



Early impacts of the largest Amazonian hydropower project on fish communities

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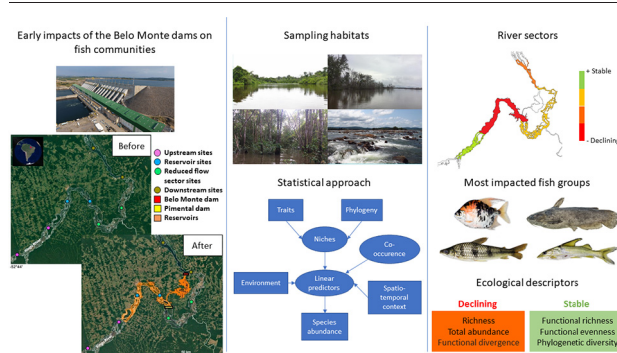
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HIGHLIGHTS

- Richness declined ~12% in lentic and ~16% in lotic habitats after dams' operation.
- Reservoir (~24%) and downstream (~29%) sectors had the steepest richness declines.
- Serrasalminae, Anostomidae, Auchenipteridae and Pimelodidae were the most impacted.
- Dams' impacts were related with changes in fish body size, shape, and trophic level.
- Changes in functional diversity were subtle with a reduction in functional divergence.

GRAPHICAL ABSTRACT



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ABSTRACT

Hydropower is a threat to freshwater fishes. Despite a recent boom in dam construction, few studies have assessed their impact on mega-diverse tropical rivers. Using a *before-after* study design, we investigated the early impacts of the Belo Monte hydroelectric complex, the third-largest hydropower project in the world, on fishes of the Xingu River, a major clear-water tributary of the lower Amazon. We explored impacts across different river sectors (upstream, reservoir, reduced flow sector, and downstream) and spatial scales (individual sectors vs. all sectors combined) using joint species distribution models and different facets of diversity (taxonomic, functional, and phylogenetic). After 5 years of the Belo Monte operation, species richness declined ~12% in lentic and ~16% in lotic environments. Changes in abundance were of less magnitude (<4%). Effects were particularly negative for species of the families Serrasalminae (mainly pacu), Anostomidae (headstanders), Auchenipteridae, and Pimelodidae (catfishes), whereas no taxonomic group consistently increased in richness or abundance. The reservoir and downstream sectors were the most impacted, with declines of ~24–29% in fish species richness, overall reductions in fish body size and trophic level, and a change in average body shape. Richness and abundance also declined in the reduced river flow, and changes in size, shape, and position of fins were observed. Relatively minor changes were found in the upstream sector. Variation in functional and phylogenetic diversity following river impoundment was subtle; however, across sectors, we found a reduction in functional divergence, indicating a decline in the abundance of species located near the extremities of community functional space. This may be the first sign of an environmental filtering process reducing functional diversity in the

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region. Greater changes in flow and habitats are expected as hydropower operations ramp up, and continued monitoring is warranted to understand the full scope and magnitude of ecological impacts.

1. Introduction

Hydropower contributes to about 70% of all renewable energy generation (24% of global electricity production) and is still among the most reliable and efficient renewable technologies (International Hydropower Association, 2018; Chala et al., 2019; Mulligan et al., 2020). There remains considerable potential for hydropower development, with only 22% of the technically feasible hydropower potential currently utilized (Zarfl et al., 2015). This hydropower potential, however, is largely concentrated in the Global South (e.g., Southeast Asia, South America, and Africa) where mega-dams are being planned and constructed to generate energy primarily for urban populations and industries (Moran et al., 2018). Nonetheless, mega-dam projects are controversial with arguments that socio-ecological impacts and implementation costs have been greatly underestimated (Ansar et al., 2014). A major environmental concern is the recent boom of large hydropower projects in the world's most biodiverse river basins: the Amazon, Congo, and Mekong (Winemiller et al., 2016).

Tropical rivers harbor the world's greatest diversity of freshwater fishes, with many species still undescribed, but hydropower dams' expansions pose a major threat (Arthington et al., 2016). Dams obstruct fish migration corridors (Liermann et al., 2012) and attenuate seasonal flood pulses that are essential for lateral connectivity that provides fish with access to crucial foraging and nursery habitats (Goulding, 1980; Timpe and Kaplan, 2017). Dams reduce fluvial habitat heterogeneity (Schmutz and Moog, 2018) and trap sediments (and nutrients), which affects river productivity and water quality within the reservoir and downstream reaches (Maavara et al., 2017). Dam installation contributes to deforestation when large areas are cleared to build roads and associated infrastructure (Laurance et al., 2009). Finally, reservoirs created by dams facilitate the establishment of exotic species (Havel et al., 2005; Johnson et al., 2008; Caiola et al., 2014).

Dam impacts on fish biodiversity are not uniform across space and time. During the first several years after impoundment, aquatic primary productivity generally surges within the reservoir as labile nutrients leach from decomposing vegetation and soil organic matter. This initial trophic upsurge often leads to an increase in overall fish abundance and biomass (Agostinho et al., 2008, 2016). With time, primary and secondary production, including fish biomass, declines as nutrients are depleted, and species diversity often declines (Agostinho et al., 2008). However, recent global meta-analyses have found contrasting results regarding the impact of dams on fish abundance and diversity, with results varying from negative to positive depending on the biome and the introduction of non-native species (Liew et al., 2016; Turgeon et al., 2019).

Impacts on freshwater biodiversity tend to be more evident at locations closer to the dam. Whereas the integrity of fish community structure may persist in distant sectors of the riverscape (e.g., free-flowing tributaries and upstream reaches) (Agostinho et al., 2007), fish diversity often decreases in downstream reaches, especially in areas near the dam (Agostinho et al., 2008; Araújo et al., 2013). Within the reservoir sector, the transition from a lotic to a lentic environment imposes strong selection on fishes, resulting in a fish community that tends to be dominated by a few generalists, pre-adapted to lentic conditions (Hoeinghaus et al., 2009; Agostinho et al., 2016). Downstream to dams, fish communities are impacted by flow regulation, loss of longitudinal and lateral hydrologic connectivity, and reduced access to floodplains (Timpe and Kaplan, 2017). Despite spatial variation in the nature and degree of fish responses, to our knowledge, few studies have explicitly analyzed differential responses of fish species among river sectors with differential impacts from the dam.

Despite recognition of the impacts of dams on taxonomic diversity (Agostinho et al., 2008), and more recently on the functional and

phylogenetic structure of communities (e.g., Wang et al., 2021), investigations of multiple facets of biodiversity are rare (Arantes et al., 2019a). In some cases, functional diversity was shown to decline after impoundment, including reduced abundance or complete loss of migratory and lotic-adapted species (Oliveira et al., 2018; Montaña et al., 2020; Zhang et al., 2020). In other cases, phylogenetic diversity was found to increase due to the invasion of exotic species (Zhang et al., 2018). A comprehensive approach to understanding dams' impacts on fish communities is especially needed for highly diverse tropical rivers where responses can be complex (e.g., divergent depending on species ecology and biodiversity aspect, or non-linear) and driven by a range of interacting factors (e.g., habitats, climate, seasons, fishing pressure) (Arantes et al., 2019a; Wang et al., 2021).

Here, we investigate the early impacts of the Belo Monte hydropower operation, composed of two main dams (Pimental and Belo Monte dams; Fig. 1), on taxonomic, functional, and phylogenetic aspects of fish communities within sectors along the longitudinal fluvial gradient of the affected region. Construction of the Belo Monte dams on the Xingu River, one of the largest tributaries of the Amazon River, was completed in 2016. This clearwater river has an extensive network of channels with rocky rapids harboring more than 450 fish species, 10% of them endemic (Camargo et al., 2004; Fitzgerald et al., 2018). With an 11,233.1 MW installed capacity (Norte Energia, 2021a), Belo Monte is the largest hydroelectric project in the Amazon Basin and the third-largest in the world. Belo Monte directly affects an area of approximately 170 km, including a stretch of rapids known as the Volta Grande (Big Bend) which is considered an ecologically unique hotspot of biodiversity (Sabaj-Perez, 2015; Fitzgerald et al., 2018). Planning for Belo Monte began in 1975 to boost economic development and national energy independence (Sabaj-Perez, 2015; Hervás, 2020). Due to intense controversy regarding the economic viability and socio-ecological impacts of the project, final approval for construction was not obtained until 2011 (Sabaj-Perez, 2015; Hervás, 2020). Belo Monte was designed as a run-of-the-river hydropower system that operates without long-term water storage and relies largely on flow within the river channel to produce energy. Run-of-the-river systems have been promoted as being less environmentally damaging (Paish, 2002; BHA, 2005), but evidence to support this argument claim is scant (Abbasi and Abbasi, 2011; Anderson et al., 2015). The fish fauna of the river stretch influenced by Belo Monte has been monitored consistently since 2012 by Norte Energia SA (the concessionaire of the project), but until recently these data were not available for analysis. To date, a single study provides evidence that Belo Monte operations have negatively affected the growth and reproduction of two cichlid fishes (Mendes et al., 2021); however, no published study has investigated the impacts of Belo Monte operations on fish communities.

Our objective was to evaluate potential changes in the taxonomic, functional, and phylogenetic structure of fish communities in relation to Belo Monte operations across four river sectors (upstream, reservoir, reduced flow sector, and downstream) at two spatial scales (river sectors vs. all sectors combined) using long-term monitoring data. Specifically, we assessed potential changes in species richness, abundance, functional (functional richness [Frich], functional divergence [FDiv], functional evenness [FEve]) and phylogenetic diversity (Faith's index of phylogenetic diversity [PDI], mean phylogenetic distance [MPD], variation of pairwise distance [VPD]). Our analysis included co-variables (e.g., habitat, seasonality, climatic conditions) to control for potential confounding effects. Given that Belo Monte has been operating for the past five years, we expected moderate responses, including a small decline in community taxonomic diversity and low to moderate changes in functional and phylogenetic diversity. The strongest negative responses were expected for lotic-adapted species (e.g., inferior mouths and elongated-depressed bodies; Bower and Winemiller, 2019), such as rheophilic loricariids that inhabit rapids, and

