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BRAZIL'S BELO MONTE HYDROELECTRIC PLANT: IMPACT ON CO-OCCURRENCE OF FISH SPECIES AND IMPLICATIONS FOR ARTISANAL FISHING

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ABSTRACT

The operation of large hydroelectric dams, such as Belo Monte in the Brazilian Amazon, significantly disrupts local freshwater ecosystems, impacting the socio-economic fabric and food security of dependent communities. To investigate and simulate future dam-induced impacts on fish that are important for subsistence, this study leveraged subsistence fishing data from four areas of the Xingu River: the reservoir, upstream, the de-watered reach, and downstream. Using network analysis and graph theory, we examined the temporal and spatial variations in fish species composition, focusing on species that co-occur in fishing catches. The analysis revealed marked changes in species diversity and catch composition, with substantial shifts in heavily altered regions. For instance, in the de-watered reach, traditional species such as curimatã (Prochilodontidae) were replaced by others like pacu (Serrasalmidae), reflecting ecological shifts and the replacement of a detritivorous species by an omnivorous one. Directed simulations were employed to project the future dynamics of these changes, which suggested significant alterations in species co-occurrence and their ecological roles (centrality) within fishing networks. These projected changes were especially pronounced in the de-watered reach, where species such as pacu, pescada (Sciaenidae), and tucunaré (Cichlidae) retained central positions despite ongoing shifts in species composition. Simulation of species loss further highlighted potential changes in species interactions and their roles within the ecosystem. These results illustrate the profound transformations in fish diversity and emphasize the critical need for strategies to mitigate these impacts, ensuring the resilience of local fishing communities.

KEYWORDS: Hydroelectric dams; Fish diversity; Network analysis; Amazon; Fisheries.

INTRODUCTION

Fishing provides animal protein and other essential nutrients globally to approximately 3.3 billion people, accounting for a substantial portion of per capita consumption, particularly in developing nations (FAO, 2020; Robinson et al., 2022). Inland fisheries, which are often overshadowed by marine fisheries, support the livelihoods of countless communities, especially traditional ones in developing regions (Lam et al., 2020). However, the health of freshwater ecosystems is under threat. Significant transformations have been rapidly occurring, especially in tropical river systems, due to the construction and operation of hydroelectric dams, among other factors (Winemiller et al., 2016). River damming, regardless of technological sophistication, disrupts water flow, and what were once fast-flowing water environments frequently experience reduced river dynamics over time following the interruption of the river continuum (Abrial et al., 2021; Agostinho et al., 2016; Haghighi & Kløve, 2013; Sabo et al., 2018). This leads to disrupted fish migration, habitats loss, the introduction or replacement of species, and alterations in the physical and chemical characteristics of the water (Almeida et al., 2020; Fitzgerald et al., 2018; Pereira et al., 2023).

Disruption of the river continuum, coupled with the lack of connection between lentic and lotic environments, triggers diverse responses among fish species, shaped by both their biological traits and the surrounding environment. Observations across different river segments show extensive ecological change that affect the sustainability of fisheries and, consequently, the livelihoods of dependent communities (Almeida et al., 2020; Arantes et al., 2019; De Fries et al., 2018; Hauser et al., 2018; Lopes et al., 2023).

An effect of damming is the alteration in fishery resource diversity, resulting from shifts in community abundance, species composition, functional traits, and local extinctions, which collectively impact the fishing system (Agostinho et al., 2008, 2016; Arantes et al., 2019; Reid et al., 2019; Santos et al., 2018). The response of fisheries varies by the location with respect to the dam (e.g., the reservoir, downstream from the dam, etc.) and by the time elapsed since the dam’s construction and the beginning of its operation (Keppeler et al., 2022). Habitat losses and gains, especially in the initial years (Almeida et al., 2020), and the blockage or inhibition of fish migration, limit the distribution and trophic functions of the fish community (De Fries et al., 2018; Hauser et al., 2018). While reservoirs often sustain fish yields initially, the species contributing to these yields frequently differ from those present before the dam's construction (Leite Lima et al., 2020).

Changes in key fisheries species carry social and economic repercussions that are yet to be fully understood. The introduction of novel species and/or the loss of others may disrupt local consumption habits and impact food security (Monterrosa et al., 2020). This can lead to a decrease in market prices, affecting the income of fishing communities (Leite Lima et al., 2020). Market dynamics are also influenced by these changes, with fluctuating prices affecting not only fishers but also consumers and related industries (Leite Lima et al., 2020). The cultural significance of certain fish species adds another layer of complexity because abrupt alterations may lead to the loss of longstanding fishing traditions and intergenerational knowledge (Arantes et al., 2019). These shifts in fisheries present challenges to the conservation and management of fishery resources, highlighting the need for sustainable fishing practices to mitigate ecological imbalances (Jimenez et al., 2021). However, the practicality of adopting such practices may be constrained by the extent to which local livelihoods are impacted.

The significant adverse impacts on fish and fish-dependent livelihoods would caution against further dam implementations. Yet, there has been a rapid and persistent increase in the number of dams in tropical regions (Bertassoli et al., 2021). The Amazon basin, recognized as the world's largest biodiversity hotspot, exemplifies the dichotomy between biodiversity and threats (Jézéquel et al., 2020). While the Amazon is well-known for its role in maintaining biodiversity and climate stability, large-scale hydroelectric projects continue to proliferate, with over 300 planned in addition to existing ones (Almeida et al., 2019; Finer & Jenkins, 2012; Latrubesse et al., 2017; Winemiller et al., 2016).

Although widely criticized for their environmental and climatic impacts (Bertassoli et al., 2021), the social impacts of dams are less often considered, especially because their burden lies on impoverished riverine populations, which are especially vulnerable to loss of their fisheries and subsistence (Fearnside, 2020; Lopes et al., 2023). This means that, while we recognize that threats exist, our comprehension of the processes and their consequences is developing at a slow pace, especially concerning socio-economic changes such as impact on food security, due to the loss of key species (Asche et al., 2018; Jézéquel et al., 2020; Reid et al., 2019).

This study focuses on the Belo Monte Dam, the largest operational dam in the Amazon in terms of installed capacity and the fourth largest dam in the world. To analyze how these changes influence the formation of space-time fish networks, we explore species co-occurrence patterns in fish species classified based on their local or vernacular names in catches. We assessed how these patterns have evolved post-dam construction and according to the proximity to the dam of fishing locations. Anticipated outcomes included the gradual disappearance of certain fish species, especially in the upstream and de-wateredreaches. In the upstream reach, increased sedimentation contributes to pronounced ecological shifts, resulting in a reduction in the presence of targeted fish species (Keppeler et al., 2022). Concurrently, diminished water flow in de-watered areas affects critical processes such as migration and spawning (Keppeler et al., 2022). We also used a node-removal sensitivity analysis to investigate the potential impact of the loss of core species and to analyze the subsequent restructuring of networks. This analysis allows us to grasp how specific species' significance in the fishery sphere changes due to dam-related impacts, facilitating more effective mitigation and compensation strategies for affected fishing communities. Our study broadens our understanding of the effects of dams by considering the social and economic intricacies caused by dam-induced changes in fishery networks. By acknowledging dams' extensive effects on food security, our results establish an understanding of the species present in local fisheries and their shifting importance over time and space in affected areas. Documenting the dramatic ecological and social impacts of the Belo Monte Hydropower Project adds to the growing weight of evidence supporting a change in development policies to abandon all plans for future large dams in the Amazon (Fearnside et al., 2021).

METHODS

Study area

This study was done using fishing data from the area affected by the Belo Monte Dam, which is located on the Xingu River in the Brazilian Amazon. Belo Monte was implemented in a specific section of the Xingu River known as "Volta Grande do Xingu" (Big Bend of the Xingu), which extends for about 130 km. The distinctive morphology of the Volta Grande do Xingu, unique in the Amazon, is characterized by its rocky channels and rapids (Sawakuchi et al., 2015). The complexity of this freshwater system, which combines morphological features with significant water-level variations throughout the year (dry and wet seasons), has resulted in an extraordinarily high level of endemic biodiversity (Zuanon et al., 2021).

The construction of the Belo Monte Hydroelectric Power Plant (HEP) began in 2011, affecting 11 municipalities (counties) in the state of Pará. This is a run-of-the-river (ROR) dam, in which the plant consists of two dams (Pimental and Belo Monte) connected by a diversion channel (Sawakuchi et al., 2015; Keppeler et al., 2022). Belo Monte is the main dam, accounting for 98% of the electricity production. The ROR design allows for a smaller reservoir, which is advertised as being less environmentally damaging, although studies show that this type of infrastructure has not resulted in benefits (Baird et al.,2024).

In addition to being ecologically unique and marked by high diversity and endemism, particularly of fishes (Fitzgerald et al., 2018), the region is also home to various Indigenous groups (Fearnside, 2017a, b). The region includes both Indigenous lands and protected areas for biodiversity (the latter are known as "conservation units" in Brazil), some of which are in the "sustainable-use" category that allows the presence of traditional riverine communities. Other riverine communities outside Indigenous lands and conservation unitgs also share a long history of river dependence, particularly through their use of fish both for subsistence and sale (Poissant et al., 2024).

For this study, monitoring data were condensed into four primary areas influenced by the Belo Monte HEP:

1. "Upstream" refers to the location situated above the dams and, thus, upstream of the reservoir.
2. "Reservoir" refers to the body of water created by the Pimental and Belo Monte Dams.
3. "De-watered reach" is a stretch of about 130 km where the flow of the river is significantly reduced (between 20 and 30%, depending on the season) (Baird et al.,2024), encompassing the Volta Grande do Xingu. In this section, the river flow is diverted into a channel to power the turbines (Fitzgerald et al., 2018).
4. "Downstream" refers to a 171 km after the river flow is reinstated below the Belo Monte Dam (Fitzgerald et al., 2018).

