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Fisheries and trophic structure of a large tropical river under impoundment

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ABSTRACT

Impacts on tropical rivers affect biodiversity and ecosystem services negatively impacting many economic activities, such as small-scale fisheries. Ecosystem-based fisheries management (EBFM) has been applied to maintain ecosystem flows and services for fisheries, to support social and economic sustainability. The suitable employment of the EBFM approach requires the understanding of the ecosystem by quantifying the trophic interactions and simulating environmental and fishery alterations. In this paper, to evaluate the early changes resulting from damming for hydroelectric power generation on the Madeira River food web, we compared two Ecopath models: before (pre) and after (post) the dam construction in November 2011. We analyzed the changes using several ecosystem attributes: fish biomass, catches, exchange of matter/energy, transfer efficiency, and, especially, the potential direct and indirect relationships among species. We also carried out simulations of the increase in the catches of several stocks in the models. Our analysis allowed us to identify several differences between before (2010–2011) and post (2012–2013) periods: an increasing of the ecosystem's respiration and consumption, a reducing of net production, transfer efficiency among Trophic Levels (TL), and total biomass of fish species by half. There was also an exchange of key species that were previously mostly non-fish compartments and became top predator fish, including *B. rousseauxii*, which was considered a key species in both periods. Fish species with an intermediate TL had their biomass reduced via top-down control, especially because of the increased biomass of non-migratory top predators (*Hoplias malabaricus* and *Plagioscion squamosissimus*). Noticeably, damming clearly reversed possible impact linkage among species, since one-third of indirect and almost one-half of direct (trophic) relations changed of signal, leading to unexpected turns in the system. Also, simulation revealed that increasing in catches strongly impact on fish biomass in the post-dam model more than in the pre-dam model. The ecosystem context of these results and the fact that they are pioneers in assess Amazonian damming can help the local managers and government to understand the impoundment effects and simulate changes in catches to foresee future impacts of reservoirs on Amazon.

1. Introduction

Impacts on tropical rivers affect both biodiversity and ecosystem services driving new trends for ecological indicators and ecosystem attributes (Philippsen et al., 2018; Tuda and Wolff, 2018). Major environmental impacts in rivers come from the invasion by alien species, habitat loss, hydrological shifts, and habitat fragmentation, which are on the bulk of the threats plaguing the freshwater biodiversity (Pelicice et al., 2017; FAO 2016; Pelicice et al. 2015). Cumulative effects of these environmental impacts within a watershed may disrupt important economic activities such as fishing and pose a risk to key ecological processes played by fish in tropical rivers, posing negative effects on the ecosystem functioning and on income, food security and livelihood for millions of people in tropical regions (Arantes et al., 2019; Tallis et al., 2015; Villarroya et al., 2014; Brismar, 2004).

In the Brazilian Amazonian region, a small-scale fishery is a low-cost family activity (FAO, 2014), which provides income, job, and food security for thousands of people (FAO, 2016; Isaac et al., 2015). More than 175,000 workers are directly and indirectly employed by the fishing activity (Ruffino, 2014). Disregarding fish consumption, they capture approximately 140,000 tons of fish per year (Berkes et al., 2006; MPA, 2011).

Life history of Amazonian fish species is strongly associated with the hydrological cycle, which is the main driver of the ecosystem,

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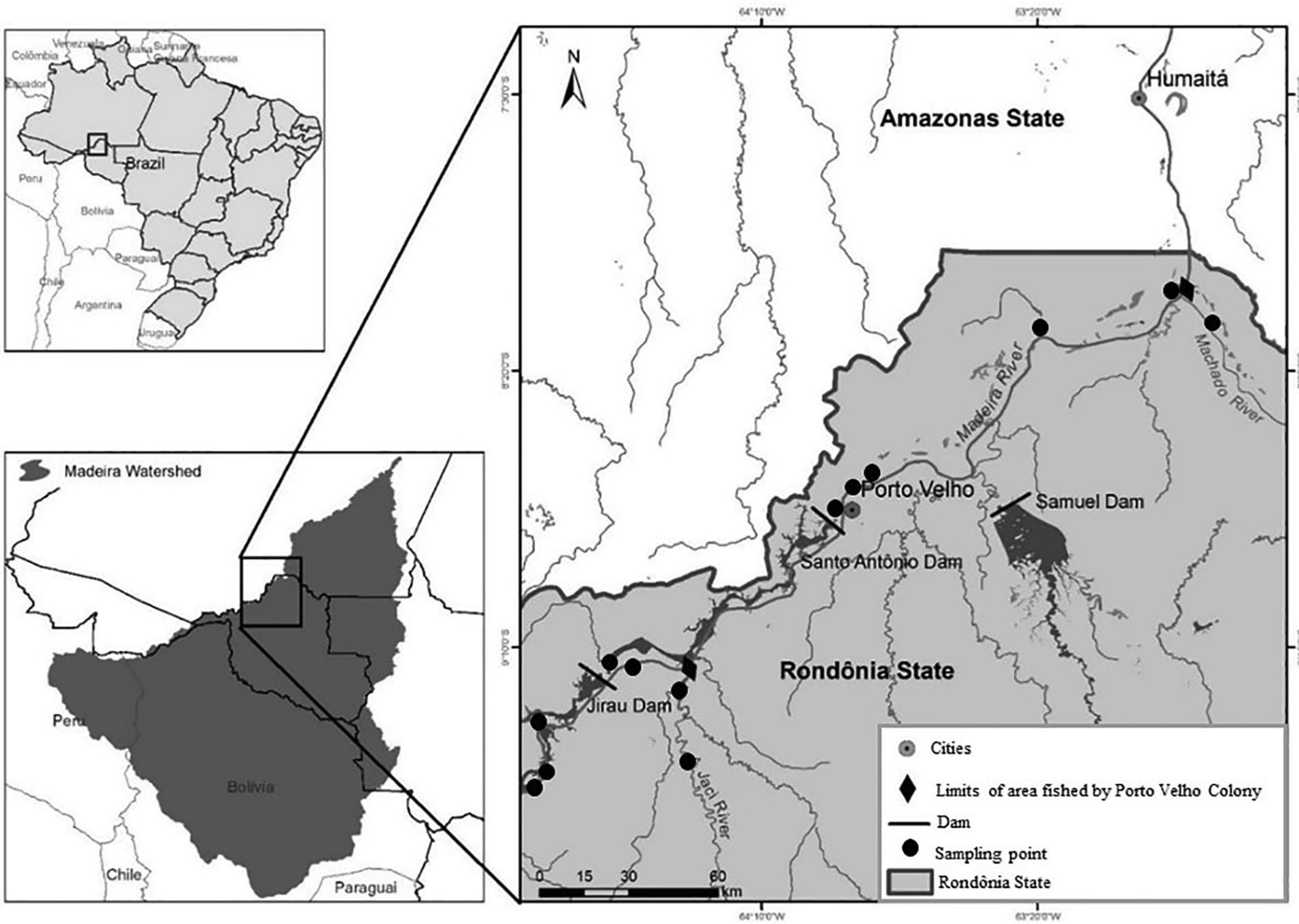

Fig. 1. Madeira River Basin (study area) with the borders of Rondônia State (Brazil)

influencing community structure, trophic organization, growth, and migration patterns (Delong and Thoms, 2016; Halls and Welcomme, 2004; Jiménez-Segura et al., 2010; Junk et al., 1989; Lima et al., 2017; Silva et al., 2013). The hydrological cycle also connects freshwater ecosystems allowing the dispersal and colonization of fish species through the river channel to the floodplain lakes (Hurd et al., 2016; Torrente-vilara et al., 2011). These environments are subject to local and regional factors that change the morphological configuration of the river channel.

The main factor currently threatening Amazonian freshwater environments is the establishment of hydroelectric dams, which strongly modify water biogeochemistry (Kondolf et al., 2014) and the patterns of river discharge and fluviometry (Fearniside, 2014; Junk & Mello, 1990; Winemiller et al., 2016), also affecting the ecological and biological dynamic in the environment. Ecological impacts of river impoundment in Amazon includes the loss of fish diversity (Castello and Macedo, 2016), interruption of migratory routes essential for the life history of the species (Barthem et al., 2017; Winemiller et al., 2016), and change the pulse of seasonal flooding (Agostinho et al., 2008; Isaac et al., 2016). The implications of such impacts are the change in fish abundance, composition and trophic configuration of fish communities. In the course of the impoundment, abundance of some species may increase, but to other species, the population may greatly shrink or even become extinct (Agostinho et al., 1999). All these aspects act in an integrated way, which requires a global analysis, capable of understanding the functioning of the system as a whole (Lassalle et al., 2014; Vasslides and Jensen, 2017).

For many years, impacts assessment and the focus on sustainability of fish stocks was performed strictly evaluating one single species, usually the most affected or valuated, ignoring its trophic relationships or indirect influences, such as those related to the climate or the environment (Angelini and Moloney, 2007). Likewise, fisheries management for long has focused on a single target species disregarding habitat, predators, and prey of the target species and other ecosystem components and interactions. In the early 2000s, this vision gradually was replaced by the Ecosystem-based fishery management (EBFM), which considers the broad ecosystem aiming to minimize environmental impact, reach sustainability and consistently manage fisheries (Pikitch et al., 2004; Link, 2010).

Such approach maintain flows and services, reaching an ecosystem assessment, besides to promote the sustainability of target species, as well as social and economic sustainability (Long et al., 2015; Marshall et al., 2018; Patrick and Link, 2015; Trochta et al., 2018). The EBFM approach seems to be even more needed in freshwater environments, given that terrestrial and floodplain systems directly influence the dynamics of aquatic populations, and ultimately, the fish stocks (Arantes et al., 2018; Carvalho Freitas et al., 2018; Collie et al., 2016).