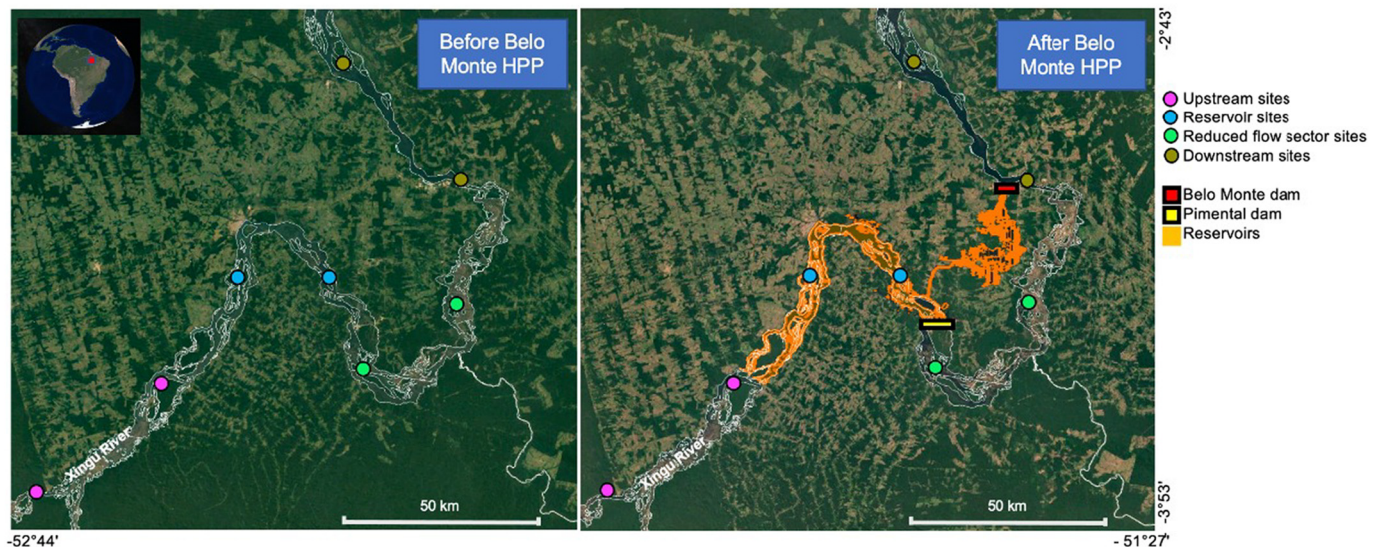


Fig. 1. Map of the study area in the Middle Xingu River Amazon basin (shown in the left upper panel). Left and right panels show the region before (12/2011) and after (04/2022) the Belo Monte hydropower project (HPP), respectively. Sampling sites and areas that were modified for hydropower are highlighted. Satellite images: Landsat/Copernicus.

fish that depend on floodplain forests, such as detritivores and frugivorous species (Goulding, 1980; Arantes et al., 2019b). We hypothesized that lentic-adapted species (e.g., deeper bodies with long dorsal and anal fins; Bower and Winemiller, 2019), such as cichlids, would increase in abundance, especially within the reservoir sector. We also expected greater changes in sectors nearest to the dams, especially with the reservoir and the Volta Grande reach downstream from the Pimental Dam where flows were projected to be reduced to a fraction of historic levels due to water diversion to the main powerhouse at the Belo Monte Dam (Fig. 1).

2. Methods and materials

2.1. Study area

The Xingu River watershed contains ancient and eroded granitic rock beds of the Brazilian Shield and, consequently, its waters have a low concentration of suspended solids and nutrients (Junk et al., 2011). The river has also a low concentration of phytoplankton and most of the autochthonous production entering the aquatic food web is from aquatic macrophytes, with major contributions from allochthonous material from the riparian zone (Camargo and Ghilardi, 2009; Andrade et al., 2019). We studied a section of 284 km along the Middle Xingu River (Fig. 1) that encompasses the area where the Pimental and Belo Monte dams were built. The climate is tropical humid with an average annual temperature of around 26 °C (Peel et al., 2007; Camargo and Ghilardi, 2009). Natural river flow varies greatly during the year (Fig. 2) with high average values (~ 8000 to $10,000 \text{ m}^3 \text{ s}^{-1}$) during the rainy season (between December and May) and low average values ($\sim 2000 \text{ m}^3 \text{ s}^{-1}$) during the dry season (between June and November) (Camargo and Ghilardi, 2009).

2.2. Fish surveys

A before-after study design was established with multi-year fish monitoring surveys in the stretch of the Xingu River influenced by the Belo Monte hydropower project. This study area was divided into four main sectors: upstream (reach above the Pimental and Belo Monte dams), reservoir (created by the Pimental Dam), sector of reduced flow (encompassing the Volta Grande), and downstream (reach below the Belo Monte Dam) (Fig. 1). This division was based on the environmental characteristics of the river and the expected impacts of Belo Monte installation and operation. In each sector, two survey sites were selected. At each site, four habitats

were sampled: lakes (water bodies located in low areas that are isolated during the dry season and that may be connected to the river via channels during the wet season), backwaters (shallow habitats near river margins with slow-flowing water, including back eddies), flooded forest (seasonal habitats formed during the wet season when river water enters floodplains), and rapids (rocky channel areas with fast-flowing water) (Fig. S1).

Surveys were conducted from 2012 to 2020 (9 years): 4 years before and 5 years after the initiation of the Belo Monte operation (Fig. 2). In lentic habitats (lakes, backwaters, and flooded forests), fish were surveyed twice each year (wet and dry season) using three sets of gillnets (Fig. S2). Each set of gillnets was composed of seven panels (each 20 m long by 2 m deep) with different mesh sizes (2, 4, 7, 10, 12, 15, and 18 cm between opposite knots). Gillnets were deployed at ~ 1700 h and retrieved at ~ 0900 h. To avoid predation of captured fish, gillnets were inspected every 2–3 h. In lotic habitats (rapids), surveys were conducted only during the dry season, and unsafe conditions of rapids with high, swift water precluded surveying during the wet season. In rapids, three areas of $5 \times 5 \text{ m}$ (25 m^2) were sampled by experienced local divers who captured benthic fishes (mainly loricariid catfishes) by hand (Fig. S2). After July 2014, the number of plots sampled increased from three to six per survey site.

Captured fishes were anesthetized with a lethal dose of clove oil, measured for total length (precision 0.1 cm), weighed (1 g), fixed in a 10% formalin solution, and transported to the laboratory (Departamento de Zoologia do Campus de Altamira da Universidade Federal do Pará) where they were preserved in ethanol (70%) and identified to the lowest taxonomic level feasible (usually species, but sometimes genus). Voucher specimens were later deposited in the Museu Paraense Emílio Goeldi and in the Laboratório de Ictiologia de Altamira.

2.3. Environmental variables

Water flow ($\text{m}^3 \text{ s}^{-1}$) was measured at stations within each sector of the Middle Xingu River during all years of our study (Fig. 2). We used the Indicators of Hydrologic Alteration (IHA; The Nature Conservancy, 2009) software to derive the following metrics from water flow data: mean monthly flow, date (in Julian format) of the maximum flow recorded in each year, annual rate of flow increase (average of all positive differences between consecutive daily values), highest flow recorded in each year (median of 7 days), lowest flow recorded in each year (median of 7 days), and length of the wet season (number of days in the year that the flow was above $8000 \text{ m}^3 \text{ s}^{-1}$).

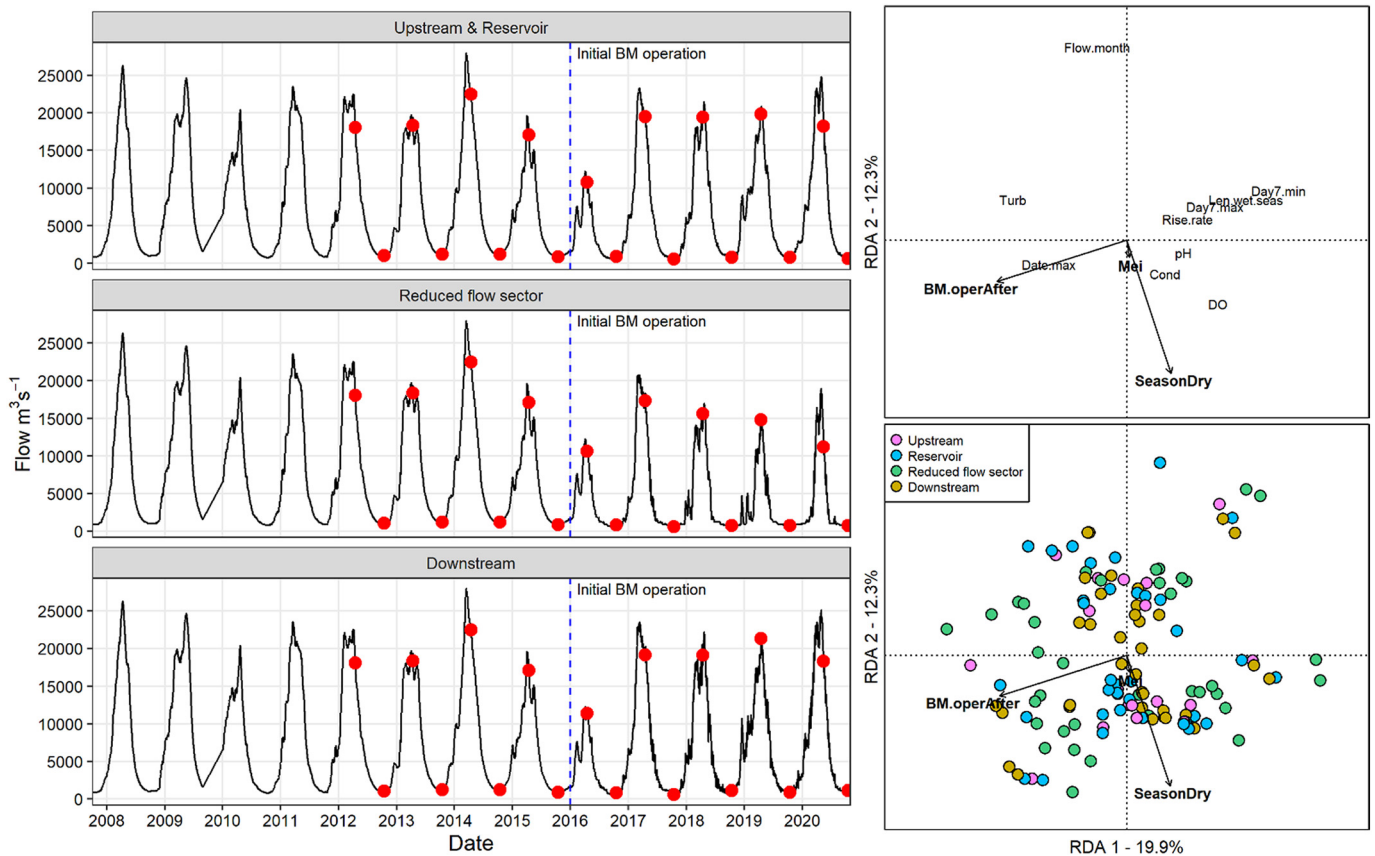


Fig. 2. Left panels show the variation in water flow over years with indications of the Belo Monte (BM) initial operation (blue dotted lines) for each river sector (upstream and reservoir, reduced flow sector, and downstream). Red dots highlight fish surveys. Upstream and reservoir sectors have essentially the same river flow and, therefore, are presented together. Right panels show the result of an exploratory RDA analysis linking the Belo Monte operation (before-after), season (wet-dry), and the Multivariate ENSO Index (MEI) to variation in hydrological and physical-chemical water parameters. Response variables were scaled to unit of variance for RDA analysis. The number of RDA axes for analysis was determined based on a scree plot that indicated disproportionate importance of the first two axes (proportion explained = 32.2%). The RDA model was significant overall ($F_{(3, 119)} = 20.74$, $P < 0.001$, permutations = 999) and the Belo Monte operation was significantly associated with the response variables ($F_{(1, 119)} = 32.91$, $P < 0.001$, permutations = 999). Date.max: Date (in Julian format) of the maximum flow recorded in the year, Rise.rate: Annual rate of flow increase (average of all positive differences between consecutive daily values); Day7.max: Highest flow recorded in the year (median of 7 days); Day7.min: Lowest flow recorded in the year (median of 7 days); Len.wet.seas: Length of the wet season (number of days in the year that the flow was above $8000 \text{ m}^3 \text{ s}^{-1}$); Flow.month: Mean monthly flow; Turb: Turbidity; Cond: Conductivity; DO: Dissolved oxygen.

