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DISSERTAÇÃO NÍVEL MESTRADO

MODELO ECOTRÓFICO DO BAIXO RIO TAPAJÓS:
análise da teia trófica e dos impactos associados à pesca e desmatamento

Leonardo Capitani

Porto Alegre, 31 Maio 2017

MODELO ECOTRÓFICO DO BAIXO RIO TAPAJÓS:
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Leonardo Capitani

Dissertação apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Mestre em Ecologia.

Orientador:

Prof. Dr. Renato de Azevedo Matias Silvano
Dep. de Ecologia, UFRGS, Porto Alegre, RS

Comissão Examinadora:

Profa. Dra. Luciane Oliveira Crossetti - Limnologia, UFRGS
Prof. Dr. Gonzalo Velasco Canziani - Oceanografia, FURG
Prof. Dr. Ronaldo Angelini - Engenharia Civil, UFRN

Porto Alegre, 31 Maio 2017

DEL RIGOR EN LA CIENCIA[1]

…En aquel Imperio, el Arte de la Cartografía logró tal Perfección que el mapa de una sola Provincia ocupaba toda una Ciudad, y el mapa del imperio, toda una Provincia. Con el tiempo, esos Mapas Desmesurados no satisficieron y los colegios de Cartógrafos levantaron un Mapa del Imperio, que tenía el tamaño del Imperio y coincidía puntualmente con él. Menos adictas al Estudio de la Cartografía, las Generaciones Siguientes entendieron que ese dilatado Mapa era inútil y no sin Impiedad lo entregaron a las Inclemencias del Sol y de los Inviernos. En los desiertos del Oeste perduran despedazadas Ruinas del Mapa, habitadas por Animales y por Mendigos; en todo el País no hay otra reliquia de las Disciplinas Geográficas.

Suárez Miranda, *Viajes de varones prudentes*
Libro cuarto, cap. XLV, Lérida, 1658

Jorge Luis Borges: El Hacedor. 2ª ed. - Buenos Aires - Debollsillo Editora, 2011.

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Irei aproveitar esta pagina para fazer memória do tempo passado no departamento de Ecologia da Universidade Federal do Rio Grande do Sul. Foi aluno discente do programa de pós graduação em Ecologia entre os anos 2015 e 2017. Escolhi ser orientado pelo Professor Renato Silvano e formei parte do Laboratório de Ecologia Humana e Peixes. É com grande felicidade e emoção que faço memória deste período. Trabalhar com o Prof. Renato foi uma grande oportunidade e um sonho realizado. Agradeço-lhe pela liberdade na pesquisa e apoio econômico nas viagens. Conheci uma pequena porção do grande e maravilhoso ecossistema Amazônico. Fiz pesquisa numa área interdisciplinar e complexa, qual é a Ecologia Humana e uso dos recursos naturais derivados da pesca.
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Pela primeira vez na minha vida foi bolsista. Um privilegio que espero poder valorizar com o meu trabalho de pesquisador e divulgador cientifico aqui no Brasil. Agradeço portanto a CAPES pela ajuda econômica durante os dois anos letivos paralelamente ao Programa Nacional de Cooperação Acadêmica (Procad)/Ação Novas Fronteiras (NF 883/2010) que financiou a coleta de dados no rio Tapajós.

Construir um modelo ecotrófico resulta ser uma tarefa desafiadora. Uma grande quantidade de dados empíricos e colaborações sempre abertas são elementos essenciais para levar a cabo um bom trabalho de pesquisa nesta área. Quero portanto citar aqui alguns dos colaboradores imprescindíveis que durante os dois anos hão estado ao meu lado. O Prof. Ronaldo Angelini (quase coorientador) e o Prof. Gonzalo Velasco Canziani pelas ajudas especificas com o software Ecopath. Não menos importantes: Prof. Dr. Sergio Camiz, Friedrich Wolfgang Keppeler, Prof. Dr. Tommaso Giarrizzo, Prof. Dr. Simone Libralato, Prof. Dr. Gustavo Hallwass, Prof. Dr. William Crampton, Prof. Dr. Peter Henderson, Profa. Dr. Victoria Judith Isaac Nahum, Maria Alice Leite Lima, Prof. Dr. Ronaldo Barthem, Junior Alberto Chuctaya Vasquez, Josele Trindade da Silva e Joelson Leall.

Imprescindível a presença firme da minha mãe, Nara Zanoli. A ela devo a minha presença no Brasil. A ela devo o grande amor para este gigante país, junto com os valores de luta e resistência para cuidar a natureza.

Dedico esta dissertação a minha tia *Zia* Graziella: estou certo dela estar orgulhosa do que eu fiz nestes dois anos de pesquisa. É per te, Zia.

SÚMARIO

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RESUMO

O rio Tapajós é o quinto maior afluente do rio Amazonas e apresenta uma das faunas de peixes mais diversas do mundo. Esses peixes realizam funções ao longo de toda a bacia hidrográfica da Amazônia, como a dispersão de sementes, a ciclagem de nutrientes e o transporte de biomassa entre rios pobres e ricos em nutrientes. Porém, a pesca e o desmatamento podem afetar esses serviços ecossistêmicos. Para o baixo rio Tapajós ainda não se conhece os efeitos da pesca e do desmatamento nas dinâmicas populacionais das principais espécies de peixes consumidos pelas populações ribeirinhas. Definir e quantificar a estrutura da teia trófica do baixo rio Tapajós é fundamental para a compreensão da sua capacidade produtiva, e da transferência de energia para sustentar os níveis tróficos superiores. O presente estudo teve como principais objetivos analisar a estrutura da teia trófica do baixo Rio Tapajós, e avaliar a dinâmica populacional de algumas espécies de peixes simulando o incremento da pesca e do desmatamento. Para modelar a teia trófica foi utilizado o programa Ecopath com dados de desembarques pesqueiros e analise de conteúdo estomacal de peixes. Os resultados mostraram que a transferência de energia na teia trófica do Rio Tapajós se dá igualmente entre as cadeias de herbivoría e detritivoría. As espécies-chave são piscívoras- insetívoras: *Acaronia nassa*, *Cichla* spp., *Pellona castelnaeana* e também predadores de topo, como os botos (*Inia geoffrensis*, *Sotalia fluviatilis*). As simulações para os próximos 30 anos indicaram que: o desmatamento é o maior fator de estresse para a teia trófica, reduzindo entre 10% e 100% a biomassa dos principais grupos biológicos; o aumento da pesca incidiu negativamente na dinâmica populacional de quelônios, pirarucu, dourada e pescada levando uma diminuição de biomassa entre 40% e 100%. Os resultados deste estudo quantificam com maior precisão a função da pesca e desmatamento na dinâmica populacional dos principais peixes de importância alimentar e comercial das populações ribeirinhas do baixo Rio Tapajós, sendo relevantes para iniciativas de manejo desse ecossistema.

Palavras-chave: Rio Tapajós, Ecopath e Ecosim, interações tróficas, pesca de pequena escala, desmatamento

Introdução Geral

Ecossistemas tropicais de água doce são descritos entres os ambientes mais produtivos e biologicamente diversificados do planeta (Downing, 2014; Likens, 1975), tendo taxas de produção primária de pelo menos uma ordem de magnitude maior que as dos ecossistemas temperados (Davies et al., 2008), por causa dos constantes aportes de nutrientes, luz e altas temperaturas (Winemiller, 2004).

Dentre os ecossistemas de águas doce, tem-se que as maiores taxas de produção primária ocorrem nas planícies de inundação dos rios tropicais (Wetzel and Ward, 1996). Estes são influenciados pelo pulso de inundação que determina fases distintas, expandindo e contraindo a área ocupada pelos sistemas lênticos das planícies (Junk et al., 1989), onde ocorre a produção de detrito, o aporte e reciclagem de nutrientes. Toda a comunidade biológica do sistema rio-planície está adaptada e se beneficia deste padrão hidrológico temporalmente regular (Bayley, 1995; Junk and Wantzen, 2004).

Um dos maiores exemplos da influência do pulso de inundação é a Amazonia brasileira. Os lagos amazônicos associados a planície de inundação desempenham um papel importante no ciclo do carbono orgânico do Rio Amazonas e efluentes. Os lagos são os principais locais de produção primária dos organismos autótrofos (macrófitas, fitoplâncton e perifiton; Junk, 1997). Representando uma área total de aproximadamente 10370.0 km^2, os ambientes lênticos amazônicos possuem uma das maiores taxas de produtividade primária bruta do mundo: 300 g C / m*ano (Abril et al., 2014; Melack and Forsberg, 2001). Esta produtividade é representada em boa parte pelas macrófitas aquáticas (± 65 %) e a seguir pelas florestas inundadas (±28 %) (Junk, 1985; Bayley and Petrere 1989; Melack and Forsberg, 2001), que então formam a base para a produção secundária de bactérias e de níveis superiores das cadeias tróficas associadas.

A alta produtividade primária amazônica é portanto o principal fator explicativo para suportar uma elevada produtividade secundária representada fundamentalmente por altos valores de biomassa e diversidade da ictiofauna (Bayley, 1989; Mérona and Rankin-de-Mérona, 2004; Petry et al., 2003). As pescarias comerciais e de subsistência presentes em toda a bacia hidrográfica beneficiam-se disto (Almeida et al., 2003; Welcomme et al., 2010), sendo que o consumo per capita de pescado na região é um dos maiores do mundo, alcançando uma média de 462 g/persona*dia em comunidades ribeirinhas (Isaac et al., 2015). Cerca de 60% de desembarques pesqueiros na região Amazônica é oriundo da pesca em pequena escala (Bayley and Petrere; 1989), que é a principal atividade econômica das populações ribeirinhas (Batista et al., 1998).

Os ecossistemas amazônicos são capazes de decompor grandes quantidades de matéria orgânica para níveis tróficos inferiores, gerando emissões de CO_2 e acumulando energia / biomassa em níveis tróficos superiores, estimulando a produção pesqueira (Fittkau, 1973; Gagne-Maynard et al., 2017). Pesquisas pioneiras nos anos 70 (Fisher and Parsley, 1979; Fittkau et al., 1975; Stark and Holley, 1975), depois 80 (Henderson and Walker, 1986; Sioli, 1984; Walker, 1985) e 90 (Melack and Fisher, 1990; Quay et al., 1992; Victoria et al., 1992), enfatizaram importância do entendimento dos padrões de ciclagem dos principais nutrientes, como fósforo, carbono e nitrogênio para uma melhor compreensão da produtividade primária e secundária dos ecossistemas aquáticos amazônicos.

Apesar de grandes extensões da Amazônia permanecerem em boas condições ecológicas, a degradação e modificação no uso da planície de inundação associada a um aumento da população humana pode impactar a ictiofauna amazônica devido à redução na quantidade e diversidade de fontes alimentares disponíveis e especialmente à alteração do pulso de inundação, com a construção de usinas hidrelétricas (Bojsen and Barriga, 2002; Goulding et al., 1988a; Hurd et al., 2016). Outro fator antropogênico são as atividades pesqueiras, e já existem evidências que a pesca excessiva tem reduzido o tamanho e a abundância de alguns peixes comerciais de grande porte na bacia amazônica (Castello et al. 2011, 2013). Por causa disso, são criadas áreas de proteção ambiental e atualmente cerca de 43.9% da Amazônia Brasileira (2.2 milhões de km^2) estão em unidades de conservação, de diversas categorias como proteção integral, uso sustentável e terras indígenas (Veríssimo et al., 2011).

A composição e o estado de conservação das florestas inundadas e a pesca são variáveis importantes na quantificação da eficiência dos ecossistemas amazônicos. Desta forma, alterações nestas variáveis podem acarretar implicações diretas no metabolismo aquático, já evidenciadas em estudos exploratórios com modelos para ecossistemas de planície de inundação (Agudelo, 2015; Angelini et al., 2013). Esta dissertação é apresentada em forma de artigo científico e seu objetivo é quantificar a teia trófica do baixo rio Tapajós (afluente de águas claras do Rio Amazonas), analisando sua estrutura quanto aos atributos ecossistêmicos como resiliência e maturidade, e em seguida simular o impacto sobre a teia trófica de aumento no esforço pesqueiro e do desmatamento de suas margens, com foco principal nas espécies de peixes mais usadas pelos ribeirinhos da região. Para a modelagem e posterior simulação, foi utilizado o software "Ecopath with Ecosim".

ARTIGO[1]

Food web modelling indicates impact of deforestation and fisheries changes over time in the Tapajós River, Brazilian Amazon

ABSTRACT

Tapajós River is fifth largest freshwater affluent ecosystem in the eastern Amazon basin and receptacle of impressive biodiversity. However, there is surprisingly little knowledge of its ecosystem structure and functioning. The main objective of the current work was to develop the ecosystem food web model of the lower Tapajós River and analyse it using specific model-based indicators. Using the temporal-dynamic module of Ecopath software, another objective was to evaluate the future responses of the lower Tapajós River food web to increasing fishing effort and deforestation rate for the main fish species catch by the riverine inhabitants. The results indicate that the lower Tapajós River food web may be structurally characterised by donor control, through the use of basal compartments: detritus, algae, plus fruits and seed which enters the system through flood pulses (wet season). The energy transfer in the Tapajós food web was co-based on the grazing food chain (58%) and the detrital food chain (42%), with an average transfer efficiency of 8.57 %. In addition, the highest values of the keystone species index highlight the role of piscivore-insectivore fish guild and top predator freshwater mammals (river dolphins). Temporal dynamic simulations for the next 30 years also indicate that both changes in fishing pressure and deforestation rate played an important role in driving species dynamics. Yet, deforestation rate was the strongest driver upon the lower Tapajós River ecosystem showing in between 10 % and 100 % biomass reduction for all the species analysed. Fishing increase reporting higher biomass decrease for top fish predators, such as giant catfishes of the genus *Brachyplatystoma* and important commercial species such as *Pellona castelnaeana* and *Plagioscion squamosissimus.* These dynamic simulation results indicate that the lower Tapajós River can sustain only moderate fishing increase and null deforestation increase rate. Each one of these anthropogenic stressors reduces the biodiversity and can negatively impact not only iconic species and top predators but also the most important commercial fish species of the ecosystem.

Keywords: Tapajós river, Ecopath with Ecosim, Trophic interactions, small-scale fisheries, deforestation

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[1] O artigo segue as regras de formatação do periódico *Acta Amazônica*, Instituto Nacional Pesquisa Amazonia.

Introduction

Freshwater ecosystems represent less than 1% of the world's surface area, being the habitat of approximately 10% of all described species (Balian et al., 2008; Collen et al., 2014; Strayer and Dudgeon, 2010). These ecosystems support biogeochemical processes that are pivotal to life on Earth (Downing et al., 1999; Naiman, 1995; Triska and Higler, 2009). The freshwater biota function within food webs where energy flows through ecosystems, from its capture by autotrophs in the process of photosynthesis to its ultimate dissipation by heterotrophic respiration (Belgrano, 2005; Elser et al., 2000). Interactions between this biota and its environment enable matter to be recycled and energy to flow through the ecosystem.

The primary, annual energy source supporting overall metazoan production and species diversity in mid- to higher-trophic levels of most rivers is autochthonous primary production entering food webs via algal-grazer and decomposer pathways (Thorp and Delong, 2002). Growing body of research conducted in tropical rivers indicated that biomass production of mid- to higher-trophic levels is principally supported by an algal-grazer (phytoplankton and periphyton) pathway that is only weakly linked to the decomposer pathway (Araujo-Lima et al., 1986; Hamilton et al., 1992; Lewis et al., 2000; Richey et al., 1990). The reason the algal-grazer pathway supports the majority of metazoan biomass is that allochthonous carbon is mostly recalcitrant, whereas carbon from autochthonous primary production, though much less plentiful, is commonly more labile (easier to assimilate), contains more energy per unit mass, and is typically preferred by aquatic biota (Thorp et al., 2010).

Specifically, freshwater fish of lower and higher trophic levels depend on both autochthonous and allochthonous (terrestrial) energy sources to grow while the balance in food sources to freshwater ecosystems is tightly linked to hydrology (Brett et al., 2017; Carpenter et al., 2005; Lewis et al., 2000; Power et al., 1995; Tanentzap et al., 2014). For example, large turbid river systems such as the Amazon present predictable and seasonal fluctuation of water level, termed flood pulse (Junk et al., 1989). During the flooding, nutrients from the main river channel and the recently inundated "terrestrial" zone become available for aquatic primary producers, thereby increasing ecosystem productivity (Bayley, 1995; Kern et al., 2010). This predictable hydrological phenomenon may be related to the fact that comparing to temperate river fish, tropical fish show proportionally more herbivorous, detritivorous, and omnivorous feeding behaviours (Layman et al., 2005; Winemiller, 1991; Wootton and Oemke, 1992).

