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RESEARCH ARTICLE

Functional responses of fisheries to hydropower dams in the Amazonian Floodplain of the Madeira River

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Abstract

1. Tropical river fisheries support food security for millions of people but are increasingly threatened by hydropower development. How dams affect these fisheries remains poorly known in most regions. Here, we used a functional traits approach to evaluate the extent to which compositions of fishery yields in the Madeira River Basin, the largest sub-basin in the Amazon, respond to dam construction. We also explored how dams affected the monetary value of yields and fishing-based income of the communities.
2. We collected fishing data in 17 locations distributed over 300 km across upstream, reservoir and downstream zones during pre-and post-dam construction periods. We interviewed 711 fishers from 13 communities to assess fishing income during pre- and post-dam periods.
3. Catch-per-unit effort (CPUE) declined significantly, that is, by 37%, after dam construction. Multivariate analysis yielded six species clusters according to trait syndromes related to life history, migration, swimming performance/habitat-use and economic value that were associated with the environmental data characteristic of pre- and post-dam periods. Comparison of CPUE of each cluster indicated that large species with periodic life-history strategy and regional or long-distance migratory behaviour were most affected by dam construction, with CPUE declining by, on average, 31%. Declines in yields and shifts in functional composition of the fishery yields resulted in average decline of 21% in the monetary value of functional clusters and 30% in fishing income.
4. *Synthesis and applications*. Our study indicates that the implementation of the dams affected the functional composition of yields and reduced catches, negatively affecting the fishing-based income of communities in the Madeira River. These results imply that hydropower expansion will cause detrimental effects for fisheries and the livelihoods they sustain. Our results underscore the urgent need for considering alternative sources of renewable energy (e.g. solar power and in-stream turbines) to avoid irreversible socio-environmental damages of large dam projects. In river reaches where dams are already in operation or under

construction, minimizing impacts will require improving operational protocols to reduce hydrological alterations and developing research and technology to improve the functionality of fish passages. In these locations, addressing losses in fishery value and fishing-based income will also require the implementation of fair compensation measures. Maintaining fish production requires conserving flow pulses and free-flowing rivers and tributaries critical for completing life cycles of fish species with vulnerable traits.

KEYWORDS

Amazon, dams, ecological impacts, fish production, functional diversity, river impoundment, small-scale fisheries, socio-economic impacts

1 | INTRODUCTION

Tropical river fisheries are increasingly threatened by hydropower development (Zarfl et al., 2014; Ziv et al., 2012). Hydropower dams disrupt lateral and longitudinal connectivity of rivers, alter flow regimes and sediment transport, thereby impacting aquatic biodiversity and productivity (Forsberg et al., 2017; Vörösmarty et al., 2010). Dams have led to shifts in spatial temporal patterns of fish assemblage structure and biotic homogenization through declines, or losses, of species and their ecological traits (i.e. any feature of organisms that affect its performance or fitness; Arantes et al., 2019). Consequently, dams have been affecting the nature of fisheries that sustain livelihoods and food security for millions of people (Welcomme, 1999; Ziv et al., 2012). Improved understanding of dams' impacts on fisheries is imperative to mitigate the social and ecological effects of these projects, and to inform planning and decision-making on future dams.

Fish stocks responses to changes in environmental conditions caused by river impoundment vary according to their ecological traits, resulting in relatively predictable shifts in assemblages composition (Arantes, Fitzgerald, et al., 2019). Because fish traits can be functionally linked to species environmental tolerances and habitat requirements (e.g. Allan et al., 2005; Gatz, 1981; Winemiller et al., 2015), traits can be used to understand differential responses of species to river impoundment (Arantes, Fitzgerald, et al., 2019; Villéger et al., 2017). Fishes with traits adaptive for habitats with swift-moving water (e.g. rapids-dwelling and benthic species) can decline when rapids are submerged by reservoirs (Lima et al., 2018). Species possessing traits that are linked to migratory behaviour (e.g. long-distance or regional migrators) require hydrological connectivity for completion of the life cycle, and therefore, are strongly affected by physical barriers imposed by dams (Agostinho et al., 2016). Fishes that depend on natural flow regimes to trigger migration and reproduction (e.g. periodic life-history strategists) can become rare following dam construction (Oliveira et al., 2018; Zhong & Power, 1996). Conversely, species with traits associated with low dispersal ability but good manoeuvrability (e.g. many sedentary or short-distance migrators) tend to increase in abundance following river impoundment (Agostinho et al., 2016; Dos Santos et al., 2017).

A shift in functional composition of fish assemblages can affect fisheries yields; however, no evaluations of functional responses in composition of yields have yet been made (Villéger et al., 2017). Species with traits that are well adapted to lentic environments can thrive in reservoirs and enhance overall fish production. Conversely, vulnerable species including long-lived and migratory stocks can collapse, resulting in declining biomass available for harvesting (Arantes, Fitzgerald, et al., 2019; McCann et al., 2016). Due to differential functional responses of fishes to dams and shifts in species composition of catches, the outcomes for total yields can be uncertain, with declines, similar levels, or even increases being reported after dam construction in tropical rivers (Hoeinghaus et al., 2009; Okada et al., 2005; Zhong & Power, 1996). Yet, because many vulnerable species may be of high economic value (Hoeinghaus et al., 2009), evaluating impacts of dams based on functional approaches can not only provide insights on fish yields in response to dams, but also on consequences to fisheries value. Finally, because many traits have well-established form–function relationships that reflect adaptation to environmental conditions (Reich et al., 2003), understanding of fisheries responses to dams based on functional relationships may be transferable across biogeographical regions.