The Multivariate El Niño Southern Oscillation (ENSO) Index Version 2 (herein, MEI), which is an extension of [Wolter and Timlin's \(2011\)](#) index, was obtained from NOAA's website ([NOAA, 2021](#)) and used to track seasonal and interannual variation caused by large-scale climatic patterns. Specifically, the MEI measures ENSO and was created from an empirical orthogonal function of five oceanic and atmospheric variables (outgoing longwave radiation, surface meridional winds, surface zonal winds, sea surface temperature, and sea level pressure) from the tropical Pacific (30°S – 30°N and 100°E – 70°W ; [NOAA, 2021](#)). ENSO has been shown to lead to extreme interannual changes in climate in the Amazon Basin during our study period and, therefore, is a potential confounding variable to control for in our analysis ([Jiménez-Muñoz et al., 2016](#)).

Turbidity (unt), conductivity (mS/cm), pH, and dissolved oxygen (mg/L) were obtained for each survey site and period. During each survey, water parameters were measured three times using a multiparameter YSI. These consecutive measurements were then averaged for statistical analyses. Finally, we estimated the fishery yield for each river sector and survey period by recording the total fish landing (kg) by commercial fishers in the region [data available from the fishery monitoring program funded by [Norte Energia \(2021b\)](#)]. The total catch was recorded by technicians that inspected all fishing boats that arrived at landing ports along the river during the study period. Fishery yields are influenced by fishing effort, which, when sufficiently intense, can affect fish community structure in the

Amazon Basin ([Castello et al., 2013](#); [Keppeler et al., 2018](#); [Capitani et al., 2021](#)).

2.4. Functional traits

Twelve morphological traits were measured on each species: body mass, body elongation, eye position, eye size, oral gape position, maxilla length, body shape in the lateral dimension, pectoral fin position, pectoral fin size, caudal peduncle throttling, rostral elongation, and caudal fin aspect ratio. Average body mass (g) and standard length (mm), which were used for the calculation of some of the functional indices, were measured directly from fish specimens obtained during our surveys, and the other traits were measured on fish photos using the software ImageJ ([Schneider et al., 2012](#)). In cases where photos were not available (e.g., for rare or putative undescribed species), we used average measurements of closely related species in the same genus. Estimates of vertical trophic position were obtained from FishBase ([Froese and Pauly, 2021](#)) using R (Version 4.1.2: [R Core Team, 2021](#)) and the package rfishbase ([Boettiger et al., 2012](#)). Trophic position estimates from FishBase are often crude but have reasonable correlation levels with more precise estimates from stable isotope analyses ([Carscallen et al., 2012](#); [Mancinelli et al., 2013](#)) and have been used extensively by other studies (e.g., [Romanuk et al., 2011](#); [Dantas et al., 2019](#); [Kopf et al., 2021](#)). The fish traits measured here were selected

based on well-documented associations with feeding, locomotion, and habitat use (Toussaint et al., 2016; Bower and Winemiller, 2019; Keppeler and Winemiller, 2020; see Tables S1 and S2 for definition, function, and references). Therefore, changes in the structure and diversity of these traits in local fish assemblages following Belo Monte operation may infer the loss of ecological roles (Toussaint et al., 2016).

2.5. Phylogeny

The phylogeny of fishes from the Middle Xingu River was based on a supertree obtained from the R package *fishTree* (Chang et al., 2019). This supertree was created from molecular data (multiple genes) of ~11,000 ray-finned fishes (marine and freshwater species) and time-calibrated using fossil records (Rabosky et al., 2018). Because the supertree did not include Chondrichthyes, we added a clade of freshwater stingrays (Potamotrygonidae, 4 species) to the phylogeny based on their time of divergence from the ancestor of ray-finned fishes (~473 MYA; Kumar et al., 2017). The phylogenetic tree was resolved to the genus level due to the absence of many of the sampled species in the original supertree and the lack of certainty regarding species identification for some taxa. Previous studies have shown that phylogenies resolved at the genus level are appropriate in studies investigating patterns of phylogenetic structure of species in ecological communities (Qian and Jin, 2021). Overall, 82.5% of the genera studied were in the original supertree. The remaining unsampled genera were attached to the tree as basal polytomies of either their family or sub-family (if present). The phylogeny for fishes of the Middle Xingu appears in Fig. S3. This tree was significantly correlated with a tree based solely on taxonomy and with a simpler phylogeny (without branch lengths) generated from the Open Tree of Life (see Table S3; Hinchliff et al., 2015).

2.6. Data analysis

2.6.1. Species occurrence, abundance, and richness

We analyzed the effect of the Belo Monte operation on fish local distribution using Hierarchical Modeling of Species Communities (HMSC; Ovaskainen et al., 2017) in the R package HMSC (Tikhonov et al., 2020). HMSC is a joint species distribution modeling approach that facilitates the assessment of how species responses to environmental variables depend on functional traits and phylogeny (Abrego et al., 2017). This method is conceptually linked with community assembly theory and considers spatial and temporal autocorrelation (Ovaskainen and Abrego, 2020).

The community matrix (sites \times species) was the response variable in our HMSC models. Because lentic (lake, backwaters, and flooded forest) and lotic habitats (rapids) were sampled using different methods, we analyzed them separately. In addition, given that species response to the Belo Monte operation and other environmental variables may vary according to spatial scale (Levin, 1992), we conducted analyses for each sector separately (upstream, reservoir, reduced flow sector, and downstream) and also for all sectors combined (herein, "All"). The exception was for models of lotic habitats, which were run only with all sectors combined ("All") due to the small number of sampling units.

We used a hurdle model approach given its higher flexibility in modeling datasets containing a disproportional number of zeros, such as our data for fish abundance. A hurdle model is a two-part model that specifies one process for species occurrence (presence-absence, herein, PA) and another for abundance data conditioned to presence (herein, ACP). The PA model component was built with a Probit distribution, whereas the ACP component was built with a Gaussian distribution after data were log-transformed and scaled to zero mean and unit variance (Ovaskainen and Abrego, 2020). Rare species (site occurrence < 2) were removed from the models because their presence disproportionately increases computer processing time without any relevant gain of information (Brasil et al., 2020; Ovaskainen and Abrego, 2020).

In the lentic HMSC models, final explanatory variables included the Belo Monte operation (assigned as before or after), fishery yield, season

(dry and wet), habitat (flooded forest, reservoir, and lake), and the MEI. For lotic models, we used the Belo Monte operation, fishery yield, sampling effort (3 vs 6 samplings), and the MEI as exploratory variables. Before developing the models, we first conducted an exploratory RDA analysis in the R package *vegan* (Oksanen et al., 2021) to test whether the Belo Monte operation had already altered the hydrology and water quality of our study area in the Middle Xingu. This analysis was performed primarily to reduce redundancy and the number of variables in the analysis, assuring model parsimony.

The results of the RDA suggested strong relationships between the Belo Monte operation period and IHA variables. After the dams were constructed, the minimum and maximum water flow declined, the rate of the rising flow decreased, the length of the wet season was shortened, and the date of maximum river flow was delayed (Fig. 2). These hydrological changes varied according to the river sector analyzed with stronger effects observed downstream from the Pimental Dam (i.e., the reduced flow sector, Fig. 2). Therefore, in the models, the explanatory variable 'Belo Monte operation' summarizes the overall hydrological alterations caused by early dam operation into a single variable with easier interpretation. The RDA results also showed that water quality parameters (turbidity, conductivity, pH, and dissolved oxygen) were only weakly associated with the early operation phase of the dams. Based on this result, and the fact that water parameters were measured at only one location per survey site and disregarding possible differences between habitats, we also excluded these variables from the models. Finally, in the RDA, the monthly average flow was strongly associated with wet and dry seasons (Fig. 2). Thus, we decided to include season rather than monthly average flow in our HMSC models because the level of variation in the latter is also driven by the Belo Monte operation, which could lead to confounding effects in our analysis.

Our HMSC models also included two random effects to incorporate spatial (position along the longitudinal river gradient) and temporal structure (survey month and year). Species traits (12 morphological traits, described in the *Functional traits* section plus trophic position) and phylogeny also were incorporated into the models. Adding phylogeny and species traits served three purposes. First, these variables are expected to improve model fitting by allowing infrequent species to borrow information from more abundant and closely related species. Second, it allows assessment of the importance of phylogeny (p) and traits ($R^2T - \beta$) to explain species responses to environmental variables, also measuring the amount of trait effect that is propagated to species PA and ACP ($R^2T - Y$). Third, it permitted us to assess the influence of each exploratory variable on each functional trait. We also assessed the phylogenetic signal associated with each functional trait using Abouheif's C_{mean} statistic (Abouheif, 1999).

We configured HMSC models with default non-informative priors following Ovaskainen and Abrego (2020). We opt for using non-informative priors to maintain consistency and avoid biases due to misspecified priors given the current scarcity of ecological studies in tropical clear water rivers. The posterior distributions were sampled with 5 chains (Markov Chain Monte Carlo – MCMC). For PA models, each chain was composed of 50,000 iterations, from which 50% was burn-in and from the remaining only 250 were retained with a thin value of 100. For ACP models, we increased the number of iterations to 150,000 to ensure convergence. MCMC convergence was verified using the Gelman-Rubin statistic (Gelman and Rubin, 1992) and trace plots.

A variable was considered significant when the 95% credible intervals of its respective parameters did not encompass zero. We also tested the significance of our richness predictions by calculating the posterior probability that richness is greater before than after Belo Monte operation ($Pr [pred [Before] > pred [After]]$; Ovaskainen and Abrego, 2020). We considered the prediction significant when the probability was greater than 0.95.

We assessed the explanatory power (i.e., focusing on the in-sample error) of each species in each PA model using the Area Under the Curve (AUC; Pearce and Ferrier, 2000), Tjur R^2 (Tjur, 2009), and Root Mean Square Error (RMSE). For ACP models, we used RMSE and R^2 . We compared the ability of our HMSC models to predict new data (i.e., focusing

Table 1

List of HMSC models created for different types of habitat (lentic, lotic) and data (PA: presence/absence, ACP: abundance conditioned to presence). Root Mean Square Error (RMSE), Area Under the Curve (AUC), Tjur's coefficient of determination (Tjur R2), and the Widely Applicable Information Criterion (WAIC) are presented for PA models. RMSE and the coefficient of determination (R2), and WAIC are presented for ACP models. Models were ranked according to their explanatory power (Tjur R2 for PA data and R2 for ACP data). ~1 indicates intercept models (without any explanatory variables and any additional compartments, e.g., time, space, traits). Env: Environmental variables (Belo Monte operation, fishery yield, season, habitat [only for lentic data], MEL, sampling effort [only for lotic data]); Traits: 11 morphological and ecological traits associated with feeding, locomotion, and habitat preference; Phy: Species phylogeny; Space: Longitudinal position of sites along the river; Time: Date when sites were sampled.