Fish has always been the principal source of protein for the Amazon populations (Barletta et al., 2016), reaching up to 0.8 kg/capita*day for riverine people in western Amazon (Fabré and Alonso, 1998). In central Amazon, fish intake reaches 0.55 kg/capita*day (Batista et al., 1998) and 0.4 kg / capita*day in the lower Amazon (Cerdeira et al., 2000). Two main fish orders (Characiformes and Siluriformes) are exploited in the Amazon basin by different fishing categories (Barletta et al., 2016; Welcomme, 2008). The main group has been the characiformes, represented in the Amazon Basin by at least 38 species used as food for direct consumption or sold in regional markets (Barletta et al., 2016). Moreover, the consumption of some siluriformes species belonging to Pimelodidae and Hypophthalmidae families (*e.g. B. rousseauxii* and *Hypophthalmus* spp.) is commonly by riverine inhabitants (Barthem and Fabré, 2004). Other orders are less important, although there are exceptions as the perciforms genus *Cichla* spp. (Cichlidae) and *Plagioscion* spp. (Scianidae) and the osteoglossiforms *Arapaima gigas* and *O. bicirrhosum* (Barletta et al., 2016).

Noticeably, most of the main fish species caught in Amazon fisheries are migratory, including both pimelodid catfish and characins (Almeida et al., 2003; Barthem and Goulding, 2007; Hallwass and Silvano, 2016). Fish such as *Arapaima gigas* (Arapaimidae) and *Prochilodus nigricans* (Prochilodontidae) live in floodplain lakes or river channels, respectively, during low water periods, and migrate laterally into vegetated floodplain habitats during high water (Fernandes, 1997). Winemiller and Jepsen (1998) suggest that migratory herbivorous fishes originating from the Amazon eutrophic, productive ecosystems may subsidise resident predators of oligotrophic Amazon tributaries ecosystems, which may result in cascading direct and indirect effects on other species in the oligotrophic tributaries food webs.

Fishing in the Brazilian Amazon basin is still far from reaching a level of exploitation corresponding to its estimated potential (Mérona and Gascuel, 1993; Pinaya et al., 2016). But there is evidence of a substantial threat to the sustainability of the fisheries resources such as the excessive concentration of fishing effort on just some few target species (Castello et al., 2011; Hallwass and Silvano, 2016). Correa and collaborators (2015) point out that fishing activities have reduced population sizes of some frugivore fish species by up to 90% and have likely altered populations to younger, smaller individuals in Amazon and Pantanal wetlands. These overexploitation practices on the Amazon fish communities may lead to fishing-down process: historical increases in fishing effort reduce the mean body size of harvested species through the gradual replacement of depleted large-bodied species with small-bodied ones (Castello et al., 2013; Welcomme et al., 2010).

However, others anthropogenic stressors may cause severe alterations to Amazon freshwater ecosystems. In this regard, floodplain degradation via deforestation or land use conversion cause direct and indirect impacts to the fish community due to the reduction in the amount and diversity of food available and due to the alteration of the hydrological cycle (Bojsen and Barriga, 2002; Goulding et al., 1988b; Hurd et al., 2016). Scientific research demonstrates that an increase in forest biomass leads to an increase in fish biomass, with some species increasing their predominance in the fish communities (Araujo-Lima and Goulding, 1998; Claro-Jr et al., 2004; Lobón-Cerviá et al., 2015; Power et al., 1995; Waldhoff et al., 1996). Ethnoichthyological survey indicates that fishermen recognise the ecological linkages between fish and flooded forests in the Amazon, suggesting that deforestation could prejudice fisheries (Silvano et al., 2008). The impact of deforestation on the stability of the aquatic ecosystem is greater than that of fishing, even on ichthyofauna species that do not depend directly on the forest, such as those in the family Pimelodidae (Roubach and Saint−Paul, 1994; Saint-Paul et al., 2000).

In the Tapajós River, an oligotrophic tributary of the Amazon River, future scenarios of deforestation are planned by several development projects which include a series of hydropower dams and waterways to transport soybeans (Fearnside, 2015). Yet, deforestation of sensitive floodplain vegetation had also changed lake–river hydrology in several sites along the Tapajós River (Oestreicher et al., 2017). Moreover, non-registered private areas, land reform settlements and private properties were the main drivers of deforestation in the middle section of the Tapajós River (Alencar and Pientokowski, 2014). Conversely, Tapajós River's indigenous territories and state nature protected areas were the land designation categories that contribute to preserve Tapajós River basin forests (Alencar and Pientokowski, 2014). Because these stressors are rapidly increasing throughout most of the Tapajós River basin, understanding how human interactions, the environment, and freshwater species interact and influence each other, and how such dynamics affect the sustainability of goods and services they provide, is of urgent importance.

Actually, under the growing need to provide guidance for biodiversity conservation and ecosystem based management, ecological modelling have been increasingly used to predict marine and freshwater ecosystem changes and for scenario testing anthropogenic impacts (Lauenroth et al., 2013; Petts et al., 2016). Ecopath with Ecosim modelling is an alternative to experimental approaches that can be used to predict ecosystem responses to perturbations and to identify higher-level properties of the ecosystem that are not readily measurable (Heymans et al., 2016; Steenbeek et al., 2016). Also, with ecosystems where data quality and quantity are insufficient, this modelling software can describe the most critical data gaps, design research strategies, and test uncertainties in unknown parameters (Bevilacqua et al., 2016; Coll et al., 2015). Moreover, Ecopath with Ecosim approach can be used to sets a baseline to further develop ecosystem analyses in order to facilitate the implementation of management policies and explore future plausible scenarios (Heymans et al., 2016; Villasante et al., 2016). For the Amazon Basin, few scientific studies using Ecopath approach address the same questions proposed in this study (Agudelo, 2015; Angelini et al., 2006; Camargo and Ghilardi Junior, 2009; Petrere and Angelini, 2009). In the specific case of the lower Tapajós River ecosystem, this study can be considered the first that describes and analyses its food web structure and its temporal dynamics with Ecopath and Ecosim modelling tool.

This study applies the Ecopath with Ecosim (EwE) modelling approach to the lower Tapajós River ecosystem with the the main objective to evaluate the structure of its food web and temporal responses of species abundances and ecosystem dynamics to changes in fisheries and deforestation rate.

Using the Ecopath module, my specific goal is to develop:

1. the ecosystem food web model of the lower Tapajós River and analyse it using model based indicators to identify resilience and ecosystem maturity.

Using the temporal-dynamic module of Ecopath, namely Ecosim, my specific goal is to simulate and explore:

2. the future responses of the lower Tapajós River ecosystem to increasing harvest effort for the main fish species caught by the riverine inhabitants and, separately, to increasing deforestation rate.

Methods:

The lower Tapajós River

The study area is the lower course of the Tapajós River, Pará State, eastern Amazon Basin (Fig. 1). The Tapajós River is a clear water river and it drains the archaic and precambrian formations of the central Brazilian shields (Wittmann and Junk, 2016). The lower course of the Tapajós River is relict of deeply incised river system with a length of 150 km and a width of 15 km, although there are also thousands of floodplain lakes whose lengths barely exceed 1 km (Fricke et al., 2017; Irion et al., 2010; Sioli, 1984).

The Tapajós River basin can be generally separated into two geomorphological sections: the upstream riverine section (lotic system), from the headwaters down to the Aveiro city region; and the downstream section (semi-lentic system), from Aveiro City to the mouth of the river where it merges with the Amazon River at Santarém city (Fig. 1).

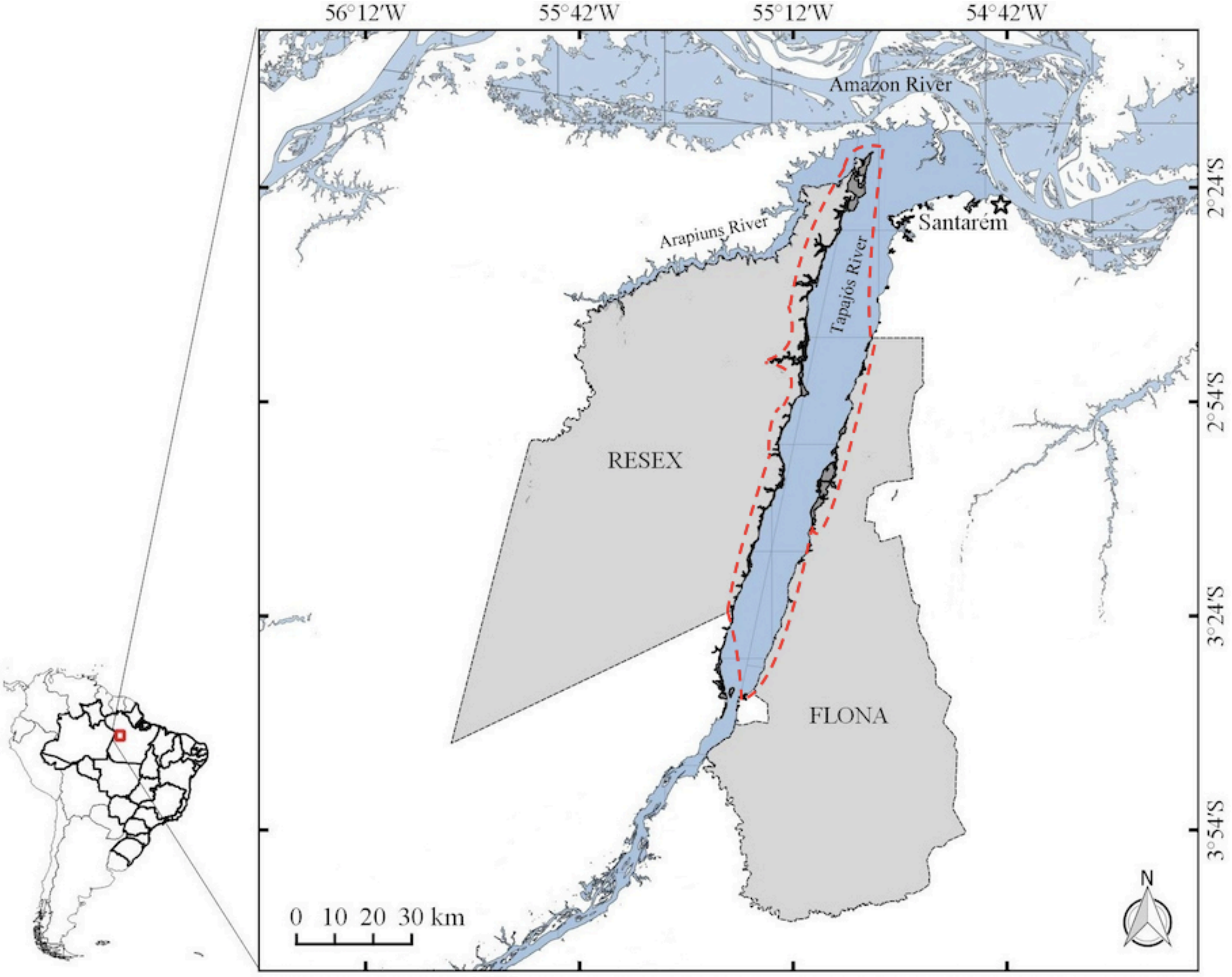

Fig. 1 A representation of the lower Tapajós River's study area with FLONA and RESEX protected areas. Map was originated using the GIS (Geographical Information System; ArcMap version 10.3; www.esri.com) by Joelson Leall, Universidade Federal do Oeste do Pará.

There are two protected areas of sustainable use in the lower section of the Tapajós River: National Forest of Tapajós (FLONA) and Extractive Reserve of Tapajós-Arapiuns (RESEX). The riverine human population of both protected areas relies on a diversified system of subsistence, including small-scale agriculture, extractive forest production, livestock farming, fishing and hunting (Hallwass, 2015). Fish is a fundamental source of protein for the Tapajós riverine population with an average consumption of 0.2 kg/capita*day (Nevado et al., 2010; Sampaio Da Silva, 2008; Sampaio Da Silva et al., 2011). Sá Leitão (2012) reported high selective fishing pressure on turtles (Podocnemididae) by riverine inhabitants in the confluence of the Tapajós and Amazon rivers.

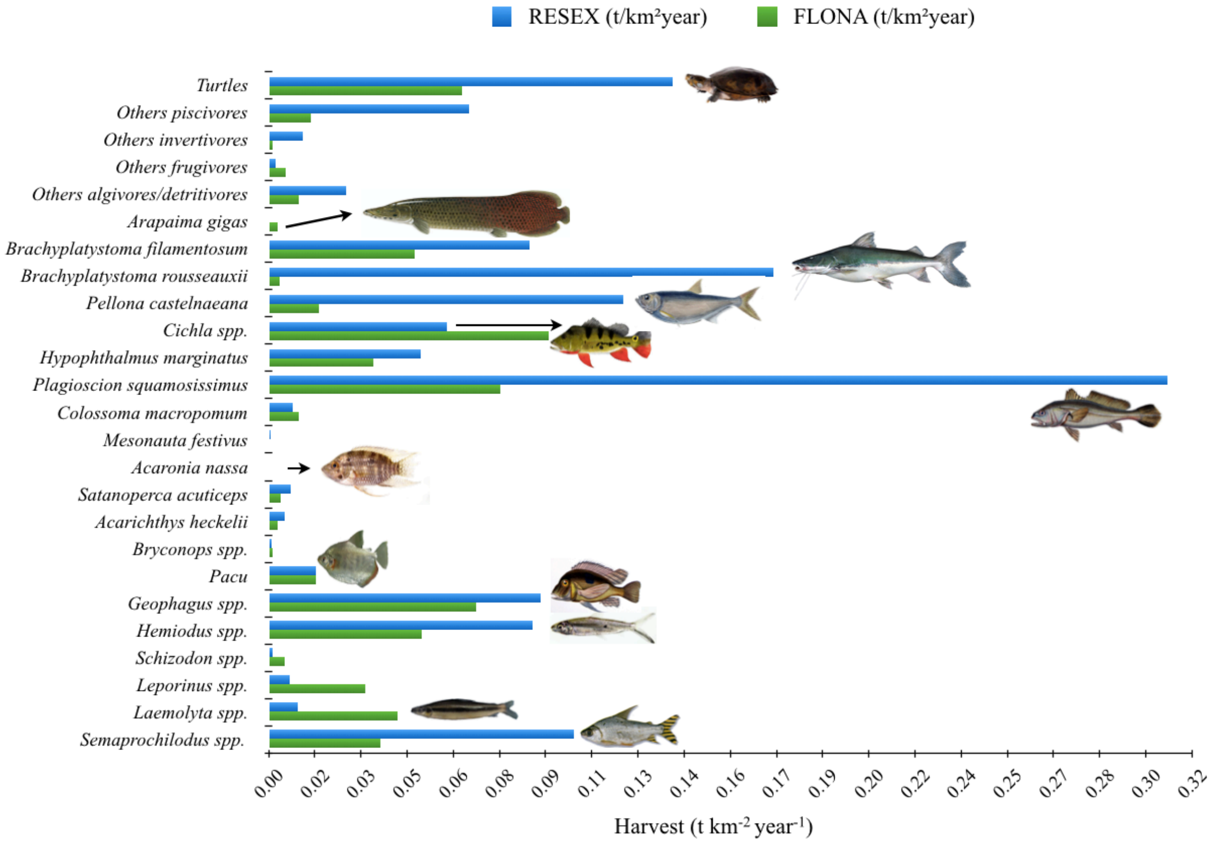

Fig.2 Fisheries landings for the different target fish groups included in the Tapajós River ecosystem model, for the reference year 2013. Landings from protected areas, FLONA and RESEX, are reported with blue and green colours, respectively.

Modelling approach

In this study, we first describe and quantify trophic structure of the lower Tapajós River using Ecopath software as a modelling tool. We then simulate, with Ecosim dynamic module, a series of anthropogenic impacts (i.e. increasing fishing pressure and increasing deforestation rate), to analyse possible future scenarios.

Ecopath with Ecosim version 6.5 (http://ecopath.org) was used to elaborate the Tapajós food web model. This modelling software was initially developed by Polovina (1984), and has been further developed in the last 30 years and it has grown into a complex and capable modelling framework (Christensen and Pauly, 1992; Pauly et al., 2000; Villasante et al., 2016). Ecopath is used to construct a mass-balanced description of a food web at a single point in time, based on biomass, production, and consumption data for each modelled species group (Christensen et al., 2008). The Ecopath data inputs, along with parameters reflecting how mortality rates change with predator biomass (i.e., vulnerabilities) are then used as input to Ecosim, which simulates the biomass, mortality, consumption, diet, and other characteristics of the modelled groups through time (Christensen et al., 2008).