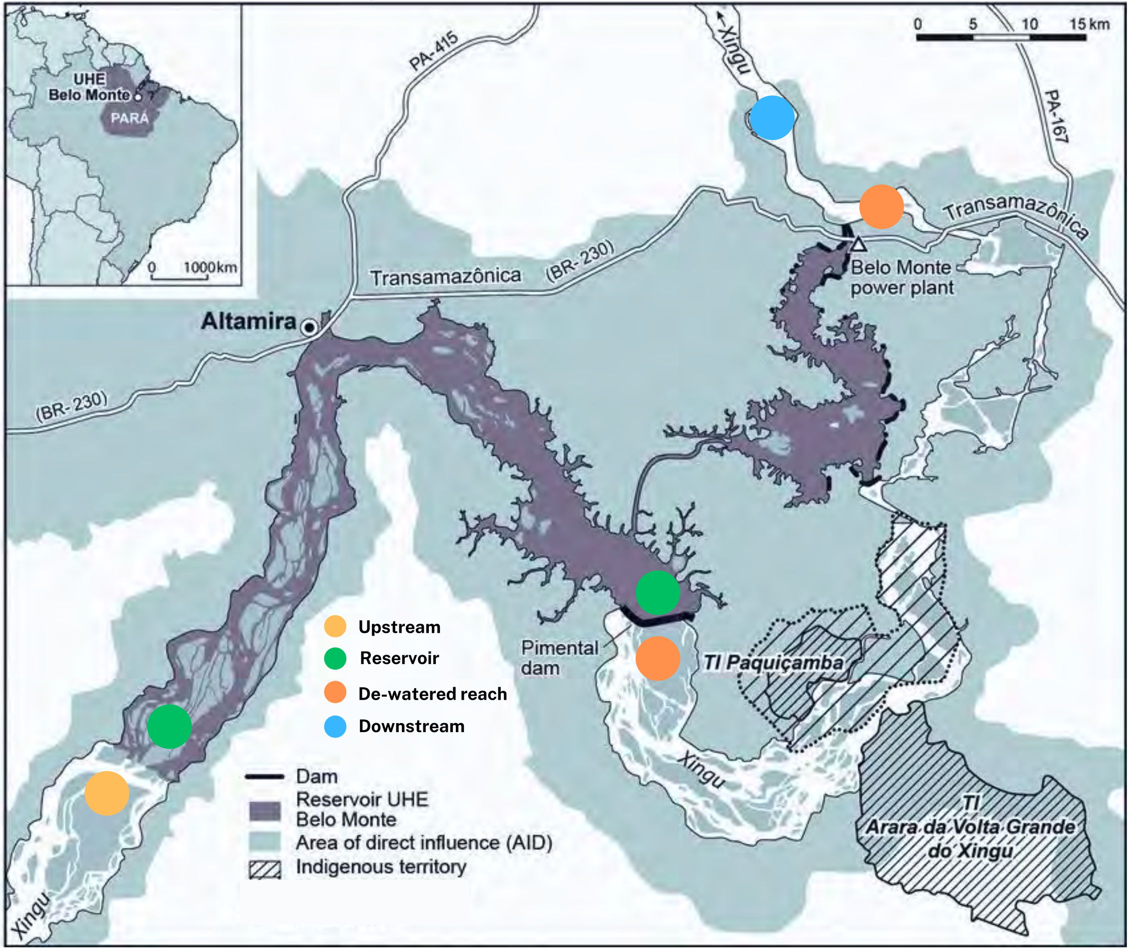


Fig. 1 - Location map of the Belo Monte hydroelectric plant, with selected sections marked by colored points.

Following the installation of the HEP, significant changes have been occurring in all sections. The increased sedimentation upstream, due to reduced water velocity, is expected to reshape the floodplains at the confluence of Xingu with other rivers (i.e., the Iriri River) (Zuanon et al., 2021). In the reservoir, water storage has led to permanent flooding of the islands and tributaries of the Xingu River. The influx of water in the reservoir directly influences increased sediment deposition, changes in water temperature, and other associated factors (Zuanon et al., 2021).

The de-watered reach, characterized by unique biotic and abiotic features, is considered to be the most impacted. The rerouting of river flow for reservoir creation has significantly decreased water input to this area. Consequently, this alteration undermines its function as an ecological corridor, substantially impacting its biodiversity and ecological connectivity (Zuanon et al., 2021).

Lastly, downstream of the Belo Monte HEP, the water level remains nearly unchanged. However, the possibility of erosion and sediment transport downstream is heightened due to sediment restrictions in this section (Zuanon et al., 2021).

Fishing Database

The data used in this study depict the subsistence fishing monitoring conducted by the Consórcio Norte Energia SA, the operating company of the Belo Monte HEP. Monitoring is required by the Brazilian environmental agency (IBAMA) and should continue indefinitely. The regions and settlements to be monitored were selected based on information gathered during the environmental impact assessment, done before construction, in addition to accumulated knowledge of previous large dams in the Amazon and elsewhere (Winemiller et al., 2016). These data are regularly submitted to IBAMA and become publicly available. The recorded information includes the catch of each fish group (fish identified by their vernacular names), the power plant's influence areas, and the year of recording. All data were collected along the Xingu River, spanning the stretch from the municipalities of Altamira (upstream from the dam) to Porto de Moz (downstream) (Fig. 1).

For comparative purposes, the data were divided into pre-operation and operation periods. However, this does not fully correspond to a *before and after* study design because the monitoring started only when the dam construction began, and thus covers a region already under impact. The pre-operation period corresponds to 2012 to 2015, whereas the operation period encompasses 2016 to 2020, although the turbines started operating partially. It was only at the end of 2019 that all 18 turbines in the main powerhouse were in full operation. Fish captures are recorded only by their vernacular names, which means that a single vernacular name might include multiple scientific species (e.g., tucunaré, known to sports fishers as "peacock bass," includes at least three species in the genus *Cichla,* in the family Chiclidae). The genera and families of the other major commercial fish groups are: acará (*Geophagus*, Chiclidae), aracu (*Leporinus*, Anostomidae), acari amarelinho (*Baryancistrus*, Locariidae), ariduia (*Prochilodus*, Prochilodontidae), curimatã (*Prochilodus*, Prochilodontidae), pacu (*Myleus* and *Myloplus*, Serrasalmidae), pescada (*Plagioscion*, Sciaenidae), pirarara (*Phractocephalus*, Pimelodidae), and surubim (*Pseudoplatystoma*, Pimelodidae). We will refer to these vernacular names as "species" or "species groups" (*Table S1*).

The diverse geomorphological characteristics of the regions impacted by the dam give rise to significant variation in fishing practices. According to data from this study, fishing trips range from 1.1 and 1.8 days in duration, varying across locations and time periods (2012-2015 and 2016-2020). Fishers use various types of small boats, including motorized boats, paddled canoes, 'rabetas' (small longtail motorized canoes), 'voadeiras' (small aluminum motorboats), and they often fish on foot as well. Among these, the 'rabeta' is the most commonly used, particularly in the upstream, downstream, and reservoir areas. Regarding fishing gear, handlines are the most frequently employed, followed by gillnets, which are especially prevalent in the downstream reach. In terms of fishing environments (rivers, lakes, streams, and floodplain lakes), rivers stand out as the most commonly used across all reaches, while lakes are the least represented, occurring specifically in the de-watered reach. These findings highlight the continuity of fishing practices in the regions affected by the dam, with variations depending on the area and period under analysis.

Data analyses

We applied graph theory concepts to understand how fishery composition has been changing over time and according to the regions subjected to different effects of the dam. Network analysis was used to establish a non-trophic relationship among the subsistence fish catches and to examine the underlying network structure of co-occurrence connections. Here, networks are represented by nodes (species) and edges (connections between species). Patterns of fish co-occurrence were examined using adjacency matrices for each region and period. Data matrices were organized to create simple and directed networks. Weighting was based on the captured biomass (kg) so that the parameters used considered how much of one species was captured in co-occurrence (i.e., in the same fishing trip) with another.

The relationship between each pair of nodes was identified through a link, with the origin of the co-capture determined by the direction of the link (Pocock et al., 2016). The analysis defines the main species for each period and region based on both the number of species co-captured simultaneously and the biomass (kg) captured over all fishing events during the period. Therefore, the arrow points from the main species to the other concurrently captured species, indicating the direction of co-capture. Directionality is indicated by an arrow pointing to the concurrently captured species. Each edge (node) was weighted by the biomass (kg) across all fishing events over time (Marai et al., 2019; Pocock et al., 2016). The node size represents the relevance of the speciesin the subsistence capture network based on the sum of biomass-weighted links flowing to or from each species (i.e., node strength or weighted node degree). Data were normalized to indicate relevance rather than raw values. In the normalization process, the minimum value for each species was transformed to 0, the maximum to 1, and other values were scaled accordingly between these limits (Ospina-Alvarez et al., 2022).

Parameters for co-occurrence network analysis

Centrality measures were used to quantify the significance of species and their interconnected relationships (Hansen et al., 2020; Ospina-Alvarez et al., 2022). Here, for each pair of co-occurring species, the number of co-captures that occurred in each period was obtained and summed. Thus, a value was estimated for each species pair per period. In a co-occurrence network, some species are essential for the network's structure because they are connected to critical species in the network and, in turn, do not have other relevant connections.

We computed five standard centrality measures for the topological structure of the co-occurrence network: 1) Eigenvector Centrality (Hansen et al., 2020), which measures the influence of a node within a connected network by considering the relative scores of each node. In essence, nodes connected to others with higher values are considered to have greater centrality within the network; 2) Edge Strength (Freeman, 1977), which quantifies paths between species groups, emphasizing connections in networks with weak links, where the shortest paths between different groups rely on a few short edges; 3) Average Distance Between Nodes (Pocock et al., 2016), which identifies the shortest path between any two species groups; 4) Graph Density (De Nooy et al., 2018), which assesses density and the maximum ratio of connections, reflecting network resilience. Higher density implies more connected species groups, but it is inversely proportional to network size, with added groups potentially increasing connections but facing limitations regarding species richness; and 5) Average Degree (De Nooy et al., 2018), which is closely tied to density, represents the number of connections by a species group. The network's average degree is double the total connections divided by the number of species groups.