Model structure	RMSE	AUC	R2	Tjur R2	WAIC
All - PA (lentic)					
Env + Traits + Space + Time	0.251 (0.110)	0.850 (0.081)	–	0.134 (0.105)	49.73
Env + Traits + Phy + Space + Time	0.251 (0.110)	0.846 (0.081)	–	0.131 (0.105)	49.77
Env + Space + Time	0.251 (0.110)	0.852 (0.081)	–	0.131 (0.104)	49.76
Env + Phy + + Space + Time	0.252 (0.110)	0.848 (0.081)	–	0.128 (0.104)	49.70
Traits + Phy + Space + Time	0.264 (0.118)	0.772 (0.107)	–	0.075 (0.082)	52.95
Space + Time	0.264 (0.118)	0.773 (0.103)	–	0.074 (0.081)	53.12
~1	0.279 (0.130)	0.500 (0.000)	–	0.000 (0.000)	58.54
Upstream - PA (lentic)					
Env + Traits + Space + Time	0.308 (0.086)	0.849 (0.082)	–	0.188 (0.123)	46.35
Env + Traits + Phy + Space + Time	0.311 (0.086)	0.832 (0.088)	–	0.176 (0.121)	46.42
Env + Space + Time	0.310 (0.085)	0.855 (0.077)	–	0.175 (0.118)	46.25
Env + Phy + Space + Time	0.314 (0.086)	0.837 (0.079)	–	0.162 (0.118)	46.10
Traits + Phy + Space + Time	0.335 (0.094)	0.745 (0.112)	–	0.084 (0.088)	49.08
Space + Time	0.335 (0.094)	0.744 (0.113)	–	0.083 (0.088)	49.10
~1	0.358 (0.104)	0.500 (0.000)	–	0.000 (0.000)	52.50
Reservoir - PA (lentic)					
Env + Traits + Space + Time	0.332 (0.084)	0.831 (0.088)	–	0.159 (0.102)	49.41
Env + Traits + Phy + Space + Time	0.334 (0.084)	0.825 (0.089)	–	0.154 (0.101)	49.36
Env + Space + Time	0.334 (0.084)	0.829 (0.088)	–	0.147 (0.100)	48.75
Env + Phy + Space + Time	0.336 (0.084)	0.820 (0.089)	–	0.141 (0.098)	48.84
Space + Time	0.358 (0.092)	0.722 (0.100)	–	0.065 (0.080)	50.67
Traits + Phy + Space + Time	0.358 (0.092)	0.723 (0.098)	–	0.064 (0.080)	50.73
~1	0.377 (0.099)	0.500 (0.000)	–	0.000 (0.000)	53.13
Reduced flow sector - PA (lentic)					
Env + Traits + Space + Time	0.308 (0.069)	0.866 (0.072)	–	0.208 (0.129)	42.68
Env + Traits + Phy + Space + Time	0.310 (0.069)	0.860 (0.072)	–	0.201 (0.129)	42.51
Env + Space + Time	0.310 (0.069)	0.870 (0.068)	–	0.191 (0.126)	42.46
Env + Phy + Space + Time	0.313 (0.069)	0.862 (0.072)	–	0.184 (0.126)	42.31
Traits + Phy + Space + Time	0.351 (0.088)	0.723 (0.099)	–	0.045 (0.058)	48.53
Space + Time	0.351 (0.088)	0.724 (0.100)	–	0.045 (0.057)	48.53
~1	0.364 (0.094)	0.500 (0.000)	–	0.000 (0.000)	50.05
Downstream - PA (lentic)					
Env + Traits + Space + Time	0.287 (0.075)	0.878 (0.067)	–	0.191 (0.098)	41.18
Env + Traits + Phy + Space + Time	0.290 (0.075)	0.867 (0.071)	–	0.181 (0.098)	41.20
Env + Space + Time	0.290 (0.075)	0.880 (0.068)	–	0.172 (0.092)	40.84
Env + Phy + Space + Time	0.293 (0.075)	0.870 (0.072)	–	0.163 (0.092)	40.71
Traits + Phy + Space + Time	0.319 (0.092)	0.765 (0.107)	–	0.064 (0.069)	44.92
Space + Time	0.319 (0.092)	0.766 (0.107)	–	0.063 (0.069)	44.81
~1	0.335 (0.097)	0.500 (0.000)	–	0.000 (0.000)	47.00
All - ACP (lentic)					
Env + Traits + Phy + Space + Time	0.383 (0.270)	–	0.364 (0.302)	–	56.99
Env + Phy + Space + Time	0.390 (0.275)	–	0.343 (0.286)	–	55.87
Traits + Phy + Space + Time	0.416 (0.283)	–	0.301 (0.270)	–	335.57
Env + Space + Time	0.418 (0.278)	–	0.295 (0.267)	–	88.58
Env + Traits + Space + Time	0.415 (0.279)	–	0.272 (0.246)	–	79.11
Space + Time	0.466 (0.303)	–	0.149 (0.210)	–	58.14
~1	0.466 (0.304)	–	0.000 (0.000)	–	57.66
Upstream - ACP (lentic)					
Env + Phy + Space + Time	0.351 (0.257)	–	0.509 (0.307)	–	69.8
Env + Traits + Phy + Space + Time	0.338 (0.262)	–	0.500 (0.327)	–	70.2
Env + Space + Time	0.388 (0.264)	–	0.461 (0.264)	–	174.1
Traits + Phy + Space + Time	0.422 (0.280)	–	0.442 (0.306)	–	66.3
Env + Traits + Space + Time	0.375 (0.260)	–	0.439 (0.301)	–	893.9
Space + Time	0.467 (0.303)	–	0.143 (0.178)	–	67.4
~1	0.476 (0.305)	–	0.000 (0.000)	–	62.4
Reservoir - ACP (lentic)					
Env + Traits + Phy + Space + Time	0.349 (0.263)	–	0.559 (0.294)	–	479.17
Env + Phy + Space + Time	0.361 (0.269)	–	0.527 (0.310)	–	557.29
Env + Traits + Space + Time	0.391 (0.257)	–	0.443 (0.280)	–	405.10
Env + Space + Time	0.398 (0.256)	–	0.440 (0.261)	–	280.74
Traits + Phy + Space + Time	0.441 (0.296)	–	0.395 (0.300)	–	74.55
Space + Time	0.481 (0.303)	–	0.177 (0.220)	–	82.45
~1	0.492 (0.307)	–	0.000 (0.000)	–	72.29

Table 1 (continued)

Model structure	RMSE	AUC	R2	Tjur R2	WAIC
Reduced flow sector - ACP (lentic)					
Env + Phy + Space + Time	0.268 (0.209)	–	0.635 (0.298)	–	58.19
Env + Traits + Phy + Space + Time	0.260 (0.208)	–	0.621 (0.311)	–	81.78
Env + Space + Time	0.328 (0.206)	–	0.516 (0.300)	–	4388.41
Env + Traits + Space + Time	0.313 (0.205)	–	0.506 (0.323)	–	213.72
Traits + Phy + Space + Time	0.375 (0.239)	–	0.456 (0.317)	–	56.70
Space + Time	0.427 (0.262)	–	0.191 (0.248)	–	62.58
~1	0.440 (0.264)	–	0.000 (0.000)	–	54.54
Downstream - ACP (lentic)					
Env + Traits + Phy + Space + Time	0.271 (0.255)	–	0.659 (0.315)	–	174.87
Env + Phy + Space + Time	0.293 (0.258)	–	0.637 (0.303)	–	2683.00
Traits + Phy + Space + Time	0.387 (0.298)	–	0.572 (0.337)	–	50.66
Env + Space + Time	0.351 (0.264)	–	0.547 (0.296)	–	1740.91
Env + Traits + Space + Time	0.337 (0.265)	–	0.522 (0.307)	–	5982.28
Space + Time	0.457 (0.321)	–	0.246 (0.292)	–	456.98
~1	0.464 (0.326)	–	0.000 (0.000)	–	47.08
All - PA (lotic)					
Env + Traits + Space + Time	0.258 (0.085)	0.888 (0.103)	–	0.256 (0.215)	16.09
Env + Traits + Phy + Space + Time	0.261 (0.085)	0.881 (0.106)	–	0.250 (0.215)	15.79
Env + Space + Time	0.264 (0.084)	0.885 (0.106)	–	0.225 (0.216)	16.07
Env + Phy + Space + Time	0.267 (0.084)	0.877 (0.108)	–	0.219 (0.215)	15.86
Traits + Phy + Space + Time	0.279 (0.084)	0.854 (0.105)	–	0.170 (0.215)	16.39
Space + Time	0.279 (0.083)	0.856 (0.105)	–	0.168 (0.214)	16.47
~1	0.332 (0.088)	0.500 (0.000)	–	0.000 (0.000)	20.08
All - ACP (lotic)					
Env + Traits + Phy + Space + Time	0.265 (0.296)	–	0.730 (0.271)	–	171,822.69
Env + Phy + Space + Time	0.279 (0.296)	–	0.721 (0.266)	–	51.74
Space + Time	0.448 (0.333)	–	0.610 (0.249)	–	302.78
Traits + Phy + Space + Time	0.353 (0.320)	–	0.561 (0.339)	–	36.73
Env + Space + Time	0.376 (0.321)	–	0.443 (0.330)	–	1847.07
Env + Traits + Space + Time	0.368 (0.324)	–	0.443 (0.317)	–	79,006.36
~1	0.449 (0.334)	–	0.000 (0.000)	–	37.40

on the out-of-sample error) to intercept models (with only the response matrix) and other nested-structured models (e.g., without explanatory variables or phylogeny structure) using the Widely Applicable Information Criterion (WAIC; Watanabe, 2010). WAIC is an extension of the Akaike Information Criterion (AIC) that can be applied for both singular and regular models and has the same asymptotic behavior as the Bayes cross-validation loss. The lower the WAIC, the greater the predictive power of the model. We opted for WAIC rather than cross-validation to avoid fitting the same model multiple times.

2.6.2. Functional and phylogenetic diversity indices

We assessed functional diversity using three main metrics: functional richness (Frich), functional divergence (FDiv), and functional evenness (FEve). These three metrics have shown to be largely independent and represent the main aspects of functional diversity (Mouchet et al., 2010). Frich, FDiv, and FEve measure, respectively, the volume of the functional space occupied by the community, the divergence in the abundance of the functional space, and the regularity in the distribution of abundance in the functional space (Villéger et al., 2008). Frich, FDiv, FEve were all calculated in the R package FD (Laliberté et al., 2014).

Phylogenetic diversity was assessed with three metrics that are considered to be fairly independent: Faith's index of phylogenetic diversity (Pfd), mean phylogenetic distance (MPD), and variation of pairwise distance (VPD) (Tucker et al., 2017). Pfd is the sum of all branch lengths in the phylogenetic tree that connect all species in a community (i.e., a measure of phylogenetic richness; Faith, 1992). MPD and VPD are the mean and variance of the phylogenetic distance among species, respectively (Webb, 2000; Clarke and Warwick, 2001). Pfd was calculated in the R package picante (Kembel et al., 2010), whereas MPD and VPD were calculated in the R package lirr (Li, 2018).