In this sense, the suitable employment of EBFM approach, requires the understanding on ecosystem by quantifying the trophic interactions (Libralato et al., 2008), and simulating environmental and fishery alterations (Alexander et al., 2015; Coll et al., 2016; Heymans et al., 2014; Plagányi et al., 2012), to reach a broad evaluation of the ecosystem features (Coll et al., 2015; Pauly et al., 2000). An important tool to support EBFM is the Ecopath with Ecosim software (EwE), which has been widely used for quantitative assessments of the structure and functioning of aquatic ecosystems (Plagányi, 2007) but also to analyze and forecast impacts of fishing, climate change, and other anthropic changes (Christensen and Pauly, 1993; Heymans et al., 2016; Sánchez and Olaso, 2004). EwE has been applied to more than 400 ecosystems and in all kinds of environments around the world (Coll et al., 2015; Colleter et al., 2015).

In the Amazon, EwE was been previously applied basically to simulate the impact of fishing on target species (e.g. Angelini et al., 2006; Camargo and Ghilardi, 2009; Córdoba, 2014; Petrere Jr. and Angelini, 2009). In the present paper, to evaluate the early effects of the damming for hydroelectric power generation on the Madeira River food web, we compared two Ecopath models: before (pre) and after (post) the dam construction in November 2011. We analyzed the changes using several ecosystem attributes: fish biomass, catches, exchange of matter/energy, ecological efficiency, and, especially, the potential direct and indirect relationships among species. We also carried out simulations of the increase in the catches of several stocks in the models. The dam focused here, is one of the first to be built of 243 hydroelectric dams proposed for the entire Amazon region in the next two decades (Lees et al., 2016).

2. Materials and methods

2.1. Study area

The Madeira River (Fig. 1) is one of the most important white water tributaries of the Amazon River. It flows by 1.4 million km^2 through Brazil, Bolivia, and Peru contributing to the high rate of water flow and sediment (Latrubesse et al., 2005; Siqueira Jr. et al., 2015). Along Madeira watershed there are roughly 18 rapids which are important geographical barriers controlling fish species distribution and migration in the main stretch of the Madeira River (Goulding et al., 2003; Siqueira Jr. et al., 2015; Torrente-vilara et al., 2011). The two dams focused here to evaluation through modeling are Santo Antônio (formed in November 2011; Fig. 1), close to Porto Velho (Rondônia State capital) and Jirau, that was constructed upstream from Santo Antônio reservoir in 2012 (Hauser et al., 2019). Such impoundments inundated two significant waterfalls (Teotônio and Caldeirão do Inferno).

The Madeira River basin has the highest richness of fish species in the world, encompassing 1008 fish species (Ohara et al., 2015). Fishing landings from Madeira River represent approximately 4% of the total Amazonian fish landings (Barthem and Goulding, 2007). The most important fishery stretch of Madeira River in Brazilian portion is at Porto Velho (Rondônia State), where approximately 60 species were recorded (Doria et al., 2012). Most of the catches (566.5 ± 193.6 tons per year) are landed at Porto Velho fish market (named *Cai N'água*), which is under the Fishermen's Colony Z-1 administration (Doria and Lima, 2015).

2.2. Methodological procedure

To assess the effect of Madeira River impoundment upon the food web, on the species interaction and on the fishery, we performed a modeling and simulation through Ecopath software (EwE). Specifically, two Ecopath models were elaborated. The first referred to the period before the dam formation (pre-dam model) and used data from 2010 to 2011. The second referred to the period soon after the dam construction (post-dam model) and uses dataset referring to 2012 and 2013.

Thus, through the analysis of (i) local dataset sampled into two periods (such as fish diet composition and biomass) and (ii) Supplementary information from literature for some groups, we performed pre- and post-dam Ecopath models to inspect changes resulting from the impoundment over ecosystems attributes and indexes, and on direct and indirect species interactions. After, we simulate the effect of increasing catches on the fish biomass (stocks). Total area used was the same for both models (1171.27 km^2) and estimated with satellite images Landsat in 2012. We calculated the areas during the flood and the dry seasons, and used the average area obtained between these two periods.

2.2.1. Modeling approach

The modeling approach used a biomass balance model (EwE; www.ecopath.org) to quantify energy flows among functional groups and to estimate relevant ecosystem attributes. Basically, EwE model considers that Production of *a group i* = Mortality by predation over *i* + other mortalities of *i* + export of *i* taking into account trophic interactions between the groups based on fractions of the diet item of each group through a diet composition matrix (DC). Liner equation describing mass balance along trophic interactions is:

$$B_i \times PB_i \times EE_i - \sum j_i (B_j \times QB_j \times DC_{ji}) - EX_i = 0 \quad (1)$$

where: B_i is biomass of prey *i*, PB*i* represents the Production/Biomass rate or natural mortality (M) of *i* and EE*i*, is the Ecotrophic Efficiency of *i*, representing the fraction of the production of *i* transferred to higher Trophic Levels (TLs) or exported. Consumption/Biomass rate (QB*j*) is the consumption of predator *j* and DC*ji*, represents the fraction of *i* in the diet of *j*. The EX*i* is the export of *i* (fishing mortality or migration to other ecosystems). In both baseline models, the biomasses are expressed in tons × km^{-2}, while the flows are calculated in ton × km^{-2} × $year^{-1}$.

2.2.2. Input data and functional groups

Functional groups to Madeira River model were chosen according to: a) importance in fishing landings in 2010 or sampled biomass along the period; b) food item in the diet of the most important caught species; c) 'non-fish' organisms present in the diet and with biomass data available; and d) charismatic species (turtles, dolphins, alligators). Other fish species were grouped in functional groups according to their trophic categories (Supplementary Material 1 (SM1), Table SM 1.1). Aiming to better understand biomass variation and the dynamics of the groups, both models were standardized by same compartments. If the group was not filling some aforementioned criteria in one period but meet criteria in other, the group was added to both periods under modelling.

2.2.2.1. Fish groups. Data included fish species biometrics (length and weight), stomach contents, locality, and gear. All the collected biological material was fixed in formalin (10%), packed in plastic bags, and properly identified in the Laboratory of Ichthyology and Fisheries of the Federal University of Rondônia. Experimental fishing was done using gillnet, trawl net and throw net in 13 sampling points 150 km upstream and 75 km downstream from dam position (Fig. 1). This procedure was repeated monthly between July 2010 and March 2011 (pre damming period) and between July 2012 and March 2013 (after damming period).

Biomass values for 23 functional groups of fishes were estimated using weight supplied by throw net to each species caught divided by the total estimated area (number of throws × throw net area). These biomass values were adjusted to balance the final models and Ecopath estimated the value biomass for other 15 fish species in pre-model and 24 species in post-model. Other data gears were used just to confirm the species presence.

The Production/Biomass (PB) rate is similar to the natural mortality (M) (Allen, 1971), and for fish compartments were estimated using the empirical equation of Pauly (1980; see SM1). Likewise, Consumption/Biomass (QB) rate, i.e. the food amount required by the organism in relation to its own weight, was calculated through empirical regression from Palomares and Pauly (1998; see SM1). Fish biometric data were used to estimate the parameters required by PB and QB equations (K, L_∞, and W_∞), using the FISAT program (Gaynilo Jr. et al., 2005) for the follow species: *Pinirampus pirinampu, Mylossoma duriventre, Prochilodus nigricans, Brycon amazonicus, Brachyplatystoma rousseauxii, Brachyplatystoma filamentosum, Semaprochilodus insignis, Pseudoplatystoma punctifer, Cichla pleiozona,* and *Schizodon fasciatus*. For other fish species, these parameters were based on estimates from similar floodplains ecosystems (for details, see Table SM 1.2).

The Diet Composition matrix (DC) was built using data from our analysis for gut content (for the number of stomachs analyzed by species, see Table SM 1.3). The frequency of food items was estimated for the pre- and post-dam period. To five fish-compartments (*Hoplosternum littorale, Astronotus crassipinnis, Arapaima gigas, Brycon melanopterus*, and *Hypophthalmus* sp.) we used literature information (Angelini et al., 2010, 2006; Angelini and Agostinho, 2005; Petrere Jr. and Angelini, 2009; Watson et al., 2013) and FishBase platform (Froese and Pauly, 2019).

2.2.2.2. Non-fish groups. Biomass values in both periods for most non-fish groups (Phytoplankton, Zooplankton, Macrophytes, Aquatic Invertebrates, Dolphins, Turtles, Aquatic Birds, Alligators and Otters) were based on local reports provided by Santo Antônio Energy Company (Ecology Brasil, 2011; INPA, 2011; PROBIOTA, 2011; SETE, 2014). For example, phytoplankton was estimated using the mean of biovolume per taxonomic group (Ecology Brasil, 2011, 2012). Using conversion rates from Angelini et al. (2018) biomass values was estimated in 1.68 $g*m^{-2}$ for the pre-dam period value and 1.89 $g*m^{-2}$ for the post-dam phase. For estimate Dolphins biomass, the two local species (*Inia geoffrensis* and *Sotalia fluviatilis)* were grouped. Local census recorded 250 and 213 individuals in pre- and post-dam periods (INPA, 2011; SETE, 2014), totaling 46.250 tons and 39.405 tons for the periods respectively (mean individual weight = 0.185 ton). This census was done in a stretch with 226 km (width = 1.2 km), resulting in an area of 271.2 km^2. Initial input biomass was 0.17 in the pre-dam period and 0.15 in the post-dam stage.

