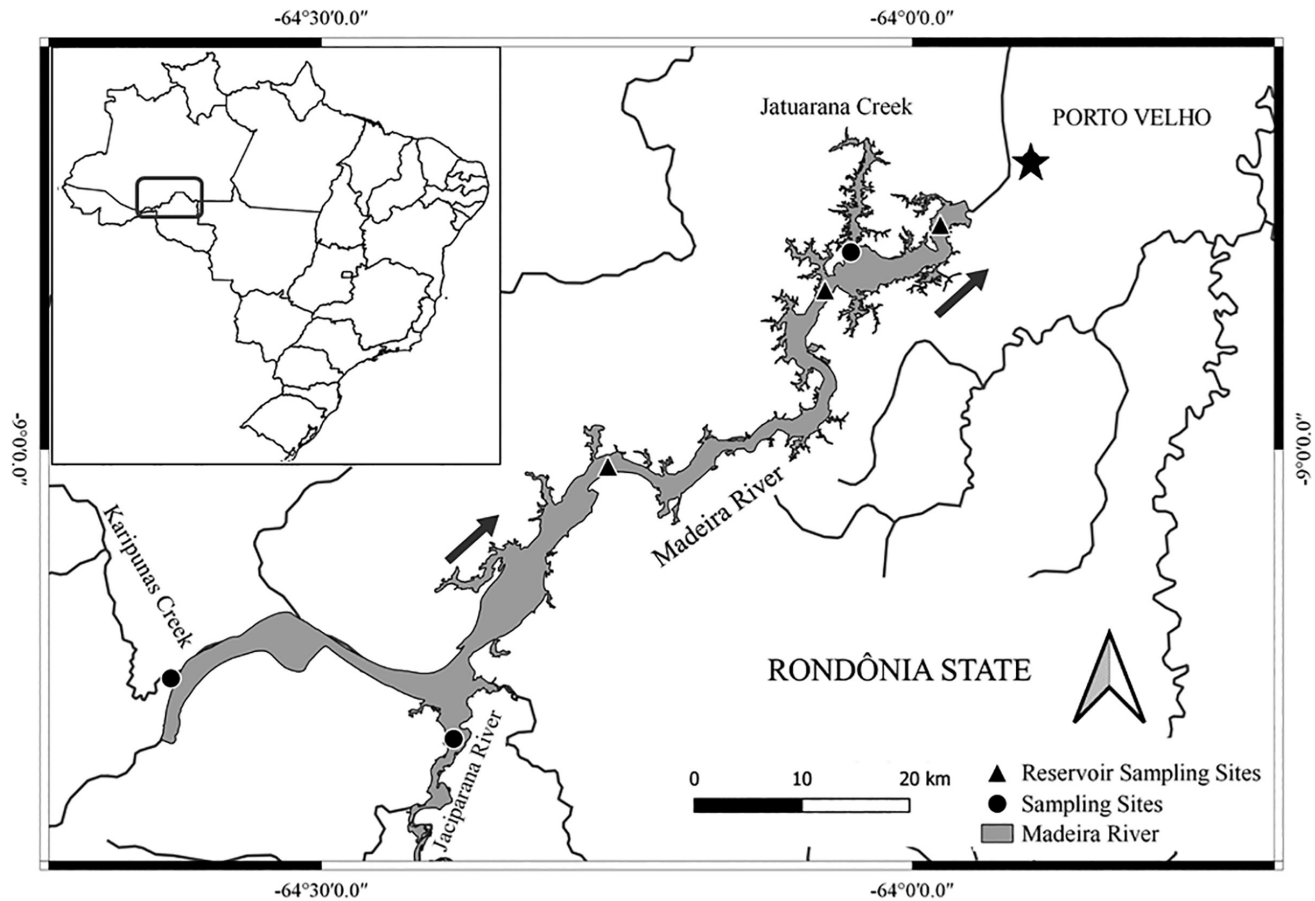


FIGURE 1 | Study area in the Madeira River portion. Black points representing fixed sampling sites for both pre-and post-damming phases. Triangles represent the sampling sites located in the reservoir area in the post-damming phase. Arrows indicate the river flow.

24 hours per sampling event (fish remotion occurred every six hours) (Cella-Ribeiro *et al.*, 2017).

Voucher specimens were transferred to 70% ethanol and deposited in the fish collection of the Universidade Federal de Rondônia under the catalog numbers: *A. falcirostris* UFRO-I 1823, 2025 and 3407; *A. heterolepis* UFRO-I 1389 and 3144; *H. scomberoides* UFRO-I 10157 and 10479; *R. vulpinus* UFRO-I 518 and 520.