Future scenarios of co-occurrence networks

We used the co-occurrence networks for the 2016-2020 period, which is the more recent one, in each region to project new networks in the future, by simulating the loss (removal) of central groups (Figure 2). The objective was to demonstrate how co-occurrence patterns change after the loss of a group of species that is considered to be important by the fishing community, i.e., the one that they have been catching the most. We conducted these projections up to five times for each region. In each iteration, we removed a single species based on the normalized eigenvector centrality value and recalculated the parameters (Figure 2).

The "netdist" function in the *igraph* package in R (Ali et al., 2014) was used to calculate distances between weighted networks. The dissimilarity metric only considers networks with the same number of nodes to calculate the distance. This measure hinges on the evaluation of subgraphs referred to as "graflets."

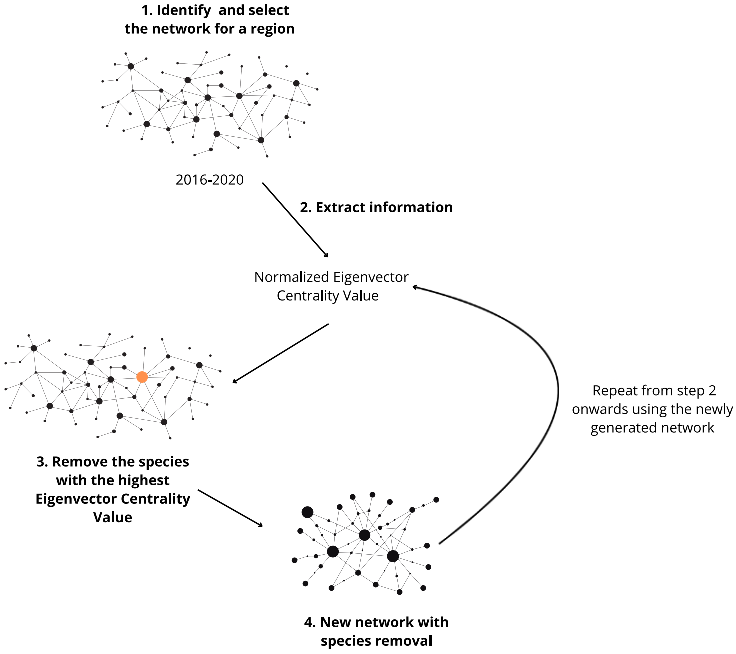


Fig. 2 - Step-by-step procedure for generating simulated networks.

Graflets are randomly selected non-isomorphic connected subgraphs containing 3, 4, or 5 nodes from each of the networks under consideration. The "netdis" measure leverages the comparison of these graflets to quantify dissimilarity, providing a nuanced perspective on the structural distinctions between the networks (Ali et al., 2014; Pržulj, 2007). The result of the comparison between the graflets of the networks ranges from 0 to 1, where 1 represents identical distribution networks and 0 represents distinct distribution networks (Ali et al., 2014; Pržulj, 2007). In this study, we chose a conservative approach for generating the subgraphs, using only those composed of 5 nodes because the limited data could potentially overestimate or underestimate the results.

Statistical Packages

All analyses were conducted using the R Statistical language version 4.1.2 (R Core Team, 2021) and the following packages: "igraph" (Csárdi et al., 2024), "ggrepel" (Slowikowski, 2023), "networktools" (Jones, 2023), "ggplot2" (Wickham, 2016),"plyr" (Wickham, 2016), "dplyr" (Wickham, 2016), "ggraph" (Pedersen, 2022), "RColorBrewer"

(Neuwirth, 2022), "scales" (Wickham, 2016), "ggpubr" (Kassambara, 2023), "rockchalk" (Johnson, 2022), and "NetEMD" (Xu & Reinert, 2019).

RESULTS

Trends in the Co-occurrence of Species in Subsistence Fishing Events

The fishing practices in the Belo Monte-impacted reaches show considerable variation both between periods (2012-2015 and 2016-2020) and across different areas (Upstream, Reservoir, De-watered, and Downstream). The total capture across all reaches was 8442.51 kg in the 2012-2015 period and 5537.42 kg in the 2016-2020 period, indicating an overall decrease in total biomass captured over time (Supplementary Material - *Table S2*).

Within these periods, different species emerged as the most frequently captured in each region. In the Upstream region, *tucunaré* (*Cichla spp.*) dominated during 2012-2015, whereas in 2016-2020, *pacu* (*Myleus spp.*) became the most captured species. In the Reservoir reach, pacu was consistently the most captured species in both periods, with a significant increase in total biomass from 468.50 kg to 1,174 kg. The De-watered reach saw *curimatã* (*Prochilodus spp.*) as the dominant species in 2012-2015, while pacu emerged as the most prominent in the following period. In the Downstream reach, *pescada* (*Plagioscion spp.*) was the most captured species in both periods, although there was a marked decrease in total capture, from 6818.11 kg to 3741.62 kg, reflecting fluctuations in capture rates across species. These results highlight both shifts in species dominance and changes in total catch, with pacu emerging as the species most frequently captured species in the later period (*Table S2*).

Table. 1 Centrality measures among regions for the periods 2012-2015 and 2016-2020. The values obtained result from the co-occurrence of species in fishing events, weighted by captured biomass (Kg) and the number of co-captures (connections).

Region	**Period**	**N° of Vertices**	**N° of Connections**	**Density**	**Average Distance**	**Average Degree**	**% difference between periods**
Upstream	2012-2015	21	146	0.35	2.94	13.9	1.10%
Upstream	2016-2020	15	82	0.39	3.52	10.93	
Reservoir	2012-2015	19	90	0.26	4.58	9.47	19.0%
Reservoir	2016-2020	13	100	0.64	2.87	15.38	
De-watered	2012-2015	5	14	0.7	1.42	5.6	50.0%
De-watered	2016-2020	11	44	0.4	2.75	8	
Downstream	2012-2015	37	461	0.34	2.39	24.9	1.25%
Downstream	2016-2020	33	230	0.21	5.10	13.94	

The following analyses used biomass (kg) for each species across all regions and periods. However, in the network analysis, the central species is not defined by biomass alone. The number of co-captures (connections) between species is also considered, which can lead to differences between the most-captured species and the central species, depending on both biomass and co-capture connections. The network approach revealed that fishing events, including species with central roles and the percentage changes in catches, varied across locations and time. Additionally, some species were recorded in certain reaches but not in others (Table 1).

Overall, the number of species present in the catches has declined over time, as indicated by a decrease in vertex count when comparing periods in each region (Table 1). The exception is the de-watered reach, which included six new species in catches after the dam started (Table 1) operating. In areas undergoing greater physical transformation, such as the reservoir and de-watered reach, there is an increase in connection numbers, albeit for potentially different reasons. Conversely, areas supposedly undergoing fewer transformations also experienced a decrease in connections, and percentage change between periods was lower.

Non-random Co-occurrence: Species Relationships in Fishing

The upstream region is the one that showed the lowest percentage (1.1%) of structural difference between the networks for the two periods, prior and during dam operation (*Fig. 3a*). Normalized strength revealed that *pacu* was the most relevant species for both periods, in the upstream region, followed by *aracu*. The detected relationships between species are not trophic, but rather are simply relationships of species co-occurrence in fishing events.

The structural differences in co-occurrence networks before and during the operation of the Belo Monte Hydroelectric Power Plant were 19.0% for the reservoir (*Fig. S1*) and 1.3% for the downstream section (*Fig. S2*). In the reservoir, *pacu* was the central species before the dam operation, but it was replaced by *pescada*, after the dam started operating. Similarly, in the downstream region, *aracu* was replaced by *pescada*.

The de-watered reach showed the most significant structural difference between the networks compared across the periods, with a 50% alteration between them (*Fig. 3b*). This difference was reflected in the number of species captured in each period, with the first period having only five species and the second period having 11 species. In the period prior to dam operation, *curimatã* was the central species, being later replaced by *pacu*.

Overall, in the initial period, *pacu*, *aracu*, and *curimatã* held central positions in the regional networks, based on eigenvector centrality. After the dam started operating, *pacu* (in the upstream and de-watered reaches) and *pescada* (in the reservoir and downstream reaches) emerged as dominant species.