Biomass for Flooded Forest, Periphyton and Terrestrial Invertebrates were obtained from the literature. Terrestrial Invertebrates biomass was either estimated by the model (pre model) or achieved in the literature (post model). Biomass for Macrophytes, Aquatic Invertebrates, Zooplankton, Dolphins, Turtles, Aquatic Birds, and Otters are original data from local sampling. Supplementary Material 2 shows the parameterization details for all non-fish groups.

2.2.2.3. Fisheries data. We used three types of fisheries data in the models: i) fishing landings in the main port of Porto Velho city, sampled by the Laboratory of Ichthyology and Fisheries at the Federal University of Rondônia; (ii) commercial data from riverine families; and (iii) familiar fish consumption recorded in fishing communities. Commercial and consumption data were sampled by monitoring of 60 families living upstream and downstream stretches of the Madeira River between 2010 and 2013. Thus, it was also possible to obtain a catch estimate per species for 2010–2011 and 2012–2013 periods, and standardize the values by model area. The short time series on catches did not allow calibration in Ecosim module.

2.2.3. Balance and confidence model

The pre-balance approach (PREBAL), based on the eco-physiological principles of the ecosystem components (Link, 2010), was used to evaluate the consistency of the input values in both models. Accordingly, PB and QB rates and Biomass data were expected to decline at higher trophic levels, while Production/Consumption (P/Q) rate would maintain similar values.

2.2.4. Ecosystem indicators and indexes

Three ecosystem indicators calculated by EwE and six indexes were used to evaluate the dam's impact on the Madeira River ecosystem. Indicators were mainly (1) Total System Throughput (TST), which refers to the total fluxes in the system; (2) Total Primary Production (TPP)/Total Respiration (TR) rate, which describes the systems development indicates maturity if has value closer ~1; (3) Total Biomass/TST rate, whose high values would indicate that the flows support more biomass and the system would be more mature or developed.

The main indexes applied to evaluate the impoundment impact were (4) Connectance Index (CI), which is the ratio between observed and possible links, and shows the degree of connection into the trophic web; (5) the System Omnivory Index (OI), which is a measure of how food interactions are distributed between trophic levels; (6) Finn's cycling index, which measures the fraction (in %) of flows recycled within the system (> 10% shows high recycling, and thus, high system resilience); (7) Ascendency (A), which measures the growth and development of the ecosystem; and (8) Overhead (O), which is also a measure of resilience since it represents the strength of energy available into the system to be accessed in response to unexpected perturbations (Ulanowicz, 1986). Lastly, we used (9) Transfer Efficiency (TE), to measure the flow of assimilation efficiency from a trophic level on the previous level (%).

2.2.5. Mixed trophic impact (MTI)

The outputs of MTI were used to unveil the impact of one species on others, regardless direct (consumer-prey) or indirect. Indirect ones refer to trophic cascade among components without food connection, given that any predator consumption affects other prey's and predators, changing overall biomass available (Gloeckner and Luczkovich, 2008). Specifically, the interaction among components (positive and negative signals) for MTI matrixes in pre- and post-dam models was compared to evaluate the effect of damming on the Madeira River food web.

The MTI approach was firstly developed to analyze direct and indirect interactions in the US economy (Leontief, 1951). Later, Ulanowicz and Puccia (1990) developed a routine to EwE calculate direct and indirect trophic impacts from one compartment over all others and quantify the changes in all components (impacted) following an increase of 20% of biomass values at each one (impacting group). Positive values occur when the 20% impact increases the biomass for the impacted group, while negative values happen if the 20% impact in the biomass of one group decreases the biomass for impacted group (Gamito and Erzini, 2005; Khan and Panikkar, 2009; Mavuti et al., 1996).

The MTI is calculated through an n × n matrix, where n is the number of components in the model:

$$MTI_{ji} = DC_{ji} - FC_{ij} \quad (2)$$

where: DC_{ji} is the diet composition expressing how much *i* contribute to the diet of *j*, and FC_{ij} is the proportion of the predation on *j* that is due to *i*. The terms *j* and *i* represent the interaction between the impacting group *j* and impacted group *i*.

Using the MTI values, Libralato et al. (2006) developed the keystoneness species index (KSi), which assigns high values to functional groups with low biomass but high effect on the trophic network. Later, changes in KSi (by Valls et al., 2015) enhanced the relevance of species of high trophic levels. The distribution of biomass between the trophic levels was also analyzed and compared between pre- and post-dam periods using the EcoTroph routine (Gascuel and Pauly, 2009). To each trophic level, the flows in the trophic chains by sources (detritus or primary producers), flow of respiration and flow of detritus production were synthetized by Lindeman spine.

2.2.6. Simulation analysis (Ecosim approach)

Following Ecopath model balancing, the Ecosim routine was used to simulate the temporal dynamic of system variables, such as biomass, predation, and production (Walters et al., 1997) and the impacts of increased fishing catch. Ecosim approach expresses the dynamic of the ecosystem over time (Christensen et al., 2005), and it is defined by a series of differential equations:

$$\frac{dB_i}{dt} = gi \sum_j Q_{ji} - \sum_j Q_{ji} + I_i - (MO_i + F_i + e_i) \times B_i \quad (3)$$

where: dB_i/dt represents the change in the biomass of functional group *i* (B_i) over time d_t; g_i is the net growth efficiency (production/consumption ratio); Q_{ij} is the consumption of group *i* by group *j*; I_i is the immigration of functional group i; $M0_i$ is the non-predation rate of natural mortality; F_i is the fishing mortality; e_i is the emigration of functional group i.

In order to test the biomass dynamic over increasing fishing impact, it was simulated from baseline model an increase on landing in both models by 10%, 12.5%, 15%, 17.5% and 20%. These increasing values seem realistically reasonable since fish consumption and human population are increasing in the region. Relative biomass dynamics was analyzed after simulating increasing catches for catfish species (*Brachyplatystoma rousseauxii, Brachyplatystoma filamentosum, Brachyplatystoma platynemum, Brachyplatystoma vaillantii, Pseudoplatystoma punctifer, Pinirampus pirinampu,* and *Zungaru zungaru*) and other relevant species in the landings (*Mylossoma duriventre, Prochilodus nigricans, Potamorhina latior, Triportheus auritus, Semaprochilodus insignis, Arapaima gigas,* and *Cichla pleiozona*).

3. Results

Groups with Trophic Level (TL) values between 2 and 2.9 held most biomass in pre-dam period (96%) and the post-dam period (86%). However, the basic input for pre- and post-dam models (including those estimated by the EwE), showed remarkable biomass increasing in basal compartments after impoundment (Table 1). The greater biomass values in the post-dam period were observed to nine Fish groups and to compartments Other insectivorous, Phytoplankton and Zooplankton (Table 1). On the other hand, biomass declined to most fish compartments, and variations in diet composition lead to overall change in community TL from 2.64 to 2.80 (see details in Tables SM 3.1 and 3.2).

Overall fish biomass has dropped by nearly half in the post-dam model. Mainly biomass and catches of large catfish (especially from *Brachyplatystoma* genus) were affected, dwindling by around 50%. As a whole, total catch declined by 42% (Table 2). Likewise, large proportion (−88%) of total fish caught per fisher' family dwindled in the post-dam model, while fish consumption has had a slightly decrease (−8%), likely leaded by the reduction in catches landed at Porto Velho City (−50%).

Catches of the most caught species in the pre-dam model decreased by 63%, 52%, and 70%, respectively (i.e. *M. duriventre, P. nigricans*, and *Brycon amazonicus*). Catches however increased from the pre- to the post-dam model to the species *S. insignis* (+40%), *Pterygoplichthys* spp. (+50%), and *Colossoma macropomum* (+125%).

After models mass-balancing, the PREBAL procedure showed that B, PB, and QB values were negatively related to the trophic levels underlining both models consistency (see SM 4). Attributes of ecosystem maturity (Table 3) showed the increasing in Total Consumption and Respiration followed by decreasing values of Total Primary Production/Total Respiration rate (8.75 to 2.28) and of Transfer Efficiency (7.8% to 4.8%). Also, Madeira River was proved to be a resilient system in both periods especially due to the high cycling values (Table 3).

3.1. Mixed trophic impacts (MTI)

In both periods, changes in detritus and lower TL groups produced greater impact upon the other components (Figs. 2 and 3). Broadly, in pre-dam period Other Carnivorous group produced larger positive impact over the system together with *Calophysus macropteus* and *Phractocephalus hemioliopterus* (Fig. 2). In the post-dam period, the species *P. hemioliopterus* and Other Carnivorous group kept to produce positive impact on the largest number of groups, along with, Omnivorous, and Piscivorous categories (Fig. 3). Though, the strongest positive impacts were produced by Flooded Forest. Aquatic birds produced the strongest negative impact in the pre-period, while in the post-dam period the greatest negative impact was caused by *B. rousseauxii* (values in SM 5).

Each impact matrix contains 3422 positive or negative interactions. Most interactions (3019) were indirect and trophic interactions (i.e. direct) happened in 403 cases. In the post-dam model, 1233 direct or indirect interactions in the food web matrix interchanged from positive to negative or vice versa (Table 4 and Fig. 4). Negative indirect relationships did not change (approximately 60%). Whole direct positive interactions in the pre-dam model (50%) turned into 31% in the post-model. Also 34% positive indirect relations were inverted after damming (Table 4 and Fig. 4).