We measured each specimen at a standard length (in cm), removed the stomachs, and kept them in 70% ethanol. Stomach fullness (percent of fullness) was visually estimated on a scale from 0 to 3 (Hahn *et al.*, 1999) considering the amount of food filling the stomach: 0 (empty), 1 (< 25%), 2 (25–75%) and 3 (> 75%). Stomach contents were analyzed under an optical stereomicroscope and identified to the lowest possible taxonomic level following keys (Queiroz *et al.*, 2013) and reference materials by several experts. Each food item had its relative volume visually estimated by the proportion of the item in the stomach contents considering the total volume of the items as 100% and later multiplied by stomach fullness score (Goulding *et al.*, 1988).

Data analysis. We estimated species capture per unit of effort (CPUE – number of individuals/341m² of nets/24h) before and after damming to identify variations in abundances. This estimate is universally used and allows direct comparison between species abundances to evaluate population size is increasing or decreasing tendencies. We used a Wilcoxon test to examine if species abundance differed between periods (prediction i), with *wilcox.test* function. It is an equivalent test to paired t-test because our data did not reach assumptions for the parametric test.

Alterations in species diet composition were evaluated between phases (pre- and post-HPP) with the percent volumes of items as dependent variables and species and periods as independent variables. We transformed volume values by log (x+1) before building a Bray-Curtis dissimilarity matrix of diet composition because of the high number of zeros. With that matrix, we applied a multivariate permutation analysis of variance (PERMANOVA; Anderson, 2006) to test possible differences in species diet composition between periods (prediction ii). PERMANOVA is sensitive to differences in multivariate dispersion even under unbalanced designs; then, we applied a PERMDISP to evaluate the homogeneity of multivariate dispersions (Anderson, 2006). Despite the unbalanced design between damming phases (*i.e.*, unequal number of examined stomachs), PERMDISP indicated that variances between periods were homogeneous, thus supporting the robustness of the PERMANOVA results (Anderson, Walsh, 2013). Finally, to check which food item contributed the most to dietary differences, we applied the percentage similarity method (SIMPER, Clarke, 1993) with 9999 randomizations.

Additionally, we used the percent volume of each food item to estimate the dietary niche breadth and overlap among species before and after the dam construction. A high number of stomach contents were in an advanced digestion stage that precluded taxonomic identification, thus we applied all analyses using prey grouped in the family taxonomic level. It was imperative to do that because of the high degree of prey digestion found in stomachs, which is a typical pattern of piscivorous (Arrington *et al.*, 2002; Luz-Agostinho *et al.*, 2009). The high occurrences of items, such as unidentified fish, lead to difficulties studying piscivores diet (Hahn *et al.*, 1999; Pacheco *et al.*, 2009), even employing high attempted sampling. We excluded from the analyses those items described as unidentified fish (Fish NI) and those identified until Order level because of the uncertainty it would add. For example, the consumption of Characiformes was elevated and could lead to high niche overlap between species pairs feeding on different families within the order.

We performed a PERMDISP using the Bray-Curtis dissimilarity matrix of diet composition to test for differences in dietary niche breadth between periods considering four species (prediction iii). We measured dietary niche breadth as the average distance of individuals from a group to the group centroid in a principal coordinate analysis (PCoA) (Silva *et al.*, 2017). We conducted the statistical analyses using the *adonis2* (PERMANOVA), *betadisper* (PERMDISP), and *simper* (SIMPER) functions from the *vegan* package (Oksanen *et al.*, 2017).

The dietary overlap for each species pair (congeneric and non-congeneric) in each phase was calculated according to Pianka (1974), with the equation $O_{jk} = (\sum p_{ij} \times p_{ik} / \sqrt{\sum p_{ij}^2 \times \sum p_{ik}^2})$, where O_{jk} is Pianka's index of species j and k ; p_{ij} is the proportion of food item i in the overall food items of species j ; p_{ik} is the proportion of food item i in the total food items of species k ; n is the total number of food items. Dietary overlap

ranges from 0 (no overlap) to 1 (full overlap). We considered values greater than 0.6 as high, values from 0.4 to 0.6 as intermediate, and values below 0.4 as low (modified from Grossman, 1986). We used *niche.overlap* function from the *spaa* package and the *rda3* algorithm to perform niche overlap analyses. All statistical analyses were performed in the R programming environment (R Core Team, 2020), considering the level of statistical significance of $p < 0.05$.