Defining an Ecopath food web model involves two main steps: i) a decision on what species should be included in the food web and ii) a characterisation of these species in terms of abundances, biological characteristics (growth rate, natural mortality, consumption rate) and feeding habits. As for any modelling choice, the final food web needs to reconcile the two competing needs of accounting for ecosystem complexity and simplifying the analysis to make it understandable. Step (i) needs to be carried out first and is commonly done by selecting the functional groups which satisfactorily describe the behaviour of the overall food web. Here, a functional group is defined as a number of species of comparable ecological or feeding behaviour which can be treated as 'functionally' similar (sensu Heymans et al., 2016). Which functional groups are selected is also determined by the purpose of the analysis as functional groups can at times include individual species of specific socio-economic or conservation interest. In this study, we consider of special interest, fish species caught by Tapajós's riverine local population plus river dolphins and turtles (charismatic species).

Once the functional groups and their composition have been chosen, step (ii) needs to characterise these in terms of abundances, biological characteristics and diets. The output of this process, as discussed above, is a snapshot of what scientific community know about the system and the data gaps highlight what we don't know about the system. Data gaps can be partly filled by expert knowledge, local ecological knowledge and by mass balancing the model, that is by ensuring that basic energy and mass conservation laws and functional groups stability are respected when the model runs.

Ecopath models parameterisation is based in two master equations, one describing the production term and the other the energy balance for each functional group. The first master equation ensures a mass balance between groups and expresses production as a function of the catch, predation, net migration, biomass accumulation and other mortality (Equation 1). The second master equation is based on the principle of conservation of matter within each group (Equation 2; Christensen et al., 2008).

$$B\left(\frac{P}{B}\right)_i = Y_i + \sum_j B_j\left(\frac{Q}{B}\right)_j DC_{ij} + E_i\, BA_i + B_i\left(\frac{P}{B}\right)_i (1 - EE_i) \qquad (1)$$

$$Consumption\ (Q_i) = production\ (P_i) + respiration\ (Ri) + unassimilated\ food\ (Ui) \qquad (2)$$

Each group is parameterised with its biomass (B, t/km^2), production over biomass ratio or production rate (P/B, year^{-1}), consumption over biomass ratio or consumption rate (Q/B, year^{-1}), the prey-predator interaction in the form of a diet composition (DC) table, ecotrophic efficiency (EE_i), the biomass accumulation rate (BA_i, year^{-1}) and the net migration rate (E_i ,year^{-1}). If one of the other parameters (for example, biomass for an entire group) is missing, it is necessary to enter a value (between 0 and 1) for ecotrophic efficiency. A value close to one indicates that a group is being heavily preyed or grazed upon and/or fishing pressure is high so that few individuals die of old age. Conversely, a value close to zero means that any other group does not consume the group within the system. Therefore, for groups that are heavily exploited or predated upon, EEs it should generally be close to one whereas top predators and phytoplankton typically have lower EEs (Heymans et al., 2016).

Ecosim: temporal simulations

Ecosim expresses biomass dynamics based upon the initial parameters of the Ecopath master equation [Equation (1)] using a series of coupled differential equations which take the form:

$$\frac{dB_i}{dt} = g_i \sum_J Q_{ji} - \sum_J Q_{ij} + I_i - (M_i + F_i + e_i)B_i, \qquad (3)$$

where dB_i/dt is the biomass growth rate of group (i) during the interval dt, g_i the net growth efficiency (production/consumption ratio), I_i the immigration rate, M_i and F_i the natural and fishing mortality rates of group (i), and e_i the emigration rate. The consumption rates Q_{ji} are calculated based on the “foraging arena” concept (animals optimise the way they spend their time, balancing predation risk with foraging) where B_i’s are divided into vulnerable and invulnerable components (Christensen et al., 2008). The second Ecosim equation defines the value of consumption (i.e. functional response), which in its form is modelled as:

$$Q_{ij} = \frac{v_{ij} \cdot a_{ij} \cdot B_i \cdot B_j \cdot T_i \cdot T_j \cdot S_{ij} \cdot M_{ij}/D_j}{v_{ij} \cdot v'_{ij} \cdot T_i \cdot M_{ij} + a_{ij} \cdot M_{ij} \cdot B_j \cdot S_{ij} \cdot T_j/D_j} \tag{4}$$

where v_{ij} and v'_{ij} is the vulnerability and expresses the rate with which prey move between being vulnerable and not vulnerable, respectively, a_{ij} is the effective search rate for i (prey) by j (predator), T_i and T_j are the relative feeding time for prey and predator, S_{ij} are the seasonal or long term forcing effects, M_{ij} are the mediation forcing effects and D_j are the effects of handling time as a limit to consumption rate. The vulnerability term controls the effect on a prey group for a given increase in predator biomass (Ahrens et al., 2012). Vulnerability values range from 1 to infinity, with a default value of v = 2 (indicating neither a trophic cascade in response to harvesting at the top of the food chain nor donor control of a predator–prey interaction).

Basic assumptions for the Tapajós food web model

- The Tapajós food web model is based on average parameters for 2013 baseline year (temporal frame where most data for the model is available);
- The modelled ecosystem includes the habitat area of the main species of concern (Fig. 1; approximately 2000 km^2).
- For migratory fish species, such as *Brachyplatystoma filamentosum*, *Brachyplatystoma rousseauxii*, *Hypophthalmus marginatus*, *Pellona castelnaeana*, *Semaprochilodus* spp. and for river dolphins an “import” value is reflected in the diet composition of these species (Table 2); In Ecopath, 'import' to a system is the consumption of preys that are not a part of the system as it is defined (for example for species that spend fractions of the year feeding outside the area of the model);

- Phytoplankton and zooplankton are distributed uniformly in the first two metres of the water column (euphotic zone);
- Microbial loop (bacterial and fungi biomass) it is considered part of the detritus group;
- 95.5 % of the study area is open water (Melack and Hess, 2010);
- 4.5% of the study area is covered with flooded igapó forest (Melack and Hess, 2010);
- 50% (1000 km^2) of the study area is used by the FLONA's riverine population for fishing activities. The other 50% of the study area is used by the RESEX's riverine population for subsistence fishing practices; note that a minor part of the modelled area (200 km^2) is outside of the conservation area's limits (Fig. 1).
- Functional groups excretion/egestion rate is 20%, except for zooplankton (40%) and for aquatic and terrestrial invertebrates (30%). This values follow criteria suggested by Heymans and collaborators (2016).
- For fish groups where biomass parameter was not available, assumed values of 0.95 for ecotrophic efficiency (EE) were used as input for the model (for many groups in Polovina (1984) original model; based on Ricker (1968)). By using an EE of 0.95 as input, Ecopath solves the mass-balance equation (Eq. (1)). It calculates the biomass required for predator groups' consumption and catches, plus 5% corresponding to other mortality (1 − EE). In this this study, these were the fish groups whose biomasses were unknown: *Arapaima gigas*, *Brachyplatystoma filamentosum*, *Brachyplatystoma rousseauxii*, *Pellona castelnaeana, Hypophthalmus marginatus*, *Plagioscion squamosissimus, Colossoma macropomum.*
- Average population in the National Forest of Tapajós (FLONA) is 8250 inhabitants (IBAMA, 2004).
- Average population in the Extractive Reserve of Tapajós-Arapiuns (RESEX) is 17250 inhabitants (ICMBio, 2014).
- Average consumption for lower Tapajós's riverine population is 0.200 g/inhabitant*day (Sampaio Da Silva, 2008; Sampaio Da Silva et al., 2011; Cerdeira et al., 2000);

- 432 t/km^2*year of igapó forest biomass is extracted representing the modelling deforestation scenario (Scenario 2). This absolute value is equivalent to 10 % annual deforestation rate for the Tapajós River basin (Trancoso et al., 2009).

Model construction

We have considered 35 groups of species in the model ecosystem. Some of these groups consisted in several species of the same genus (such as fish species caught by riverine local population), whereas others consisted of several species called functional groups (Table S1). For some of these functional groups, species are incorporated into trophic guilds while other groups are formed on the basis of general taxonomic similarities (i.e. river dolphins, turtles, otters). Fish species lists were compiled from more recent ichthyofauna biodiversity studies of the Tapajós lentic and lotic ecosystems and personal communication with scientific experts (ICMBio 2014, Keppeler et al. 2017, Dr. Ronaldo Barthem, Dr. Victoria Isaac). Phytoplankton biomass value in terms of chlorophyll *a* was taken from Freitas da Silva (2012). The average value presented in this study (4.43 µ/L) was converted into t/km^2 units using empirical equivalences (Table S2). For non fish groups, the biomass parameter was estimated according to scientific literature or from others Ecopath ecosystem models.

The biomass parameter of the fish groups was calculated considering data (the number of individuals per species caught and the sampled fishing area) from Ferreira da Costa Ph.D thesis (2005). In the mentioned study, samples were taken from nine lakes from the lower Tapajós River, in between the years of 2002 and 2003 using seine net and purse-seine net fishing techniques. We have used an empirical length frequency-distribution of fish from Henderson and Hamilton (1995) to estimate an average weight per individual and then, multiplied it by the number of caught individuals per species. The total weight caught of each species and the total sampled area were used to calculate the biomass density per species (t/km^2). For seven fish species, the biomass parameter was estimated indirectly, using the Ecopath Software mass balance routine with ecotrophic efficiency parameter equal to 0.95, following ecological and thermodynamic rules for balancing Ecopath models (Heymans et al., 2016) (*Arapaima gigas, Brachyplatystoma filamentosum, Brachyplatystoma rousseauxii, Pellona castelnaeana, Hypophthalmus marginatus, Plagioscion squamosissimus, Colossoma macropomum*).

The detritus biomass was calculated as a function of primary production and euphotic depth by employing the relationship suggested by Christensen and Pauly (1993):

$$\ln B_{detritus} = [(0.954 \cdot \log PP) + (0.863 \cdot \log E)] - 2.41 \qquad (5)$$

where $B_{detritus}$ is the standing stock of detritus, in t C/km^2, PP the primary production in t C/km^2 *year and E is the euphotic depth in meters (= 2 m) with log as the natural logarithm. For the PP value, we used net aquatic primary productivity of 113.0 t C/km^2*year (McClain et al., 2001).

Production rate (P/B) and consumption rate (Q/B) were estimated from scientific papers, reports, theses, governmental reports, online databases, and other Brazilian Ecopath models. For the fish groups, production rate (P/B) and consumption rate (Q/B) were estimated by empirical equations using fish life history parameters, such as asymptotic weight (g), asymptotic length (cm), fin aspect ratio and von Bertalanffy growth rate at which asymptotic length is approached (Christensen et al., 2008; Froese and Binohlan, 2000; Pauly, 1980). The diet composition parameter (DC) was summarised as the percentage of each group in terms of the total wet weight (or volume) in the diet of the predator. A diet matrix was assembled using preferentially a local field study on stomach content analyses for fish species (Friedrich Keppeler unpublished data) completed with Fishbase online database (Froese and Pauly, 2017) and other studies of the same group of species and from the same ecological regions. For the Igapó forest group, habitat area fraction, which is the habitat area to total model area ratio was calculated using an average estimate of 4.5% of flooded area (Melack and Hess, 2010). Also,

Since there are no historical data on fishery catches in the study area, annual fish biomass harvested by riverine population was estimated through indirect approach. FLONA or RESEX annual harvest biomass per fish species (Y_i) was estimated as follow:

$$Y_i = \frac{0.2 \cdot h_i \cdot 365 \cdot f_i}{1000} \qquad (6)$$

where h_i is the number of inhabitants for RESEX or FLONA protected areas. f_i is the relative proportion of fish species abundance obtained from the landing volumes reported by Tapajós riverine fishermen who recorded the composition of catch (species of fish caught) between 2013 and 2014 years (Hallwass, 2015). Absolute value 0.2, refers to the average daily fish consumption per capita of the Tapajós riverine inhabitants (grams/inhabitant*day). Absolute value 1000 refers to the ecosystem area used by RESEX or FLONA fishermen (square kilometres unit).

Balancing and validation of the model

Initial inputs to Ecopath, including estimates for biomasses, production to biomass ratios, consumption to biomass ratios, and diets, rarely produce mass balance, and thus ad hoc changes to inputs are required to balance the model. "PREBAL" or pre-balancing analysis (Link, 2010) assesses whether data are coherent to the system level by respecting some basic laws, rules, and principles of ecosystem ecology (Fig. S1; Fig. S2 and Fig. S3). It is argued that by using PREBAL diagnostics, problems in initial model balancing can be headed off before progressing to dynamic simulations. Three diagnostics were used in this study, after the initial Ecopath model was created, including: assessing biomass across taxa/trophic levels (where biomass should span 5 –7 orders of magnitude and slope on log scale should be 5–10% decline); and vital rates such as production to biomass ratio and consumption to biomass ratio. As these vital rates are strongly related to body size and biomass (Denney et al., 2002; Link, 2010; Pauly, 1980; Pauly, 1989), they tend to follow some of the same properties as noted above for biomass estimates.

Also we calculated the model pedigree describing the origin and quality of each parameter and we used it to analyse which inputs are least reliable or most likely to achieve mass balance. The pedigree routine allows to mark the data origin using a pre-defined table for each type of input parameters (Table S3). Specifying the pedigree of data is useful to provide a basis for the computation of an overall index of model 'quality', a model being of high quality when it is constructed mainly using precise estimates of various parameters, based on data from the system to be represented by the model. Although Pedigree values can be used as coefficients of variations (CVs) in the Monte Carlo routine to test uncertainty in Ecosim simulations, we chose the same approach and criterions of Kohen and collaborators (2016) to establish the coefficients of variation for the Ecopath input parameters (for each functional group, CVs are listed in Table 1; data quality rankings and multipliers are listed in Table S4).

With these preliminary analysis, we checked if the ecotrophic efficiency (EE) was less than one for all compartments, as values >1.0 are inconsistent (it is impossible that, under conditions of steady state, more biomass is used than produced by a compartment); if inconsistencies were detected, we adjusted specifically the Biomass parameter (B) or Diet Composition (DC) values, following the recommendations of two studies about balancing procedures in Ecopath modelling approach (Ayers and Scharler, 2011; Langseth et al., 2014).

The Monte Carlo approach was used to test for sensitivity of Ecosim's outputs to Ecopath input parameters (Christensen and Walters, 2004). We assigned a coefficient of variation (CV) to each input parameter (B, Q/B, P/B, and Diet). We ranked data according to degree of confidence and assigned precision levels accordingly to the approach of Koehn and collaborators (2016, but see Table 1 and Table S4). We made 100 random simulations trials from range of possible input values to determine whether the set of parameters resulted in a balanced model (EE tolerance = $5*10^{-4}$). Then we ran the Ecosim simulation based on the new randomly selected parameters. The output from the Monte Carlo simulations was plotted (percent biomass change over time for each group). The percent change in biomass for each group was calculated for each of the 100 Monte Carlo simulations and then ordered. The 5th and 95th ranked trails were then selected to provide the upper and lower 90 % confidence intervals.

Model outputs: analysis of the structure of the Tapajós River food web

In the Result section of this study we first present the relationships visually within the food web by highlighting fish species group and each of its direct predators and prey, as well as the strength of the interactions. To do this, we use the Ecopath flow diagram tool. We use the results of the static food web model to evaluate the trophic level (TL) and role of the species to place it within the continuum of apex predator to low trophic level prey. Then, we use the food web model to partition sources of mortality for a single species group. In this way, we evaluate fishing mortality relative to predation mortality and the remaining mortality not explained by the food web model to determine the extent of impact of fishery mortality by riverine inhabitants. Sources of mortality are evaluated in terms of proportion of total mortality for each functional group. We also present and analyse trophic spectra, i.e. the continuous distribution of biomass at the ecosystem scale and as a function of continuous trophic levels (Gascuel et al., 2011; Gascuel and Pauly, 2009).

Model outputs: Ecopath indexes of trophic structure and networks

Several indexes are produced by Ecopath, which are useful for determining an ecosystem`s structure, maturity, and stability (Odum, 1969; Ulanowicz, 1980). For this, the entire modelled ecosystem is aggregated into discreet trophic levels as proposed by Lindeman (1942). Results of this analysis are the calculated absolute flows, which can be aggregated to create useful summary statistics that can then be compared to other systems. Here, the description of the indexes considered in this study:

We consider food web structure indexes such as connectance index (CI), which is the ratio of the number of actual links between groups to the number of possible links; the system omnivory index (SOI), which is calculated as the mean omnivory of all consumers weighted by the logarithm of each consumer's food intake (Christensen et al., 2008) and the transfer efficiency, which is calculated as the ratio between the sum of the exports from a given trophic level, plus the flow that is transferred from one trophic level to the next, and the throughput of the trophic level (Christensen et al. 2008; Table 2). These indexes characterises the extent to which a system displays web-like features, and high values indicate that the groups are not highly specialised and feed on many different trophic levels (De Mutsert, 2010).