Based on a functional perspective, here we addressed three questions: How do fishery yields respond to dams? To what extent have dams impacted the composition of fisheries' yields? And, how do impacts, if any, affect fishery value and fishing-based income? Our study focuses on riverine fisheries of the floodplain of the Madeira River in the Brazilian Amazon. People living in riverine areas of the Amazon depend on fisheries to survive. In the Brazilian Amazon, fish consumption is high: it averages 67 kg/year per capita, a rate that is about four times above the world average (Isaac & Almeida, 2011). In the Madeira River, two large hydropower projects, Santo Antônio and Jirau (Figure 1) with production capacities of 3,568 and 3,750 MW were completed in November 2011 and September of 2012, respectively (Cella-Ribeiro et al., 2017). Although the dams were designed as run-of-the-river, their construction expanded flooded area by 78% (576 km^2), submerging significant areas of riparian forests (Cochrane et al., 2017). The

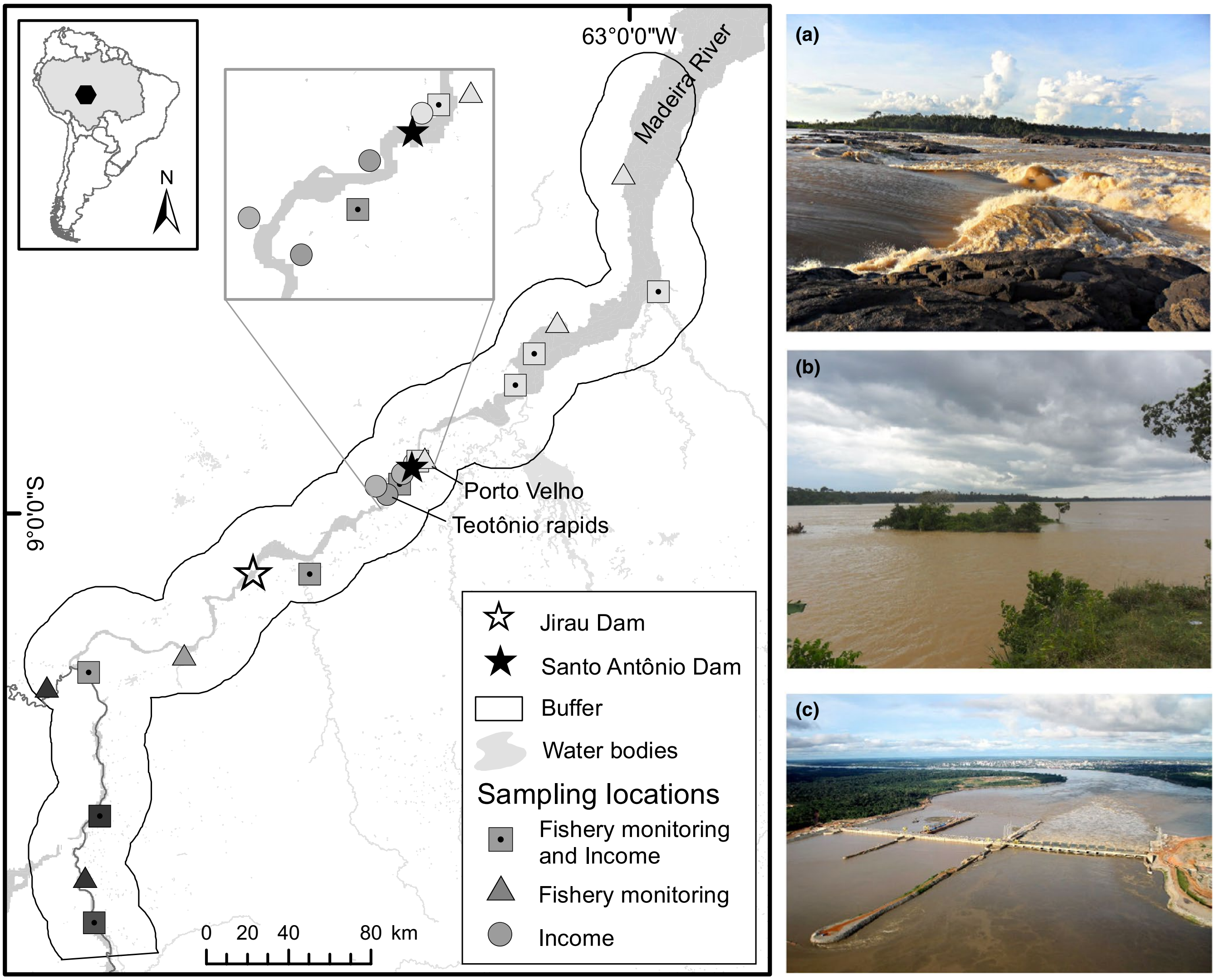

FIGURE 1 Study area in the floodplain of the Madeira River in the Brazilian Amazon, showing sampling and dams locations. The different symbols indicate locations where either, or both, fishery data (fishery monitoring) and fishing income (income) were collected. The buffer area where land cover was mapped is indicated. Gradients of grey, from dark to light grey, represent the sampling location in relation to the dam, or the 'zones' (upstream, reservoir and downstream, respectively). Inserts in the upper left show the location of the study area in the Amazon Basin and the surveyed communities near the Santo Antônio dam to improve visualization. Panel in the right shows photos of the same location of the river in periods pre-dam (a) Teotônio rapids (see indication in the map) and post-dam (b) when the rapids were flooded by the Santo Antônio dam (c). Photographs: Tais Melo Da Silva; Journal O observador (http://www.oobservador.com.br)

dams also altered physical–chemical conditions of the river and its tributaries (Almeida et al., 2019), led to changes in the structure of fish assemblages and caused declines in the biomass of several fish species (Cella-Ribeiro et al., 2017; Lima et al., 2020). Commercial fishing landings at two major cities (Porto Velho and Humaitá) showed signs of declines (Lima et al., 2020; Santos et al., 2018, 2020). These changes likely impact more than 50,000 people who live in riverine communities and depend on fisheries to sustain their livelihoods (Doria et al., 2018).