RESULTS

Fish abundance changed among the piscivorous species between pre- and post-HPP (Tab. 1; Fig. S1 and S2). Even so, only *R. vulpinus* showed a significant increase in capture in the post-HPP phase ($V = 91.5$; $p = 0.0028$). From the 1,776 examined individuals, only 146 had stomach contents: 51 from *A. falcistrostris*, 54 from *A. heterolepis*, 16 from *H. scomberoides*, and 25 from *R. vulpinus* (Tab. 2; Fig. S3).

The congeneric species pair has fed exclusively on fishes, while the non-congeneric species has fed primarily on fishes and occasionally ingested other items as microcrustaceans, insects, and vegetables. A high percentage of stomachs was composed of fish in high-level digestion that hampered identification. Some of them could be identified only at the Order level, which allowed identifying high percentage values of Characiformes as prey (Tab. 2).

TABLE 1 | Abundance, Capture Per Unit of Effort (CPUE – individuals/10,000m²/24h), and the number of empty and analyzed stomachs with alimentary content.

Species	Number of collected specimens		Number of empty stomachs		Number of analyzed stomachs
	N	CPUE	N	%	N
<i>Acestrorhynchus falcistrostris</i>					
Pre-damming phase	528	3.00	423	80.11	43
Post-damming phase	194	1.50	171	88.14	8
<i>Acestrorhynchus heterolepis</i>					
Pre-damming phase	455	2.59	339	74.51	41
Post-damming phase	127	1.12	101	79.53	13
<i>Hydrolycus scomberoides</i>					
Pre-damming phase	73	0.42	42	57.53	7
Post-damming phase	250	2.20	173	69.20	9
<i>Rhaphiodon vulpinus</i>					
Pre-damming phase	271	1.54	193	71.22	12
Post-damming phase	408	3.59	324	79.41	13
Total	2,306		1,766		146

TABLE 2 | List of consumed prey by *Acestrorhynchus falcistrostris*, *A. heterolepis*, *Hydrolycus scomberoides*, and *Rhaphiodon vulpinus*. V% = Volume percentual, PRE = pre-HPP (before damming) and POST = post-HPP (after damming); NI = not identified. Numbers below species name are the range of species body size in standard length measured in centimeters (values based on specimens with stomach content).

Food Items	<i>Acestrorhynchus falcistrostris</i> (13.0–37.4)		<i>Acestrorhynchus heterolepis</i> (12.3–38.8)		<i>Hydrolycus scomberoides</i> (16.4–34.3)		<i>Rhaphiodon vulpinus</i> (15.5–51.4)	
	PRE	POST	PRE	POST	PRE	POST	PRE	POST
	%V	%V	%V	%V	%V	%V	%V	%V
Characiformes NI	16.26	27.27	19.83	33.33	20.69	4.00		33.33
Acestrorhynchidae								
<i>Acestrorhynchus</i> spp.	2.44							
<i>Acestrorhynchus microlepis</i>			5.17					
<i>Acestrorhynchus</i> cf. <i>pantaneiro</i>			5.17					
<i>Acestrorhynchus falcistrostris</i>	11.38							
<i>Acestrorhynchus heterolepis</i>	2.44							
Characidae NI	2.44			8.33			16.13	
Characidae								
<i>Aphyocharax avarii</i>						12.00		
<i>Brachyhalcinus copei</i>						9.60		
<i>Charax gibbosus</i>			2.59					
<i>Ctenobrycon spirulus</i>						8.40		
<i>Moenkhausia</i> gr. <i>lepidura</i>							9.68	
Curimatidae								
<i>Cyphocharax</i> spp.	7.32							
<i>Potamorhina</i> spp.	2.44							
<i>Curimata inornata</i>	4.88	12.00						
<i>Potamorhina latior</i>			2.59					11.11
<i>Psectrogaster rutiloides</i>		12.00						11.11
<i>Psectrogaster amazonica</i>	2.44		2.59					
<i>Psectrogaster essequibensis</i>	1.63		5.17	8.33				
Cynodontidae NI			2.59					
Hemiodontidae								
<i>Anodus orinocensis</i>		12.00						
Gymnotiformes NI	3.66	4.55					6.45	
Sternopygidae								
<i>Sternopygus macrurus</i>			1.72					
Siluriformes NI							9.68	
Auchenipteridae NI							9.68	
Doradidae NI								7.41
Hypostominae NI								11.11
Loricariidae NI				8.33				
Pimelodidae NI					6.90			
Fish NI	42.69	27.27	52.59	41.67	23.62	29.44	41.94	21.59
Insect NI						0.37		0.11
Microcrustacean								0.04
Vegetable NI					7.41	5.63	6.45	0.18
Scales						8.00		0.04