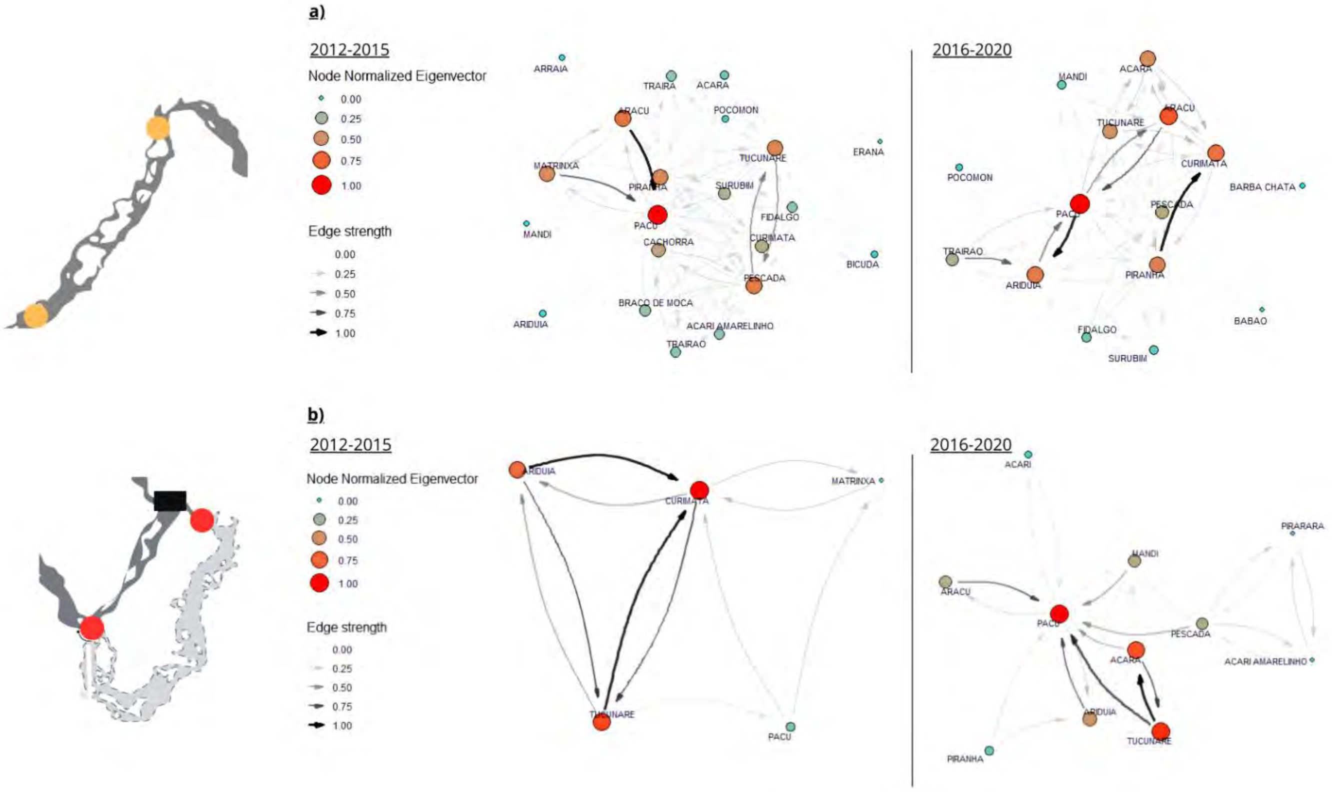


Fig. 3 Interaction networks in the 'upstream' reach (a) and 'de-watered reach' (b) sections of the Belo Monte Hydroelectric Plant, covering the periods 2012-2015 and 2016-2020. These two reaches represent the sections with the smallest and the greatest structural differences in co-occurrence networks, respectively (for the other reaches, refer to the Supplementary Material). Species are represented as circles, with colors close to 1 indicating greater importance based on eigenvector centrality. Larger, more orange circles represent greater eigencentrality, while smaller, greener circles indicate lower values. Connections between species during fishing seasons are represented by arrows, with darker shades representing stronger co-occurrence between two species. In the side maps the location of each reach is highlighted.

Directed Simulations: Changes in the Co-occurrence and Centrality of Species by Reach

To simulate the non-availability of species due to the dam and/or intensified fishing, we followed a stepwise process of removing central species and observing network rearrangements (Supplementary Material). In the upstream reach, the species removed by simulation and their respective difference percentages compared to the original network were *pacu* (1.9%), *curimatã* (5.5%), *aracu* (10.7%), *pescada* (24.8%), and *ariduia* (35.6%) (*Fig. S3*). The cumulative difference between the original network and the last simulation was 78.5%, with an average change of 15.7% per simulation (*Fig. 4*).

For the reservoir, the removed species, in order, were *pescada*, *curimatã*, *tucunaré*, *pacu*, and *surubim*. The differences between the simulations and the original co-occurrence network were 3.7% in the first simulation, 6.2% in the second, 11.6% in the third, 23.4% in the fourth, and 29.2% in the last (*Fig. S5*). When considering the total difference between the 2016-

2020 network and the simulations, a total of 74.1% was obtained. The average per simulation was 14.8% (*Fig. 4*).

The de-watered reach showed the highest average difference of 17.6% between the original network and the simulated ones. Here only four simulations were run because the analysis requires a network composition that contains at least five nodes and only three were present after the fourth simulation (*Fig. 4*). The species removed for this reach were, respectively, *pacu* (with a difference percentage compared to the original network of 14%), *acará* (19.5%), *pirarara* (16.6%), and *acari amarelinho* (20.3%) (*Fig. S4*). The cumulative difference between the networks when compared to the 2016-2020 period network was 70.4%. In contrast to other reaches, the de-watered reach showed a constant and greater increase in network changes throughout the simulations. Initial differences were low, but in the final simulations they were up to four times higher.

The downstream reach showed the lowest percentage differences in simulations compared to the networks calculated for the period during the dam operation. The average difference per simulation was 8.7%, with a cumulative total of 43.4%. The species removed were *pescada* (2.2%), *acará* (4.3%), *aracu* (11.2%), *tucunaré* (12.8%), and *pacu* (12.9%) (*Fig. S6*), in each iteration, respectively (*Fig. 4*).

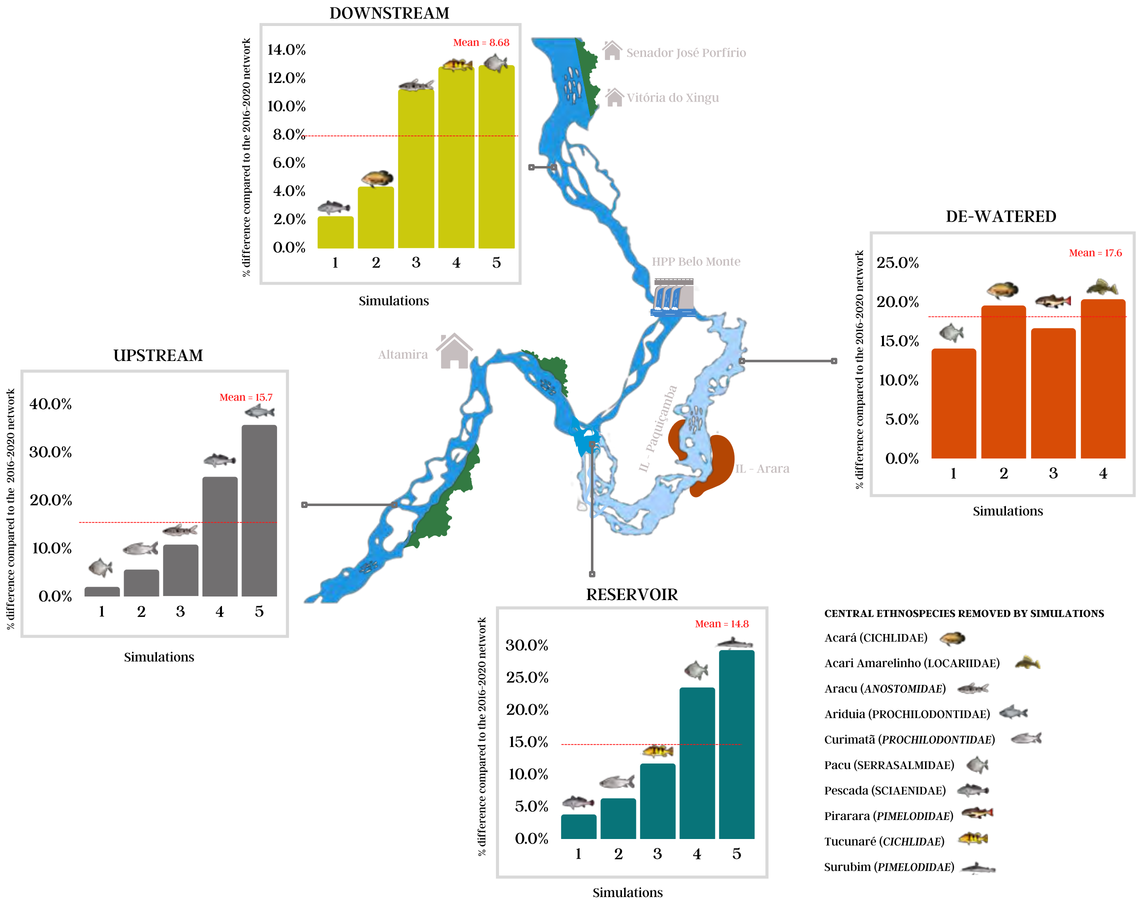
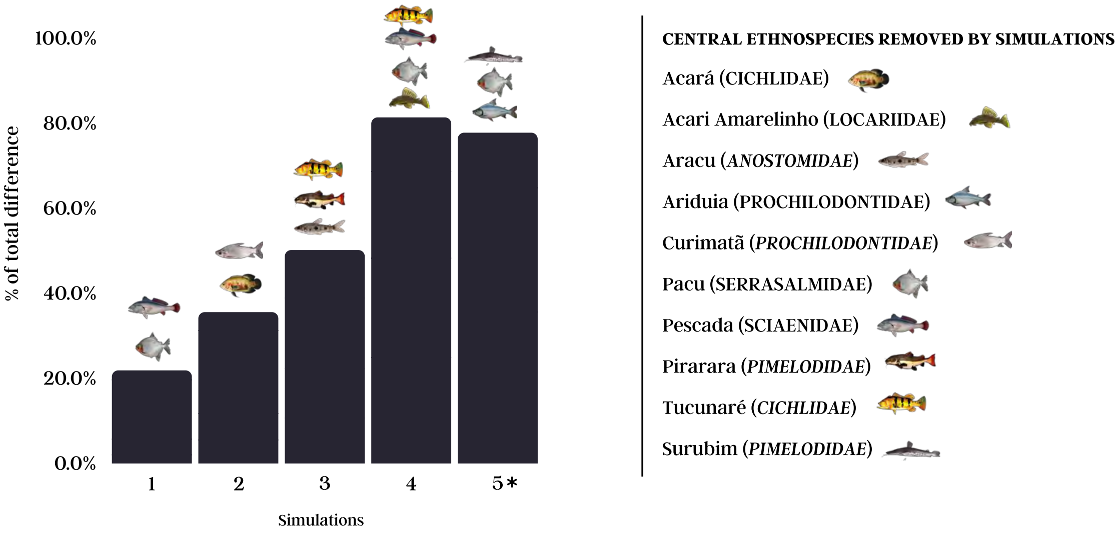


Fig. 4 - Differences in the co-occurrence networks between the dam operation period (2016-2020) and simulations in which the central species is removed (i.e., lost). The values, in each graph, represent the percentage difference between each simulation and the original network for each region. The red dashed lines correspond to the overall average difference of the simulated networks compared to the 2016-2020 period. The fish icons represent the species removed in each simulation.