To analyze variation in all six diversity metrics, we used the same Bayesian hierarchical model structure described above, including the explanatory variables (Belo Monte operation, fishery yield, season, habitat, MEI, sample size), random variables (space and time), and non-informative

priors. The only exception was the exclusion of phylogeny and functional traits from the models since the response variable was composed of a single diversity index rather than multiple species. Given that all diversity metrics were continuous and normally distributed, we used a Gaussian distribution. Again, we conducted separate analyses for lentic and lotic habitats.

3. Results

A total of 236 fish species (30,516 specimens) were obtained from lentic habitats (lakes, backwaters, and flooded forests). In lotic habitats (rapids), 79 fish species (5713 specimens) were collected; among these, 29% were not encountered in lentic habitats. Species accumulative curves indicate that even after 9 years of study, the total number of species captured is still increasing, especially in lotic habitats (Fig. S4). Forty (15.4%) species are considered endemic to the Xingu River Basin. No exotic species were detected during our study.

3.1. HMSC models

3.1.1. Model assessment

HMSC models explained a small to moderate amount of variation in the fish community structure, but values varied greatly among species (Table 1). In lentic habitats, models explained, on average, from 13% to 21% of PA data and from 36% to 66% of ACP data. The average amount of variation explained was higher at smaller scales (river sectors; PA: 15% to 20%, ACP: 50% to 66%) than at larger scales (all sectors combined; PA: 13%, ACP: 36% Table 1). For lotic habitats, HMSC models explained on average 25% and 73% of PA and ACP data, respectively. Eliminating environmental variables and functional, phylogenetic, and space-time information from the models led to a significant loss of explanatory power (Table 1). The same pattern was observed for predictive power (indicated by WAIC) in PA models. However, ACP models tended to have lower predictive power than intercept models (except for lentic models encompassing all sectors; Table 1).

3.1.2. Belo Monte effects on species occurrence, abundance, and richness

Belo Monte operation had a significant effect on PA and ACP for several fish species in both lentic and lotic habitats and across different scales (Fig. 3). Most of these species had a lower frequency of occurrence and/or reduced abundance (Fig. 3, Figs. S5 to S10). Serrasalminids (mainly pacus), anostomids (headstanders), auchenipterids (driftwood catfishes), and pimelodids (long-whiskered catfishes) consistently declined in occurrence and abundance in lentic habitats (Fig. S11). Occurrence and abundance of curimatids declined in all sectors, except the reservoir (Fig. S11). There were no consistent increases in abundance or occurrence after the Belo Monte operation for any fish family, but a few taxa were more commonly captured, including *Pachypops* spp. (drum) and *Spatuloricaria tuiara* (loricariid catfish) (Figs. S5 and S11). In addition, some cichlids (e.g., *Crenicichla* spp., *Geophagus altifrons*) and loricariids (e.g., *Limatulichthys griseus*, *Spectracanthicus* spp.) increased in occurrence in the upstream sector after the Belo Monte operation (Fig. S6). In lotic habitats, cichlids (*Teleocichla* spp. and *Crenicichla dandara*), as well as most loricariids, consistently declined in occurrence and abundance (Figs. S10 and S11). *Spectracanthicus zuanoni* was the only taxa with significant positive responses to the Belo Monte operation (Fig. S10).

Predictions of our HMSC models showed that species richness and total abundance declined within most of the river sectors after the Belo Monte operation (Fig. 4). Richness declined on average 11.6% ($\text{Pr} [\text{pred} [\text{Before}] > \text{pred} [\text{After}]] = 0.999$) in lentic habitats, the decline was ~16.2%, but changes were only marginally significant ($\text{Pr} =$

0.93; Fig. 4). The reservoir and downstream sectors were the most impacted, with average declines in richness of 29.6% and 24.2% ($\text{Pr} > 0.997$), respectively, whereas no significant changes were observed for the upstream sector ($\text{Pr} = 0.82$; Fig. 4). Total abundance (all species combined) declined 3.6% in lentic habitats ($\text{Pr} = 0.98$) and showed no significant differences in lotic habitats ($\text{Pr} = 0.89$; Fig. 4). Greater differences in total abundance were observed in the downstream and reduced flow sectors (12% and 9%, respectively; $\text{Pr} = 0.996$), whereas no difference in total abundance was found in the reservoir and upstream sectors ($\text{Pr} < 0.84$; Fig. 4).

When compared to the other explanatory variables in the models, Belo Monte operation explained only a relatively moderate proportion of species distribution variation (PA data - Lentic: 8.7% [relative contribution]; PA data - Lotic: 25.9%; ACP data - Lentic: 7.0%; ACP data - Lotic: 22.4%) (Fig. 5).

3.1.3. Belo Monte effects on traits

HMSC models indicated that the effect of the Belo Monte operation on fish traits varied according to the river sector (Fig. S12). In the upstream sector, we found increases in rostral elongation, relative maxillary length, and body lateral shape, indicating an overall increase in the number and abundance of fishes with a relatively large head after the Belo Monte operation. In the reservoir, we found a reduction in the abundance of fishes with large and elongated bodies. In the reduced flow sector, changes were mainly associated with an increase in the occurrence of species with large and more central-positioned pectoral fins, and with an increase in the

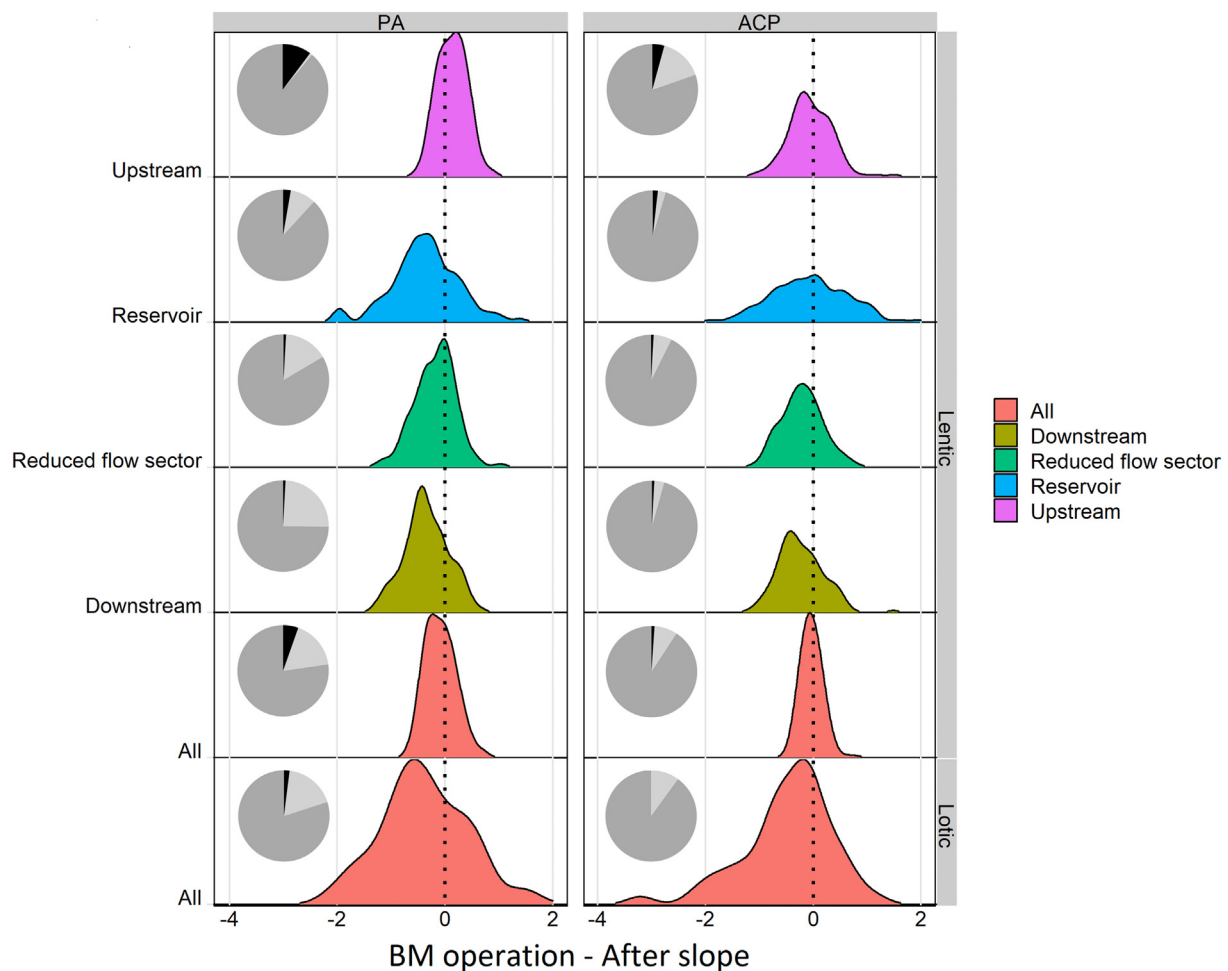


Fig. 3. Density plots show the variation in species response (slope) to the Belo Monte operation for each model component (PA: Presence-Absence, ACP: Abundance conditioned to presence), sector (Upstream, Reservoir, Reduced flow, Downstream, All), and environment (Lentic, Lotic). Pie charts show those species with significantly negative responses (light gray), positive responses (black), and neutral responses (dark gray). BM operation = Belo Monte operation.