From all analyzed stomachs with food content, only 50 of them had prey identified at the family level. Regarding the recognized items, the congeneric species pair consumed mostly other *Acestrorhynchus* and Curimatidae species. The non-congeneric species ingested an elevated amount of fish families such as Characidae, Curimatidae, Auchenipteridae, Doradidae, and Loricariidae.

We observed differences in diet composition among species (PERMANOVA $p = 0.016$) and phases (PERMANOVA $p = 0.036$), but not for the interaction between these factors (PERMANOVA $p = 0.266$) (Tab. 3; Fig. 2). There were no differences in the dispersion among groups between phases or species (PERMDISP; $p > 0.05$), corroborating the patterns detected by PERMANOVA (Tab. S4).

Regarding species differences indicated by PERMANOVA, SIMPER analyses identified significant differences in diet similarity of congeneric species in the consumption of Acestrorhynchidae ($p = 0.01$), Cynodontidae ($p = 0.02$), and Sternopygidae ($p = 0.02$). Non-congeneric species showed different diets in the consumption of vegetables ($p = 0.01$) (Tabs. S5, S6, S7, and S8).

Concerning the effect of the HPP phase, congeneric species consumed mainly Characiformes. They had explored a broader range of prey species and families in the pre-HPP phase, including five taxonomic families (Cynodontidae, Acestrorhynchidae, Characidae, Curimatidae, and Sternopygidae; Tab. 2; Fig. 2). In the post-HPP, both species consumed prey within four families. *Acestrorhynchus falcistrostris* fed primarily on Curimatidae and Hemiodontidae and *A. heterolepis* ingested Curimatidae, Characidae, and Loricariidae only in the post-HPP phase (Fig. 2). Congeneric species had intra-genus predation and *A. falcistrostris* had cannibalism in the pre-HPP.

Hydrolycus scomberoides consumed mainly Pimelodidae during the pre-HPP and limited diet to Characidae prey in the post-HPP phase. They also have eaten vegetables, insects, and microcrustaceans at minor volumes (Tab. 2; Fig. 2). *Rhaphiodon vulpinus* in turn, ingested mostly Characidae and Auchenipteridae in the pre-HPP, while in post-HPP, there was a predominant consumption of Curimatidae, followed by Doradidae and Loricariidae.

TABLE 3 | Permutational Multivariate Analysis of Variance (PERMANOVA) applied to percent volume of the diet of four piscivorous fishes from Madeira River before and after damming. Significant p-values are indicated by (*).

	Df	SumOfSqs	R2	F Pr(>F)	p
Species	3	2.2983	0.12154	2.1140	0.016 *
Dam	1	0.8270	0.04374	2.2822	0.036 *
Species: Dam	3	1.2889	0.06816	1.1856	0.266
Residual	40	14.4953	0.76656	2.1140	
Total	47	18.9095	1.00000		