Here, we tested the hypothesis that fish yields of riverine communities (capture per unit effort [CPUE]) in the Madeira River declined in the post-dam period possibly due to declines in catches of species with traits that convey vulnerability to the conditions of the river after the impoundment. Because many vulnerable species are large, long-lived species, including migratory fishes and apex predators (e.g. *Brachyplatystoma* spp.), they contribute greatly to weight in the catches. We further tested the hypothesis that the functional composition of fishery yields was related to environmental data associated with the dams. Finally, we hypothesized that the monetary value of the fishery and fishing-based income of the studied communities declined after the dams. We expected that the functional composition in catches would be associated with periods pre- and post-dam. We also expected to observe declines in multispecies CPUE and more prominent declines in the CPUE of vulnerable functional groups after dams. That, in turn, would result in declines in fishery monetary value and in fishing-based income of the riverine communities. Our findings reveal the potential vulnerability of fish yields, their functional traits and monetary value to river impoundment and, thus, can provide insights on the likely impacts of dams on fisheries across geographical regions.

2 | MATERIALS AND METHODS

2.1 | Study area and data collection

The study was conducted in the floodplain of the Madeira River, one of the largest tributaries to the Amazon River, in Rondônia State, Brazil (Figure 1). The annual river flood pulse is monomodal and varied on average 9.4 m (±4.3 m) over the study period as measured at Porto Velho's gauging station (ANA, 2020). The study area covers a 300 km stretch of the river with distinct characteristics in its upstream and downstream portions. Upstream from Porto Velho up to Guajara-Mirim, the river has a series of rapids and waterfalls, several of which have been flooded by the hydropower dams Santo Antônio and Jirau (Figure 1). Downstream from Porto Velho, the river flows freely through a deep channel with a narrow floodplain until it reaches the Amazon River (Doria et al., 2018). This ecosystem supports high fish diversity, containing at least 1,057 identified species (Queiroz et al., 2013). Fish yields comprise 51 fish taxa groups (a single species, or a variety of species that usually have similar morphologic aspects) and are commonly classified in the region by unique names (e.g. jaraquis, *Semaprochilodus* spp.; see Table S1). From these taxa groups, about 32 that dominate the catches were included in this study (Table S1).

2.1.1 | Fishery data

The fishery data were collected by a monitoring programme coordinated by the Ichthyology and Fisheries Laboratory of the Federal University of Rondônia that included 17 locations from November 2003 to February 2005, and again from April 2008 to November 2013 (Figure 1; Table S2). This dataset consists of standardized interviews conducted with fishers on a daily basis after their return from fishing trips. Data from before closure of the dam, November 2003 to November 2011, represented pre-dam period and data from after closure of the dams, December 2011–2013, represented post-dam construction, following Cella-Ribeiro et al. (2017). Data for years 2006 and 2007 were excluded due to data limitations. The data recorded included yield (total kg/fishing trip), taxon (common names of species, or of species group, Table 1) and effort (fishers/day) of fishing trips as well as market value (price/kg) of each taxa caught in each fishing trip that took place in each location during the monitoring period. The analysed dataset included 27,689 fishing trips of the main fishery type in the region, which is multispecies and multi-gear performed in the river. This fishery is conducted by fishers mainly in motorized boats and using a variety of gears, including gillnets, long lines, hook-and-line and cast nets in combination. We calculated catch-per-unit effort (CPUE) for every month (CPUE = monthly yields of fish divided by monthly fishing effort; Petrere et al., 2010) for all taxa together (multispecies) and for each taxa group and period (pre- and post-dam).

2.1.2 | Functional traits data

We classified or quantified species traits that have been shown to confer sensitivity of species to hydrologic and other environmental disturbance (Arantes, Fitzgerald, et al., 2019; Arantes, Winemiller, et al., 2019; Table 1; Table S1). We classified species into three functional groups based on life history defined by consistent patterns of trait intercorrelations, particularly, those related to reproduction (e.g. size at maturation, parental investment per individual offspring): equilibrium, intermediate and periodic strategists following Winemiller (1989) and Röpke et al. (2017) (Table 1). We also classified taxa according to four migratory strategies (i.e. sedentary, local, regional and long-distance migrators) that are often related to reproduction and/or feeding ecology and influenced by environmental conditions of habitats in the riverscape following Arantes et al. (2018) and Arantes, Winemiller, et al. (2019). We then measured morphological traits related to degree of body compression and eye position, which are associated with swimming performance and vertical position within the water column during foraging and represent phenotypes that influence fitness along environmental gradients following Gatz (1981) and Winemiller (1991) (Table 1; Table S1). These measurements were taken from 3 to 5 specimens (adult size class) from each taxon obtained from the museum of the Ichthyology and Fisheries Laboratory from the Federal University of Rondônia. Finally, we used two indicators of a taxon's economic value: market value data for each taxon from the fishery data described above (average market value considering its value in all fishing trips) and taxon maximum size (total length-TL, from the FishBase database www.fishbase.org; Froese & Pauly, 2016) as fish length tends to be related to its economic value (Welcomme, 1999). Pearson correlation tests showed no multicollinearity among traits.

2.1.3 | Environmental data

Water-level data were obtained from gauges of the Brazilian water agency (Agência Nacional de Águas ANA, http://www.snirh.gov.br/hidroweb). Gauges were selected according to their proximity to the fishery monitoring locations. Obtained data were aggregated at a monthly scale to derive a 'seasonal hydrology' indicator for the study area. We used land cover data from the European Space Agency Climate Change Initiative's Land Cover project (ESA-CCI; http://maps.elie.ucl.ac.be/CCI/) as described in Chaudhari et al. (2019). The data comprised an annual time series of land cover mapped at a 300m spatial resolution based on combinations of map from several remote sensing instruments. The classification follows the LULC classes defined by the UN Land Cover Classification System (LCCS). Based on these classes, we calculated annual areas of forest cover, urbanization and flooding (flooded area) at two scales: the floodplain