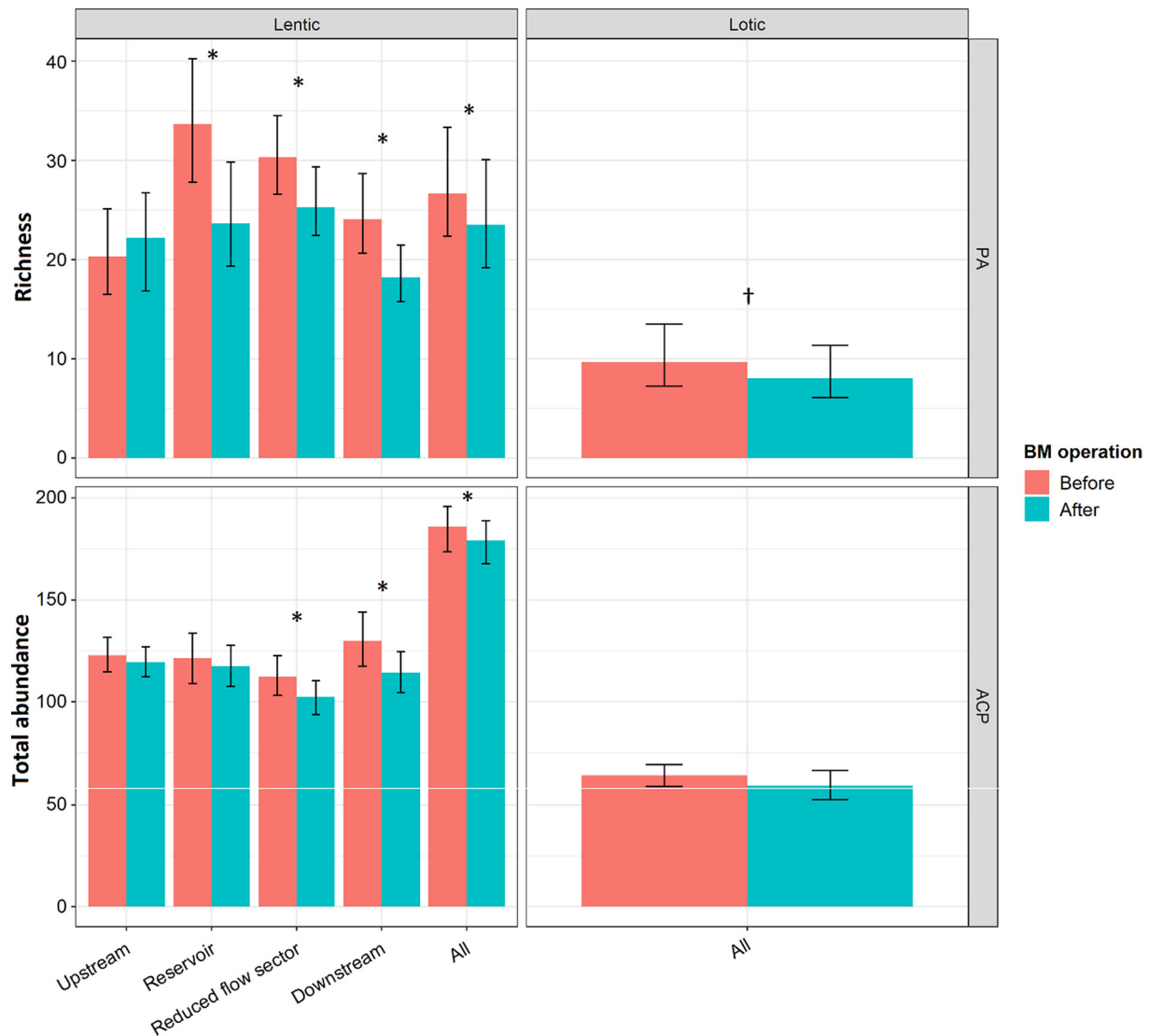


Fig. 4. Predictions about changes in fish total abundance (ACP) and richness (PA) after Belo Monte (BM) operation. Predictions are provided for each river sector (Upstream, Reservoir, Reduced flow, Downstream, All) and environment sampled (Lentic, Lotic). Predictions were generated by setting the other variables to their most likely values. Error bars are 95% credibility intervals. * Indicates significant differences ($\Pr[\text{pred}[\text{Before}] > \text{pred}[\text{After}]] > 0.95$). † Indicates marginally significant differences ($\Pr > 0.9$).

abundance of fishes with high caudal fin aspect ratios. In the downstream sector, we found a reduction in the occurrence of species at high trophic levels. When analyses were based on responses at a large spatial scale, responses were weaker with non-significant associations for both lentic and lotic habitats.

3.1.4. Effects of other variables

Habitat was, on average, the most important variable explaining variation in PA (relative average contribution of $40\% \pm 10\%$) and ACP ($23\% \pm 3\%$) in lentic habitats across scales, followed by season (PA = $18\% \pm 5\%$, ACP = $16\% \pm 3\%$; Fig. 5). Overall, occurrence and abundance increased for a large proportion of species ($\sim 43\%$) in the dry season (Figs. S5 to S9). Species occurrence was also higher for most species ($\sim 54\%$) in flooded forests than in lakes, however, the abundance of some species ($\sim 9\%$) was higher in the latter (Figs. S5 to S9). Differences between flooded forests and backwaters were less pronounced but more complex and scale-dependent (Figs. S5 to S9). Fishery yield was also an important environmental variable (PA = $10\% \pm 4\%$, ACP = $14\% \pm 3\%$), with its effect varying according to the river sector. For example, species association with fishery yield tended to be positive in the reservoir sector with 15

species ($\sim 8\%$) increasing in occurrence, but negative in the downstream sector as 10 species ($\sim 5\%$) reduce in occurrence (Figs. S7, S9).

In lotic habitats, Belo Monte operation (26%) and sample size (16%) were the most relevant variables influencing PA data, whereas MEI (28%) and Belo Monte operation (22%) were the variables most strongly associated with ACP data (Fig. 5). As expected, sample size tended to increase species detection (Fig. S10). The MEI had a mixed effect on species abundance, with some responding positively (*Hypancistrus* spp.) and others negatively (*Ancistrus* spp.) (Fig. S10). Associations between co-variables and specific fish traits appear in the supplementary material (Figs. S13 to S18).

3.1.5. Phylogenetic signal and traits effect on fish response and distribution

Overall, traits explained more than a third of the variance associated with species responses to environmental variables ($R^2_T - \beta$), with values depending on the model and the environmental variable analyzed (PA lentic: $34\% \pm 15\%$, ACP lentic: $45\% \pm 17\%$, PA lotic: $51\% \pm 18\%$, ACP lotic: $53\% \pm 15\%$; Table S4). Traits also explained from ~ 20 to 50% of the variance associated with species occurrence ($R^2_T - Y$; lentic: $23\% \pm 4\%$ SD, lotic: 44%) and abundance (lentic: $46\% \pm 9\%$, lotic: 48% ; Table S5). Phylogenetic signal (p) in species response to the environmental variables was statistically significant for all HMSC models (PA lentic: 0.68 average \pm

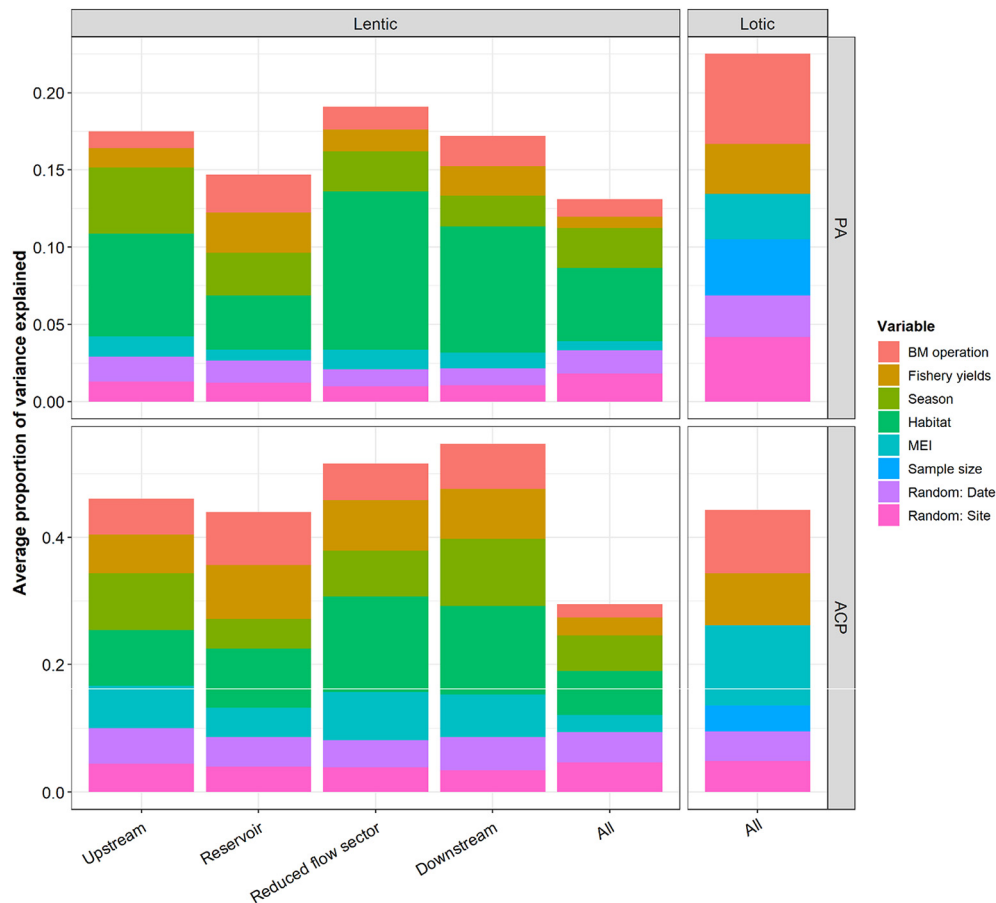


Fig. 5. Average proportion of variance explained by the explanatory variables for each model component (PA, ACP), sector (Upstream, Reservoir, Reduced flow, Downstream, All), and environment (Lentic, Lotic). For lentic environments, models were conducted for each sector (upstream, reservoir, reduced flow, and downstream) and with all sectors combined (All). Conversely, due to the small sample size, models for lotic environments were constructed only with all sectors combined (All). PA = Presence-Absence data, ACP = Abundance conditioned to presence data, BM operation = Belo Monte operation.

0.09 SD, ACP lentic: 0.81 ± 0.15 , PA lotic: 0.64, ACP lotic: 0.77; Table S6). Phylogenetic signal (Abouheif's C_{mean} statistic) was detected for all functional traits ($P < 0.001$; Table S7).

3.1.6. Spatial and temporal components

In lentic habitats, the temporal component (i.e., sampling date) had a relative contribution of $\sim 8\%$ ($\pm 3\%$) for PA and 11% ($\pm 3\%$) for ACP data (Fig. 5). The contribution was similar in lotic habitats, with values of 12% for PA and 11% for ACP data (Fig. 5). The contribution of the spatial component (i.e., site location) varied according to the scale of analysis. For models encompassing all sectors, space had a relative contribution of 14 to 16% in lentic habitats and 11 to 19% in lotic habitats (Fig. 5). For models at the sector scale, the average relative contribution of space was 7% ($\pm 1\%$; Fig. 5). However, it is noteworthy that the temporal and spatial effects are estimated after accounting for the influence of environmental variables that have considerable spatial and temporal variation.

3.2. Functional and phylogenetic diversity indexes

3.2.1. Models assessment

Our models explained up to 57% of the data variation and were slightly higher for phylogenetic (PDF = $46\% \pm 8\%$, MPD = $38\% \pm 12\%$, VPD = $35\% \pm 11\%$) than for functional diversity (Fric = $35\% \pm 9\%$, FDiv = $23\% \pm 12\%$, FEve = $20\% \pm 9\%$). There were relatively minor differences in the explanatory power between different sectors (All = $32\% \pm 14\%$, Upstream = $23\% \pm 7\%$, Reservoir = $35\% \pm 10\%$, Reduced flow sector = $34\% \pm 14\%$, Downstream = $40\% \pm 15\%$) and different habitat types (Lentic = $31\% \pm 13\%$, Lotic = $40\% \pm 14\%$).

3.2.2. Belo Monte effect on functional and phylogenetic diversity

Among functional and phylogenetic diversity metrics, functional divergence (FDiv) was lower following the Belo Monte operation in both lentic and lotic habitats. Conversely, variation of pairwise distance (VPD) and mean phylogenetic distance (MPD) increased in lentic habitats across all sectors and the upstream sector, respectively (Fig. 6). The other functional metrics did not show a significant change after the Belo Monte operation.