The key species index ranking (Table 5) indicated which *B. rousseauxii* was the second key component of the system in the pre-dam model, turn out to be the first in the post model. Likewise, some fishes' groups (*A. gigas*, "Other Piscivorous," and *C. pleiozona*) became key components in the post-dam model, replacing Aquatic Birds, Cladocera and *B. vailantii*, which were important key species in the pre-dam model.

The Detritivory:Herbivory relationship in post-dam model is twice the value in pre-dam model (Lindeman spine, Fig. 5), underlining the increase of the detritus chain triggered by damming (as previously showed in Fig. 2 and 3).

3.2. Ecotroph

Total biomass was distributed over 4.5 TLs in both periods, pre- and post-dam (Fig. 6). In the pre-dam period, the trophic network presented higher biomass at intermediate TLs, while in the post-dam phase, besides having reduced biomass, the highest concentration was at lower TLs, except for organisms at TL > 3.3, which presented higher biomass.

3.3. Simulations of the catch increasing

The increase in the fish catch in both models reduced the relative biomass values for catfish. Values sharply decreased in the post-dam period mainly for *B. filametosum, B. rousseauxii*, and *Z. zungaru* (Fig. 7). Also, the increase in fisheries reduced the biomasses for *P. latior* and *T. auritus* in the pre-dam period and for *S. insignis* and *A. gigas* in the post-dam period (see details for other species in SM 6).

4. Discussion

4.1. Model overview

This study presents the early effects of impoundment in Madeira River, the major branch of Amazon River through Ecopath modeling and simulation of changes in the ecosystem, in species biomass, and trophic trends observed among compartments before and after damming. Many studies have used the same modeling approach used here to analyze impact of impoundment on other ecosystems such in an estuary ecosystem (e.g. Han et al., 2017) and to evaluate reservoir ecosystems around the world with regards to fishing impacts (Bornatowski et al., 2017; Philippsen et al., 2018; Tuda and Wolff, 2018; Wang et al., 2019), temporal dynamics (Gamito and Erzini, 2005; Guo et al., 2018), invasive species impact (Bezerra et al., 2017; Khan and Panikkar, 2009; Tesfaye and Wolff, 2018), and maturity development (Gubiani et al., 2011). To our knowledge, this is the first time Ecopath is used to assess the same ecosystem before and after damming. Focusing on the same ecosystem may contextualize changes and steer reservoirs planning and management, especially in the Amazon region, which will receive more than a hundred of them in the next decade (Winemiller et al., 2016).

The pre- and post-dam Ecopath models were developed with analyses of stomach contents of the fish sampled before and after the damming, highlighting small but important TL changes among consumers (see below). Likewise, biomass, one of the most difficult estimates to obtain and the main and most sensitive input parameter in Ecopath, was obtained from data sampled in the region and to the specific study periods, providing reliability to results achieved. All other input parameters supplied by fieldwork were sampled as part of a

Table 1
Input parameters values for the groups in the Madeira River models: pre and post dam implementation. B, biomass; PB, production/biomass; QB, consumption/biomass; TL: Trophic Level; EE: Ecotrophic Efficiency. Bold values were calculated by Ecopath.

		TL		B (t km^{-2})		PB (year^{-1})	QB (year^{-1})	EE	
No.	Group name	Pre	Post	Pre	Post			Pre	Post
1	Phytoplankton	**1.00**	**1.00**	1.680	1.893	205.00		**0.00**	**0.25**
2	Flooded forest	**1.00**	**1.00**	9800	9800	0.10		**0.10**	**0.05**
3	Macrophytes	**1.00**	**1.00**	178.02	71.75	4.00		**0.00**	**0.20**
4	Periphyton	**1.00**	**1.00**	2.300	2.000	8.80		**0.42**	**0.57**
5	Terrestrial invertebrates	**2.00**	**2.00**	**1.129**	2.400	25.00	180.00	0.61	**0.12**
6	Aquatic invertebrates	**2.00**	**2.00**	0.350	2.400	25.00	180.00	**0.80**	**0.12**
7	Cladocera	**2.00**	**2.11**	0.008	0.465	54.70	230.00	**0.70**	**0.26**
8	Copepoda	**2.00**	**2.11**	0.009	0.250	54.70	230.00	**0.63**	**0.48**
9	Rotifer	**2.00**	**2.11**	0.008	0.230	54.70	200.00	**0.73**	**0.54**
10	Protozoa	**2.00**	**2.11**	0.006	0.200	54.70	190.00	**0.73**	**0.65**
11	Alligator	**3.40**	**3.68**	0.002	0.005	0.25	1.50	**0.00**	**0.00**
12	Dolphins	**3.48**	**3.67**	0.171	0.145	0.08	0.80	**0.00**	**0.00**
13	Turtles	**2.03**	**2.27**	3.640	3.046	0.17	1.00	**0.29**	**0.35**
14	Aquatic birds	**3.35**	**3.54**	0.028	0.028	0.30	2.00	**0.00**	**0.00**
15	Otters (*Lontra longicaudis*)	**3.31**	**3.47**	0.0004	0.0004	1.50	5.00	**0.00**	**0.00**
16	Otters (*Pteronura brasiliensis*)	**3.54**	**3.59**	0.001	0.0008	1.50	5.00	**0.00**	**0.00**
17	*Pinirampus pirinampu*	**3.01**	**3.14**	**0.053**	**0.003**	0.65	5.69	0.80	0.80
18	*Mylossoma duriventre*	**2.00**	**2.43**	0.988	0.043	4.00	16.73	**0.02**	**0.18**
19	*Prochilodus nigricans*	**2.03**	**2.04**	0.500	0.104	2.31	13.09	**0.14**	**0.12**
20	*Brycon amazonicus*	**2.00**	**2.71**	0.060	0.081	1.06	8.85	**0.90**	**0.20**
21	*Brachyplatystoma rousseauxii*	**3.17**	**3.60**	**0.024**	**0.007**	1.16	4.56	0.80	0.80
22	*Brachyplatystoma filamentosum*	**3.45**	**3.38**	**0.015**	**0.008**	1.11	2.92	0.80	0.80
23	*Semaprochilodus insignis*	**2.00**	**2.00**	0.068	**0.043**	1.29	10.00	**0.33**	0.80
24	*Pseudoplatystoma punctifer*	**3.18**	**2.95**	**0.024**	**0.026**	0.50	4.00	0.80	0.80
25	*Cichla pleiozona*	**2.67**	**3.58**	0.090	0.053	0.47	3.00	**0.39**	**0.43**
26	*Schizodon fasciatus*	**2.03**	**2.00**	0.200	**0.016**	1.64	14.00	**0.08**	0.80
27	*Brachyplatystoma platynemum*	**3.35**	**3.71**	**0.010**	**0.002**	1.20	7.46	0.80	0.80
28	*Potamorhina latior*	**2.06**	**2.06**	**0.024**	0.061	1.55	10.36	0.80	**0.15**
29	*Zungaro zungaro*	**3.31**	**3.67**	**0.014**	**0.003**	1.02	4.42	0.80	0.80
30	*Hoplosternum littorale*	**3.00**	**2.42**	**0.018**	**0.006**	1.02	7.00	0.80	0.80
31	*Astronotus crassipinnis*	**2.31**	**2.32**	**0.013**	**0.004**	0.74	5.00	0.80	0.80
32	*Phractocephalus hemioliopterus*	**3.37**	**2.86**	**0.023**	**0.012**	0.60	2.00	0.80	0.80
33	*Pterygoplichthys* spp.	**2.00**	**2.00**	**0.003**	**0.004**	1.00	10.00	0.80	0.80
34	*Triportheus auritus*	**2.68**	**2.39**	0.380	0.730	1.40	13.35	**0.09**	**0.08**
35	*Colossoma macropomum*	**2.00**	**2.25**	0.010	0.023	1.40	8.30	**0.27**	**0.27**
36	*Arapaima gigas*	**2.20**	**2.94**	0.016	0.003	1.50	3.90	**0.26**	**0.26**
37	*Calophysus macropterus*	**2.59**	**3.25**	0.280	0.003	2.63	9.41	**0.06**	**0.25**
38	*Brachyplatystoma vaillantii*	**3.04**	**3.43**	**0.010**	**0.001**	1.02	7.75	0.80	0.80
39	*Hypophthalmus marginatus*	**3.00**	**3.06**	**0.002**	0.023	0.55	2.00	0.80	**0.17**
40	*Pygocentrus nattereri*	**2.89**	**2.79**	0.005	0.005	2.00	7.05	**0.27**	**0.27**
41	*Brycon melanopterus*	**2.50**	**2.52**	0.230	**0.002**	1.06	8.85	**0.05**	0.80
42	*Piaractus brachypomus*	**2.40**	**2.37**	0.012	0.052	1.40	8.30	**0.27**	**0.02**
43	*Hoplias malabaricus*	**3.41**	**3.48**	0.054	0.145	0.97	6.05	**0.28**	**0.15**
44	*Plagioscion squamosissimus*	**3.88**	**3.67**	**0.005**	0.085	1.02	7.99	0.80	**0.10**
45	*Triportheus* sp.	**2.43**	**2.89**	0.450	**0.032**	1.76	13.98	**0.17**	0.80
46	*Hypophthalmus* sp.	**2.50**	**2.56**	**0.012**	**0.000**	1.75	8.87	0.80	0.80
47	*Pimelodus* sp.	**2.48**	**3.05**	0.040	**0.039**	0.90	5.00	**0.36**	0.80
48	Other carnivorous	**2.88**	**2.67**	1.500	**1.305**	1.50	6.20	**0.60**	0.80
49	Other detritivorous	**2.04**	**2.20**	1.000	**0.505**	1.00	8.00	**0.27**	0.80
50	Other insectivorous	**2.92**	**2.99**	0.090	**0.142**	1.50	8.50	**0.17**	0.80
51	Other omnivorous	**2.63**	**2.77**	1.450	**0.515**	1.90	8.30	**0.58**	0.80
52	Other piscivorous	**2.66**	**3.44**	1.000	**0.048**	0.99	8.00	**0.53**	0.80
53	Other planktivorous	**2.10**	**2.66**	0.195	**0.401**	0.55	5.50	**0.06**	0.80
54	Other herbivorous	**2.00**	**2.24**	0.080	**0.001**	1.45	7.44	**0.04**	0.80
55	Animal detritus	**1.00**	**1.00**					**0.01**	**0.00**
56	Detritus	**1.00**	**1.00**					**0.10**	**0.49**