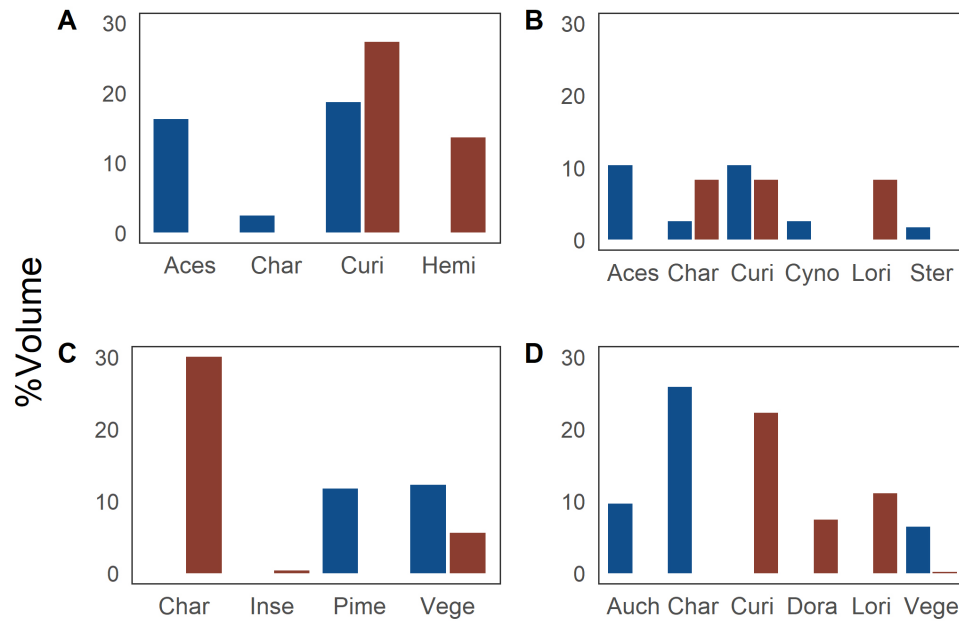


FIGURE 2 | The percent volume of prey consumed by four piscivorous fishes in Madeira River. **A.** *Acestrorhynchus falcirostris*, **B.** *Acestrorhynchus heterolepis*, **C.** *Hydrolycus scomberoides*, and **D.** *Rhaphiodon vulpinus*. Blue bars correspond to the pre-damming period and red bars to the post-damming period. Items are Aces = Acestrorhynchidae, Cyno = Cynodontidae, Char = Characidae, Curi = Curimatidae, Ster = Sternopygidae, Hemi = Hemiodontidae, Lori = Loricariidae, Auch = Auchenipteridae, Dora = Doradidae, Pime = Pimelodidae, Inse = Insects, Vege = Vegetable.

We did not find differences in niche breadth values besides the variations between periods ($F = 0.22$; $p = 0.63$). *Acestrorhynchus falcirostris* exhibited niche breadth (Average Centroid Distance-ACD) of 0.50 in the pre-HPP and 0.33 in the post-HPP. On the other hand, we detected a broader range of resources used by *A. heterolepis*, displaying a niche breadth value of 0.58 in pre-HPP conditions and no apparent variation in the post-HPP phase (ACD = 0.57). *H. scomberoides* remained some variation before and after damming (ACD = 0.51 in pre-HPP; ACD = 0.41 in post-HPP), while *R. vulpinus* demonstrated an increase of the niche breadth (ACD = 0.41 in pre-HPP; ACD = 0.58 in post-HPP) (Fig 3).

Trophic niche overlap was remarkably high (0.91) in congeneric acestrorhynchids in pre-HPP and intermediate (0.45) in the post-HPP period. While the non-congeneric cynodontids revealed low niche overlap in the pre-HPP phase (0.31) and extremely low (0.019) in the post-HPP phase (Tab. 4).