The simulations revealed how much the networks are likely to change if species continue to be lost due to the mounting direct and indirect consequences of the dam, particularly in the de-watered reach. They also showed that some groups of species, such as *pacu*, *pescada* and *tucunaré,* occupied centrality in more than one simulation and location (*Fig. 5*). In general, the networks were altered by up to about 78%, with the loss of a total of 10 species over 19 simulations and with the three species highlighted above being removed in more than one region.



*In the fifth simulation it was not possible to generate results for the De-Watered Reach due to the requirements of the comparative analysis.

Fig. 5 Percentage (shown in bars) of difference between the 2016-2020 networks and the simulated networks. The fish on top of the bars represent the species removed in each simulation. Throughout the simulations, there is an increase in the percentage difference, with a maximum peak of 77.7% in the fourth simulation. Only in the fourth simulation did the removed species differ, with a different species removed for each location. On the right, the association between the representative fish figures and their respective names and families is presented.

DISCUSSION

The present study investigated interaction networks among fish species using data from fishery monitoring in areas influenced by the Belo Monte Hydroelectric Plant, in the Brazilian Amazon. This approach enabled the identification of co-occurrence relationships among captured species, i.e., which species are often caught together and how these co-occurrences vary according to the area under the impact of a dam and with the operational periods of the plant (before and during operation). Additionally, the study explored how the composition of fish catches, in terms of species co-occurrence, may change in case some of the most-sought species (the central ones) are lost.

The results obtained in this study are consistent with previous research showing the influence of species diversity on fishers' ability to add new species to their catches (Caballero et al., 2023). Particularly in regions and periods with higher diversity (i.e., abundance and richness), fewer new species are added (as seen in *Fig.4*), while in the de-watered reach, there is an increase in species capture, indicating the adaptive behavior of fishers. This phenomenon arises from the depletion of target species within ecosystems, prompting fishers to rely on alternative species as substitutes in both catch composition and consumption patterns (Lopes et al., 2023), even if these are not the most desirable ones. Network analysis identified the most important species and the peripheral species, which is a crucial step in understanding the implications of changes in interaction networks and simulating alternative scenarios in case of loss of central species.

Construction of hydroelectric plants, such as Belo Monte, has substantial impacts on fish richness and abundance, leading to ecological, social, and economic consequences (Pezzuti et al., 2024; Reid et al., 2019). These challenges extend beyond the Amazon region, particularly affecting countries in the Global South. This region faces these issues more acutely due to two key factors: significant socioeconomic and cultural dependence on fishery resources (Juan et al., 2021; Zhang et al., 2020), and the presence of many rivers with substantial hydroelectric potential that still flow freely or have large free-flowing stretches. One of the negative impacts of the Belo Monte Dam is the loss of species that are important for the local subsistence (Lopes et al., 2023).

The initial concentration of fishing activity on *pacu* and *pescada* is evident, while other species are marginally exploited. These preferred species typically inhabit shallow floodplain lakes and environments that share similar characteristics with the littoral zones of newly formed reservoirs, providing an abundance of food and suitable spawning sites (Agostinho et al., 2016). Additionally, their generalist diets allow them to exploit a wide range of available food resources, offering a significant advantage during the initial ecological transition periods (Agostinho et al., 2016). As these main species are removed due to environmental deterioration and intensified fishing, the time required for fish community structure to stabilize once more varies greatly, with no consensus on the duration indicated in the literature (Agostinho et al., 2016). Consequently, a significant change in fishing dynamics occurs, with peripheral species ascending to a central position. This phenomenon has significant implications for the diet and economy of riverine communities, underscoring the importance of previously overlooked species, either for nutritional supplementation or due to emerging fishing opportunities influenced by the specificities and challenges associated with their capture. For example, *pacu* alone represents 49.8% of the entire local fishing output (Pezzuti et al., 2018), corroborating what was found in co-occurrences in which the group was central at some years in all reaches.

At the Belo Monte Hydroelectric Plant, peripheral species that emerge as central in fishing activity may be subject to substitutions over time due to environmental changes resulting from plant construction. Therefore, the implementation of specific, but adaptive monitoring and management programs is essential to understanding and managing these changes in fishing communities to ensure the sustainability of fishing activities and the conservation of aquatic resources in the affected area (Asche et al., 2018; Jézéquel et al., 2020).

Belo Monte, as is the case for many other major dams, has been at the center of heated debates for various reasons, mostly originating from the consequences that the extensive river flow control can have and is having on forest regeneration, particularly in the floodplains (Xiandie et al., 2018), loss of turtle habitats, birds and general loss or change in the fish community (Pezzuti et al., 2022, 2024). It is important to connect such changes and losses to human subsistence and livelihood (Zuanon et al., 2021; Lopes et al., 2023). This is particularly important in the case of the Amazon because this is a socioecological hotspot where societies have evolved with intrinsic partnership and dependency on its aquatic ecosystems (Lopes et al., 2021). Yet, studies connecting the consequences of Belo Monte to fishing may prove difficult due to the scarcity of historical data or a truly pre-impact assessment (Arantes et al., 2019).

Although causality may be difficult to demonstrate, there is growing evidence of cumulative impacts after the installation and operation processes of Amazonian dams on subsistence fishing (Agostinho et al., 2016; Duponchelle et al., 2021; Winemiller et al., 2016; Lopes et al., 2023). Any alteration in the ecosystem exerts a direct influence on resource availability, thereby shaping the dietary and economic choices of local communities (FAO, 2020; Fiorella et al., 2014; Lynch et al., 2020; Roberts et al., 2022). The results of this study illustrate the substitution of species groups, both among different locations and, more prominently, over different periods.

Species substitution has been well-documented in numerous hydroelectric ventures, not only in Brazil but also in other parts of the world (e.g., Winemiller et al., 2016; Zarfl et al., 2014). These changes encompass not only the abundance of functional groups and the structure of food chains, which vary in response to different flow regimes (Arantes et al., 2019; Sabo et al., 2018), but also affect species richness, biomass availability, mean fish size, and species loss rates (Latrubesse et al., 2017; Reid et al., 2019; Reis et al., 2016; Zhang et al., 2020). Some studies reveal diverse population responses to damming, suggesting no uniform reaction (Agostinho et al., 2016). Although no single life-history trait explains the variation, there is some indication that maximum body length of a fish and nest guarding behavior respond slightly negatively to the construction of dams (Fernandez et al., 2024).

The filling of reservoirs changes water's physical and chemical properties, acting as environmental filters that favor certain ecological traits such as trophic guilds, reproductive strategies, and habitat fidelity (Fearnside et al., 2021; Fernandez et al., 2024). Successful colonizers often find suitable environments in lotic tributaries or littoral zones and adapt their strategies accordingly (Agostinho et al., 2016). Fish tend to occupy habitats that match their physiological needs, especially those that concern dissolved oxygen levels and water temperature (Agostinho et al., 2016). During the first year after impoundment, stratification can cause species to occupy atypical habitats, but reassembly typically occurs within a few years, forming new diversity patterns. In neotropical reservoirs, species richness and abundance initially rise but then decline due to environmental filtering, species sorting, and trophic depletion (Agostinho et al., 2008). It appears that environmental factors are more critical in determining species availability than are the species' life-history traits (Fernandez et al., 2024).

Identifying key species in space-time networks provides valuable insights into species interactions over time and space (Canning & Death, 2017; Hansen et al., 2020; Ospina-Alvarez et al., 2022). This approach is particularly useful for understanding the impact of human activities, such as building hydroelectric plants, on species communities (Canning & Death, 2017). This knowledge supports the management of ecosystems under human pressure and helps anticipate and monitor impacts from large infrastructure development.

Understanding the significance of these key species and how they shift as a consequence of a major ecosystem change, such as the one caused by dams, is fundamental because they are species of economic and cultural importance for human communities (Agostinho et al., 2016; Moreira et al., 2019; Jézéquel et al., 2020). A comprehensive assessment of the populations of these species is warranted. There is a noticeable decline in their centrality in the studied periods, possibly due to changes in fishing dynamics due to dwindling resources, seasonal variations, or increased distance to fishing grounds.

The term "run-of-the-river" (ROR), often used to describe hydropower projects advertised as ecologically less impactful, can obscure the true extent of environmental and social damage these projects cause, including community displacement and habitat destruction (Baird et al.,2024). The case of Belo Monte exemplifies this disconnection; while promoted as a sustainable solution, it resulted in significant ecosystem degradation and loss of fishery resources (Baird et al., 2024). \

During the reservoir-filling phase, we observed a variation in species composition that is critical for understanding species colonization (Agostinho et al., 1999, 2016). However, in contrast to expectations from studies suggesting greater species availability in reservoir areas (Albieri & Araújo, 2021; Lima et al., 2017), our data indicate that, in the context of subsistence fishing, the downstream reach of the hydroelectric plant offers a richer resource pool. An alternative explanation could be that this reach maintains flow rates similar to the natural ones (Debona et al., 2021; Prysthon & Vieira da Cunha, 2019), which do not significantly disrupt the life cycles of species (Almeida et al., 2020).

The findings of the present study have significant implications for conservation efforts in the context of subsistence fishing in regions affected by hydroelectric dams (Agostinho et al., 1999; Almeida et al., 2020). By elucidating the dynamics of species and their co-occurrence patterns within space-time networks, we gain some insights into the functioning of subsistence fishing ecosystems (Almeida et al., 2020; Araújo et al., 2009; Silva et al., 2019). Although here the longitudinal distances between fishing locations within the areas influenced by the hydroelectric plant were not assessed, previous research has identified changes in ichthyofauna assembly structures over both long (~250 km) (Araújo et al., 2009) and very short (~1 km) distances (Albieri & Araújo, 2021). The identification of core species, such as *aracu*, *curimatã*, *pacu*, *pescada*, and *tucunaré*, reinforces their roles in sustaining local communities' food security, socio-cultural significance, and economic livelihood (Early-Capistrán et al., 2020; Koehn et al., 2022; Silva et al., 2019). These species not only serve as fundamental resources but also act as indicators of the overall health of the ecosystem (Lees et al., 2016; Reid et al., 2019). These findings provide a deeper understanding of shifts in local fishing practices and food security, which is crucial for developing more effective and targeted conservation strategies. Such strategies should be tailored to the specific needs of communities that rely on subsistence fishing in regions impacted by hydroelectric dams (e.g., Abrial et al., 2021; Almeida et al., 2020; Doria et al., 2021; Moran et al., 2018). This underscores the importance of adaptive management approaches that promote the sustainability of fishery resources and strengthen community resilience (Agostinho et al., 2016; Athayde et al., 2019; Moreira et al., 2019; Jézéquel et al., 2020).