from a single research project that standardized the samples of all groups, allowing reliable comparisons between periods and avoiding problems on scales and aggregation of compartments (Abarca-Arenas and Ulanowicz, 2002; Angelini and Agostinho, 2005; Winemiller, 2007). As a result, the basic data set of the models has consistency and locally-oriented reflecting the ongoing environmental changes in the process of impoundment. This was also reflected and confirmed for both models in the PREBAL procedure, which showed the eco-physiological coherence in Ecopath models estimated here (Link, 2010; SM 4).

Damming considered here increased the ecosystem's respiration and consumption, reducing net production, transfer efficiency among Trophic Levels, and reducing total biomass of fish species by half. There was also an exchange of key species that were previously mostly non-fish compartments and became top predator fish, including *B. rousseauxii*, which was considered a key species in both periods. Fish species with an intermediate TL had their biomass reduced via top-down control, especially because of the increased biomass of non-migratory top predators (*Hoplias malabaricus* and *Plagioscion squamosissimus*). Noticeably, damming clearly reversed possible impact linkage among species, since one-third of indirect and almost one-half of direct (trophic) relations changed of signal, leading to unexpected turns in the system. Also, simulation revealed that increasing in catches strongly

Table 2
Familiar fishing for commerce and own consumption (t km-2 year-1); Landings in the main port of Porto Velho City, for the periods' pre (2010–2011) and post (2012–2013) dam implementation on the Madeira River (Brazil).

Group name	Familiar commerce		Familiar consumption		Landings		Total	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Turtles			0.182	0.1820			0.182	0.1820
Pinirampus pirinampu	0.002	0.0001	0.002	0.0003	0.024	0.001	0.028	0.001
Mylossoma duriventre	0.007	0.001	0.004	0.001	0.057	0.023	0.068	0.025
Prochilodus nigricans	0.007	0.001	0.003	0.001	0.042	0.024	0.053	0.025
Brycon amazonicus	0.013	0.001	0.001	0.0003	0.043	0.016	0.057	0.017
Brachyplatystoma rousseauxii	0.007	0.001	0.0002	0.00004	0.015	0.006	0.022	0.007
Brachyplatystoma filamentosum	0.004	0.001	0.0001	0.00003	0.009	0.006	0.013	0.007
Semaprochilodus insignis	0.003	0.0003	0.0003	0.00004	0.020	0.032	0.023	0.032
Pseudoplatystoma punctifer	0.002	0.0002	0.001	0.0001	0.006	0.008	0.009	0.009
Cichla pleiozona	0.007	0.0002	0.001	0.0001	0.009	0.011	0.017	0.011
Schizodon fasciatus	0.002	0.0001	0.001	0.0001	0.005	0.003	0.007	0.003
Brachyplatystoma platynemum	0.001	0.0004	0.0001	0.0001	0.009	0.001	0.010	0.002
Potamorhina latior	0.001	0.0002	0.0002	0.0001	0.017	0.007	0.018	0.007
Zungaro zungaro	0.002	0.0003	0.0001	0.00002	0.009	0.003	0.011	0.003
Hoplosternum littorale	0.001	0.000005	0.0003	0.00002	0.013	0.004	0.014	0.004
Astronotus crassipinnis	0.001	0.00004	0.0001	0.00001	0.004	0.002	0.005	0.002
Phractocephalus hemioliopterus	0.003	0.001	0.0001	0.0002	0.007	0.005	0.010	0.006
Pterygoplichthys spp.					0.002	0.003	0.002	0.003
Triportheus auritus	0.0003	0.00003	0.0001	0.00001	0.013	0.004	0.013	0.004
Colossoma macropomum	0.0004	0.0001	0.0002	0.0001	0.003	0.009	0.004	0.009
Arapaima gigas	0.002	0.0002	0.0001	0.0001	0.005	0.001	0.006	0.002
Calophysus macropterus	0.000004	0.000002	0.00002	0.00001	0.012	0.002	0.012	0.002
Brachyplatystoma vaillantii	0.001	0.0001	0.0004	0.0002	0.007	0.0002	0.008	0.001
Hypophthalmus marginatus	0.0002	0.00001	0.00003	0.000004	0.001	0.001	0.001	0.001
Pygocentrus nattereri	0.0001		0.0001	0.000003	0.003	0.003	0.003	0.003
Brycon melanopterus	0.0002	0.000004	0.00003	0.00001	0.001	0.001	0.002	0.001
Piaractus brachypomus	0.001	0.0001	0.0004	0.0001	0.003	0.002	0.005	0.002
Hoplias malabaricus	0.001	0.001	0.0003	0.0002	0.003	0.002	0.005	0.002
Plagioscion squamosissimus	0.0004	0.00002	0.0001	0.00001	0.003	0.002	0.004	0.002
Hypophthalmus sp.	0.0004				0.001		0.0014	
Other carnivorous	0.0014	0.0003	0.001	0.0002	0.006	0.001	0.008	0.002
Other detritivorous	0.0080	0.00003	0.001	0.00001	0.015	0.001	0.024	0.001
Other omnivorous	0.0034	0.001	0.002	0.0001	0.01	0.002	0.01	0.002
Other piscivorous	0.0058	0.0003	0.001	0.0001	0.01	0.005	0.02	0.005
Other planktivorous						0.0004		0.0004
Other herbivorous		0.0001		0.0003	0.0001	0.0003	0.0001	0.001
Total caught	**0.089**	**0.011**	**0.203**	**0.187**	**0.387**	**0.192**	**0.676**	**0.386**

Table 3
Attributes of the ecosystem maturity for the Ecopath models calculated for pre and post dam implementation on the Madeira River (Brazil). Changes: bold values increased and italic values decreased.

Parameter	Values		
	Pre	Post	Change
Sum of all consumption (t km^{-2} year^{-1})	362.71	1153.21	**3.18**
Sum of all *exports* (t km^{-2} year^{-1})	0.67	0.38	*0.57*
Sum of all respiratory flows (t km^{-2} year^{-1})	235.02	733.22	**3.12**
Sum of all flows into detritus (t km^{-2} year^{-1})	3951.05	3143.65	*0.80*
Total system throughput (t km^{-2} year^{-1})	4549.46	5030.46	1.11
Sum of all production (t km^{-2} year^{-1})	2111.87	1862.04	0.88
Gross efficiency (catch/net p.p.)	0.00	0.0002	1.00
Total net primary production (t km^{-2} year^{-1})	2056.72	1672.70	*0.81*
Total primary production/total respiration	8.75	2.28	*0.26*
Net system production (t km^{-2} year^{-1})	1821.70	939.48	*0.52*
Total primary production/Total biomass	0.21	0.17	*0.81*
Total biomass/Total throughput (year^{-1})	2.20	1.97	0.90
Total biomass (excluding detritus) (t km^{-2})	9996.31	9889.35	0.99
Total biomass of fish (t km^{-2})	8.93	4.51	*0.51*
Total catch (t km^{-2} year^{-1})	0.67	0.38	*0.57*
Connectance Index	0.11	0.11	1.00
System Omnivory Index	0.17	0.19	1.12
Finn Cycling Index (%)	39.83	32.73	*0.82*
Overhead (%)	59.16	69.07	1.17
Ascendency (%)	40.84	30.93	*0.76*
Mean trophic level catch	2.35	2.43	1.03
Transfer Efficiency (%)	7.80	4.83	*0.62*

impact on fish biomass in the post-dam model more than in the pre-dam model.

Environmental impacts from dam construction are expected to change Amazon freshwater ecosystems, resulting in physical, chemical, and biological alterations on many habitats down and upstream (Poff et al., 1997). Here, the changes unveiled in the attributes, indexes and trophic linkages indicated that the system under impoundment must be understood as another ecosystem. Despite new condition (post-dam) originated from pre-dam condition, features and interactions may change at least by half until other dams are placed upstream or downstream.

4.2. Trophic Level, food web control, and biomass change

Most fish biomass was concentrated in species with TL < 2.9 in pre-dam model, but in the post-dam model 89% of fish biomass were grouped in species with TL < 3.67. Species of highest TL and contribution of biomass in the post-dam model were traíra (*H. malabaricus*), pescada (*P. squamosissimus*), and curimatã (*P. nigricans*). Historically, these species had established in other dammed river systems in Brazil mainly during the formation of reservoirs (Cecilio et al., 1997), due to their generalist food habit (Kong et al., 2016).