TABLE 1 Functional traits and indicators of economic value classification or quantification. Trait descriptions are adapted from Arantes, Winemiller, et al. (2019). Number of taxa are shown in parenthesis for categorical traits ('Migratory behaviours' and 'Life-history strategies'). Traits related to habitat-use strategies and indicators of economic value are quantitative and specific to each taxon

Functional groups/traits		Functional traits description
Migratory behaviours	Sedentary (5)	Resident species that spend their entire life cycles within floodplain habitats eventually performing short-distance movements. Sedentary species were small-bodied species, or had territorial behaviour, or are known to be strongly associated with substrates or complex structures (e.g. tree branches and aquatic vegetation), or pelagic habitats
	Local migrators (18)	Diverse group of fishes that migrate laterally from floodplain lakes or river channels onto flooded floodplain habitats following closely the dynamic 'pulsing' of water levels
	Regional migrators (8)	Species that migrate onto flooded floodplain habitats during high waters, but also conduct longitudinal migrations (often hundreds of kilometres) along river channels to spawn, particularly during falling waters
	Long-distance migrators (4)	Species that migrate thousands of kilometres along river channels, though their juveniles often inhabit floodplain habitats
Life-history strategies	Equilibrium (4)	Moderate to long generation time, variable body size, low batch fecundity, large egg size and high investment per offspring (e.g. parental care), high juvenile survivorship
	Intermediate (5)	Batch fecundity between 1,000 and 9,000, relatively large oocytes, and intermediate development of parental care. Intermediated strategy within the continuum triangle of life history represented by three end-points (periodic–equilibrium–opportunistic, Winemiller, 1989), many of which have generalist habits
	Periodic (26)	Long generation time, large body size, high batch fecundity, low investment per offspring (e.g. no parental care), low juvenile survivorship with large interannual and spatial variation in recruitment, usually perform migration
Habitat-use strategies	Relative body depth, or degree of lateral compression (BC)	Body height divided by SL. Higher ratios indicate the species has a laterally compressed body, indicating pelagic habitat, manoeuvrable capacity and lower dispersal ability. Lower ratios are related with dorsoventrally flattened bodies that are typical of rheophilic/ rapids-dwelling and benthic species
	Relative eye position (EP)	Distance from the eye to the ventral head margin divided by head depth. Higher ratios indicate laterally positioned eyes typical of species with pelagic habitat. Lower ratios indicate dorsally located eyes that are typical of rheophilic/Rapids-dwelling and benthic species
Economic value	Total length (TL)	Total length values for each taxon were extracted from FishBase database
	Market value (MV)	Determined based on market prices (US$) of each taxon obtained from the fishery monitoring system (see Section 2.1.1)

(locally called 'várzea') and a 20 km buffer to each side of the river. This buffer size was shown to encompass the expansion of the reservoir (Cochrane et al., 2017). We used Pearson correlation tests to evaluate collinearity among land cover variables. Flooded area was negatively correlated (−0.97) with forest cover and positively correlated with urban areas (0.94). These correlations were expected because during and after the construction of the dams, forests were submerged (see Section 1 and Cochrane et al., 2017), and the population and urbanization have increased substantially. To avoid data multicollinearity and assure visualization of results in biplots, we used flooded area and excluded forest and urban areas from the analyses.

2.1.4 | Income data

We assessed fishing-based income through interviews with 711 fishers from 13 communities (average of 54.7 fishers per community) in periods pre- (year 2009) and post-dam (years 2017, 2018 and 2019) construction (Figure 1; Table S2). These interviews included a question for fishers to estimate their average monthly fishing income. Incomes were corrected based on inflation rates from the National Index of Consumer Prices of Brazil (IPCA).

This study collected data during fishery activities conducted by local fishers, as such, it did not require approval from an animal ethics committee. However, all necessary sampling protocols were followed, and a collection permit was granted by the 'Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis'—IBAMA (the Brazilian Environmental Federal Agency) to the Ichthyology and Fisheries Laboratory of the Federal University of Rondônia (approval number 12759-2).

2.2 | Data analyses

We used linear mixed-effect models to explore possible differences in multispecies CPUE and fishing-based income between pre- and post-dams periods. We performed log (natural logarithm) and square root transformation of the response variables, CPUE and fishing-based income, respectively, to meet normality and homoscedasticity assumptions and considered the monitoring location in relation to the dam (upstream, reservoir, downstream, herein three different 'zones') as a random effect in the analyses. Zones were included as a random effect to account for zone-specific variation in the different periods.

We used partial RLQ analyses (Dolédec et al., 1996; Wesuls et al., 2012) to investigate possible associations of species and functional traits in the composition of fishery yields with environmental data related to the implementation of the dams. RLQs were used encompassing environmental data in two different scales of land cover mapping (buffer and floodplain, as described above). RLQ is an extension of co-inertia analysis that searches for a combination of traits and environmental variables of maximal co-variance, which is weighted by the abundances of species, in our case CPUE of each fish taxon. This multivariate analysis involves the ordinations of three data matrices: environmental data (seasonal hydrology and flooded area at buffer or floodplain scales, and the pre- or post-dam periods; R table), CPUE of each taxon (L table), species trait attributes (Q table). Tables R and Q were submitted to Hill–Smith analysis (Hill & Smith, 1976). Table L was submitted to correspondence analysis (CA). Prior to this analysis, we applied a Hellinger transformation and excluded rare taxa which have insignificant contributions to yields. These rare taxa were those contributing to <0.5% of the total CPUE and occurring in only 0.003%–0.62% of the fishing trips. In the partial RLQ, we used 'zone' as a covariable in order to control for the effects of spatial variability on the traits–environment relationship (Wesuls et al., 2012). The co-correlation between the three tables (R, L and Q) was summarized into major correspondence axes. Permutation (999) tests were used to evaluate the significance of the traits–environment relationships. In the RLQ biplots, we examined the relative position of taxa along the first two axes. We then performed a trait-based clustering of species to investigate how species cluster together in this multi-dimensional space following Kleyer et al. (2012). Species and traits were clustered via Ward's hierarchical clustering and optimal number of groups determined based on Calinski–Harabasz stopping criterion. Based on these analyses, we identified trait syndromes (herein 'functional clusters') related to environmental data associated with pre- and post-dam construction. Because results for the two scales of land cover mapping (buffer and floodplain) were consistent, we only present the buffer scale results (but see result for the floodplain scale in Supporting Information, Figure S2).