3.2.3. The effects of other variables

For sectors with lentic conditions, habitat type explained the greatest proportion of variation in phylogenetic (average relative proportion explained = $40\% \pm 18\%$) and functional diversity ($32\% \pm 15\%$), followed by season (Phylogenetic: $13\% \pm 10\%$, Functional: $12\% \pm 8\%$). Flooded forests had higher phylogenetic (MPD, PDF, and VPD) and functional diversity (mainly FRic) than lakes (Fig. S19). Conversely, functional and phylogenetic diversity were similar between flooded forests and backwaters (Fig. S20). The dry season was positively associated with FRic, PDF, and VPD, but negatively related with MPD (reservoir and downstream sectors) (Fig. S21).

In lotic habitats, the Belo Monte operation ($32\% \pm 20\%$) and sample size ($10\% \pm 1\%$) were the variables that were most strongly associated with functional diversity. For phylogenetic diversity, fishery yield ($14\% \pm 5\%$) and the MEI ($13\% \pm 5\%$) were the most important variables. Fishery yield had a negative association with MPD (Fig. S22). Conversely, sample size and the MEI had weak, non-significant, associations with functional and phylogenetic diversity (Figs. S23, S24).

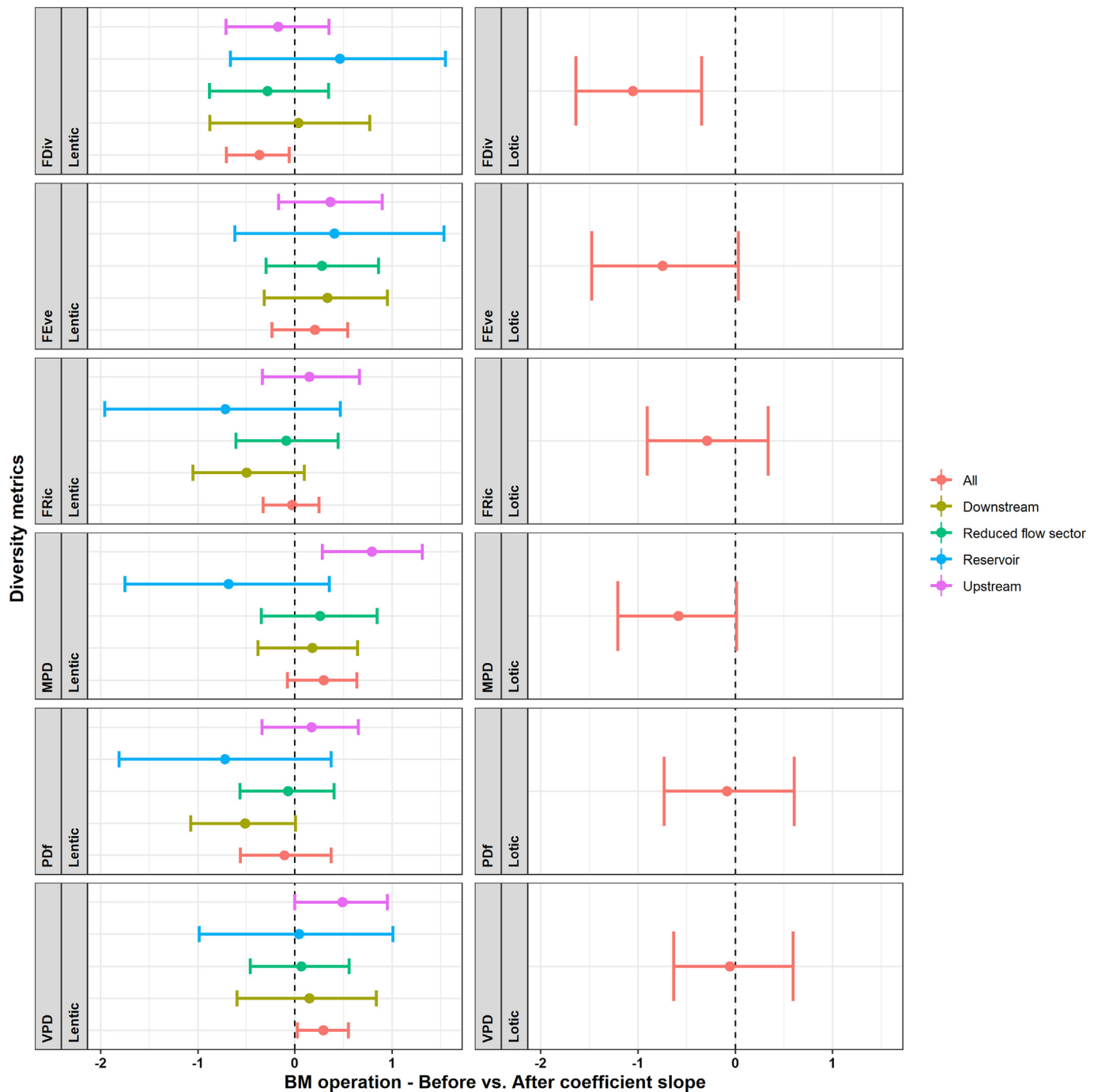


Fig. 6. Coefficient slopes associated with functional and phylogenetic diversity responses to Belo Monte (BM) operation. Points are averages and error bars are 95% credibility intervals. Consistent negative values (i.e., credibility intervals not encompassing zero) indicate a reduction in diversity indices after BM operation. FRic = Functional richness, FDiv = Functional divergence, FEve = Functional evenness, Pdf = Faith's index of phylogenetic diversity, MPD = Mean phylogenetic distance, VPD = Variation of pairwise distance (VPD). BM operation = Belo Monte operation.

3.2.4. Spatial and temporal components

In lentic habitats, the temporal component contributed $\sim 8\%$ ($\pm 5\%$) and $\sim 12\%$ ($\pm 8\%$) towards models explaining phylogenetic and functional diversity, respectively. The spatial component had a relative contribution of $\sim 24\%$ ($\pm 11\%$) for phylogenetic diversity and $\sim 15\%$ ($\pm 10\%$) for functional diversity when sectors were analyzed together. These estimates were reduced to $\sim 8\%$ ($\pm 2\%$) and $\sim 11\%$ ($\pm 5\%$), respectively, when the analysis was performed on individual sectors.

In lotic habitats, the relative contribution of time to explain phylogenetic and functional diversity was $\sim 7\%$ ($\pm 2\%$) and $\sim 12\%$ ($\pm 7\%$),

respectively. Conversely, the spatial component had a relative contribution of $\sim 49\%$ ($\pm 7\%$) for phylogenetic diversity and $\sim 28\%$ ($\pm 24\%$) for functional diversity.

4. Discussion

Five years of Belo Monte operation produced major changes to the flow regime, aquatic habitats, and biota of the Middle Xingu River. Declines in flow magnitude and flood duration during the wet season were followed by declines in fish species richness, abundance, and functional diversity.

Similar to studies conducted in other regulated rivers (e.g., Pyron et al., 1998; Agostinho et al., 2008; Araújo et al., 2013), our results suggest that changes in fish communities varied according to river sector and were usually greater within the reservoir and sites located downstream from the dams.

Species richness declined, on average, 12% in lentic and 16% in lotic habitats in the Middle Xingu River after the commencement of dam operations. Although changes in fish abundance were of lesser magnitude, they nonetheless were statistically significant in lentic habitats (reduction of ~4%). Compared to a recent synthesis, the impacts of the Belo Monte project on richness are similar to what was observed in other tropical rivers over the same time frame (reduction of ~14.6% in the first five years; Turgeon et al., 2019). The observations reported herein are largely consistent with qualitative expectations described in the environmental impact assessment performed prior to the approval of the Belo Monte project (Rima, 2009). Nonetheless, fish community changes documented for the Middle Xingu were larger than most of those reported in a global meta-analysis of changes in species richness and abundance after impoundment (Liew et al., 2016). Because most of the studies reviewed by Liew et al. (2016) and Turgeon et al. (2019) dealt with conventional dams with storage reservoirs, the relatively high impact of the Belo Monte dams (Pimental Dam in particular) raises doubts about whether run-of-the-river hydropower dams actually reduce ecological impacts. Two large run-of-river dams (Santo Antônio and Jirau, each with ~3600 MW installed capacity) were built in the Madeira River, another large tributary of the Amazon River, leading to the submersion of extensive tracts of riparian forests (Cochrane et al., 2017) and a shift in fish community structure (Cella-Ribeiro et al., 2017; Arantes et al., 2021). Later, fishery yields declined, especially for high-value migratory species (e.g., dourada *Brachyplatystoma rousseauxii* and curimatã *Prochilodus nigricans*), leading to reductions in the income of riverine communities (Lima et al., 2020; Arantes et al., 2021). To better guide future hydropower projects, there is an urgent need for studies that compare the environmental impacts of conventional vs. run-of-river dams over long time periods, particularly, in highly diverse tropical rivers.

Impacts of the initial operation of Belo Monte were particularly negative for fish species of the families Serrasalminidae (mainly pacus), Anostomidae (headstanders), Auchenipteridae (driftwood catfishes), and Pimelodidae (long-whiskered catfishes) (Fig. S25). This result may be related not only to observed changes in flow patterns and losses of hydrologic connectivity but also to potential reductions of important habitat areas after impoundment. Flooded forests and rapids were shown here, and elsewhere (Sabaj-Perez, 2015; Fitzgerald et al., 2018; Arantes et al., 2019b), to strongly affect fish communities in Amazonian rivers. Most of the affected serrasalmids were herbivorous species (e.g., *Colossoma macropomum*) that occupy primarily slow waters and sustain their energetic demands by consuming allochthonous material from the flooded forest (e.g., seeds, fruits). Other herbivorous serrasalmids, such as *Myleus setiger*, occupy rapids where they exploit periphyton and aquatic plants as food resources (Andrade et al., 2019). Anostomids and auchenipterids are omnivorous and frequently inhabit flooded riparian forests where they feed on allochthonous material (e.g., insects, fruits, seeds), decaying material, and periphyton on submerged logs and roots (Goulding, 1980). Anostomids and pimelodid catfishes are dependent on seasonal flood pulses and associated hydrologic connectivity for reproduction, and therefore, are especially vulnerable to dams (Winemiller, 1989; Arantes et al., 2019a). The family Pimelodidae is of special interest because it includes large migratory species of high commercial importance, such as dourada (*Brachyplatystoma rousseauxii*) and piraíba (*Brachyplatystoma filamentosum*) (Petrere et al., 2004).

There were no consistent positive responses to the Belo Monte operation as only a few unrelated species increased in abundance within certain sectors. Cichlids are generally more common in lentic habitats or slow-flowing areas in rivers and, therefore, were expected to increase in abundance within the reservoir sector. However, several cichlid species declined in both abundance and occurrence throughout the region. This finding agrees with a previous study demonstrating reductions in growth and reproduction rates of two cichlids (*Geophagus argyrostictus* and

Geophagus altifrons) after the Belo Monte operation (Mendes et al., 2021). The negative response of cichlid fishes to the Belo Monte operation is likely explained by reductions in resource availability driven by shorter wet seasons, reduced lateral expansion of aquatic habitat, and changes in water quality (Mendes et al., 2021).