Ratios of some of the summary statistics can provide information as well. The ratio of total system biomass to the total system throughput is directly proportional to system maturity (Christensen 1995), which becomes higher with increasing maturity. Another maturity index is the ratio of net primary production to total respiration, which decreases to 1 with increasing maturity (Odum 1969). We also consider indexes such as ascendency, system capacity, and system overhead, which is based on ascendency and capacity. Ascendency measures the structure of an ecosystem in terms of the amount and organisation of biomass flow within the system. Based upon Odum`s (1969) interpretation of the attributes of ecosystems, more speciation, longer retention, and more cycling within the system indicate that an ecosystem is more mature. Higher ascendency values indicate that there is an increase in one or more of these properties. The upper limit to ascendency is the development capacity of the ecosystem. System overhead is the difference between capacity and ascendency. System overhead is the upper limit to how much ascendency can increase to counteract unexpected perturbations. Higher overhead indicates that a system has a larger amount of energy reserves with which it can react to perturbations, so that the system should be more able to maintain stability when perturbed.

Model outputs: mixed trophic impact analysis

We present the effect that changes the biomass of a group will have on the biomass of the other groups in the Tapajós River food web with the Mixed Trophic Impact analysis (MTI). The MTI for living groups is calculated by constructing an *n* x *n* matrix, where the *i,j* th element representing the interaction between the impacting group *i* and the impacted group *j* is :

$$MTI_{i,j} = DC_{i,j} - FC_{j,i} \qquad (7)$$

where DC_{ij} is the diet composition term expressing how much *j* contributes to the diet of *i*, and FC_{ji} is a host composition term giving the proportion of the predation on *j* that is due to *i* as a predator. When calculating the host compositions the fishing fleets are included as 'predators'. For detritus groups the DC_{ij} terms are set to 0. For each fishing fleet a 'diet compositions' is calculated representing how much each group contributes to the catches, while the host composition term as mentioned above includes both predation and catches.

Model outputs: key functional groups

Using the keystone species index proposed by Valls and collaborators (2015), we select and present the first five keystone species of the Tapajós River ecosystem. Moreover, the Relative Total Impact (RTI) index was used to identify the groups that may have large biomass and a large impact to other food web components per change in unit biomass. These are the functional groups of which a minor change in their biomass would result in significant changes in other food web components (Valls et al., 2015). RTI is calculated from the mixed trophic impact (MTI) matrix (m_{ij}) (Eq. 8). MTI is the inverse of the matrix of net impacts (Christensen and Pauly 1992) that is composed of the net impacts (net_{ij}) calculated between each functional group in the food web model as the difference between the positive (the fraction of prey i in the predator j diet, d_{ij}) and negative (the fraction of prey i diet that coincides with the predator diet, f_{ij}) effects as proposed by Ulanowicz and Puccia (1990) (Eq. 9).

$$RTI = \sqrt{\sum_{j \neq i}^{n} m_{ij}^2} \qquad (8)$$

$$net_{ij} = d_{ij} - f_{ij} \qquad (9)$$

Identifying the key functional groups allow to focus the sensitivity and uncertainty analysis on groups likely to have large impact on the model structure and output.

Model outputs: simulation increase fishing harvest and deforestation rate:

After Ecopath model was balanced, we performed a set of simulations on the Tapajós River food web model to assess the ecosystem changes induced by fishing and deforestation. We used the Ecosim vulnerability parameters equal to one ($v = 1$), to represent the empirical evidence that all levels of trophic chains in nature respond to enrichment at the bottom positively (Ahrens et al., 2012; Arditi and Ginzburg, 2012; White, 2013). The duration of simulations was 30 years

(2013-2043 years). We set the minimum foraging time at 0.01. I established two simulation scenarios:

Scenario 1: The fishing mortality was increased linearly from the Ecopath baseline value F_0 to $F_t = F_0 * a$ (where a is a multiplier), and then maintaining the last value of F_t for the last 10 years of the simulation. The multiplier a was set between 1.0 and 2.0 values, corresponding, respectively, to a range between 0% and 100% fishing increase with respect the initial baseline value (Fig.3).

Scenario 2: With an initial baseline value of 10 % deforestation biomass loss (B_0 = 432 t/km^2), we increased linearly the baseline value from B_0 to $B_t = B_0 * a$ (where a is a multiplier), and then maintaining the last value of B_t for the last 10 years of the simulation. The multiplier a was set between 1.0 and 2.0 values, corresponding, respectively, to a range between 0% and 100% deforestation increase. The fishing mortality was fixed and it maintained constant to the baseline value.

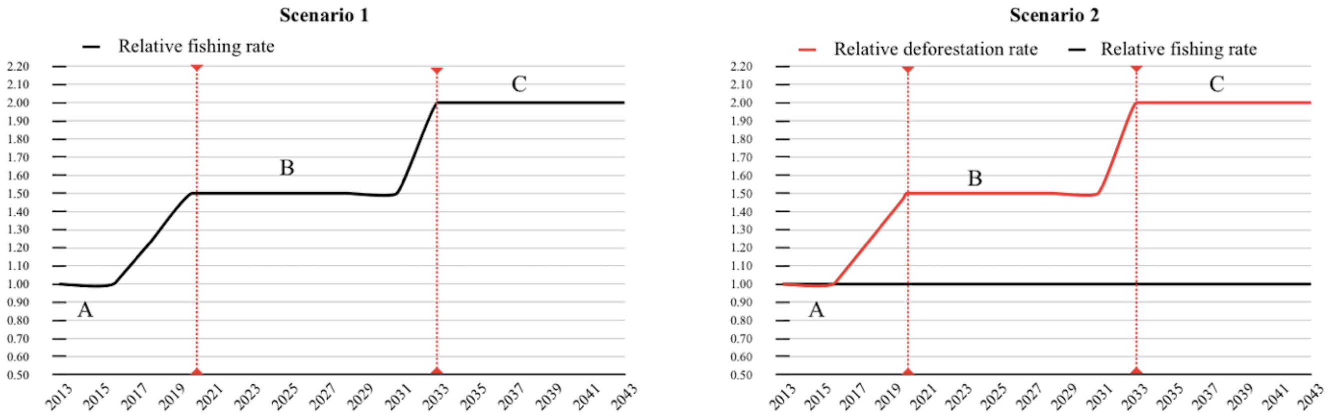

Fig.3 Schematic representations of the Scenario 1 (left side) and Scenario 2 (right side) used in the Ecosim simulations. (A) baseline initial value (B) 50 % increase rate for year 2020-2030 (C) 100 % increase rate for years 2033-2043.

Results

The food web of the lower Tapajós River ecosystem

The flow diagram shown in Figure 4 represents a balanced model of the trophic connections within lower Tapajós River in the reference year 2013 with the groups arranged by trophic level.

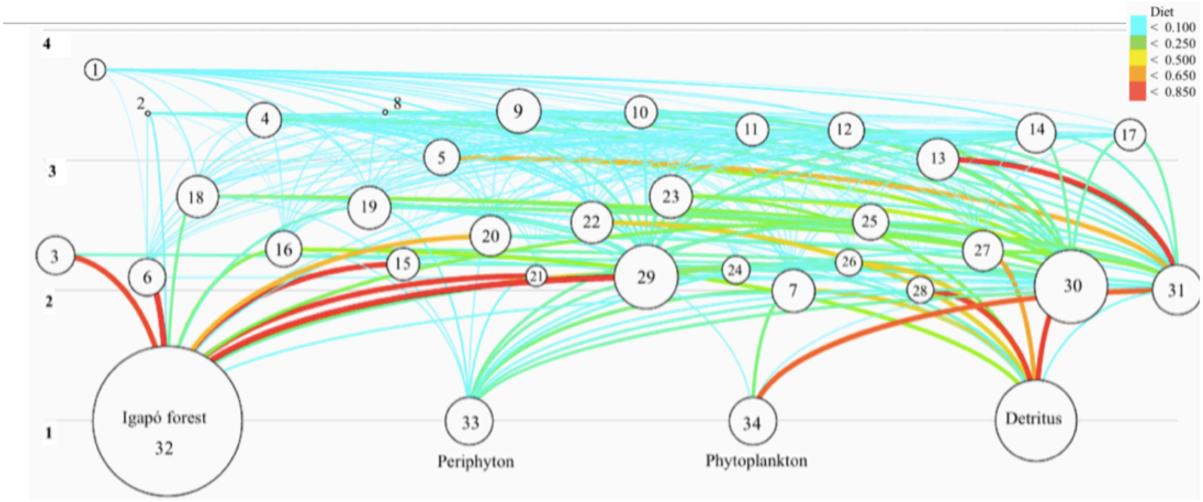

Fig. 4 Flow diagram of the lower Tapajós River (year 2013). Each functional group is shown as a circle and its size is proportional to the logarithm of its biomass. The functional groups are represented by their trophic levels (y-axis) and linked by predator-prey relationships showed as coloured lines representing the relative prey's contribution in the predator diet.

Numbers in the figure: 1. River dolphins; 2. Otters; 3. Turtles; 4. Other piscivore fish; 5. Other invertivore fish; 6. Other frugivore fish; 7. Other algivore detritivore fish; 8. *Arapaima gigas*; 9. *Brachyplatystoma filamentosum*; 10. *Brachyplatystoma rousseauxii*; 11. *Pellona castelnaeana*; 12. *Cichla* spp.; 13. *Hypophthalmus marginatus*; 14. *Plagioscion squamosissimus*; 15. *Colossoma macropomum*; 16. *Mesonauta festivus*; 17. *Acaronia nassa*; 18. *Satanoperca acuticeps*; 19. *Acarichthys heckelii*; 20. *Bryconops* spp.; 21. Pacu; 22. *Geophagus* spp. ; 23. *Hemiodus* spp. ; 24. *Schizodon* spp.; 25. *Leporinus* spp.; 26. *Laemolyta* spp.; 27. *Loricariichthys* spp.; 28. *Semaprochilodus* spp.; 29. Terrestrial invertebrates; 30. Aquatic invertebrates; 31. Zooplankton; 32. Igapó forest; 33. Periphyton; 34. Phytoplankton;

Table 1. Input parameters – biomass (B), production to biomass ratio (P/B), consumption to biomass ratio (Q/B), ecotrophic efficiency (EE), and catch (C) – for each functional group in the model. Parameters in bold are estimated for by the model. Also included are the specified coefficients of variation (CV) values for each parameter based on data quality ranking in Table S4. CV ranges from 1 (i.e. low precision information) to 0 (i.e. data and parameters fully rooted in local data). D_QR states for uncertainty ranking scores for diet input data (Table S4). D_QR ranges from 0 (i.e. low precision information) to 1 (i.e. data and parameters fully rooted in local data). TL states for Trophic level. OI states for Omnivory Index.

	Group name	TL	B (t/km^2)	B_CV	P/B (year^{-1})	P/B_CV	Q/B (year^{-1})	Q/B_CV	D_QR	EE	OI	C (t/km^2 year
1	River dolphins	**3.70**	0.295	0.25	0.08	0.20	7.50	0.20	0.20	**0.00**	**0.33**	
2	Otters	**3.36**	0.017	0.40	4.30	0.20	22.46	0.20	0.20	**0.00**	**0.35**	
3	Turtles	**2.27**	**1.260**	0.35	0.17	0.20	2.54	0.20	0.20	0.95	**0.21**	0.2040
4	Other piscivore fish	**3.31**	0.950	0.35	1.00	0.10	10.0	0.10	0.20	**0.46**	**0.14**	0.0829
5	Other invertivore fish	**3.02**	1.110	0.35	3.00	0.10	18.0	0.10	0.20	**0.55**	**0.001**	0.0131
6	Other frugivore fish	**2.10**	1.202	0.35	1.50	0.10	15.0	0.10	0.20	**0.51**	**0.09**	0.0084
7	Other algivore/detritivore fish	**2.00**	1.850	0.35	1.30	0.10	20.0	0.10	0.20	**0.65**	**0.00**	0.0367
8	*Arapaima gigas*	**3.37**	**0.008**	0.5	0.41	0.10	3.61	0.10	0.40	0.95	**0.17**	0.0030
9	*Brachyplatystoma filamentosum*	**3.38**	**0.184**	0.5	1.11	0.10	3.89	0.10	0.20	0.95	**0.20**	0.1388
10	*Brachyplatystoma rousseauxii*	**3.37**	**0.220**	0.5	1.16	0.10	4.76	0.10	0.20	0.95	**0.18**	0.1761
11	*Pellona castelnaeana*	**3.24**	**0.424**	0.5	0.61	0.10	7.94	0.10	0.40	0.95	**0.11**	0.1380
12	*Cichla* spp.	**3.22**	1.122	0.25	0.83	0.10	5.06	0.10	0.80	**0.69**	**0.10**	0.1619
13	*Hypophthalmus marginatus*	**3.01**	**1.424**	0.5	1.05	0.10	9.34	0.10	0.40	0.60	**0.002**	0.0876
14	*Plagioscion squamosissimus*	**3.21**	**1.040**	0.5	0.61	0.10	5.50	0.10	0.40	0.95	**0.22**	0.3856
15	*Colossoma macropomum*	**2.20**	**0.727**	0.5	0.48	0.10	5.34	0.10	0.60	0.60	**0.16**	0.0189
16	*Mesonauta festivus*	**2.32**	1.116	0.30	1.80	0.10	14.55	0.10	0.80	**0.60**	**0.23**	0.0011
17	*Acaronia nassa*	**3.19**	0.755	0.30	1.25	0.10	10.93	0.10	0.20	**0.56**	**0.25**	0.0002
18	*Satanoperca acuticeps*	**2.72**	1.660	0.30	1.25	0.10	11.05	0.10	0.80	**0.61**	**0.22**	0.0114
19	*Acarichthys heckelii*	**2.64**	1.850	0.30	1.40	0.10	11.71	0.10	0.80	**0.49**	**0.25**	0.0084
20	*Bryconops* spp.	**2.42**	1.566	0.30	1.61	0.10	14.13	0.10	0.80	**0.50**	**0.26**	0.0027
21	*Pacu*	**2.11**	0.290	0.35	1.94	0.10	15.66	0.10	0.80	**0.63**	**0.10**	0.0376
22	*Geophagus* spp.	**2.52**	1.751	0.30	1.32	0.10	12.62	0.10	0.80	**0.65**	**0.27**	0.1636
23	*Hemiodus* spp.	**2.73**	1.897	0.30	2.87	0.10	12.85	0.10	0.80	**0.26**	**0.23**	0.1424
24	*Schizodon* spp.	**2.16**	0.571	0.30	1.11	0.10	11.76	0.10	0.80	**0.51**	**0.14**	0.0067
25	*Leporinus* spp.	**2.52**	1.120	0.30	1.01	0.10	9.66	0.10	0.80	**0.59**	**0.27**	0.0403
26	*Laemolyta* spp.	**2.21**	0.502	0.30	1.66	0.10	18.67	0.10	0.80	**0.44**	**0.18**	0.0537
27	*Loricariichthys* spp.	**2.30**	1.520	0.30	1.28	0.20	11.94	0.20	0.80	**0.61**	**0.21**	0
28	*Semaprochilodus* spp.	**2.00**	0.481	0.30	1.39	0.10	14.31	0.10	0.80	**0.57**	**0.002**	0.1425
29	Terrestrial invertebrates	**2.10**	8.400	0.35	6.00	0.20	30.0	0.20	0.20	**0.52**	**0.09**	
30	Aquatic invertebrates	**2.03**	16.800	0.40	10.40	0.20	40.0	0.20	0.2	**0.33**	**0.02**	
31	Zooplankton	**2.00**	3.22	0.25	70.0	0.20	166.0	0.20	0.2	**0.40**	**0.02**	
32	Igapo Forest	**1.00**	3,200.0	0.25	0.30	0.20				**0.22**		
33	Periphyton	**1.00**	3.0	0.30	733.0	0.20				**0.24**		
34	Phytoplankton	**1.00**	2.658	0.20	1,128.0	0.20				**0.43**		
35	Detritus	**1.00**	22.940							**0.20**		

The trophic spectra analysis showed that the Tapajós River ecosystem can be divided into three main trophic levels (Fig. 5). Most of the biomass is confined to the first trophic level (98.5 %. of the total ecosystem biomass). Terrestrial and aquatic invertebrates groups represent a great proportion of the second trophic level's biomass (52.6 %). Between fish groups, species with trophic level higher than three contribute by 36.75 % of the total ichthyofauna biomass.