We calculated CPUE of each of the clusters and explored possible trends between pre- and post-dam periods. Finally, we used information on the taxon market value that was registered for each year through the monitoring programme (see 'Section 2.1.1' above) to calculate a proxy of an average 'monetary value' of each cluster over periods pre- and post-dam (i.e. CPUEs of each taxon multiplied by its market value; the results were averaged out by all taxon in each functional cluster).

Analyses were performed in R v.4.0.0 (R Core Team, 2020). RLQ and clustering were computed using ADE4 package (Dray & Dufour, 2007) and an adapted script from Kleyer et al. (2012). Linear mixed models were fitted using LME4 package (Bates et al., 2015).

3 | RESULTS

Catch per unit of effort declined, on average, 37% in the post-dam period (Figure 2a; coefficients estimates, intercept = 2.36 and period = 0.33; $t = 27.9$; $p < 0.001$). Likewise, the fishing income of the riverine communities declined, on average, 30% after the construction of dams (Figure 2b, coefficients estimates, intercept = 27.06 and period = 6.46; $t = 5.1$; $p < 0.001$).

Species traits were significantly associated with environmental data (RLQ analysis; Figure 3; Figures S1 and S2; $p = 0.005$). RLQ biplots and clustering showed six functional clusters associated with the environmental data. One of these groups (cluster A) was dominated by large-bodied, long-distance migratory species and periodic life-history strategists (Figures 3a,b and 4; Figure S1). This cluster was positively associated with the pre-dam period, while negatively associated with flooded area and the post-dam period. This cluster was one of greatest economic importance as it was related with largest sizes and higher market values. In the opposite extreme, cluster D, that comprised intermediate life-history strategists and local migrators with higher degree of lateral compression and lower market value, was positively associated with flooded area and the post-dam period (Figures 3a,b and 4). Cluster B comprised mostly periodic strategists that perform local migrations, with only one equilibrium strategist species (*Arapaima* spp.). In this cluster, largest body sized

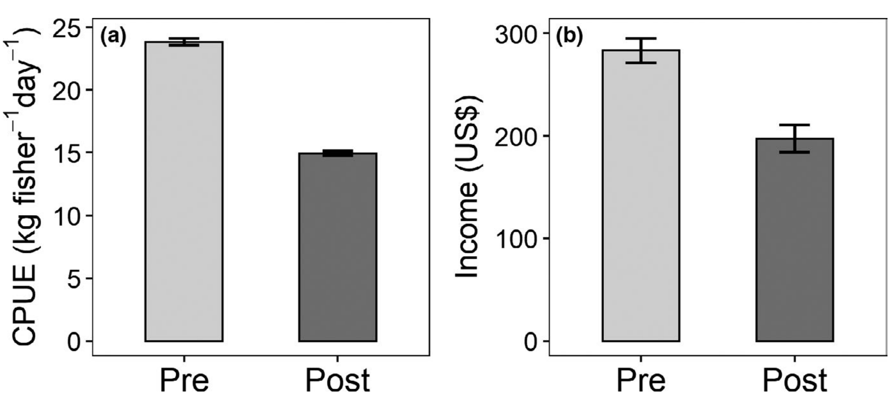

FIGURE 2 (a) Mean (+*SE*) of multispecies catch per unit of effort (CPUE) and (b) monthly fishing-based income of the interviewed fishers in riverine communities over pre- and post-dam periods (based on this data, we estimated the mean decline in the annual fishing-based income per fisher to be US$1,269.36, as described in Section 4, and see Table S2)