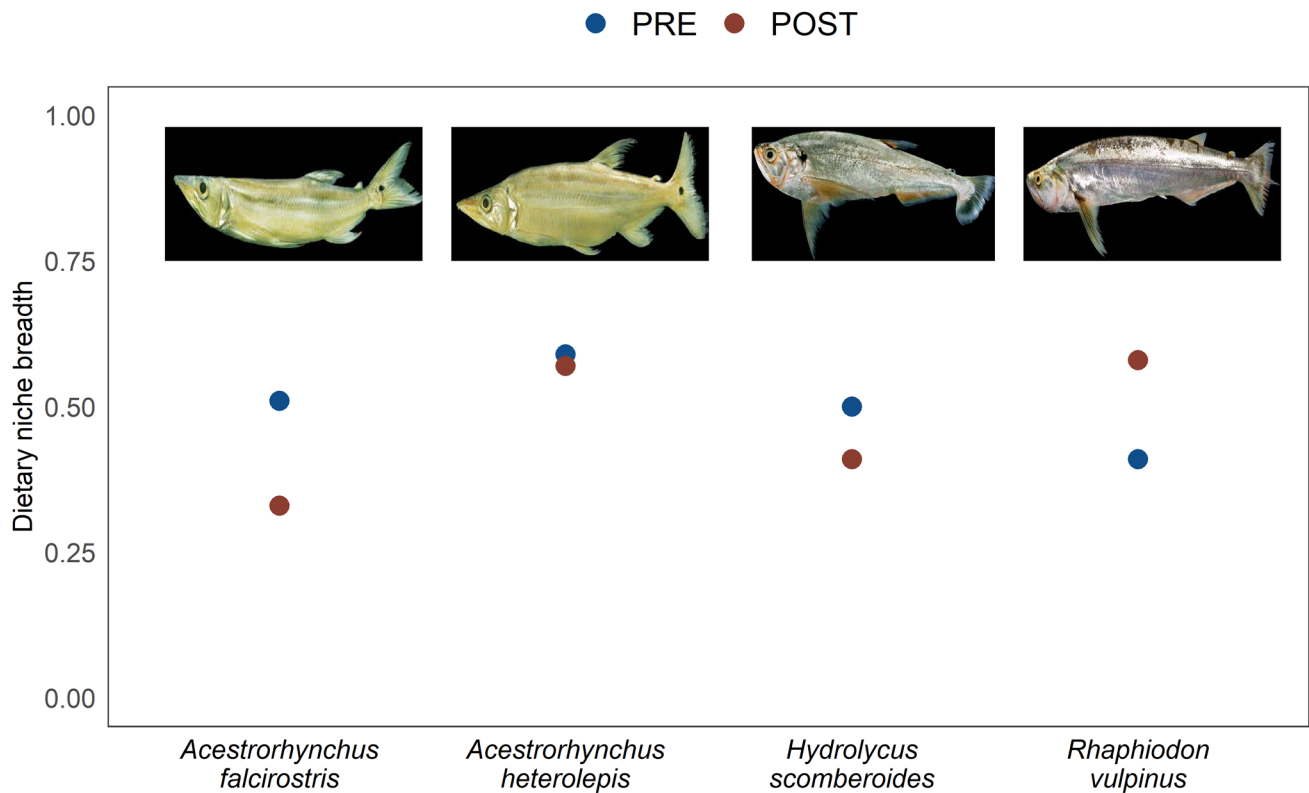


FIGURE 3 | Dietary niche breadth values of four piscivorous fishes before (pre-HPP) and after (post-HPP) dam construction in the Madeira River.

TABLE 4 | Pairwise niche overlap (NO) values using Pianka Index and p-values of niche similarity.

Pre-damming	NO
<i>Acestrorhynchus falcirostris</i> X <i>Acestrorhynchus heterolepis</i>	0.912
<i>Rhaphiodon vulpinus</i> X <i>Acestrorhynchus heterolepis</i>	0.231
<i>Rhaphiodon vulpinus</i> X <i>Acestrorhynchus falcirostris</i>	0.208
<i>Hydrolycus scomberoides</i> X <i>Rhaphiodon vulpinus</i>	0.314
Post-damming	NO
<i>Acestrorhynchus falcirostris</i> X <i>Acestrorhynchus heterolepis</i>	0.450
<i>Rhaphiodon vulpinus</i> X <i>Acestrorhynchus heterolepis</i>	0.715
<i>Rhaphiodon vulpinus</i> X <i>Acestrorhynchus falcirostris</i>	0.539
<i>Hydrolycus scomberoides</i> X <i>Rhaphiodon vulpinus</i>	0.019

DISCUSSION

The disturbance caused by impoundment led to changes in species abundances, diet composition, niche breadth, and overlap of congeneric and non-congeneric piscivorous fishes. Here, we show that diet variations recorded have modified the food spectrum of piscivores and affected their resource partitioning. Despite predicting a general increase in species abundance and niche breadth, congeneric species responded differently than non-congeneric species in these attributes. Niche overlap decreased between congeneric and non-congeneric species.

The environmental changes resulting from river damming have affected congeneric and non-congeneric in different ways. Even the piscivore habit persisted, species changed the explored prey between periods. Congeneric acestrorhynchids species displayed a typical piscivore diet, eating only fish, as reported for *A. falcistrostris* and *A. microlepis* (Schomburgk, 1841) of Negro River (Goulding *et al.*, 1988).

Nevertheless, the congeneric species were not effective in persisting at the reservoir area. We reported them in the tributary's mouths, while the non-congeneric cynodontids occurred in all sampled sites (Fig. S1), which may be, in part, explained by their diet flexibility registered after damming. Besides eating primarily fishes, cynodontids also fed on secondary items (*e.g.*, insects, microcrustaceans) and other different fish prey, which could run in a higher energy balance according to the optimal foraging theory (Gerking, 1994). The wide niche breadth and decreased niche overlap of cynodontids may have contributed to their persistence and increasing abundance in the reservoir.