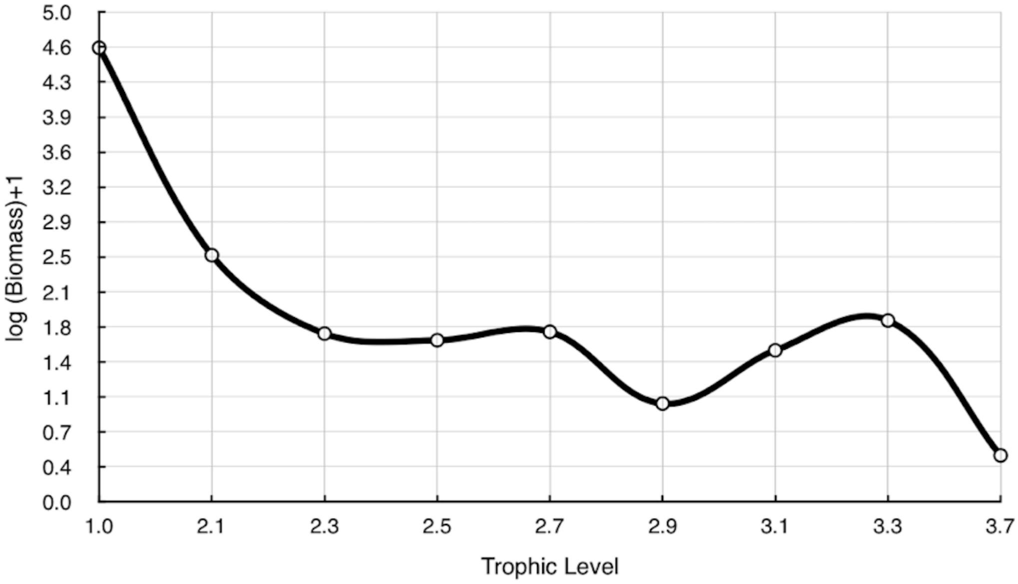

Fig. 5 Trophic spectra of the Tapajós River ecosystem model for the reference year 2013, representing the absolute biomass ($\log_{10}$ +1 scale) of different trophic levels.

The final parameters values for the balanced model of the Tapajós ecosystem are presented in Table 1**.** The highest trophic level (TL) was obtained for river dolphins (3.70) while otters have a trophic level of 3.36. Among the fish species, the highest TL values were obtained for *Brachyplatystoma filamentosum* (3.38), *Arapaima gigas* (3.37 and *Pellona castelnaeana* (3.24). The Omnivory Index, representing the variance of the trophic level estimate for each group, ranged from 0.001 to 0.333 (Table 1). Among the groups with a TL > 3, only river dolphins and otters exhibited an OI greater than 0.25. The species *Leporinus* spp., *Geophagus* spp., *Bryconops* spp., *Acarichthys heckelii*, from the intermediate TLs (between 2 and 3) has an OI greater than 0.25 too. The zero ecotrophic efficiency (EE) values for the river dolphins and otters functional groups reflect the absence of predation on these groups because these groups are considered top predators in the Tapajós River ecosystem. Fish group presents EE values ranging between 0.778 and 0.959. Primary production groups (phytoplankton, periphyton and igapó forest) presents EEs values lower than 0.5, but phytoplankton group presents a significantly higher value than the other three. Remarkably, terrestrial invertebrates group present an ecotrophic efficiency value of 0.953. The matrix of the diet composition (DC) is shown in Table 2, supplementary material section.

Several ecosystem indexes are presented in Table 3.

Table 3. Summary ecosystem indexes calculated for the Tapajós River food web model (reference year 2013)

Indexes	Tapajós River ecosystem indexes
Summary statistics	
Total biomass (excluding detritus, t/km^2)	4384.3
Total catch ($t/km^2/year$)	2.1
Sum of all consumption (t/km^2*year)	2031.0
Sum of all exports (t/km^2*year)	2302.0
Sum of all respiratory flows (t/km^2*year)	940.6
Sum of all flows into detritus (t/km^2*year)	3025.0
Total system throughput (t/km^2*year)	8299.0
Sum of all production (t/km^2*year)	3722.0
Average trophic level of the catch	2.86
Net system production (t/km^2*year)	2298.0
Total net primary production (t/km^2*year)	3239.5
Primary production required (PPR harvested groups/total primary production, %)	17.0
Ecosystem maturity	
Total primary production/total respiration (dimensionless)	3.4
Total primary production/total biomass	0.7
Total biomass/total throughput ($year^{-1}$)	0.5
Food web structure	
Connectance Index	0.3
Finn's cycling index (% of total throughput)	4.3
Finn's mean path length	2.6
System Omnivory Index	0.1
Average transfer efficiency (%) From primary producers From detritus	8.57 9.07 7.73
Ascendency (%)	31.1
Overhead (%)	68.9
Model reliability	
Ecopath pedigree index	0.48

The MTI of the lower Tapajós River ecosystem suggests that direct and indirect impacts of the RESEX riverine population's fishing activity are negative for turtles and giant catfish of the genus *Brachyplatystoma* (Fig. 6). On the other side, RESEX riverine population has a slight positive indirect effect on *Arapaima gigas*, *Acaronia nassa* and *Colossoma macropomum*. FLONA riverine population fishing activities generate negative strong impacts on *Arapaima gigas* and with less degree for turtles and *Brachyplatystoma filamentosum*. Igapó forest has direct positive impacts for many functional groups, specially for turtles, other frugivore fish, and *Colossoma macropomum*. Igapó forest also has indirectly positive impacts for the RESEX and FLONA riverine population. The *Brachyplatystoma* genus has negative impact on *Pellona castelnaeana*, *Plagioscion squamosissimus, Colossoma macropomum* but generates an indirect positive impact on *Cichla* spp. group. Top predators, like river dolphins and other piscivore fish, have similar slightly indirect negative impact on the fisheries of FLONA and RESEX protected areas.

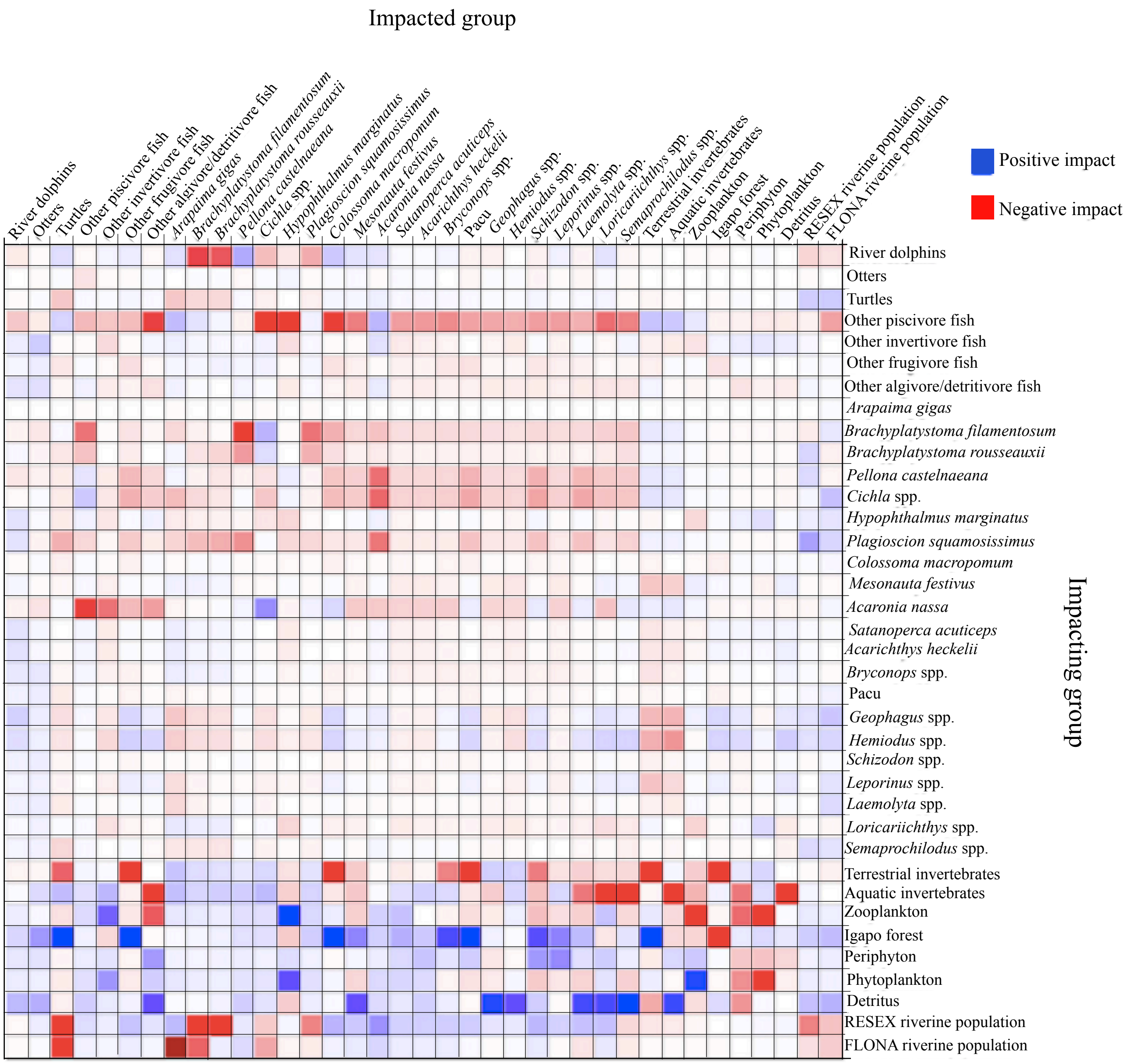

Fig. 6 Mixed trophic impact analysis showing direct (predation) and indirect (competitive) impacts of the lower Tapajós River ecosystem, for the reference year 2013. Note that intensity of the colour reflects the intensity of the impact.

Table 4 shows the Tapajós River's keystone species. They are: others piscivore fish, river dolphins, *Acaronia nassa, Pellona castelnaeana* and *Cichla* spp.

Table 4. Top five functional groups with higher keystone index for the lower Tapajós River ecosystem (year 2013). Relative total impact represents the overall effect of one group on all the other groups in the food web (without including the effect of the group on itself). Keystone index was based on Valls and collaborators (2015) operational methodology.

Group number	Ranking Functional group	Keystone index	Biomass (t km^{-2})	Relative Total Impact
4	Other piscivore	1.33	0.950	0.810
1	River dolphins	1.10	0.950	0.353
17	*Acaronia nassa*	1.09	0.755	0.398
11	*Pellona castelnaeana*	0.96	0.794	0.321
12	*Cichla* spp.	0.91	1.122	0.375

Dynamic simulations: impacts of fishing and deforestation

First we present dynamic simulation results for river dolphins and turtle functional groups, based on their ecological and socio-economic importance. Secondly, we present dynamic simulation results for functional groups of fishery importance such as giant catfish of the genus *Brachyplatystoma,* cichlids such as *Cichla* spp*.,* characins such as *Hemiodus* spp. and prochilodontid *Semaprochilodus* genus. Moreover, we present dynamic simulations results for *Acaronia nassa* and for *Arapaima gigas.* The first species mentioned is considered in this study an ecosystem's keystone species. *Arapaima gigas* is an iconic species of the Amazon basin and it is considered threatened by overfishing.

Scenario 1: increasing fishing effort

Of the groups directly impacted by fishing effort increase, dolphins, turtles, *Arapaima gigas*, *Brachyplatystoma rousseauxii,* and *Plagioscion squamosissimus* have the greatest response associated with fish mortality, decreasing in biomass more than 10 % compared to the reference biomass (Fig. 7 and Fig. 8). Turtles and river dolphins present a significant biomass reduction of 29 % and 15.5 % respectively (Fig. 7 a-b). *Brachyplatystoma rousseauxii, Arapaima gigas,* and *Plagioscion squamosissimus* decline by 47%, 35% and 10.1% respectively (Fig. 8 a-b-e). Changes in biomass to other target fish species were smaller in magnitude, having a biomass change less than 3 % (Fig. 8 g-h-j-k). Dolphins, turtles and *Arapaima gigas* show a linear and continuous decline all over the stressed period (Fig. 7 a-b and Fig. 8 b). In contrast, the other fish functional groups present alternative peaks followed by linear stabilised biomass change (Fig. 8 a-c-d-e-f-g-h-j-k). *Cichla* spp., *Pellona castelnaeana*, *Acaronia nassa* responded almost immediately to a change in fishing mortality in their fish preys (Fig. 8 c-d-f), whereas *Plagioscion squamosissimu*s had a delayed (3–4 years) response (Fig. 8 e).

Monte Carlo sensitivity analysis reports 91 trials with energetically balanced models. So, 9 % of the 100 simulations trials returns unbalanced models. Nevertheless, the observed trend in the baseline run, for all groups, was echoed by the results of the Monte Carlo simulations, even those that had large variations due to low confidence levels. The biomass change variance for each functional group presents a heterogeneous range of confidence intervals. *Cichla* spp., *Acaronia nassa*, Pacu, *Schizodon* spp., *Semaprochilodus* spp., *Hemiodus* spp. functional groups showed a confidence interval of no more than 1% of the average biomass change (Fig. 8 c-f-g-h-j-k). River dolphins and *Pellona castelnaeana* showed a confidence interval of no more than 5% of the average biomass change Fig. 7a and Fig.8d). In contrast, groups with a higher level of uncertainty associated with their data, for example turtles, *Brachyplatystoma rousseauxii*, *Arapaima gigas, Plagioscion squamosissimu*s showed large confidence intervals, reaching a biomass change outputs varying more than 10% (Fig. 7b and Fig. 8 a-b-e).

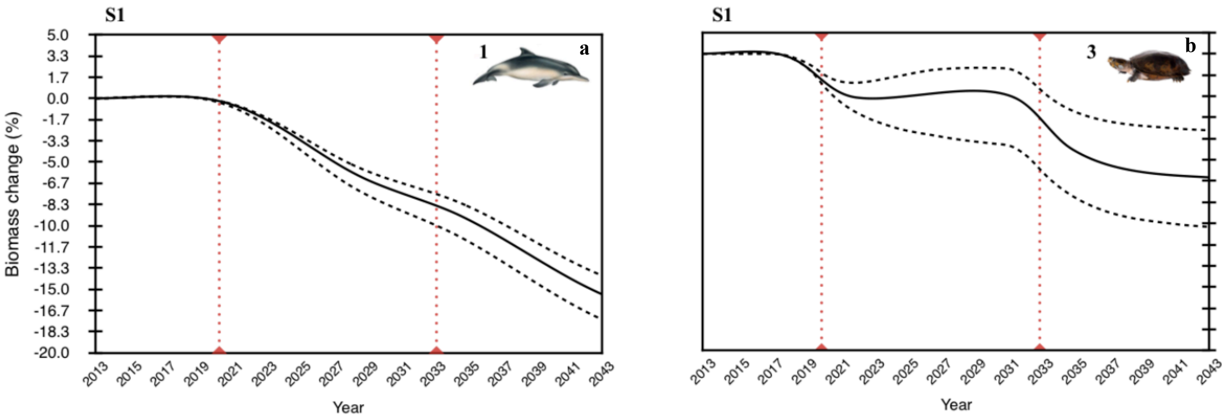

Fig. 7 **Representation of temporal dynamic simulations for river dolphins and turtles in the lower Tapajós River, reference year 2013.** Mean predicted biomass change is shown as solid line. Black dotted lines represent the 95th percentile and 5th percentile obtained through the Monte Carlo routine. S1 states for Scenario 1 (increasing fishing effort). Red dotted lines represent years when increase fishing effort corresponds to 50 % (left side) and 100 % (right side) of the baseline value. Functional codes correspond to those given in Table 1, Results section.