Our study introduces a novel approach to exploring the interaction between fishers' species choices, behavior, and their capacity to adapt to environmental change, which in this case was induced by a dam. While our analysis illuminates the dynamics of species and their co-occurrence within space-time networks, several caveats would need to be addressed in future work. One aspect is particularly relevant to be considered when designing mandatory data collection to assess impacts over time: the need to include data previous to the beginning of dam construction. Also needed are data on the longitudinal distances between fishing points within the dam's area of influence. Absence of these data, as observed here, restricts our understanding of subsistence fishing variations across regions and a clearer attribution of responsibility (Albieri & Araújo, 2021; Robertson & Midway, 2019). Nevertheless, we were able to show which species are crucial for sustaining fishing activities in the Belo Monte region, highlighting the potential ramifications in the event of their depletion.

CONCLUSIONS

This study sheds light on the complex web of interactions between Amazonian hydroelectric dams, subsistence fishing, and ecological systems, using the emblematic Belo Monte Hydroelectric Power Plant as a case study. We have demonstrated that hydroelectric dams have far-reaching ecological, social, and economic consequences, with significant implications for the subsistence fishing communities that depend on these ecosystems. Our findings underscore the global relevance of understanding the dynamics of fish species and their co-occurrence patterns within space-time networks, as they offer insights not only into the functioning of subsistence fishing ecosystems but also into broader conservation strategies. By identifying core species that serve as indicators of ecosystem health and assessing their potential losses over time, we have highlighted the pivotal roles of specific species in sustaining the food security, socio-cultural values, and economic livelihoods of local communities. In the Amazon and in other regions worldwide that are grappling with the complex interplay between subsistence fishing and hydroelectric dams, there is an urgent need for proactive conservation measures and targeted strategies to safeguard these communities' well-being. The negative impacts on aquatic ecosystems and local populations shown here add to the growing body of evidence calling for a critical revision of development policies in the Amazon and a shift away from building large hydroelectric dams.

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CO-OCCURRENCE DYNAMICS OF FISH SPECIES IN FRESHWATER ECOSYSTEMS: IMPLICATIONS FOR ARTISANAL FISHING IN HYDROELECTRIC DAM-IMPACTED REGIONS

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SUPPLEMENTARY MATERIAL

Table S1: This table presents species groups along with their corresponding species names, scientific names, and families. In some cases, species or families could not be identified due to limitations in the information provided by local fishers' common names. For those groups where identification was not possible, either the species or family names are absent.

Vernacular Species Group	Possible Local Species	Species Family
Acará	*Astronotus ocellatus* , *Caquetaia spectabilis* , *Retroculus xinguensis* , *Satanoperca spp.* , *Geophagus gr. altifrons* , *Geophagus argyrosticus*	Cichlidae, Cichlidae, Cichlidae, Cichlidae, Geophagidae, Geophagidae
Acari	*Hypostomus plecostomus* , *Pterygoplichthys pardalis* , *Pterygoplichthys xinguensis*	Loricariidae, Loricariidae, Loricariidae
Acari Amarelinho	*Baryancistrus xanthellus*	Loricariidae
Aracu	*Hypomasticus julii* , *Anostomoides passionis* , *Anostomus ternetzi* , *Laemolyta fernandezi* , *Laemolyta proxime* , *Leporellus vittatus* , *Leporinus aff. fasciatus* , *Leporinus friderici* , *Petulanos intermedius* , *Schizodon vittatus*	Doradidae, Anostomidae, Anostomidae, Curimatidae, Curimatidae, Anostomidae, Anostomidae, Anostomidae, Anostomidae, Anostomidae
Ariduia	*Semaprochilodus brama* , *Semaprochilodus insignis*	Prochilodontidae
Arraia	*Paratrygon aiereba* , *Paratrygon spp.* , *Potamotrygon leopoldi* , *Potamotrygon orbygnyi*	Potamotrygonidae
Babão	*Brachyplatystoma platynemum*	Pimelodidae
Barba Chata	*Pinirampus pirinampu*	Pimelodidae
Bicuda	*Boulengerella cuvieri* , *Boulengerella maculata*	Cichlidae
Braço de Moça	*Platystomaticthys sturio*	Pimelodidae
Cachorra	*Hydrolycus armatus* , *Hydrolycus tatauaia* , *Cynodon gibbus* , *Rhaphiodon vulpinus*	Cynodontidae
Curimatã	*Prochilodus nigricans*	Prochilodontidae
Erana	*Argonectes robertsi* , *Bivibranchia spp.* , *Hemiodus spp.*	Asterophysidae, Asterophysidae, Hemiodidae
Fidalgo	*Ageneiosus inermis* , *Auchenipterus nuchalis*	Auchenipteridae
Mandi	*Pimelodus blochii* , *Pimelodus ornatus*	Pimelodidae
Matrinxã	*Brycon falcatus*	Characidae
Pacu	*Myloplus arnoldi* , *Myloplus rubripinnis* , *Myloplus schomburgkii* , *Myloplus rhomboidalis* , *Mylossoma duriventris* , *Myleus setiger*	Serrasalmidae
Pescada	*Pachyurus junkii* , *Pachyurus schomburgkii* , *Plagioscion squamosissimus*	Sciaenidae
Piranha	*Serrasalmus rhombeus* , *Serrasalmus manueli* , *Pygocentrus nattereri*	Serrasalmidae
Pocomon	*Tocantinsia piresi*	Curimatidae
Pirararara	*Phractocephalus hemiolopterus*	Pimelodidae
Surubim	*Pseudoplatystoma punctifer*	Pimelodidae
Tucunaré	*Cichla melaniae* , *Cichla*	Cichlidae
Trairão	*Hoplias aimara* , *Hoplias curupira*	Erythrinidae
Traíra	*Hoplias malabaricus*	Erythrinidae

Table S2: *Total fish catches (kg) by species, fishing gear, boat type, and average fishing duration across regions and periods (2012-2020). The most captured species in each region and period are highlighted.*

REGION	PERIOD 2012-2015 (Kg)	PERIOD 2016-2020 (Kg)	MOST CAPTURED SPECIES (2012-2015)	MOST CAPTURED SPECIES (2016-2020)	TOTAL CATCH BY SPECIES (2012-2015)	TOTAL CATCH BY SPECIES (2016-2020)	AVERAGE NUMBER OF FISHERS (2012-2015)	AVERAGE NUMBER OF FISHERS (2016-2020)	MOST FREQUENT BOAT (2012-2015)	MOST FREQUENT BOAT (2016-2020)	MOST FREQUENT FISHING GEAR (2012-2015)	MOST FREQUENT FISHING GEAR (2016-2020)	AVERAGE FISHING DURATION (2012-2015)	AVERAGE FISHING DURATION (2016-2020)
UPSTREAM	1115.90	473.50	TUCUNARÉ	PACU	TUCUNARÉ (254.5 kg), OTHERS (861.4 kg)	PACU (148.5 kg), OTHERS (325 kg)	1.2	1.4	RABETA	RABETA	LINE	NETS	1.1 days	1.2 days
RESERVOIR	468.50	1174.00	PACU	PACU	PACU (114 kg), OTHERS (354.5 kg)	PACU (315 kg), OTHERS (859 kg)	1.2	1.5	RABETA	RABETA	LINE	LINE	1.2 days	1.8 days
DE-WATERED	40.00	148.30	CURIMATA	PACU	CURIMATA (12 kg), OTHERS (28 kg)	PACU (66.5 kg), OTHERS (81.8 kg)	1.8	1.4	RABETA	RABETA	LINE	OTHERS	1.5 days	1.4 days
DOWNSTREAM	6818.11	3741.62	PESCADA	PESCADA	PESCADA (1,415.4 kg), OTHERS (5,402.71 kg)	PESCADA (932 kg), OTHERS (2809,62 kg)	1.4	1.3	RABETA	RABETA	REDS	NETS	1.1 days	1.1 days
TOTAL (Kg)	**8442.51**	**5537.42**												

Reservoir Networks

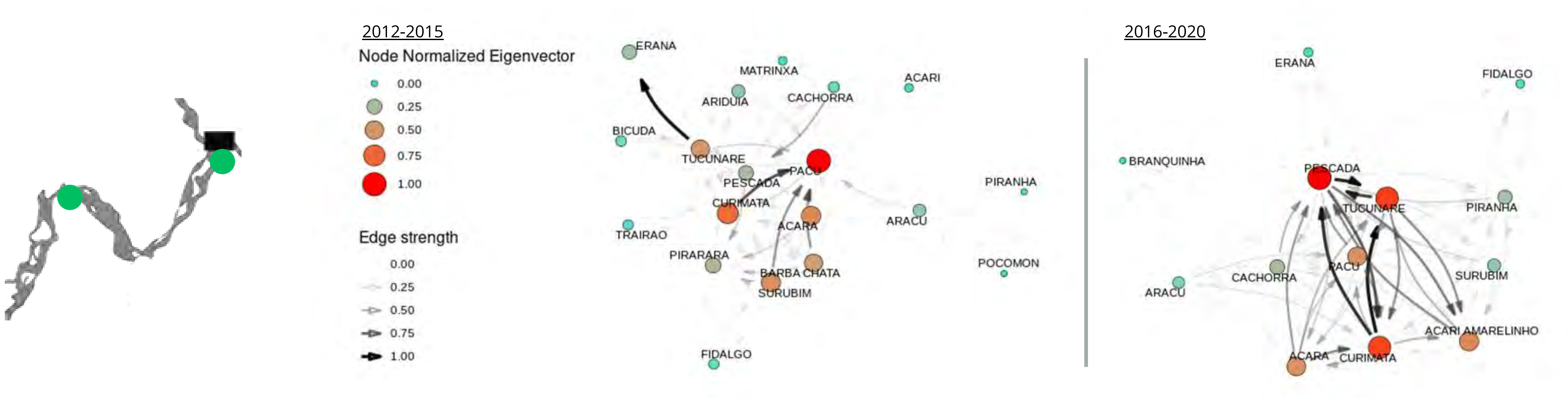

Fig. S1: Interaction networks in the ‘reservoir’ region 2012-2015 and 2015-2016 periods of the Belo Monte Hydroelectric Plant. Species are represented as circles, with colors close to 1 indicating greater importance based on eigenvector centrality. Larger, more orange circles represent greater eigencentrality, while smaller, greener circles indicate lower values. Connections between species during fishing seasons are represented by arrows, with darker shades representing stronger co-occurrence between two species. In the side maps the location of each reach is highlighted.