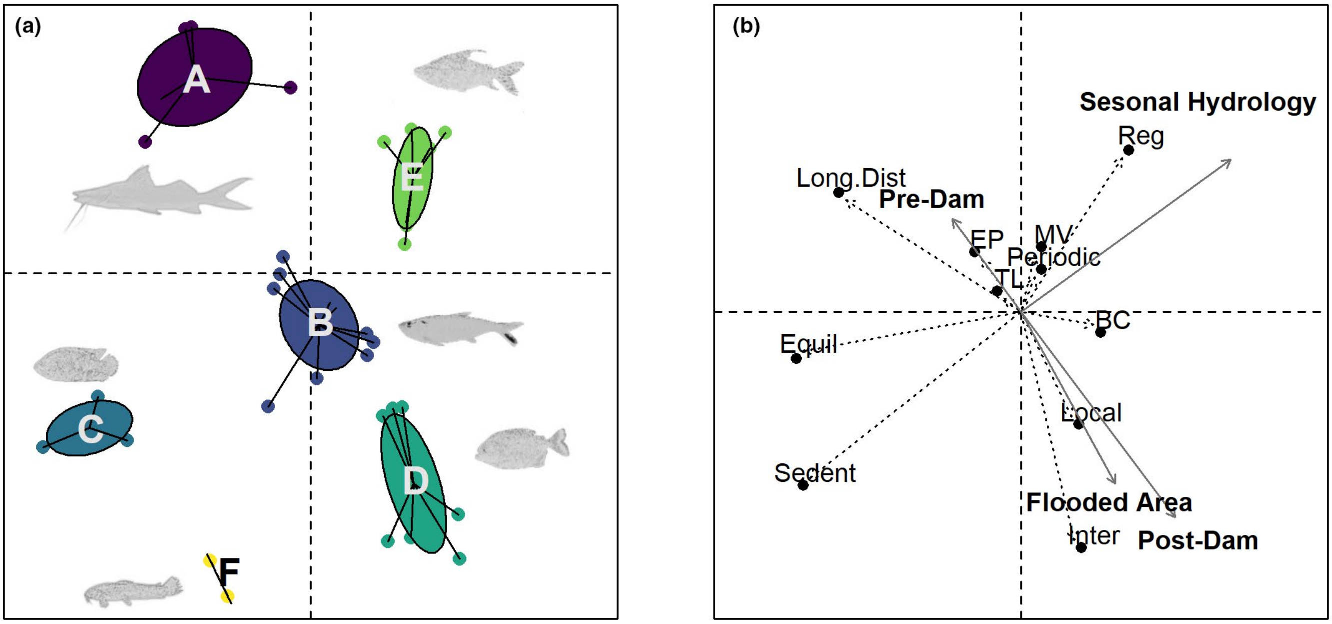

FIGURE 3 RLQ analysis of the relationships between taxa traits and environmental variables measured at the buffer scale (see Figure S2 for floodplain scale results). First and second axes summarized 68.8% and 30.6% of the co-inertia (i.e. strength of the association between traits and environmental variables), respectively. (a) RLQ biplots showing the position of each species (dots), and its combination of traits, along each of the three environmental data gradients (seasonal hydrology, flooded area, and the pre- and post-dam periods). By examining the common traits shared by species under different environmental conditions, we identified six trait syndromes (shown in different colours) associated with the environmental data. Drawings represent examples of fishes that are characteristic of each cluster. (b) RLQ biplots showing environmental gradients and species traits; BC, body compression; EP, relative eye position; Equil, equilibrium; Inter, intermediary; MV, market value; Reg, regional; Sedent, sedentary; TL, total length

taxa (average TL = 150.2 cm; Figure 4), including some benthic species (e.g. *Pinirampus pirinampu*), were positively related with the pre-dam period, while smallest sized taxa (average TL = 48.5 cm) that have compressed bodies were associated with the bottom right quadrant, which was positively related to flooded area and post-dam period. Cluster E, positively associated with seasonal hydrology, was comprised of species of high market value with periodic strategies that perform regional migrations. Clusters C and F were comprised of sedentary and equilibrium life-history strategists, which appeared to be negatively related with seasonal hydrology.

The mean CPUE and the indicator of monetary value of the functional clusters declined, on average 23.3% and 21.7%, respectively, in the post-dam period (Table 2; Figures S3 and S4). The only exception was cluster B for which monetary value showed a slight increase (1.6%).

4 | DISCUSSION

Our results indicate that the implementation of the dams and associated changes in environmental conditions affected the functional composition of yields and reduced catch-per-unit of effort in the Madeira River. Whereas catches of all functional clusters declined after the dams, some clusters appeared to be particularly vulnerable. These clusters comprised species possessing large body sizes and traits related to a periodic life-history strategy, either with long-distance or regional migratory behaviours. Because species with these traits are those of greatest economic importance, declines in their catches were accompanied by greater losses in their indicators of monetary value (compared to small-bodied taxa) and losses of fishing income of riverine communities. These impacts occurred only a few years after the construction of the dams, which raises concerns about the possible more drastic changes that are likely to occur in following years. Continued acquisition and accessibility of fishery data will be essential, thus, particularly, to assess long-term dam impacts on the large-bodied/long-lived fishes which can involve notable time-lags. Our results support the view that trait-based frameworks can aid in understating of the effects of environmental changes, in particular those caused by dams construction, on organisms and their contribution to provision of key services such as fishery yields and incomes they sustain (Luck et al., 2012).

4.1 | Multispecies yields and functional composition of yield responses to dams

Our results showing declines in mean multispecies fishery yields per unit effort are consistent with previous studies finding reductions of 30%–50% in catches after dam construction on tropical river basins (Okada et al., 2005; Ribeiro et al., 1995; Santos et al., 2018). Although in some river basins, expansions in aquatic habitat and pulse of production in newly flooded areas increased fishery production (Okada

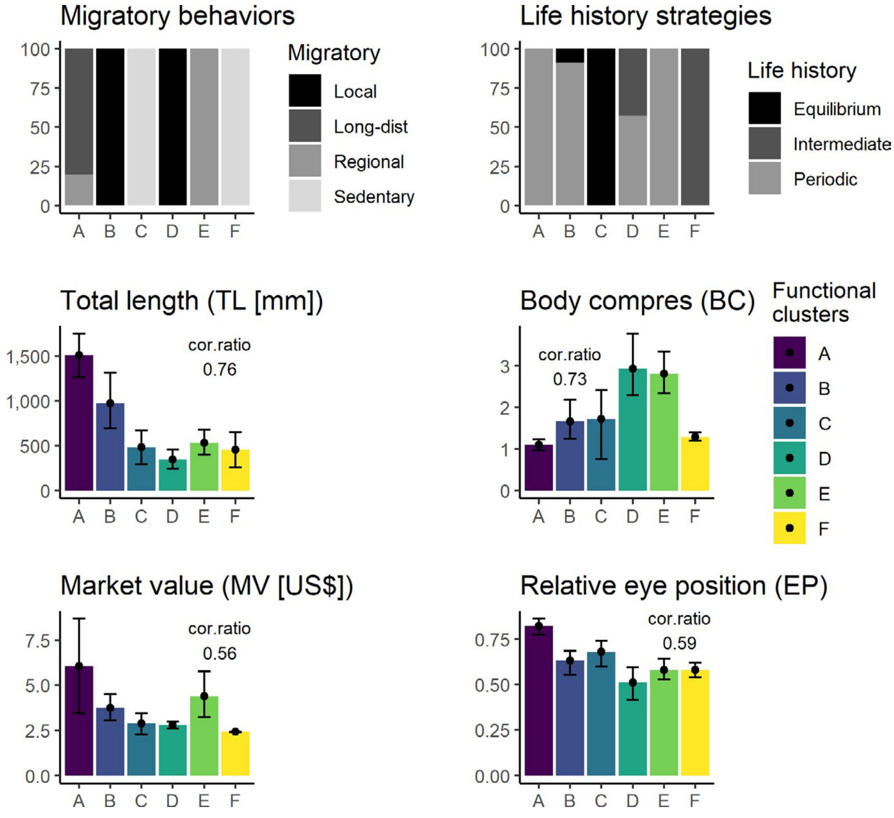

FIGURE 4 Plots for categorical traits represent the frequency of occurrence of each trait (migratory and life-history categories) in each functional cluster (see Figure 3). Plots for continuous traits represent the distribution of trait attributes (mean and standard deviation) in each cluster