The reservoir sector showed the strongest reduction in fish richness among the sectors analyzed, although total fish abundance remained nearly constant. The decline in fish richness is consistent with the sharp reduction in diversity often observed in reservoirs following impoundment likely due to the abrupt shifts from lotic to lentic conditions (Agostinho et al., 2008). Aquatic secondary production could have been sustained by the decomposition of flooded vegetation and soil organic matter as seen in other reservoirs (i.e., trophic upsurge during a heterotrophic phase; Agostinho et al., 2008, 2016). This increase in production caused by decomposition could explain the local increase in the abundance of curimatids, a family of primarily detritivorous fishes (Goulding, 1980; Soares et al., 1986). The reservoir fish community also changed functionally, with overall reductions in fish body size and elongation. These changes in body shape were likely associated with the reduction in water velocity which may have acted as an environmental filter selecting for smaller, wider bodies against streamlined forms (Bower and Winemiller, 2019). A reduction in fish body size after impoundment has been reported for other reservoirs, often associated with the gradual disappearance of migratory predators (Agostinho et al., 1999; Hoeinghaus et al., 2009; Santos et al., 2017).

In the downstream and reduced-flow sectors, we observed moderate declines in species richness and abundance probably due to flow regulation that reduced hydrologic connectivity as discussed above. Flow regulation and reduction in habitat connectivity and availability are expected to restrict seasonal fish movements that are essential for spawning and feeding success (Liermann et al., 2012; Barbarossa et al., 2020). The disappearance of fishes at high trophic levels (e.g., silver arowana *Osteoglossum bicirrhosum*, biara *Raphiodon vulpinus*, Xingu peacock bass *Cichla melaniae*) observed in the downstream sector may also be associated with a reduction in food resources from the surrounding flooded forest, which is in agreement with previous food web studies conducted in clearwater rivers (Capitani et al., 2021). Significant shifts in the position, size, and shape of pectoral and caudal fins within the trait space of the fish community within the reduced flow sector were also observed. We speculate that these changes reflect species sorting in response to changes in habitat conditions (e.g., water velocity) caused by divergence and reduction of flows by the Pimental Dam. For example, the increase in the dominance of pelagic fishes with high caudal fin aspect ratios (i.e., fork or lunate caudal fins) may indicate that the new hydrological conditions benefit fish that are relatively active swimmers in the water column (e.g., *Astyanax*, *Moenkhausia* and other characids) but were detrimental to some of the sedentary benthic fishes that inhabit rocky shoals (e.g., loricariid catfishes and crenuchid darters).

Total fish abundance and richness in the upstream sector changed relatively little following the commencement of operations of the Belo Monte dams. The Pimental Dam is a barrier to longitudinal fish movements, but the upstream sector retained essentially natural environmental conditions. Interestingly, we observed an increase in the phylogenetic diversity (mainly MPD and VPD) in the upstream community and an increase in the percentage of species with larger head proportions (i.e., increased body shape, rostral elongation, and maxillary length; e.g., pike cichlids *Crenicichla* spp. and some loricariids). Although more research is necessary to fully understand the combination of factors driving these community patterns, it is likely that suitable habitat conditions in the upstream sector provided refuge for fishes impacted by the major changes in the reservoir sector (Agostinho et al., 2008).

Changes in functional and phylogenetic diversity indices were relatively small following the completion of the Belo Monte hydropower project. Reductions in functional divergence of both lentic and lotic ecosystems indicate a decline in the abundance of species located at the extremities of functional space (Mason et al., 2005). This may be the first sign of an environmental filtering process reducing functional diversity, which can potentially impact ecosystem services including fisheries production and

seed dispersion (Mason et al., 2005; Anderson et al., 2009). For example, large pacus (e.g., *Myloplus* spp.), which were negatively associated with Belo Monte operation, are a unique group of herbivorous fish that disperse seeds of riparian plants and comprise a large proportion of fish landings in the region (Isaac et al., 2015; Correa et al., 2016). Interestingly, functional richness did not change significantly, suggesting that the total functional space was only marginally affected. This result is consistent with other findings that indicated that functional richness was weakly associated with functional vulnerability in Neotropical freshwater fishes due to high trait redundancy among species (Toussaint et al., 2016). Unlike previous studies of impounded rivers (e.g., Liew et al., 2016), we did not collect any non-native species during our surveys, therefore functional and phylogenetic patterns reflected changes involving native diversity and local community structure.

The other explanatory variables included in our models revealed similar, or even greater, relationships with fish community structure when compared to relationships to the Belo Monte operation. Habitat type and season explained most of the variation in fish occurrence, abundance, and diversity, a finding consistent with previous studies showing the importance of spatial variation in environmental conditions (e.g., structural complexity, depth, dissolved oxygen, food availability) and seasonality for structuring tropical freshwater fish communities (Junk et al., 1989; Siqueira-Souza et al., 2016). A major concern, thus, is the potential of dams to homogenize and/or isolate habitats or attenuate seasonal flood pulses (Hurd et al., 2016), potentially, causing synergistic effects on fish community dynamics that are still poorly understood. Other variables, such as El Niño–Southern Oscillation (e.g., measured by the MEI) and fishery yield (interpreted here as an indicator of fishing pressure), had secondary importance to the fish community during the nine years of our study. However, given the increasing effects of climate changes (Nobre et al., 2016) and market demand for fish driven by human population growth (Keppeler et al., 2018; Capitani et al., 2021), these variables merit further investigation.

Our study used a recently developed statistical approach (HMSC; Ovaskainen and Abrego, 2020) that facilitates the use of phylogenies and traits for impact assessment. A traditional approach calculates functional and phylogenetic diversity metrics and then analyzes the extent to which these metrics correlate with a stressor of interest (e.g., dam, pollution; Wang et al., 2021; Morelli et al., 2021). Here, in addition to this traditional approach, we also used traits and phylogeny to improve model fit. Based on this analysis, we were able to not only demonstrate patterns of occurrence and abundance of species before and after dams but also reveal the degree that functional traits and phylogeny were associated with shifts in community structure. In this regard, HMSC may be especially useful for tropical regions where studies usually lack statistical power due to high biodiversity and proportions of rare species as well as high environmental heterogeneity leading to low levels of explanatory and predictive power (Keppeler et al., 2018).

We adopted an explanatory modeling approach to test causal hypotheses of community changes after the commencement of operations of the Belo Monte hydropower project (Shmueli, 2010). PA models were shown to have better predictive power than intercept models, however, the same was not true for ACP models. Although we are confident that observed temporal and spatial patterns of abundance are reliable, we caution against the use of our ACP models to forecast dynamics. Modeling abundance in a multivariate context is challenging because community data are often zero-inflated and long-tailed (i.e., few cases with extremely high abundances). Future improvements in our models may be possible with the use of more flexible probability distributions (e.g., negative binomial; not yet implemented in the Hmsc package) as well as with the inclusion of other relevant exploratory variables (e.g., flooded forest coverage), and other functional traits that currently are not available (e.g., life-history traits).

Our study used a *before-after* (BA) design to assess the impact of the Belo Monte operation. Recent studies indicate that BA design performs 2.9–4.2 times worse than *Before-After Control-Impact* (BACI) to assess anthropogenic impacts (Christie et al., 2019). However, we highlight that at the beginning

of the project the upstream sector was considered a control in a BACI design, but we decided to use the term BA given that the upstream sector is not completely out of the range of the impacts of the Belo Monte operation. Either way, the upstream sector experienced little change compared to the downstream sectors, further indicating a negative impact of the Belo Monte dams on fish assemblages.

We collected a total of 259 fish species during our nine years of study, which is roughly 57.5% of total species richness documented for the region (Sabaj-Perez, 2015; Fitzgerald et al., 2018). Therefore, it is not surprising that our species accumulation curves did not level off completely. Our study focused on a fraction of the functional and phylogenetic space of local fish assemblages, reflecting temporal and spatial variation based on our survey dates and sites as well as the selectivity of survey methods and gear. Our survey methods were relatively inefficient for capturing small fishes from shallow water on sandbanks (e.g., small characids) and large fishes from deep areas in the main river channel (e.g., migratory catfishes) and reservoir during filling. Capture of fishes from swift rapids, especially during the wet season, also was inefficient, with some rheophilic benthic fishes likely evading capture. More surveys are needed to achieve a more exhaustive survey of fish species and assessment of the full impact of the Belo Monte dam on fishes and their habitats.

4.1. Conclusions

Despite the recent boom in hydropower projects in the Amazon (Winemiller et al., 2016), there have been few studies assessing the impacts of large dams on the region's phylogenetically and ecologically diverse fish communities. The present study was the first to analyze taxonomic, functional, and phylogenetic data to assess dams' impacts over relatively large spatial and temporal scales. We found significant reductions in fish abundance, richness, and functional diversity in the Middle Xingu River after five years of Belo Monte operation.

Findings presented here reveal only the early impacts of the Belo Monte operation, and further changes are anticipated. In tropical and sub-tropical regions, fish diversity and production generally tend to decline for an extended period of time following river impoundment (Agostinho et al., 2007, 2008; Turgeon et al., 2019). The two dams (Pimental and Belo Monte) have not yet reached total installed capacity (max. generation of ~9395 MW in March 2021), although the total amount has increased steadily over time (ONS, 2021; Fig. S26). An increase in the total amount of energy produced by the main power house at the Belo Monte Dam directly reduces water flow in the reduced-flow sector downstream from Pimental Dam. Norte Energia SA, the concessionaire of the Belo Monte hydropower project, intends to follow the consensus hydrograph as agreed in the environmental impact assessment study (Rima, 2009). That plan recommends the annual alternation of two hydrographs: Hydrograph A with a minimum peak flow of 8000 m³s⁻¹ and hydrograph B with a minimum peak flow of 4000 m³s⁻¹ (IBAMA, 2014). Both hydrographs consider a minimum annual flow of 700 m³s⁻¹ (IBAMA, 2014). If fully implemented, this implies a further reduction of 35% to 67% of the minimum peak flow recorded after the Belo Monte operation (2016; Fig. 1). This flow reduction would lead to major reductions in floodplain inundation, causing further declines in fish diversity and abundance and likely major losses in functional and phylogenetic diversity. Our study indicates that to minimize the impact on fish communities in the Middle Xingu River it will be necessary to conserve the natural habitats by emulating the natural flow regime with its seasonal variability, magnitude, frequency, and duration downstream of the dams. Continuous monitoring will be critical to assess impacts on fish communities as well as local people, including indigenous communities, that rely heavily on fishery resources.

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CRediT authorship contribution statement

Friedrich W. Keppeler: Conceptualization, Methodology, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **Marcelo C. Andrade:** Investigation, Data curation, Visualization, Writing - review & editing. **Paulo A.A. Trindade:** Investigation, Data curation, Writing - review & editing. **Leandro M. Sousa:** Investigation, Data curation, Writing - review & editing. **Caroline C. Arantes:** Methodology, Writing - review & editing. **Kirk O. Winemiller:** Supervision, Writing - review & editing. **Olaf P. Jensen:** Supervision, Methodology, Writing - review & editing. **Tommaso Giarrizzo:** Funding acquisition, Project administration, Data curation, Supervision, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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