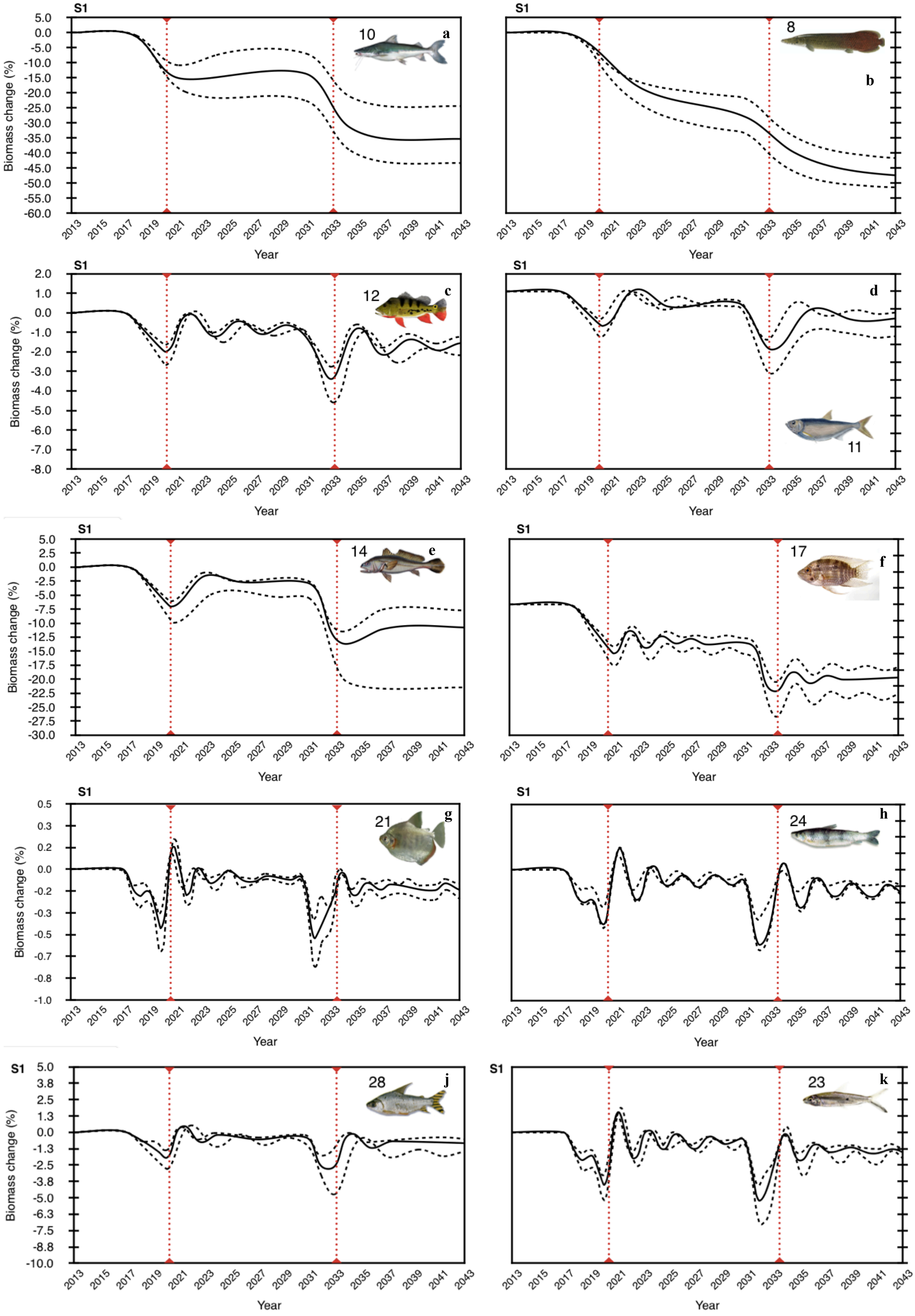

Fig. 8 Representation of temporal dynamic simulations for target fish functional groups in the lower Tapajós River, reference year 2013. Mean predicted biomass change is shown as solid line. Black dotted lines represent the 95th percentile and 5th percentile obtained through the Monte Carlo routine. S1 states for Scenario 1 (increasing deforestation rate). Red dotted lines represent years when increase fishing effort corresponds to 50 % (left side) and 100 % (right side) of the baseline value. Functional codes correspond to those given in Table 1: 8. *Arapaima gigas*; 10. *Brachyplatystoma rousseauxii*; 11. *Pellona castelnaeana; 12. Cichla* spp.; 14. *Plagioscion squamosissimus;* 17. *Acaronia nassa*; 21. Pacu; 23. *Hemiodus* spp.; 24. *Schizodon* spp.; 28. *Semaprochilodus* spp.

Scenario 2: increasing deforestation rate

In this Scenario, temporal dynamic simulations indicate that all functional groups show a negative biomass change with respect to the baseline values (Fig.9 and Fig.10).

Functional groups with high proportion of terrestrial (allochthonous) food sources in their diet showed most dramatic changes in biomass with respect to the baseline values (Turtles -39%, Fig. 10b; Pacu -35 %; *Schizodon* spp. -26%, Fig.10 g-h). The biomass of the top predators (river dolphins and piscivorous fish) also showed pronounced decrease, with *Plagioscion squamosissimu*s and *Brachyplatystoma rousseauxii* showing a considerable long-term decline in biomass (more than 20 % decrease, Fig. 9a and Fig.10 a-e).

In the Monte Carlo sensitivity analysis examining the impact of uncertainty in the basic Ecopath parameters on the effects of increase deforestation rate, the responses of most functional groups were quite similar to those in the Ecosim Scenario 1.

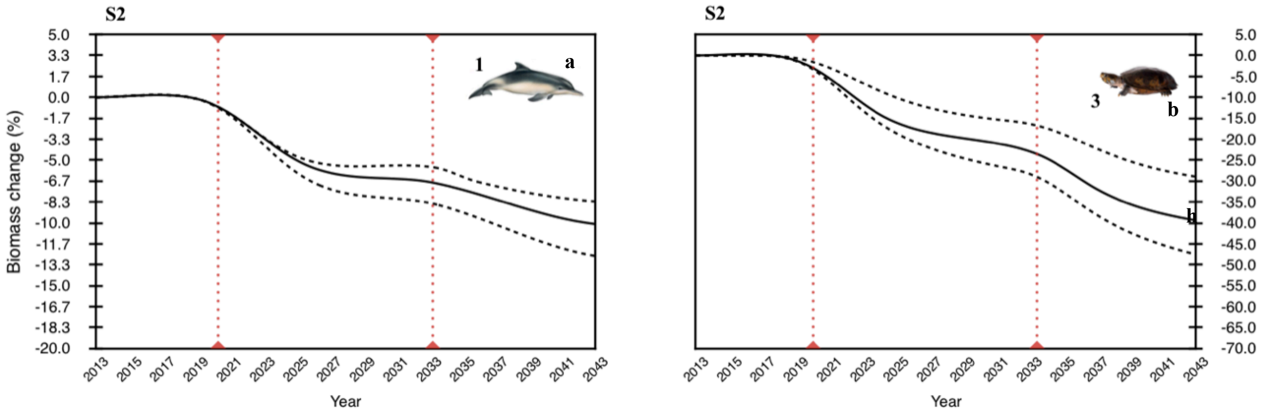

Fig. 9 Representation of temporal dynamic simulations for river dolphins and turtles in the lower Tapajós River, reference year 2013. Mean predicted biomass change is shown as solid line. Black dotted lines represent the 95th percentile and 5th percentile obtained through the Monte Carlo routine. S2 states for Scenario 2 (increasing deforestation rate). Red dotted lines represent years when increase fishing effort corresponds to 50 % (left side) and 100 % (right side) of the baseline value. Functional codes correspond to those given in Table 1, Results section.

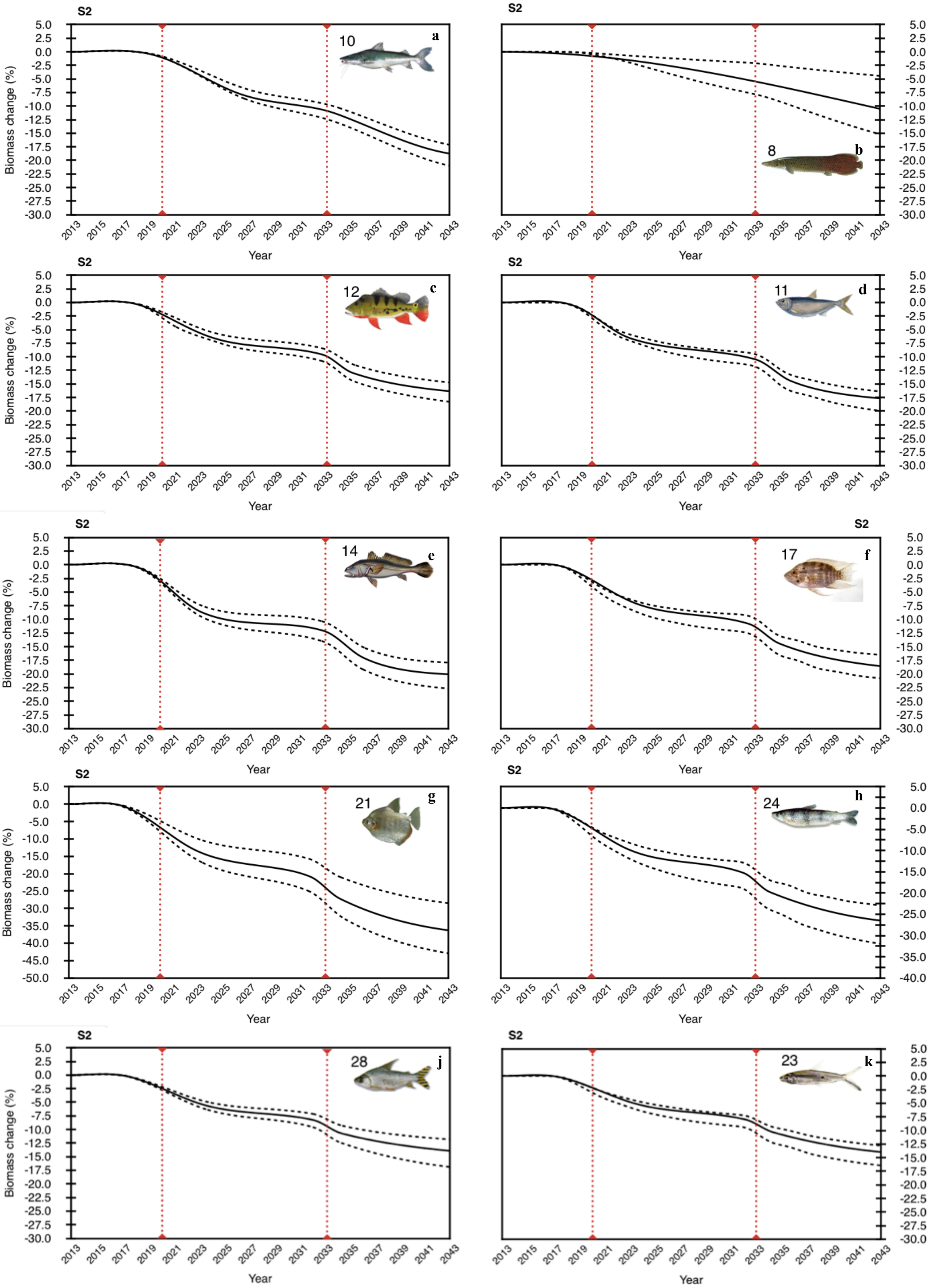

Fig. 10 Representation of temporal dynamic simulations for target fish functional groups in the lower Tapajós River, reference year 2013. Mean predicted biomass change is shown as solid line. Black dotted lines represent the 95th percentile and 5th percentile obtained through the Monte Carlo routine. S2 states for Scenario 2 (increasing deforestation rate). Red dotted lines represent years when increase fishing effort corresponds to 50 % (left side) and 100 % (right side) of the baseline value. Functional codes correspond to those given in Table 1: 8. *Arapaima gigas*; 10. *Brachyplatystoma rousseauxii*; 11. *Pellona castelnaeana; 12. Cichla* spp.; 14. *Plagioscion squamosissimus;* 17. *Acaronia nassa*; 21. Pacu; 23. *Hemiodus* spp.; 24. *Schizodon* spp.; 28. *Semaprochilodus* spp.

Discussion

We constructed a food web model with more taxonomic resolution of harvested fish species caught by lower Tapajós River's inhabitants. We focus the attention on these fish species and their predators to directly consider their ecological importance and interactions in the lower Tapajós River ecosystem. The model integrated different biological information and sources of data, including some that were not previously published. We investigated the Tapajós River's food web using Ecopath software and by simulating increasing fishing harvest and deforestation stressor using Ecosim module. The model was configured with 35 functional groups. Principals findings of this study are as follow:

- The food web of the lower Tapajós river has a compressed structure, with three defined trophic levels;
- The biomass of fish groups was estimated at 28.7 t/km^2;
- From the energetic point of view, algae (phytoplankton and periphyton) and the igapó forest supply most of the energy to the higher trophic levels;
- The average Tapajós River's energy transfer efficiency (conversion of ecosystem production from lower to higher trophic levels) was 8.57 %. The food chain based on primary producers is more efficient than detritus food chain (9.07 % and 7.73 % respectively).
- Increasing the effect of fishing in the Ecosim simulations resulted in a significant biomass decrease of river dolphins, turtles and piscivore fish such as pirarucu (*Arapaima gigas*), dourada (*Brachyplatystoma rousseauxii*), and pescada (*Plagioscion squamosissimus*).
- Lower trophic harvested fish species do not present negative biomass change under increase fishing scenario.
- Increasing deforestation rate in the simulations has a wide negative impact on frugivore guild (turtles, Pacu and *Schizodon* spp.) showing between 24 % and 40 % biomass reduction. Insectivore and piscivore fish (Cichla spp., *Pellona* spp., *Acaronia nassa* among others) also, decrease an average 15 %.

These evidences suggest that ichthyofauna of the Tapajós River is characterised by opportunistic bottom feeders rapidly changing their diet to profit from terrestrial invertebrates within high water phase, and shifting to detritus -algae- aquatic invertebrates food chain when terrestrial food items became exhausted such as demonstrated by other studies in the Amazon oligotrophic clear water tributaries (Albrecht and Caramaschi, 2003; Benedito−Cecilio and Araujo−Lima, 2002; Camargo and Ghilardi Junior, 2009; Camargo et al., 2015). Regarding anthropogenic stressors, deforestation and consequently habitat loss, is the main negative stressor for the Tapajós's food web components. It is plausible to assert that increase deforestation rate may lead to changes in the Tapajós River food web structure and functioning.

Model's quality: reliability of the input data

PREBAL diagnostics applied to this study show general coherent results of rates to trophic levels (Fig.S1; Fig.S2; Fig.S3). Nevertheless, punctual departures from rules of thumb are noted: the biomasses of top predators such as otters and *Arapaima gigas* are considerably below the trend line of biomass allocation across trophic levels. Primary producers such as phytoplankton and periphyton are above the slope-line in the PREBAL diagnostic of production rate (P/B). As stated by Link (2010), groups at the two extremes of the food web, i.e. primary producers, and mammals, present out-of-trend values compared to their trophic position and should be excluded when interpreting most diagnostics. Functional groups such as zooplankton and turtles presented high coefficients of variation because input values were taken by others Ecopath models. This fact leads to noticeable departure from PREBAL diagnostics. So, these diagnostics suggest investing extra effort particularly on parameters with high coefficients of variation that lead to noticeable departure from PREBAL diagnostics (Heymans et al., 2016). Moreover, their position regarding an expected trend line (threshold) across trophic levels (pathways) gives the main direction for revisiting those initial estimates (Lassalle et al., 2014).

The Pedigree Index, which describes the origin and quality of data used in the Tapajós River model, was estimated to be 0.48. This value is similar to the average value calculated by Colléter and collaborators (2015) in a meta-analysis research study describing critical aspects of the Ecopath models. Another meta-analysis of 50 Ecopath models showed that few models exhibited a very high pedigree (10% have a pedigree higher than 0.60, with the maximum value being 0.65) (Morissette, 2007). Pedigree Index of the Tapajós River model falls in the medium-high range as defined by Morissette (2007), i.e. between 0.4 and 1. So it testifies to an ecosystem benefiting from a sufficient amount of data. Moreover, for those models with Pedigree Index above 0.4, a closer look at the pedigree routine, i.e. values by parameters and compartments, and the PREBAL analysis would help to prioritise parameters needing improvement (Lassalle et al., 2014).

By using the Monte Carlo routine in Ecosim, the Ecopath base model was shown to be quite robust, as for 100 Monte Carlo trials, about 90 % trials return energetically balanced models. This fact suggests that the Ecopath base model is less sensitive to changes in input values, thus potential small errors in input values were not likely to significantly affect Ecosim run outcomes. For fish functional groups such as *Arapaima gigas*, *Plagioscion squamosissimus* or *Brachyplatystoma,* biomass change's inner 95th percentile range suggests high uncertainty for simulations results. Generally, Ecosim model's most critical uncertainties relate to the quality and implementation of diet data and the fitting and calibration of the vulnerability parameters that designate population and trophic behaviour of the functional groups (Stäbler et al., 2016).