TABLE 2 Mean (±*SE*) catch-per-unit effort (CPUE) and indicator of monetary value of each functional cluster over periods pre- and post-dam. Functional clusters were determined based on the RLQ analysis of the relationships between taxa traits and environmental variables (see Figure 3). Note declines of ~27%, or of US$9.93 in the monetary value of the cluster A, as described in Section 4. Negative percent changes represent declines, while the positive value represents increase from the pre- to the post-dam period

Functional cluster	CPUE (kg fisher^{-1} day^{-1})					Monetary value (US$)				
	Pre		Post			Pre		Post		
	Mean	*SE*	Mean	*SE*	Change (%)	Mean	*SE*	Mean	*SE*	Change (%)
A	4.76	0.62	3.54	0.36	−25.52	36.67	5.91	26.74	3.06	−27.08
B	5.02	0.52	4.62	0.63	−7.95	19.73	2.07	20.05	3.57	1.64
C	4.16	0.46	3.40	0.94	−18.26	11.94	1.20	9.49	2.37	−20.51
D	3.44	0.28	2.29	0.17	−33.54	9.75	0.78	6.45	0.48	−33.80
E	5.24	0.46	3.37	0.28	−35.74	22.92	2.15	15.59	1.60	−31.99
F	3.19	0.62	2.60	0.40	−18.55	7.68	1.50	6.25	0.95	−18.61

et al., 2005), our analyses indicate average declines in multispecies CPUE of 1.6 times in the first three years after completion of the dams. This decline appears to be related to decreases in yields of large-bodied species with high market value (e.g. clusters A and E) in association with an apparent lack of compensation in catches of smaller-bodied, lentic-adapted species (cluster C), as well as in catches of intermediate strategists (cluster D) that have relatively lower market value (Table 2).

Differential responses of species in fishery yields to the environmental data and dams-periods are consistent with the view that organism's responses to disturbance are driven by their functional traits (Mouillot et al., 2013). The strongest association of large, long-lived migratory fishes (cluster A) with the pre-dam period and declines in their catches in post-dam period is in line with previous studies demonstrating higher vulnerability of these species' group (Arantes, Fitzgerald, et al., 2019; Lima et al., 2020). Several large migratory species such as the Amazonian catfishes (e.g. *Brachyplatystoma rousseauxii*, *B. platynemum*) require connectivity across river basins to complete their life cycle (Duponchelle et al., 2016; Zhong & Power, 1996). Accordingly, barrier dams have disrupted the movement of these species between downstream nursery and upstream breeding grounds (Duponchelle et al., 2016). Because convergent functional traits are revealed for fish in catches of different tropical river basins (Winemiller et al., 2015), these results provide insights on likely responses of fish yields to dams across geographical regions. For example, traits we found to be vulnerable, including medium–large body size and long generation time, typical of periodic and migratory species, are found not only in the Amazon (e.g. *Brachyplatystoma* spp.), but also in many other Neotropical (e.g. *Pseudoplatystoma* spp., *Salminus* spp. in South America rivers) and Asian rivers (e.g. *Pangasius* in the Mekong River, and in the Yangtze River, sturgeons as well as the paddlefish which is now considered to be extinct from this river; Huang & Wang, 2018; Kang et al., 2009; Zhang et al., 2020).

Regional migrators (cluster E) were primarily related to seasonal hydrology, consistent with findings showing they depend on flow pulses to trigger their movements, reproduction and chances of recruitment (Lima et al., 2017). In addition, this latter cluster's CPUE declined (average 36%) following the dam construction. The effects of dams on this cluster probably have been driven not only by changes in hydrological patterns (Almeida et al., 2020), but also by other factors that might include the blockage of species attempts to migrate longitudinally to spawn. More work is needed to fully understand the mechanisms driving this functional cluster's response to dams that usually affect the flow patterns in floodplain rivers.

Our results revealed the functional clusters associated with expanded flooded area and the post-dam period, including species considered to be often associated with lentic habitats, or even habitat generalists (e.g. *Pygocentrus nattereri*, *Serrassalmus* spp.) and planktivores (*Hypophthalmus* spp.; in cluster D), or pelagic piscivores (e.g. *Plagioscion squamosissimus* and *Pellona* spp., in cluster B). These results are consistent with other findings showing these functional groups to take advantage of expanded open water habitats and increased productivity in reservoirs (Turgeon et al., 2016). However, unexpected declines in CPUE for these clusters (i.e. 33% and 7.8% declines in post-dam period, for clusters D and B, respectively) suggest that even stocks with traits known to be tolerant to changes in environmental conditions after dam construction have been negatively affected. Potential shifts in fishing pressure, from targeting stocks of high economic value to more resilient fish populations, may explain declines in these groups' catches as observed in other regions (e.g. Paraná River; Hoeinghaus et al., 2009). In addition, frequently, species with traits associated with low dispersal ability either equilibrium or intermediate strategists (i.e. traits of species in clusters C and F, e.g. *Cichla* spp.) dominate reservoirs (Agostinho et al., 2016; Oliveira et al., 2018), but in our study they were not clearly associated with either of the study periods. Yet average CPUE in these clusters slightly declined after the completion of the dams (Table 2). Stronger patterns might be revealed by not only expanding time series of data, but also addressing possible changes in fishing strategies that may have developed to compensate for reduced value of various stocks.