Biomass of 24 fish compartments decreased over the periods, reducing the total biomass of fish by 50%. Reduction in total biomass after damming contrasted with the increase in biomass of invertebrate components, which triggered a change in the diet and consequently an increase in TL for some opportunistic species, such as *M. duriventre*

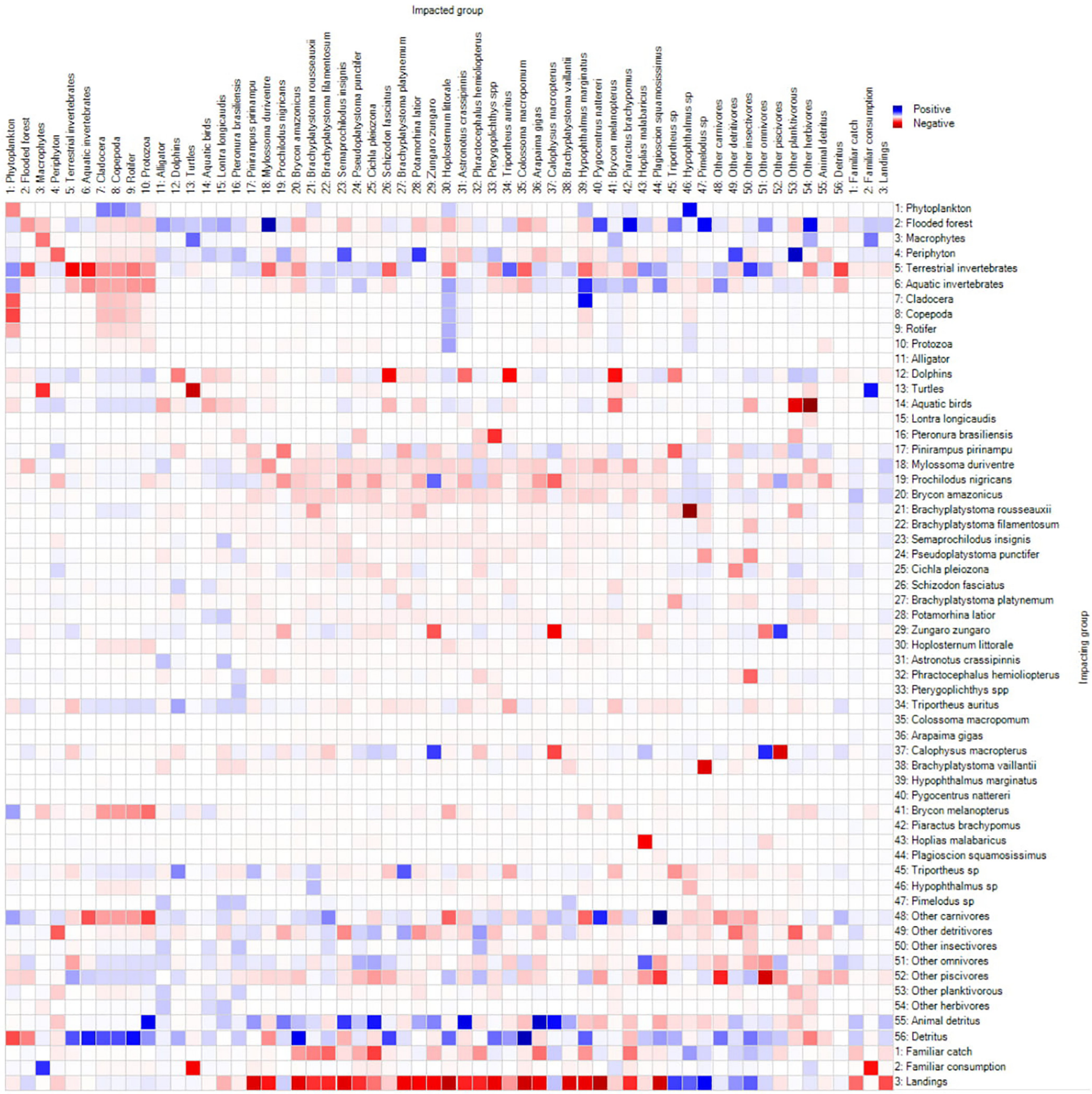

Fig. 2. Matrix Trophic Impact (MTI) of the Madeira River model for the period pre dam implementation (2010-2011).

(Melo et al., 2019) and *C. macropomum*. However, the growth of piscivorous and opportunistic species that better adapt to changes in tropical impounded areas (Agostinho et al., 1999; Gubiani et al., 2010; Luz-Agostinho et al., 2006; Pereira et al., 2016) resulted in larger biomasses for groups with TL > 3.0 in the post-model. Accordingly, after damming the trophic pyramid has a larger base (more invertebrates) and is longer (have larger predator biomass), but has lower biomass of fish with intermediate TLs (total biomass of the fish).

Thus, the increase of invertebrates biomass after damming was not enough to increase their consumers' biomass that seems to be top-down controlled by opportunistic piscivorous species, such as *H. malabaricus* and *P. squamosissimus*. These opportunistic species still benefit from the reduction in large piscivorous and migratory catfish. The pattern of reduction in general biomass of fish due to an increase in the number of piscivorous species, confirms what was previously observed to reservoirs in the Brazilian semi-arid region (Paiva et al., 1992).

The reduction of biomass and capture is one of the most negative impacts of hydroelectric reservoirs building, markedly to long-distance migrants species, which have migratory routes disrupted by damming (Fearnside, 2016). In Amazonian rivers a large number of fish species are migratory, swimming hundreds of kilometers, especially for reproduction (Barthem and Goulding, 1997). In Madeira River, damming effects upon migratory species are essentially harmful for many riverine communities that rely on these fish species (Doria et al., 2012; Santos et al., 2018). As for communities in our area of study, migratory species play important roles for food security of numerous populations (Castello et al., 2015; Doria et al., 2018) since they are valuable source of income and subsistence (Doria and Lima, 2015; Ferreira et al., 2014; Winemiller et al., 2016), directly affecting the fishing yield and income (Acreman et al., 2014). As observed here, the reduction in capture per

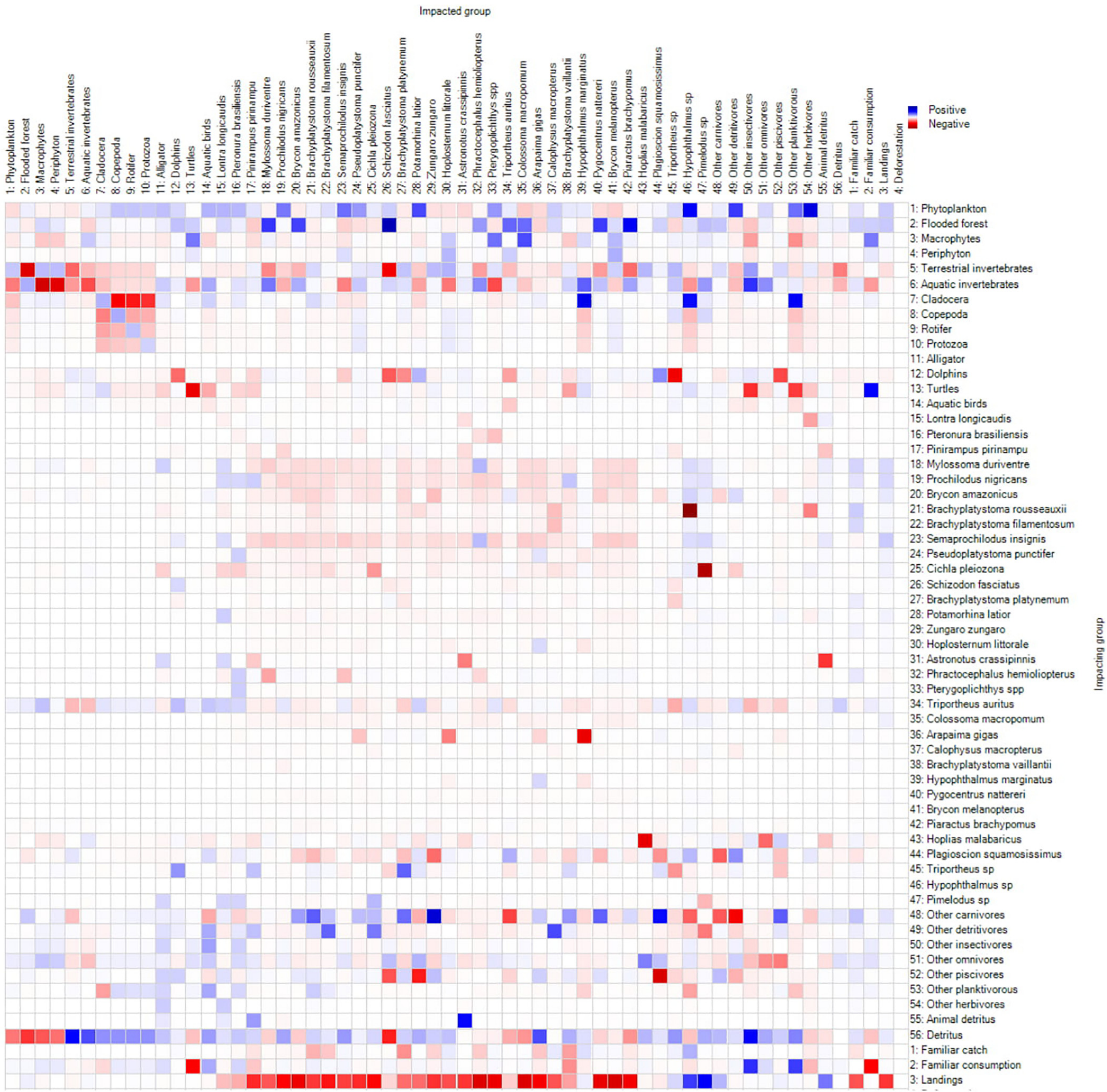

Fig. 3. Matrix Trophic Impact (MTI) of the Madeira River model for the period post dam implementation (2012-2013).