Downstream Networks

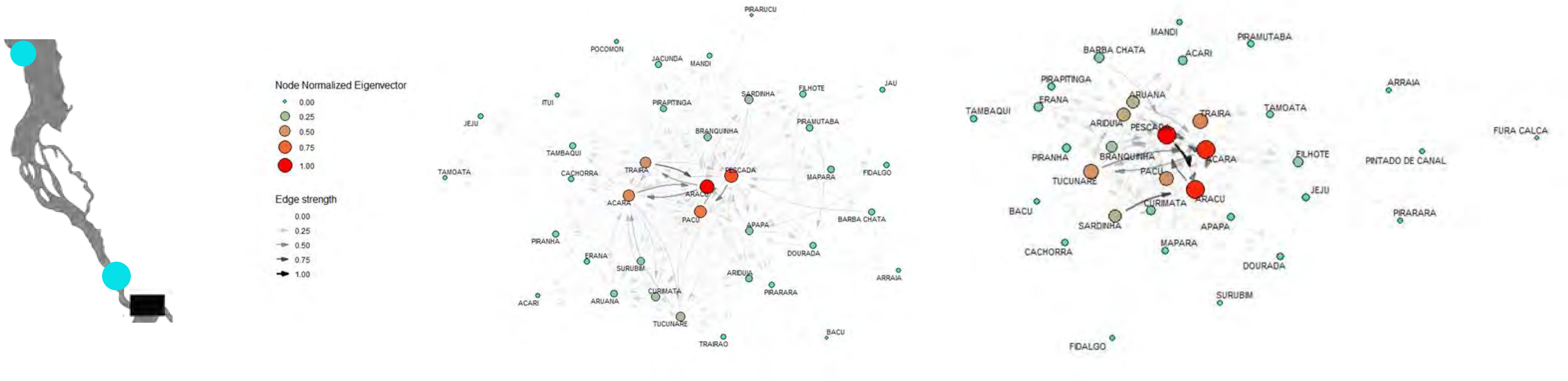

Fig. S2: Interaction networks in the ‘reservoir’ region 2012-2015 and 2015-2016 periods of the Belo Monte Hydroelectric Plant. Species are represented as circles, with colors close to 1 indicating greater importance based on eigenvector centrality. Larger, more orange circles represent greater eigencentrality, while smaller, greener circles indicate lower values. Connections between species during fishing seasons are represented by arrows, with darker shades representing stronger co-occurrence between two species. In the side maps the location of each reach is highlighted.

SUPPLEMENTARY MATERIAL – SIMULATED NETWORKS

Upstream Networks

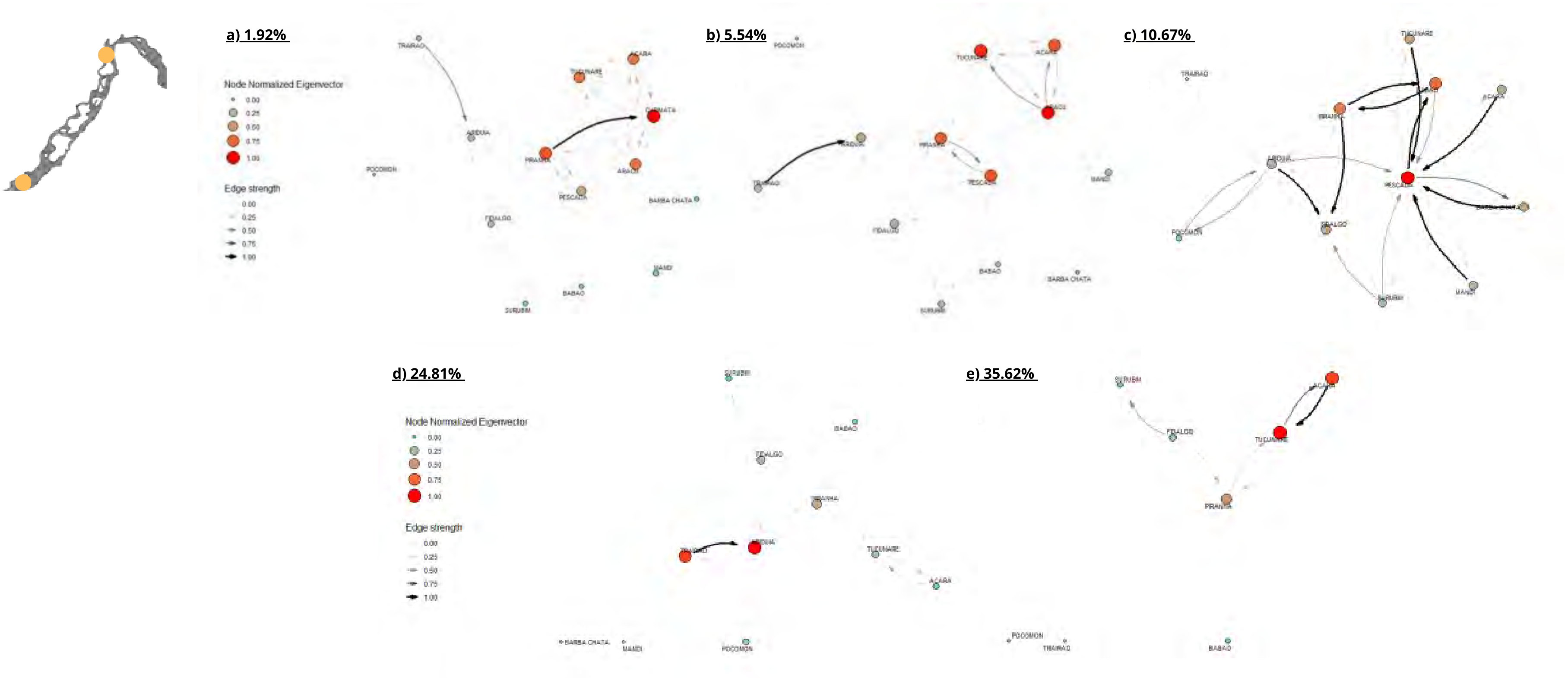

Fig. S3: Simulated networks in the 'upstream' of the Belo Monte Hydroelectric Plant. The subfigures show the percentage differences between the original network (2016-2020) and the simulated networks with the exclusion of key species: a) 1.92%, b) 5.54%, c) 10.67%, d) 24.81%, and e) 35.62%. Species are represented as circles, with larger, more orange circles indicating greater eigenvector centrality and smaller, greener circles indicating lower centrality. Connections between species during fishing seasons are represented by arrows, with darker shades indicating stronger co-occurrence. The side maps highlight the location of each reach.