4.2 | Monetary and fishing income losses

Our results demonstrating that the fishery value has been negatively impacted by the constructions of the dams support the idea that environmental and economic costs of these projects usually are underestimated (Ansar et al., 2014; Callegari et al., 2018). The comparisons of monetary values of functional clusters among periods suggest average economic losses in fishery yields of about 22% after construction of dams. This result and stronger responses of larger fishes that have higher dispersal capacity and greater economic importance are consistent with previous findings suggesting that the effects of dams on migratory fishes reduce the overall economic value of fisheries (Hoeinghaus et al., 2009). Obviously, values for the fishery quantified within this study represent catches and market tendencies at the time of the study. Processes such as temporal trends in prices are likely to affect these values, as shown by Lima et al. (2020) who found increased price per kg of exploited fish species over time. Performing an economic valuation that encompasses long-term data and diverse economic use and non-use values (e.g. Loomis et al., 2000) is beyond of the scope of this paper, but would be beneficial in the future to improve quantification of the costs of hydropower development in this region and beyond.

Similarly to studies showing hydroelectric projects leading to falling income from fisheries in the long run (e.g. Baird et al., 2015; Manatunge et al., 2009), our results suggest that the dams have negatively affected fishing-based income of fishers from riverine communities in the Madeira River. Although causal inferences must further be tested, significant declines in fishing earnings appear to be related to the shifts in functional composition of yields as well as to declines in yields per unit of effort and related monetary value of the fishery. The evident declines in fishing income of studied communities support the view that hydropower projects impact the livelihoods of people living not only upstream and around the reservoir, but also downstream from dams (Baird et al., 2015). A question that remains open, however, is whether and how compensation measures, which often fail to account for fisheries economic losses (Moran et al., 2018), can adequately address impacts to livelihoods of riverine communities in the region.

5 | CONSERVATION AND MANAGEMENT IMPLICATIONS

Our results indicate shifts in fisheries composition and declines in yields, and in its value and income for local communities after the dam construction. This implies that hydropower expansion will cause detrimental effects for fisheries and the livelihoods they sustain. Consistent with other studies based on synthesis of the literature (e.g. Agostinho et al., 2016; Arantes, Fitzgerald, et al., 2019), or on evaluations of fish assemblages' responses (Oliveira et al., 2018), our study empirically demonstrates that the more vulnerable traits in fisheries yields are those associated with a periodic life-history strategy, particularly, large, long-lived, migratory and high market value fishes. Conversely, fishes with traits related to high degree of body compression, typical of pelagic species, as well as traits associated with low dispersion capacity and lower market values appeared to be more tolerant, although their yields also declined after the implementation of the dams. In the Amazon and other tropical rivers, hundreds of large dams are under construction or being planned (Winemiller et al., 2016). In these rivers, thousands of small dams project also pose emerging threats to connectivity (Couto et al., 2021). Despite that the rivers in our study domain are key routes of migration to fish species, 32 dams are either in operation or under construction, and at least 18 others are planned to be completed by 2030 (e.g. in the Machado, Tabajara, and Esperanza rivers; Anderson et al., 2018). The species groups likely to be most affected by the cumulative effects of these existing and planned dams are those we showed to be widely vulnerable and to have declined in yields after the construction of the Santo Antônio and Jirau dams.

Therefore, to avoid irreversible socio-environmental consequences of these projects, there is an urgent need to re-evaluate plans of hydropower expansion. The demand for energy will continue to grow, but other lower costs/lower impacts sources of renewable energy such as solar power (e.g. photovoltaics) and in-stream turbines based on water kinetic energy have been shown to be a viable alternative to large dam projects and could produce up to 67% of all the energy planned using hydropower dams (Chaudhari et al., 2021). The use of floating solar panels in existing reservoirs could also increase energy production without needing to build more large or small dams. Where dams are in operation or under construction, long-term ecological losses are likely to be enormous. Improving operational protocols of dams to reduce alterations in seasonal and daily flow dynamics is essential to minimize ecological changes in the river system (Almeida et al., 2020). Fish passage structures in tropical rivers have been demonstrated to not work, with <3% making it through (Pompeu et al., 2012). However, minimizing impacts will also require the development of scientifically sound research and technology to improve the functionality of these structures (Doria et al., 2019). Socio-economic impacts must also be addressed. The Brazilian Federal Environmental Agency (IBAMA) responsible for hydropower licensing and regulation, states that any impact on fisheries must be mitigated and/or compensated to 'assure fishing sustainability and proper income for fishers' (Technical Regulation N. 060/2008 (IBAMA, 2008)). In the Madeira River, a few compensation measures including the implementation of a small fish farm in a community (i.e. Nova Teotônio) and financial returns to resettled households were put in place. However, our results showing declines in the overall fishery value and fishing-based income indicate that these measures have not adequately compensated the actual impacts. Our results showing declines of about US$1,200.00 in the annual fishing income per capita (Figure 2; Table S2) and of up to US$9 per kilogram of fish caught (see declines in the value of fish functional cluster A, Table 2) after the construction of the dams, provide a first basis for balancing compensation and losses in fishery revenue. Further research is needed to strengthen these estimates and to understand broader future impacts not only as a result of dams, but due to increasing pressures the region faces from mining, deforestation, and waterways and road building. Maintaining fishery yields in the region requires conserving flow pulses and free-flowing rivers and tributaries critical for completing life cycles of vulnerable fish species, particularly, those of greatest economic importance.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHORS' CONTRIBUTIONS

C.C.A., J.L., M.D.d.S.P., J.D.-G., E.F.M. and C.R.C.D. conceived the research; C.C.A., J.L., M.D.d.S.P., S.C. and Y.P. analysed the data; C.C.A. and J.L. took the lead in writing the manuscript with contributions and revisions of all authors.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.9p8cz8whj (Arantes et al., 2021) and Table S1.

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