The lower Tapajós River's food web structure

Twenty two percent (22%) of the modelled fish biomass is represented by herbivore and detritivore fish. 51.5 % of the modelled fish biomass is represented by omnivore-insectivore fish and 26.5 % is represented by piscivore fish guild. This trophic description of the food web is in accordance with results presented by Jepsen and Winemiller (2002) for nutrient-poor amazon freshwater ecosystems. Herbivore and omnivore/insectivore guilds depends mainly on igapó forest, detritus with its associated decomposing bacterial-fungi fauna and terrestrial invertebrates. In tropical waters, organic carbon from terrestrial forest may enter the food web after processing by the microbial loop, in which bacteria and fungi consume detritus and in turn serve as a food resource for elements of the metazoan food web (Azevedo-Silva et al., 2016; Benner et al., 1995; Thorp and Delong, 2002; Tundisi and Tundisi, 2012). A pathway that may be particularly dominant in blackwater and clearwater systems (Jepsen and Winemiller, 2007; Meyer, 1990; Walker et al., 1991). Phytoplankton is the most probable alternative carbon source in the Tapajós River. Phytoplankton may become a principal direct source for zooplankton and indirect source for fish when algal cells settle onto substrates and metabolised via microbial loop (Farjalla et al., 2002; Trevisan and Forsberg, 2007; Winemiller et al., 2006). The Tapajós River has considerably higher pH than Amazonian blackwaters rivers, and its transparency may also mean that its photic zone is wider. So, although the absence of extensive macrophytes stands in this clearwater ecosystem, microbial loop and the associated food chains probably can be related to phytoplankton primary production (Anesio et al., 1997; Farjalla et al., 2006; William Crampton pers. comm.).

Trophic level estimates for the single species fish groups were found similar to those TL estimated by stable isotope analyses (Araujo-Lima et al., 1986; Forsberg et al., 1993; Hamilton et al., 1992; Jepsen and Winemiller, 2002, 2007; Watson et al., 2013), stomach content analysis of herbivorous and insectivore fish (Anderson et al., 2009; Correa et al., 2015; Correa and Winemiller, 2014; Goulding, 1980) and Fishbase online database (Froese and Pauly, 2017). From the same study region, Keppeler (2015, pag.23) found that the average trophic level of the Tapajós fish fauna ranged from 2.3 to 3.39. As far as the ecosystem biomass trophic spectra is concerned, an important decrease in total biomass was observed from the lower to higher trophic levels (TLs). Two peaks in biomass distribution were observed between TLs 2.6 and 3.3. The first peak corresponds to small pelagic migratory fish, such as *Hemiodus* spp. and small cichlids such as *Acarichthys heckelii* and *Satanoperca acuticeps* (Lucas and Baras, 2008; Reis et al., 2003). The second peak corresponds to second order fish predators, such as *Plagioscion squamosissimus, Cichla* spp. and top carnivorous migratory catfish of the genus *Brachyplatystoma*. Around TL 2.9, a gap was observed in the biomass spectra due to the small number of trophic groups present at this point. Fish organisms belonging to this trophic level can be considered insectivore/omnivore, and it is recommended to consider the omnivore index, presented in Table 1, as the variance of these species's trophic level (Libralato and Solidoro, 2009).

System omnivory index (SOI) was 0.1 which is in between the range of values presented for the middle Amazon River (0.09-0.13; Agudelo, 2015; Petrere and Angelini, 2009; Angelini et al. 2006b). The low value for system omnivory index of the lower Tapajós River may also result from system dependence on detritus as a source of energy (Janjua et al., 2015). Ecosystems that are less dependent on detritus have higher SOI values because the organisms need to diversify their energy sources (Christensen, 1995; Vasconcellos et al., 1997). The connectivity index (CI) and the system omnivory index indicate also the internal complexity of the system with more mature ecosystems displaying stronger and more stable associations between functional groups. In scientific literature, the CI and SOI values for a mature system are both close to 1 (Christensen, 1995), and in the present study, the CI was estimated to be 0.3. These two indexes were slightly higher than those of other freshwater Amazon ecosystems (Agudelo, 2015; Petrere and Angelini, 2009).

The average Tapajós River's energy transfer efficiency (conversion of ecosystem production from lower to higher trophic levels) was 8.57 %. The food chain based on primary producers is more efficient than detritus food chain (9.07 % and 7.73 % respectively). Energy transfer efficiency is generally expected to fall in between 4% and 20 % (Heymans et al., 2014). It is assumed that systems with high transfer efficiencies often have fewer pathways between trophic levels, while systems such as lakes, lagoons, estuaries and bays often have more species at the lower trophic levels – detritivores, suspension feeders, etc., therefore reducing the average transfer efficiency (Heymans et al., 2014). This specific result support the worldwide general assumption of a 10%

transfer between neighbouring trophic levels within aquatic ecosystems (Christensen and Pauly, 1993; Pauly and Christensen, 1995).

From the basic outputs of the Ecopath model, the biomass of fish groups was estimated at 28.7 t/km^2. This value is higher than those published in the scientific literature for similar clear-water Amazonian ecosystems. For example, in the Tocantins river, fish biomass was estimated at 10.63 t/km^2 (De Merona, 1990). For Xingu River fish biomass was estimated at 2.7 ± 0.9 t/km^2 (Camargo et al., 2015). Agudelo (2015) estimated fish biomass at 10.55 t km^2 in the middle Amazon River with its muddy and productive waters. Although this estimate is the first for Tapajós River, such biomass density value has to be consider with caution. Mainly because it is the result of an indirect estimate taken from another scientific study considering only lower Tapajós lentic ecosystems (Ferreira da Costa, 2005). Others two ichthyofauna studies included in the FLONA and RESEX management plans have found different results in composition and absolute abundance of fish species and families (ICMBio, 2014; Silva-Oliveira et al. 2016). Each one of the mentioned studies differs in what kind of microhabitat is sampled and what kind of methodology is used. Scientists face a challenge in that virtually all methods of fish capture or observation are selective (Haddon, 2010). Further, most fish capture methods can be applied to only a fraction of the entire area of interest. Thus, measures such as catch per unit effort (CPUE) or catch per area can only be regarded, at best, as being proportional to the true population abundance (Hayes et al., 2007). This study estimate an average fish biomass using data from seine net samples, assuming homogeneous distribution of the ichthyofauna in the water column of the floodplain lakes annualised. So far, this is the only published scientific study, using both fishing techniques, performed in this region. Coefficient of variation associated to the fish biomass parameters used in this study should be considered as indicator of uncertainty and variability in space.

Globally, Ecopath modelling approach has been developed to study freshwater ecosystem in a minority proportion with respect marine ecosystems: 15 % of the 433 Ecopath's models analysed by Colléter and collaborators (2015) represents freshwater ecosystems. Aiming to compare Tapajós River food web model with others Ecopath models for the tropical zone, we focus the attention on published African and Asian Ecopath models mainly of lentic freshwater ecosystems.

Biomass of fish groups in the Tonle Sap Great Lake ecosystem (Mekong River Basin, Cambodia) was estimated at 58 t/km^2 higher than the estimated biomass of fish groups in African Lake Victoria (43 t/km^2) and Lake Tanganyika (35 t/km^2) while for this study, as mentioned above, fish biomass was estimated in 28.7 t/km^2 (Chea et al., 2016; Christensen and Pauly, 1993). The differences reported may be derived by different primary productivity and transfer efficiency within food webs. For example, African Lakes show higher transfer efficiencies than Tapajós River food web (Christensen and Pauly, 1993) while Tonle Sap Great Lake has a net total primary production (TNPP) higher than the TNPP of Tapajós River (Chea et al., 2016).

Nevertheless, most of the Ecopath freshwater food web models reported over-exploitation of the fishery resources suggesting that the "fishing-down" process was acting (Welcomme, 2008; Welcomme et al., 2010). Average trophic level of the catch (ATL) in the Tonle Sap Great Lake ecosystem was 2.48 (Chea et al., 2016), showing that the catch composition was dominated by the opportunist species (mud carp, small herbivores) and small size fish. In the Chinese lake Taihu, ATL is 2.92 and the composition of landings was increasingly dominated by relatively small and less valuable species with high turnover rates from lower trophic level (Chen et al., 2009; Xu et al., 2016). The same pattern is showed in Ethiopian lakes, such Lake Hayq and Lake Awasa with respectively 2.46 and 2.57 average trophic level of the catch (Fetahi et al., 2011). Tapajós River's average trophic level of the catch is estimated in 2.86 by this study. Moreover, Tapajós riverine inhabitants composition of the catch presents a notable proportion (45%) of lower trophic level fish species such as jaraqui (*Semaprochilodus* spp.) charuto (Hemiodus spp.,) and Aracu (*Leporinus* spp., *Schizodon* spp., *Laemolyta* spp.) (Hallwass and Silvano, 2016; Silvano et al., 2017). This evidences point out that more attention has to be paid at the fishing down process in the lower Tapajós River ecosystem.

Dynamic simulations

The two dynamic scenarios focus on fishing and deforestation as main stressors in the lower Tapajós River. One important conclusion is immediately evident: deforestation and consequently habitat loss, is the main negative stressor for the Tapajós's food web components. Comparing the two scenarios, negative biomass change for all the functional groups is more accentuated for Scenario 2 (deforestation) than Scenario 1 (increase fishing pressure).

When analysed separately, Scenario 1 depicts a specific ecosystem behaviour. Increasing fishing pressure has a negative impact on the top predators, such as river dolphins, *Arapaima gigas* or giant catfish of the genus *Brachyplatystoma.* Effects of an increase in fishing pressure are dampened for piscivore-invertivore fish such as *Cichla* spp. or *Pellona castelnaeana*. Small target fish species such as *Hemiodus* spp., *Schizodon* spp., *Semaprochilodus* spp., slightly oscillate in their biomass and tend to stabilise with no significant biomass reduction along the stressed period. It seems reasonable to assert that top piscivore predators (river dolphins, *A. gigas*, *Brachyplatystoma* spp.)

are sensitive to fishing mortality in the lower Tapajós River, reporting biomass decrease between 15 % and 45 %. This fact is remarkably serious for the case of river dolphins and for the genus *Brachyplatystoma*. Their modelled diet composition contemplates an allochthous input (i.e small migratory fish from the Amazon River main channel), indicating that, although using supplemental food sources, fishing activities strongly interfere on their population dynamics.

For river dolphin, basing on its model's diet composition, fishing activities can be considered a strong competitor for the same fish species. If top predators might compete with fisheries, then fisheries might also compete with predators. Indeed, it can be argued, both on the basis of predator–prey dynamics (Arditi and Ginzburg, 2012; White, 2005) and on the simple grounds that humans (unlike natural predators) have access both to powerful technology and to an abundance of alternative resources, that fisheries are more likely to affect predator populations than the other way around (Yodzis, 2001). Multispecies modelling of the Patagonian marine ecosystem showed that extreme harvest rates of hake led to clearly negative effects, including extinction of sea lion (Koen-Alonso and Yodzis, 2005). In the Amazon Basin, several studies reported growing situation of conflict with fishing activities and river dolphins (Alves et al., 2012; Loch et al., 2009; Mintzer et al., 2013). Moreover, it is known that increasing fishing pressure decreases the biomass flow in the food web, with cumulative effects for the highest trophic levels even if they are not targeted by fishing (Gascuel and Pauly, 2009).

Turtles is another group that shows strong negative decrease in biomass density along the stressed period. This functional group is directly impacted by any slight increase in fishing effort. This result can be interpreted comparing turtle's biomass to yield. During the simulated stressed period, harvest represents between 15% and 30 % of the initial turtle's biomass. Ninety five percent of the turtles's total mortality is represented by fishing activities (Table S5). Protection of turtle's adults, particularly nesting females, remains paramount to avoid the demographic declines associated with adult harvesting in species with Type III survivorship curves (the greatest mortality is experienced early in life, with relatively low rates of natural mortality; Pearse et al.,2006).

Piscivore-invertivore fish such as *Cichla* spp. and *Pellona castelnaeana* show small and dampened response to the increase of fishing harvest. For these species, fishing mortality represents about 25 % of the total mortality. Instead their predation mortality fraction (proportional contribution of individual predator to prey total mortality) is above 65 % (Table S5). In other words, these fish species suffer an intra-guild predation mortality suggesting strong interference competition among predators. This fact is described among the characteristics of the donor control mechanism that may attenuate the negative impact of the fishing mortality (Arditi and Ginzburg, 2012; DeAngelis et al., 1975).

Looking small pelagic fish species such as *Hemiodus* spp., *Semaprochilodus* spp. or *Schizodon* spp., dynamic simulations show no biomass change over the stressed period. These fish functional groups can be considered omnivores (Junk et al., 1997; Röpke et al., 2016). So their biomass densities dynamics can be driven in time and space by the quantity and quality of these food sources. This assertion is supported by the empirical evidence that tropical freshwater fish exploit food resources in a variety of ways, and many species can switch diets opportunistically in response to the relative availability of food (Jepsen and Winemiller, 2002). Moreover, omnivory can theoretically have a stabilising or destabilising effect on ecosystems, depending to some extent on where it occurs in the food chain (Abrams et al., 1996; Pimm and Lawton, 1978; Pimm, 1982). For example, omnivory species at higher trophic levels may mitigate the trophic cascade in response to harvesting at the top of the food chain in many aquatic environments (Herwig et al., 2004; Vadas, 1990). Probably, for the omnivore fish species analysed in this study, dynamic simulations report no biomass change over time because primary producer and invertebrates are constrained to maintain their initial biomass values.

Scenario 2 differs from Scenario 1 in terms of higher negative biomass change for all functional groups analysed. The negative impact of deforestation by losing igapó forest's biomass is reflected on a linear non-stop decrease along the stressed period. Considering the initial modelling hypothesis about a donor-controlled ecosystem, it seems reasonable that simulation results represent higher biomass losses for Scenario 2, where a primary producer (igapó forest) suffers high deforestation rate. In the simulations of this Scenario there is no evidence of stabilised biomass change all over the stressed period. This fact may indicates that igapó forest is a strong donor-controller component of the lower Tapajós River's food web. Agudelo (2015) finds similar biomass decrease for the central region of the Amazon River, using the same modelling approach. His study with dynamics simulation combining fishing harvest and deforestation stressors, shows a high reduction in biomass for migratory catfish and for small characins and cichlids fish. Camargo and collaborators (2014) also simulates the suppression of the floodplain forest for the Xingu River. They find that benthic scraper fish and detritivore fish biomass increased, while frugivore fish's biomass, strongly decreases.

In an important ecological feedback, the products of floodplain primary production eventually return to the main-stem river in floodplain runoff, becoming important energy sources for heterotrophic communities living there (Richey et al. 1990, Melack and Forsberg 2001). Dissolved organic carbon produced by the flooded forest is one of the main sources for detritus (Goulding et al., 1988b). Empirical evidence from stream sites in the Ecuadorian Amazon relates that the fish community changed from dominance by omnivorous and insectivorous characins at forested sites to dominance of periphyton-detritivore feeding loricariids at deforested sites (Bojsen and Barriga, 2002). This modification of the food web structure deals with the detrital-microbial loop and its fundamental role by providing both an energetic resource and habitat (Hagen et al., 2012).

Results form this study, suggest that biomass loss of igapó forest in the Tapajós River floodplain provoke a net strong biomass decrease for frugivore guild (turtles, Pacu and *Schizodon* spp.) showing between 24 % and 40 % reduction. Insectivore and piscivore fish (Cichla spp., *Pellona* spp., *Acaronia nassa* among others) also, decrease an average 15 %. This fact is suggestive of possible shifts in key species within the food web, a finding supported by field evidence in an observed lotic ecosystem food web in an Amazon Andean piedmont river located in the Orinoco basin (Taylor et al., 2006). It is plausible to assert that increase deforestation rate may lead to changes in the Tapajós River food web structure and functioning. Less nursery-shelter habitat for migratory fish and less energy sources such as fruits, seed and terrestrial invertebrates are the principal drivers of the linear decrease in biomass of the main fish caught by Tapajós riverine inhabitants.