De-watered Networks

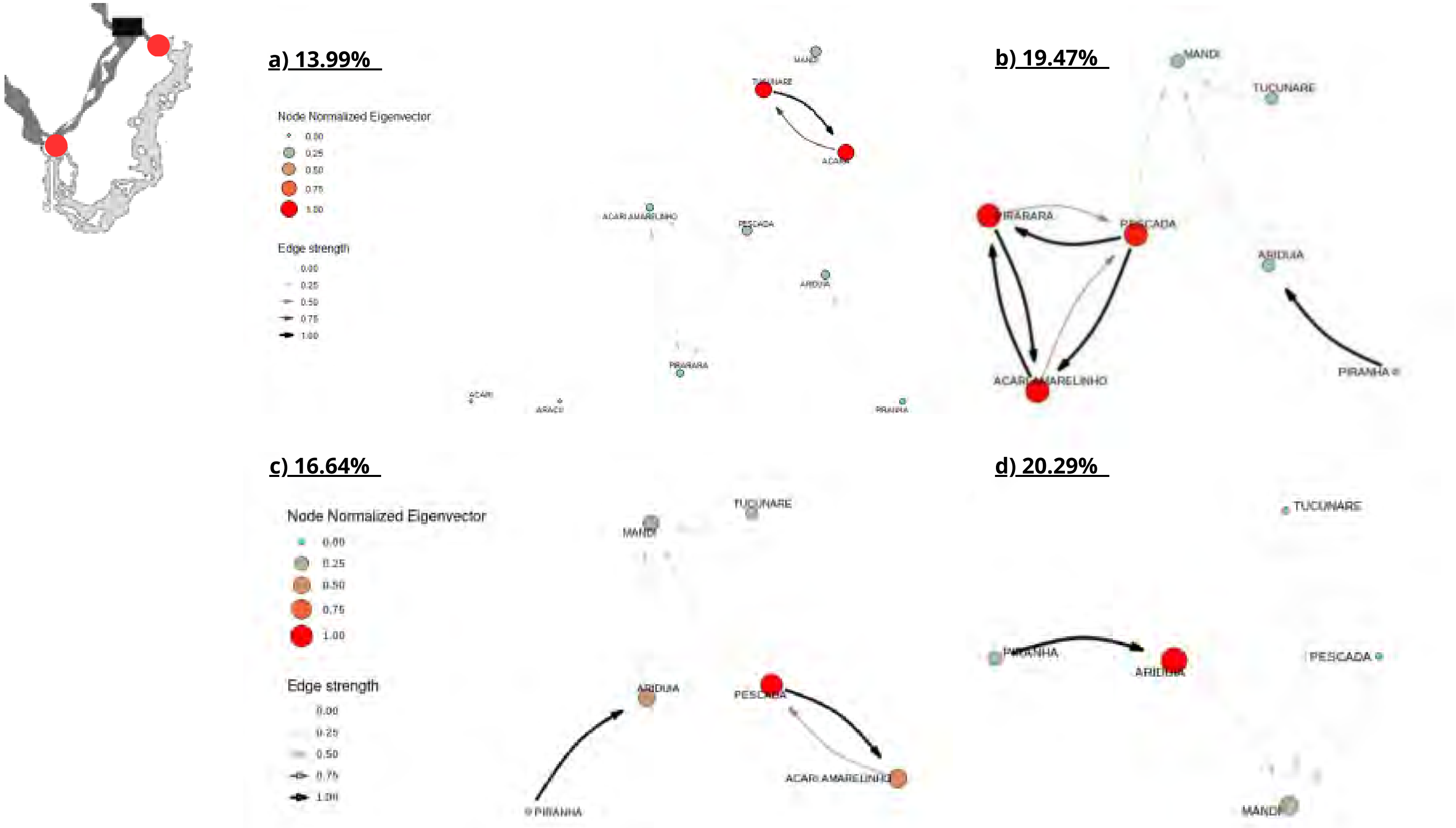

***Fig. S4**:* Simulated networks in the 'de-watered' of the Belo Monte Hydroelectric Plant. The subfigures show the percentage differences between the original network (2016-2020) and the simulated networks with the exclusion of key species: a) 13.99%, b) 19.47%, c) 16.64% and d) 20.29%. Species are represented as circles, with larger, more orange circles indicating greater eigenvector centrality and smaller, greener circles indicating lower centrality. Connections between species during fishing seasons are represented by arrows, with darker shades indicating stronger co-occurrence. The side maps highlight the location of each reach.

Reservoir Networks

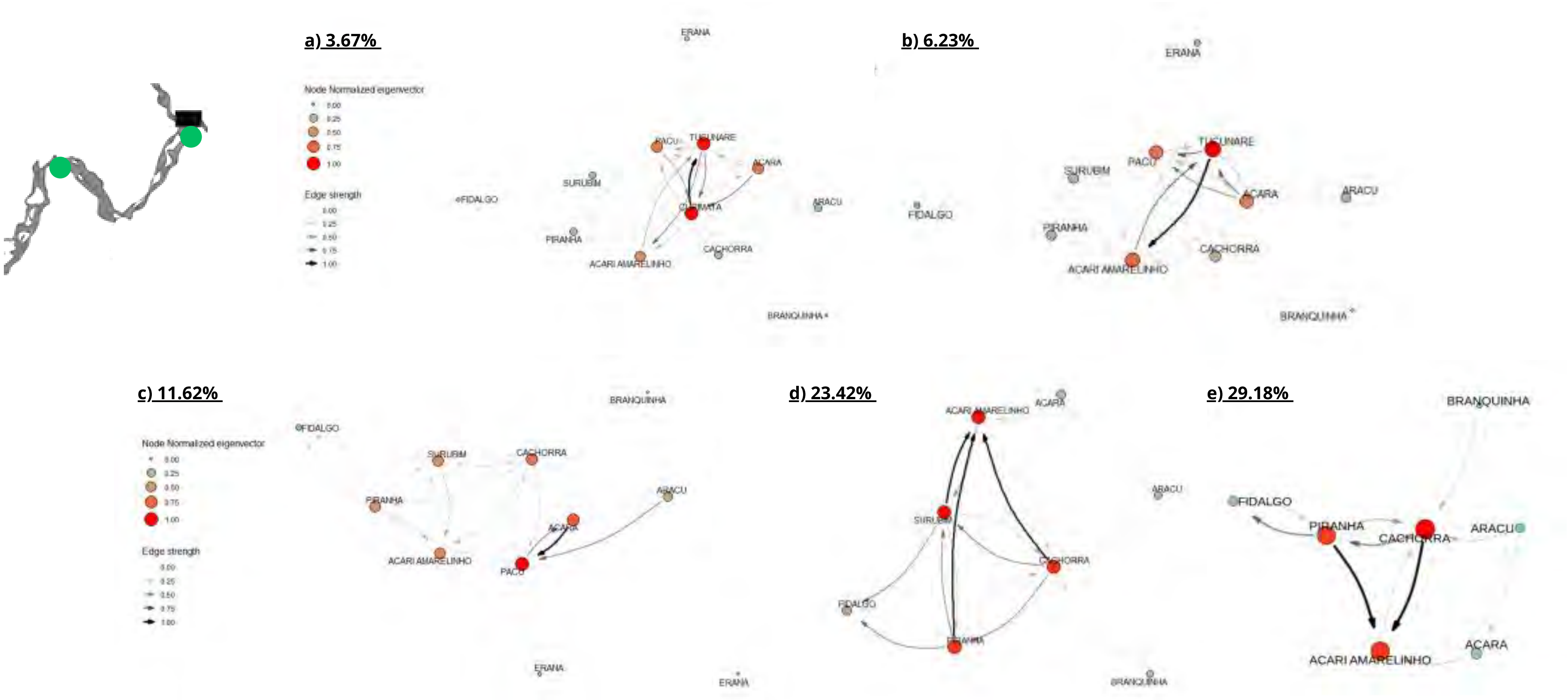

Fig. S5*:* Simulated networks in the ‘reservoir’ of the Belo Monte Hydroelectric Plant. The subfigures show the percentage differences between the original network (2016-2020) and the simulated networks with the exclusion of key species: a) 3.67%, b) 6.23%, c) 11.62%, d) 23.42%, and e) 29.18%. Species are represented as circles, with larger, more orange circles indicating greater eigenvector centrality and smaller, greener circles indicating lower centrality. Connections between species during fishing seasons are represented by arrows, with darker shades indicating stronger co-occurrence. The side maps highlight the location of each reach.

Downstream Networks

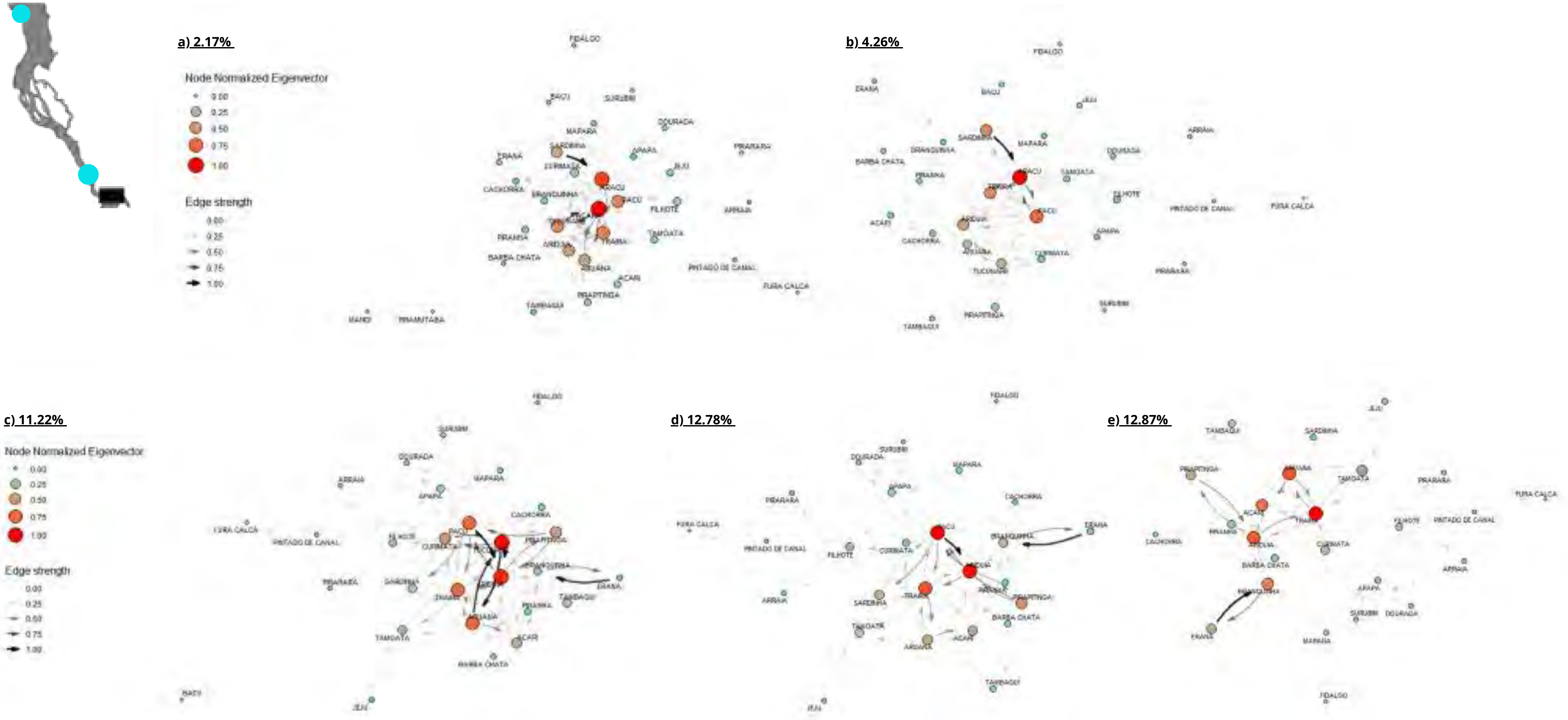

***Fig. S6**:* Simulated networks in the ‘downstream’ of the Belo Monte Hydroelectric Plant. The subfigures show the percentage differences between the original network (2016-2020) and the simulated networks with the exclusion of key species: a) 2.17%, b) 4.26%, c) 11.22%, d) 12.78%, and e) 12.87%. Species are represented as circles, with larger, more orange circles indicating greater eigenvector centrality and smaller, greener circles indicating lower centrality. Connections between species during fishing seasons are represented by arrows, with darker shades indicating stronger co-occurrence. The side maps highlight the location of each reach.