Table 4
The number and relative frequency of signals (positive and negative) of direct (feeding) and indirect relations between both Matrices of Impact Trophic, pre and post dam implementation in Madeira River (Brazil).

Post dam	Direct relationships (Trophic)	Indirect relationships	Total
Keep positive	192	633	825
Keep negative	23	1341	1364
Total	*215 (53.3%)*	*1974 (65.4%)*	*2189*
Changes to negative	74	559	633
Changes to positive	114	486	600
Total	*188 (46.7%)*	*1045 (34.6%)*	*1233*

unit of effort (CPUE) of migratory species also happened in other Amazonian impounded areas, where migrators practically disappeared (Santos and Oliveira Jr., 1999).

Piscivorous species and top predators, such as large catfish, are important in stabilizing food webs (Lima, 1998) because they influence interspecific interactions (Novak and Wootton, 2008; Pereira et al., 2016). The simulations carried out here reflected such relevance, since in the post-dam model (which had lower biomass of migratory predators) the decrease in almost all groups was more pronounced than in the pre-model, showing the importance of predators to the stability of the system, and that models are mimicking what has been observed in other regions.

The high proportion of recycled flows in the system can be a sign of stress in the environment, but also reinforces the idea that these environments are resilient and can recover rapidly (Christensen et al.,

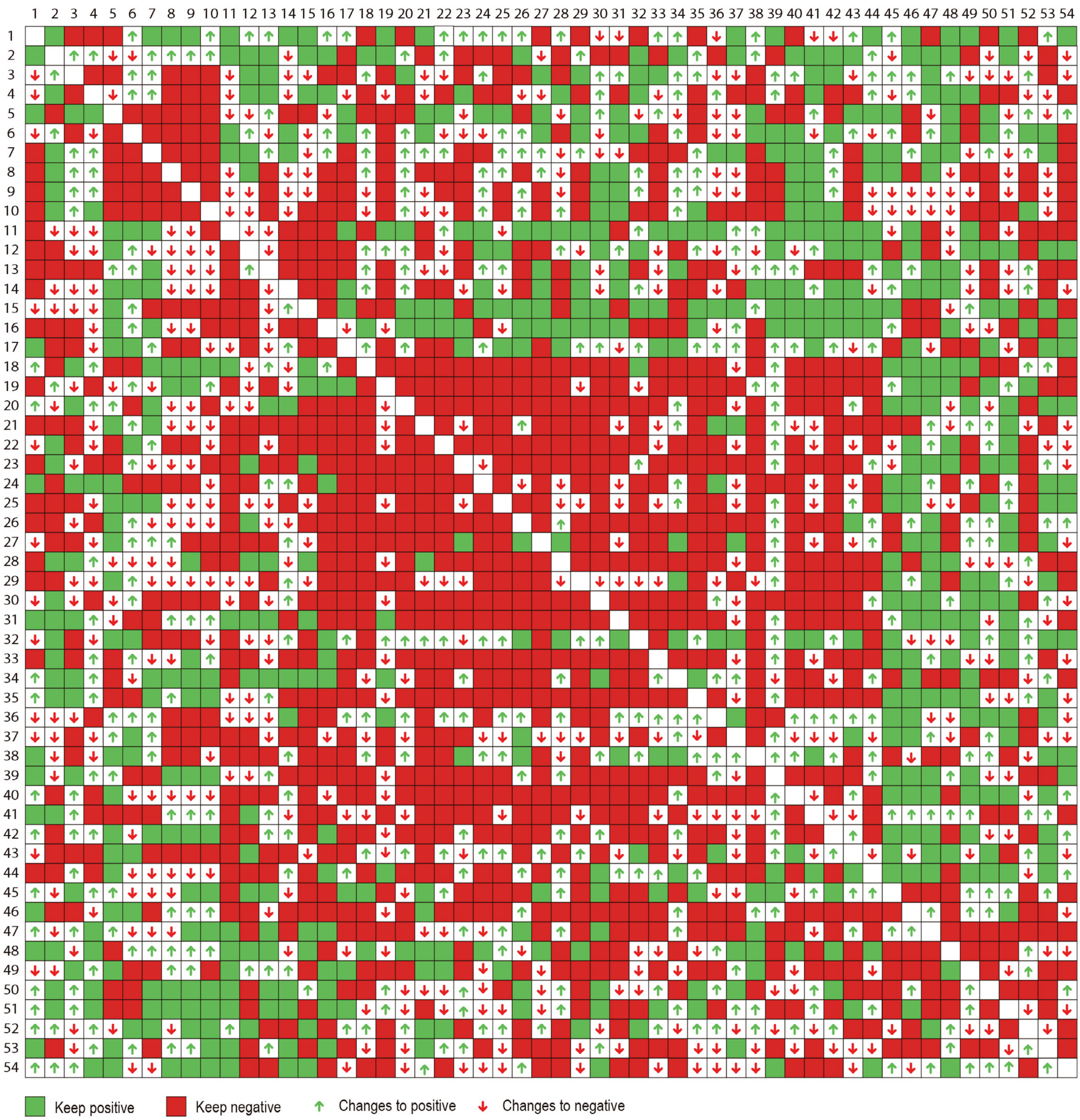

Fig. 4. Comparison between the Matrices of Trophic Impact in the pre and post dam periods of the Madeira River (Brazil). Group names can be viewed in Table 1.

2005; Finn, 1976; Odum, 1969). Moreover, the role of detritus is greater in the post-model, which has greater detritivory when compared to the pre-model. The index of omnivory also increased in the post-dam period, probably related to the species food plasticity and changes in food resource availability (Agostinho et al., 2008; Junk et al., 1989). The increases in respiration and consumption flows led to the reduction of fish biomass (see above), but without affecting the invertebrates that appear to be the group most favored by the dam.

4.3. MTI and key species (groups)

The direct and indirect trophic interactions among groups were largely modified after damming, since almost 46% of direct impacts and 34% of indirect ones interchanged between positive and negative. The fact that positive direct relationships increased by 50% to 70% shows that the larger base of the trophic pyramid (greater invertebrate biomass) can likely increase the food web growth by modifying one of its elements, such as Cladoceras and Copepods, which had higher positive impacts in the post-model. It seems that despite higher influence of top-down control because of larger number (and biomass) of top predators reducing the total fish biomass in the post-model (($TL > 3$; see above), this new ecosystem (reservoir) will have a chance to increase its biomass, especially considering the feeding plasticity of the fish species (Melo et al., 2019).

Besides, MTI showed that the key species controlling linkages and biomass in the food web were all replaced from pre- to post-dam model,

Table 5
Ranking of the main key species (compartments) of the trophic models of the Madeira River (Brazil) in the periods' pre (2010–2011) and post (2012–2013) dam implementation. The top five values of each ranking are highlighted in bold.

Species/Compartments	Pre	Post
Aquatics bird	**1°**	34°
Brachyplatystoma rousseauxii	**2°**	**1°**
Cladocera	**3°**	**5°**
Brachyplatystoma vaillantii	**4°**	46°
Zungaro zungaro	**5°**	45°
Otters	6°	15°
Dolphins	7°	6°
Copepoda	8°	22°
Pinirampus pirinampu	9°	28°
Calophysus macropterus	10°	43°
Cichla pleiozona	27°	**4°**
Arapaima gigas	46°	**2°**
Other piscivorous	19°	**3°**
Triportheus spp.	24°	7°
Plagioscion squamosissimus	44°	8°
Semaprochilodus insignis	36°	9°
Other carnivorous	22°	10°

in exception to *B. rousseauxii*, which was the second key species in the pre-dam model and became the headmost key species in the post-dam model. Given the aforementioned importance of catfishes as source of food security for numerous populations, their high market value (Acreman et al., 2014; Ferreira et al., 2014; Castello et al., 2015; Winemiller et al., 2016; Santos et al., 2018) and the wage decline of

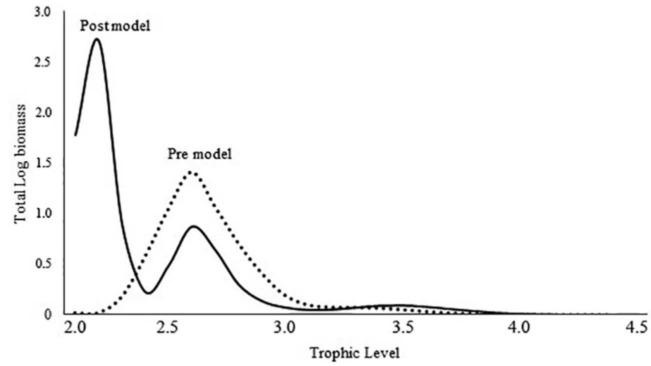

Fig. 6. Total (log) biomass of the trophic levels in pre and post dam models for Madeira River (Brazil).

capture per unit of effort (CPUE) of catfishes in impounded areas of Amazon (Barthem and Goulding, 1997; Fearnside, 2016) the unveiling of *B. rousseauxii* as leading key species is worrisome and shed light not only on the ecological impact of Madeira River damming, but on its potential economic and social damage.