Small-sized fishes can find refuges in aquatic macrophytes that usually increased after reservoirs formation (Pelicice *et al.*, 2005), and this may explain the increase of species abundance in post-damming (Cantanhêde *et al.*, 2008; Cella-Ribeiro *et al.*, 2017). This increase is followed by rising populations of slow water-dwelling piscivores, taking advantage of abundant resources (Pereira *et al.*, 2016; Dias *et al.*, 2019). Thus, piscivorous fishes can benefit from the biotic changes promoted by the reservoir formation (Hahn *et al.*, 1998; Mérona *et al.*, 2001; Dias *et al.*, 2019) by exploring the available resources. In the Serra da Mesa dam (Tocantins River), Pacheco *et al.* (2009) considered that the clear water favored the foraging behavior of *R. vulpinus*. Conversely, the muddy waters of the Madeira River may hamper the task of finding prey for visual predators, as cynodontids. However, the reduced water turbidity and higher water transparency after damming (Cella-Ribeiro *et al.*, 2017; Fig. S9) could partially explain the persistence of cynodontids within the reservoir since they could see and reach their prey and thus, expanded their niche breadth. Such conditions may also explain the abundance increase of *R. vulpinus* in the post-HPP phase.

On the other hand, acestrorhynchids species became rare in reservoir sampled sites despite some prey species (*e.g.*, *Potamorhina* spp., *Psectrogaster* spp.) kept being captured more often within the reservoir (Cella-Ribeiro *et al.*, 2017). Since prey was not limited in the reservoir area, and niche overlap decreased among acestrorhynchids species, we suppose that the congeneric species could not adapt to the new lentic environment due to changes in water conditions such as water temperature and dissolved oxygen after damming (Cella-Ribeiro *et al.*, 2017).

Phylogenetically close species can share morphological attributes that allow them an exploration of similar resources. Because of this, they may experience harsher competition

effects than the more distant ones (Darwin, 1859; Webb *et al.*, 2002), even despite the disturbance. Congeneric species presented high trophic niche overlap and explored items from five different taxonomic families of fishes before damming (including predation of the same genus, *Acestrorhynchus*), indicating they could coexist, sharing food resources in natural conditions, and avoiding severe competitive interactions. After damming, both acestrorhynchids fed on less prey, which led to a narrowed and more segregated trophic niche. Our results evidenced that closely related species may suffer harsher effects after the impoundment. Congeneric species explored Curimatidae species in both periods and, trophic relationships established in natural conditions had to rearrange accordingly to prey availability, and to prey preferences. Although not investigated in our study, trophic interactions with other piscivorous species that increased abundance (*e.g.*, *R. vulpinus*) also may have limited species adjustment to the new conditions.

Before damming, non-congeneric species fed on different prey sources, demonstrating diet segregation. These may be explained by the habitat use of *R. vulpinus* potentially, exploring the middle and the surface of the water of rivers, lakes, and flooded forests (Toledo-Piza, 2000). *Hydrolycus scomberoides* fed on catfishes indicating its skills to prey on benthic fish. The ability to explore different habitats and the trophic segregation may explain how they could persist in the reservoir. We recognized higher niche breadth when species consumed distinct prey, leading to extremely low niche overlap. These may indicate that species coexistence may be possible by avoiding competition interactions.

Optimal foraging theory (OFT) predicts that species will expand their diet to include alternative food items to meet dietary requirements (Perry, Pianka, 1997). It is acceptable that cynodontids in this study could persist at the damming area following OFT. The pattern of low overlap observed in natural conditions may be a product of past competition that promoted changes in their diet for alternative prey (*i.e.*, the ghost of past competition; Connell, 1980). Thus, we expected low niche overlap when coexistence depends on differences in resource use to minimize competition (Hutchinson, 1957). Environmental disturbances, such as river impoundment, may rearrange trophic interactions and can renew the selection process. Since the habitat seasonality (flooding) may protect and relieve species competition (Osman, 1978), river damming follows in a more stable environmental condition, as the reservoir.

Conversely, resource competition theory predicts that competing species will specialize and exploit fewer alternative resources (*i.e.*, trophic niche contraction), thereby segregating in the niche space (Pianka, 1974; Schoener, 1974). Our result supports this scenario when some preference to Curimatidae species in congeneric species (Acestrorhynchidae), but they also fed on other Acestrorhynchidae species. In this sense, interspecific interactions, as competition may have played a significant role, favoring narrow niches and, thus, impoundment might have affected closely related species more strongly.

Competition occurs when species overlap in resource use (Gotelli, Graves, 1996). It is possible to overlap in resource use without competition if resources are abundant (Raborn *et al.*, 2004). Phylogenetically related species tend to be ecologically similar but usually display temporal or spatial differences in resource use that allow local cooccurrence (Chase, Leibold, 2003).