Mixed Trophic Index had already been used to compare an ecosystem over a 50 years (Kong et al., 2016), but this approach did not show relevant changes. Similarly, results found by Colvin et al. (2015) in a study of a eutrophic lake aiming to understand the role of just two species was not revealing. Ortiz et al. (2015) compared two similar ecosystems, also using MTI, but their comparison also remained individual for some components' behaviors. In this present study, we

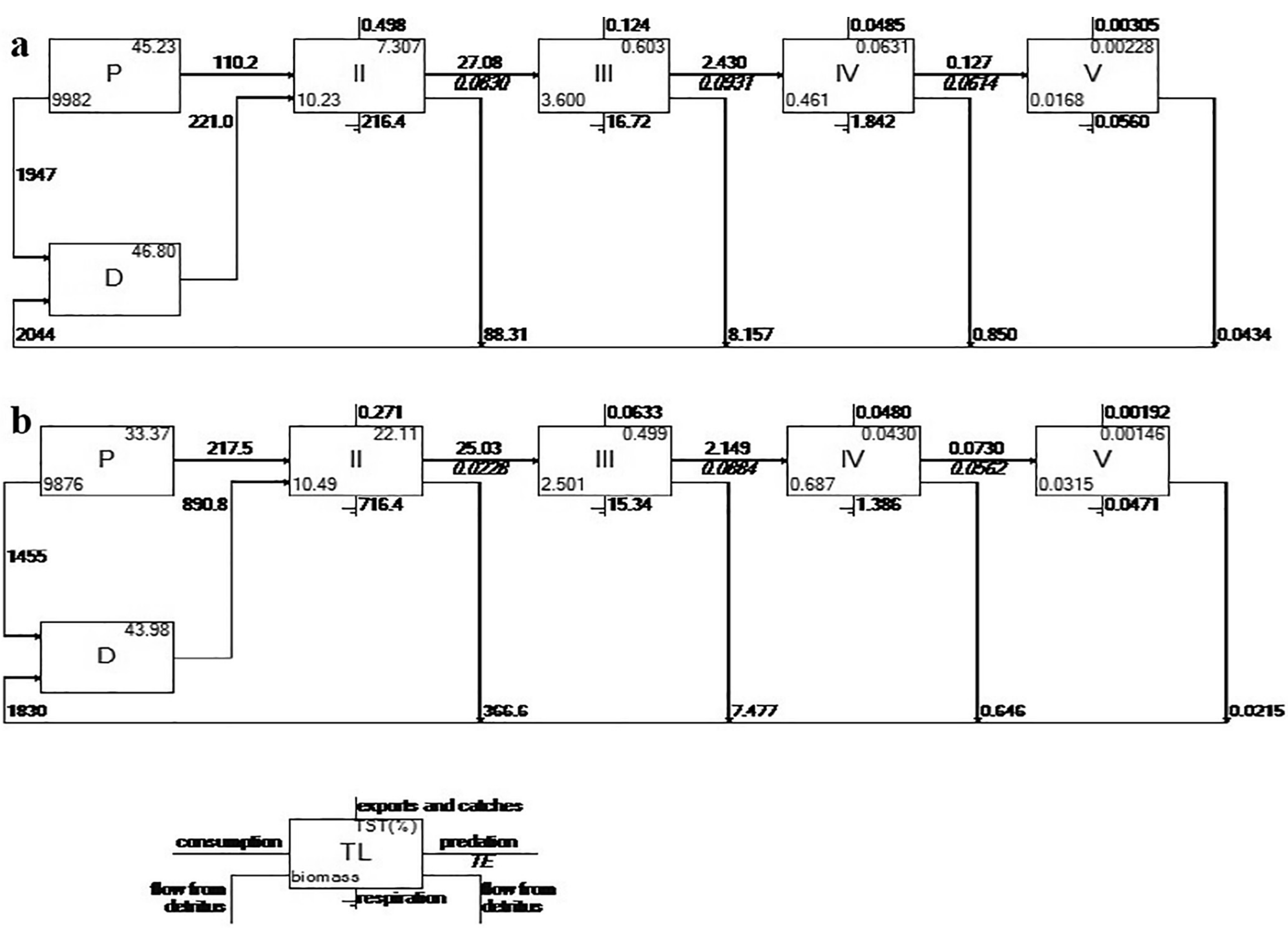

Fig. 5. Lindeman Spine for Madeira River (Brazil) in the periods pre (a) and post (b) dam implementation.

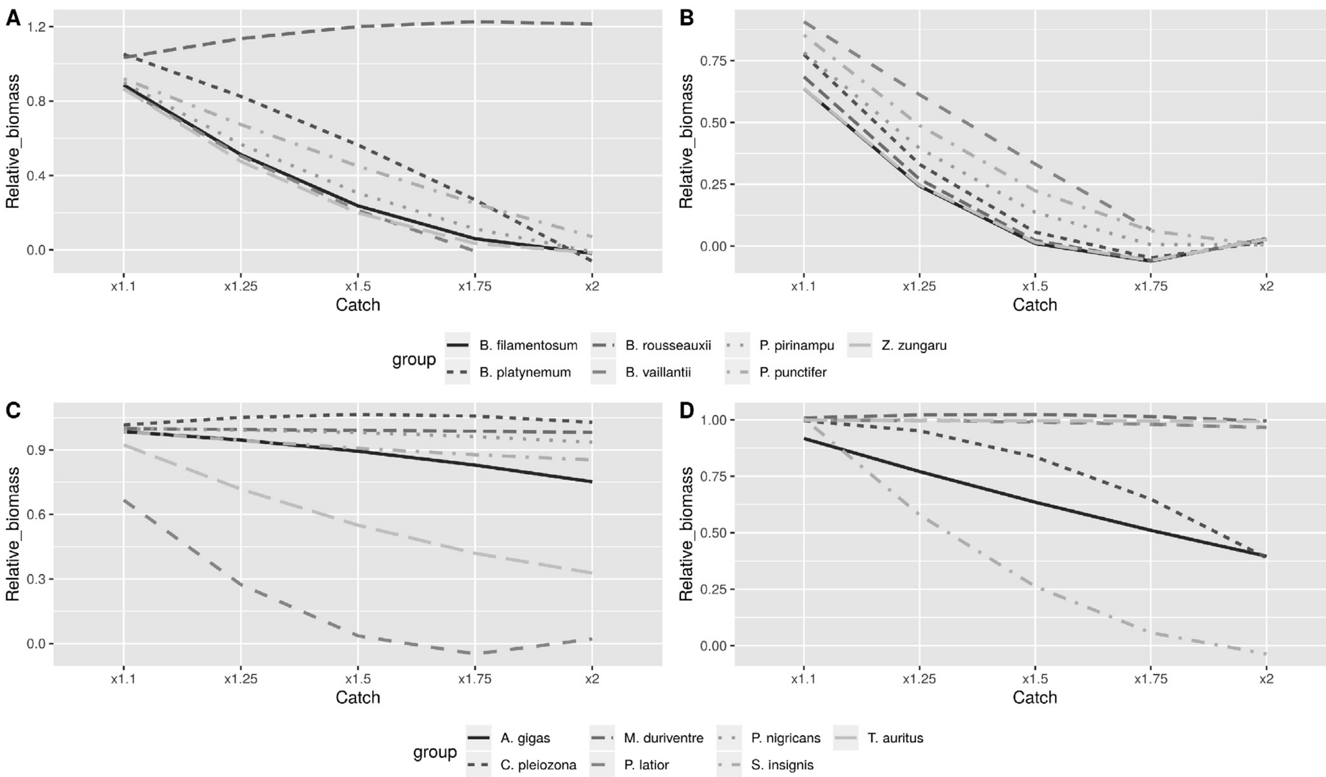

Fig. 7. Variations in the relative biomass of the functional groups in the Madeira River models with increased fishing effort for the periods' pre (2010 and 2011) and post (2012 and 2013) dam implementation.

improved this approach, indicating the signal changes and quantifying, in an overall way, the magnitude of changes caused by dams.

The use of MTI as applied here to understand the changes in trophic interaction within the ecosystem under damming is trailblazing. It first provided compelling evidence of shifting in half of all possible interactions among species. Second, it also indicates the compartments that drive the most of the changes in compartments at the whole system. Moreover, in the context applied here, MTI also allowed to find out if key species also changed under the system impoundment. Lastly, but importantly, biomass estimates used here assure reliance on the MTI responses, since biomass is the most sensitive parameter to the modeling robustness.

5. Conclusions

The EwE models developed in the Madeira River displayed the changes caused by damming in a large aquatic tropical Amazonian ecosystem. Results will be useful to inform and avert the effects of future reservoir projects in the Amazon. Yet the approach used here provided an overall understanding of the new ecosystem formed by the application of the EBFM approach, which is still little explored in freshwater ecosystems. One evident example is the need for catfish species monitoring since the post-model showed that their catches declined and the species were replaced by others better adapted to the new environment.

As future recommendations, is important to bear in mind that these fisheries have to be monitored since the environment formed in the post-dam phase appears to be less resilient when compared to the pre-dam. However, it is worth mentioning that the prediction of impacts on fish and fisheries is still complex, as shown by the inversion of the trophic relationships after dam construction. In this way, the ecosystem context of these results, and the fact that they are pioneers in assess Amazonian damming can help the local managers and government to understand the impoundment effects and simulate changes in catches to foresee future impacts of reservoirs on Amazon.

CRediT authorship contribution statement

Maria A.L. Lima: Conceptualization, Data curation, Formal analysis, Writing - original draft. **Carolina R. Doria:** Funding acquisition, Project administration, Resources. **Adriana R. Carvalho:** Visualization, Writing - original draft, Writing - review & editing. **Ronaldo Angelini:** Conceptualization, Supervision, Validation, Writing - original draft.

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

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106162.

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