Congeneric species coexisted and shared food resources demonstrating, under a

natural environment, possibly because abundant resources avoided competition. Diet modified in post-HPP due to changes in preferential items and decreasing niche breadth of *A. falcistrostris*, which may be, at least in part, a consequence of competition interactions. Hence, it is expected species to adjust their feeding to reduce niche overlap with competitors (Correa, Winemiller, 2014), not because of the decrease in the general availability of prey fish, as they tend to increase in new reservoirs, but of specific prey, such as some Curimatidae species. In this sense, competition between acistorrhynchids may be reduced through resource partitioning, as predicted by niche theory, and that differences between species are essential for their coexistence (Chase, Leibold, 2003).

Food resource partitioning is a crucial factor in structuring fish assemblages, in almost all aquatic habitats (Gerking, 1994) and one of the most relevant factors accountable for structuring populations (Agostinho *et al.*, 2003). Piscivorous fishes studied here may have the flexibility to adjust prey consumption, and predator-prey relationships might demand limited species-specific interactions. Such conditions could be essential to the piscivorous fishes' ability to cope with the drastic environmental changes resulting from river damming.

The construction of dams and reservoirs formation is one of the critical causes of environmental disturbance for Neotropical fishes because it modifies the habitats and the hydrological and ecological conditions severely and abruptly, modifying species abundances and composition (Agostinho *et al.*, 2008; Winemiller *et al.*, 2016) and the functional diversity of communities (Arantes *et al.*, 2019). Piscivorous fishes and other top predators are essential for stabilizing trophic webs (Lima, 1998) because they influence interspecific interactions (Novak, Wootton, 2008; Pereira *et al.*, 2016) and help to regulate ecosystems services. River damming endangers them through physical blockage of their reproductive routes, destruction of nursery habitats, water physical and chemical changes, and invasive fish species (Agostinho *et al.*, 2008; Winemiller *et al.*, 2016).

Waterfalls have operated as natural barriers over evolutionary time and supported speciation processes that resulted in the most diverse freshwater ichthyofauna in the world (Dias *et al.*, 2013). Damming the Madeira River flooded a sequence of waterfalls, altered biophysical processes, and species interactions that have promoted and maintained fish diversity shaped by millions of years of evolution (Torrente-Vilara *et al.*, 2011). Alternative and more ecologically effective ways of planning and building hydroelectric power plants should be employed and thus, to avoid or mitigate the environmental impacts and biodiversity loss within one of the world's most diverse biomes (Lees *et al.*, 2016; Winemiller *et al.*, 2016).

We provide insights into how interspecific interactions play a role as a possible result of phylogenetic relatedness. Despite that, it is relevant to observe some design limitations. First, the number of stomachs analyzed, which were considerably reduced in the post-HPP phase. Second, study the seasonal variation of diet since it affects the availability and consumption of food resources. Future studies may evaluate it to understand the role of the long-term environmental changes resulting from river damming that may affect piscivorous assemblage.

Water impoundment is among the most predominant and powerful ways of anthropogenic environmental alteration in the world. The construction of the Santo Antônio dam in the Madeira River modified the food spectrum of four piscivorous

fishes studied and consequently affected their resource partitioning. Our results indicate that damming affect piscivorous fishes in distinct ways. Interspecific interactions, such as predation and competition, are applicable, and understand how piscivores act in response to such environmental disturbances is essential to better deal with this impact.

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AUTHORS' CONTRIBUTION

Alessandra Pasian Lonardoni: Conceptualization, Data curation, Formal analysis, Investigation, Writing-original draf, Writing-review and editing.

Cristhiana Paula Röpke: Data curation, Investigation, Writing-original draf, Writing-review and editing.

Taís Melo: Data curation.

Gislene Torrente-Vilara: Conceptualization, Funding acquisition, Data curation, Investigation, Project administration, Writing-original draf, Writing-review and editing.

ETHICAL STATEMENT

Captured specimens were euthanized by an ice bath and transported in an icebox to the laboratory. Laboratório de Ictiologia e Pesca (LIP) of Universidade Federal de Rondônia (UNIR) sampled the biological data, under the Santo Antônio Energia (SAE) and Energia Sustentável do Brasil (ESBR) Programa de Conservação de Peixes (#51/09 authorizations from Coordenação Geral de Autorização para uso e Manejo dos Recursos de Fauna e Pesca; Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis – GFAP/IBAMA).

COMPETING INTERESTS

The authors declare no competing interests.

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