More important for the lower Tapajós River ecosystem are the nutrients entering from the nutrient-rich, productive waters of the Amazon and its floodplain, largely in the form of brooding fishes (Fittkau, 1973; Junk et al., 1997; Lucas and Baras, 2008). Many Amazon fish migrate from black-water and clear-water rivers to the main stem and other white- water rivers to spawn (Barthem and Goulding, 2007; Lowe-McConnell, 1987). These predictable migration routes are used by larger predators that congregate at the confluences of clear water and whitewater rivers, such as giant catfish of the genus *Brachyplatystoma*, turtles, and river dolphins (Fittkau, 1970; McClain and Naiman, 2008). Following the pioneer hypothesis of Ernst Josef Fittkau (1970), the greater the number and biomass of the top carnivores of the food chain is (predatory fish, reptiles, mammals), the more the allochthonous nutrients which can be collected into their biomass by feeding migratory fish from Amazon River eutrophic waters. This principle becomes more important as more allochthonous food is accumulated in the organisms and partly transformed into nutrients, or is remineralised via microbial loop, so that it is available for use in primary production.

In this study, dynamic simulations suggest that removing from the Tapajós nutrient poor ecosystem the flooded forest, results in a reduction of food sources for the fish fauna. This fact may cause a severe reduction in fish fauna biomass. This fish fauna play important roles as accumulators and transformers of allochthonous nutrition, so the original food web structure may break down (Fittkau and Klinge, 1973; Flecker et al., 2010; Winemiller et al., 2014). Cumulative effects of fishing harvest increase and deforestation, may increase the negative impact on the river dolphins and other piscivore fish from the Tapajós River ecosystem. So, the biological filter for allochthonous nutrition will be disrupted in its most effective part, and the resulting loss of biomass will diminish the metabolism of the food web and degrade its capacity for production. Lakes and the main river channel in the unprotected area were more intensely fished than protected areas in the lower Tapajós River (Hallwass, 2015; Keppeler et al., 2017). Simulation dynamic results of this study agreed with Keppeler and collaborators (2017), pointing out that the conditions provided by the protected areas in the Tapajós River, such as lower human population density, general management rules and higher environmental integrity, may act synergistically to reduce the levels of fishing pressure and deforestation rate allowing the sustainability of the riverine fisheries.

Implications to Ecosystem Management

Tapajós River food web model is not primarily intended as a management tool, but for studying the food-web structure and dynamics under different anthropogenic stressors. However, the two tested scenarios (i.e. increase fishing harvest and increase deforestation rate) can be interpreted within the ecosystem based fishery co-management (Cinner and Huchery, 2014; Jentoft, 2003; Pomeroy, 2001). Preserving the integrity of the Tapajós River floodplain benefits directly frugivore fish and indirectly all others trophic fish guilds that depend partially on the whole floodplain habitat. Increasing fishing harvest may be prejudicial for top piscivore species, such as river dolphins, giant catfish of the genus *Brachyplatystoma* and the iconic *Arapaima gigas*. In this context, priority management actions should be planned with the aim to preserve the quality and quantity of the primary production sources of the Tapajós River, including its floodplain lakes. Co-management effects have been studied in Amazon clear water tributaries such as Tocantins and Tapajós Rivers (Hallwass, 2015; Keppeler et al., 2017; Silvano et al., 2014). For example, Silvano and collaborators (2014) demonstrated that for Tocantins River, the co-management influence positively fishing yields of fishing communities and fish abundance in floodplain lakes. Keppeler and collaborators (2017) indicate that protected areas of sustainable use in the lower Tapajós River, which were designed primarily to protect terrestrial ecosystems, increased the fishing productivity of the riverine inhabitants.

The results of the dynamic simulation presented here should be consider the model uncertainties. The model developed in this study highlighted the input data that require local estimates for the fish biomass and parameters of some functional groups, such as aquatic and terrestrial invertebrates. The lack of fish yields time-series data for the lower Tapajós River did not allow a proper model calibration. Tapajós riverine communities are central actors in monitoring field assessment (Hallwass, 2015). Also, scientific community and decision makers should included biological groups understudied as priority in field investigations for the Tapajós River.

Finally, this study may also contributes to guide public fisheries management policies (e.g., defining priority fish species for conservation or avoiding conflicts with riverine population), food safety (top piscivore species that should be avoided for consumption due to potential mercury contamination), environmental impact assessment by dams, environmental education and local fishery management initiatives.

Concluding Remarks

Understanding the way an ecosystem functions in terms of internal control between components appears to be a key to predicting ecosystem effects of fishing and deforestation. The current study contributed to constructing the first food web model for the Tapajós River ecosystem where ecological information and understanding are scarce. We investigated the structure and the dynamic behaviour of this model using Ecopath with Ecosim (EwE) modelling approach. The biomass spectra, ecotrophic efficiencies, ecosystem indexes, trophic relationships impacts and ecosystem's keystone species were analysed. Long-term Ecosim simulations were performed to investigate the fishing and deforestation impacts on fish target species. Functional groups were chosen focusing on target fish species caught by Tapajós's riverine population (Hallwass, 2015). So, the model could address important ecological and socio-economic questions. Namely, characterising the food web structure of the ecosystem and whether this environment can support moderate or high fishing pressure and deforestation rates.

Through quantification of energy flow through food webs, the effect of changing species abundance can be determined, which helps to answer the question: does the structure and function of a community change in accordance with changes in basal food source supply and species composition? The EwE approach provided an understanding of the aquatic food web structure of the lower Tapajós River, which is supposed to be structurally characterised by donor control, through the use of basal compartments: detritus, fruits, seed which enter the system through flood pulses (wet season) and terrestrial and aquatic invertebrates. The ecosystem may be considered resilient due to its ecosystem attributes and is able to sustainably withstand a subsistence fishing pressure, particularly of fish species belonging to lower trophic levels.

Time-dynamic simulations across an expanded temporal scale illustrated that lower trophic level consumers were resilient to increasing fishing pressure. Otherwise, piscivore fish guild, turtles and river dolphins were more sensitive to increase harvest events than the other species in the system, and it is not known if they may eventually return to their equilibrium state. Long-term fishery perturbations, as simulated within the limitations of the Ecosim model, were shown to have the potential to reduce the long-term average biomass of key important species in this system. Habitat loss and degradation may cause a major change in the structure of the Tapajós River's food web since it should affect negatively biomass abundance of lower trophic level consumers.

Anthropogenic stressors in the lower Tapajós River ecosystem are projected to increase as the human population continues to grow along this portion of the clearwater Amazon tributary, and climate change models predict that there is a potential for alterations of precipitation patterns in this region (Nobre et al., 2016; Sorribas et al., 2016). Our analysis illustrates the importance of careful land- and water-use management in order to ensure the viability of the dynamic food web of the lower Tapajós river, and likely other clear water Amazon tributaries.

Considerações finais

Entender a estrutura, o funcionamento e a eficiência de um ecossistema é fundamental para compreensão das vias de transferência de massa e fluxo de energia nele. Nessa tentativa, o conjunto da biota e as suas relações tróficas são imprescindíveis pontos de partida para prever os possíveis impactos das atividades humanas no ecossistema. O presente estudo teve como principais objetivos analizar a estrutura da teia trófica do baixo rio Tapajós, e avaliar ao longo do tempo a dinâmica das principais espécies de peixes sob incremento da pesca ou do desmatamento. Para conseguir estes objetivos foi utilizado o programa de modelagem ecológica Ecopath e módulo de simulação dinâmica Ecosim.

A construção do modelo seguiu todo o protocolo do Ecopath para estimativa de incertezas e erros (PREBAL analise). O modelo pode ser considerado de boa qualidade, com estimativas locais para os grupos funcionais da ictiofauna. Para a construção e balanceamento do modelo foram necessários ajustes na tentativa de suplantar as lacunas da informação, principalmente em relação aos demais grupos funcionais utilizados no modelo. Desta forma, esperamos que este estudo incentive novas investigações nestas áreas através de análise quantitativas (através de estimativas de B, P/B, Q/B e composição da dieta) de fitoplâncton e zooplâncton, invertebrados aquáticos e terrestres, répteis, mamíferos.

A teia trófica do baixo rio Tapajós possui uma estrutura comprimida, com três níveis tróficos definidos. Do ponto de vista energético as algas e a floresta de igapó fornecem a maior parte de energia para os níveis tróficos superiores. A transferência de energia na teia trófica do rio Tapajós resultou ser co-baseada na sub-teia alimentar dos herbívoros (58%) e na sub-teia alimentar dos detritivoros (42%), com uma eficiência média de transferência de 9.15%. As espécies-chave do ecossistema formam parte da guilda trófica dos piscívoros-insetívoros (*Acaronia nassa*, *Cichla* spp., *Pellona castelnaeana*) e também predadores de topo como os botos (*Inia geoffrensis*, *Sotalia fluviatilis*). Entretanto, o índice de conectância (IC: 0,3) e o índice de omnívoria do sistema (SOI: 0,1) apresentaram valores intermediários comparados com outros ecossistemas tropicais de água doce. A análise de impacto trófico indicou a mortalidade por pesca como um importante fator ecológico no ecossistema do baixo rio Tapajós.

As simulações, para os próximos 30 anos, indicaram que a pressão da pesca e a taxa de desmatamento influenciam na dinâmica populacional dos peixes de maior importância para as comunidades ribeirinhas do rio Tapajós. O desmatamento foi o maior fator de estresse para o ecossistema do baixo rio Tapajós, mostrando entre 24% e 40% de redução de biomassa para peixes frugívoros.

É evidente que as mudanças que ocorrem num ecossistema causam uma reestruturação em suas comunidades locais que não podem ser preditas sem um claro entendimento dos mecanismos que permitem a manutenção e coexistência de espécies. Dessa forma estudos baseados nesta abordagem ecossistêmica, são importantes ferramentas não só para a ciência clássica, mas para o manejo de suas populações frente às perturbações ambientais como alterações no uso da floresta de igapó e a pesca.

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Supplementary material

Table S1. Description of functional groups and sources of input data

	Group name	Species aggregation	B	P/B	Q/B	Diet
1	River dolphins	*Inia geoffrensis, Sotalia fluviatilis*	Pavanato et al. 2016	Kastelein et al. 1999	Kastelein et al. 1999	Kastelein et al. 1999
2	Otters	*Lontra longicaudis, Pteronura brasiliensis,*	Evangelista and Rosas, 2011; Groenendijk et al. 2014; Groenendijk et al. 2005	Angelini et al. 2013 (Ecopath model)	Angelini et al. 2013 (Ecopath model)	Silva et al.2014
3	Turtles	*Podocnemis expansa, Podocnemis sextuberculata, Podocnemis unifilis*	Rio Madeira's Ecopath model (Lima, A. et al. 2017, unpublished data)	Rio Xingu's Ecopath model (Camargo, 2009)	Rio Xingu's Ecopath model (Camargo, 2009)	Sá-Leitão Barbosa, 2012
4	Other piscivore fish	*Acestrorhynchus* spp., *Agoniates halecinus, Boulengerella* spp., *Brachyplatystoma vaillantii, Catoprion mento, Crenicichla marmorata, Cynodon gibbus, Electrophorus electricus, Hoplias spp., Leiarius marmoratus, Oxydoras niger, Platynematichthys notatus, Pinirampus pirinampu, Pseudoplatystoma* spp., *Serrasalmus* spp.,*Triportheus rotundatus*	Indirect estimate; Ferreira da Costa, 2005; Giarrizzo et al. 2015; www.fishbase.org/	Indirect estimate; Giarrizzo et al. 2015; www.fishbase.org /	Indirect estimate; Giarrizzo et al. 2015; www.fishbase.org/	Keppeler, F. (unpubblished data); Goulding, 1980; Lowe-McConnell,1987; Junk, 1997; Mérona and Rankin-de-Mérona, 2004; Val and de Almeida-Val, 1995; www.fishbase.org
5	Other invertivore fish	*Achirus* spp., *Anchovia surinamensis*, *Apistogramma* spp., *Hassar orestis*, *Hoplosternum littorale, Ilisha amazonica, Lycengraulis* spp., *Moenkhausia* spp., *Nemadoras leporhinus*, *Pimelodina flavipinnis, Potamotrygon spp., Scorpiodoras heckelii*, *Tetranematichthys* sp., *Triportheus auritus*	Indirect estimate; Ferreira da Costa, 2005; Giarrizzo et al. 2015; www.fishbase.org/	Indirect estimate; Giarrizzo et al. 2015; www.fishbase.org /	Indirect estimate; Giarrizzo et al. 2015; www.fishbase.org/	Keppeler, F. (unpubblished data); Goulding, 1980; Lowe-McConnell,1987; Junk, 1997; Mérona and Rankin-de-Mérona, 2004; Val and de Almeida-Val, 1995; www.fishbase.org
6	Other frugivore fish	*Argonectes longiceps, Astrodoras asterifrons, Auchenipterichthys* spp*., Brycon* spp*., Hoplerythrinus unitaeniatus, Piaractus brachypomus, Pygopristis denticulata, Uaru amphiacanthoides*	Indirect estimate; Ferreira da Costa, 2005; Giarrizzo et al. 2015; www.fishbase.org/	Indirect estimate; Giarrizzo et al. 2015; www.fishbase.org /	Indirect estimate; Giarrizzo et al. 2015; www.fishbase.org/	Keppeler, F. (unpubblished data); Goulding, 1980; Lowe-McConnell,1987; Junk, 1997; Mérona and Rankin-de-Mérona, 2004; Val and de Almeida-Val, 1995; www.fishbase.org
7	Other algivore-detritivore fish	*Ancistrus spp., Caenotropus labyrinthicus, Curimata spp., Curimatella immaculata, Curimatopsis crypticus, Cyphocharax spp., Hypoptopoma elongatum, Limatulichthys griseus, Loricariichthys acutus, Micromischodus sugillatus, Potamorhina spp., Peckoltia spp.* and the taxonomic family Doradidae	Indirect estimate; Ferreira da Costa, 2005; Giarrizzo et al. 2015; www.fishbase.org/	Indirect estimate; Giarrizzo et al. 2015; www.fishbase.org /	Indirect estimate; Giarrizzo et al. 2015; www.fishbase.org/	Keppeler, F. (unpubblished data); Goulding, 1980; Lowe-McConnell,1987; Junk, 1997; Mérona and Rankin-de-Mérona, 2004; Val and de Almeida-Val, 1995; www.fishbase.org
8	*Arapaima gigas*		Ecopath estimate	Indirect estimate; www.fishbase.org /	Indirect estimate; www.fishbase.org/	Queiroz, H. L., 2000; Watson et al., 2013; Oliveira et al., 2005; www.fishbase.org
9	*Brachyplatystoma filamentosum*		Ecopath estimate	Indirect estimate; www.fishbase.org /	Indirect estimate; www.fishbase.org/	Barthem and Goulding, 1997; www.fishbase.org
10	*Brachyplatystoma rousseauxii*		Ecopath estimate	Indirect estimate; www.fishbase.org	Indirect estimate; www.fishbase.org/	Barthem and Goulding, 1997; www.fishbase.org
11	*Pellona castelnaeana*		Ecopath estimate	Indirect estimate; www.fishbase.org ; Ikeziri et al. 2008	Indirect estimate; www.fishbase.org/; Ikeziri et al. 2008	Keppeler, F. (unpubblished data); Val and de Almeida-Val,1995; www.fishbase.org
12	*Cichla* spp.	*C. monoculus, C. pinima, C.temensis*	Indirect estimate; Ferreira da Costa, 2005; Camargo et al., 2015	Indirect estimate; Giarrizzo et al. 2015; www.fishbase.org	Indirect estimate; Giarrizzo et al. 2015; www.fishbase.org/	Keppeler, F. (unpubblished data); Val and de Almeida-Val,1995; www.fishbase.org
13	*Hypophthalmus marginatus*		Ecopath estimate	Indirect estimate; Giarrizzo et al. 2015; www.fishbase.org	Indirect estimate; Giarrizzo et al. 2015; www.fishbase.org	Keppeler, F. (unpubblished data); Val and de Almeida-Val,1995; www.fishbase.org
14	*Plagioscion squamosissimus*		Ecopath estimate	Indirect estimate; Giarrizzo et al. 2015; www.fishbase.org /	Indirect estimate; Giarrizzo et al. 2015; www.fishbase.org/	Forsberg et al., 1993; Mérona and Rankin-de-Mérona, 2004; Jepsen and Winemiller, 2007; www.fishbase.org
15	*Colossoma macropomum*		Ecopath estimate	Indirect estimate; Costa et al. 2013; www.fishbase.org /;	Indirect estimate; Costa et al. 2013; www.fishbase.org/;	Mérona and Rankin-de-Mérona, 2004; Benedito-Cecilio et al.,2000;Val and de Almeida-Val,1995; www.fishbase.org
16	*Mesonauta festivus*		Indirect estimate; Ferreira da Costa, 2005; www.fishbase.org/	Indirect estimate; www.fishbase.org /	Indirect estimate; www.fishbase.org/	Keppeler, F. (unpubblished data);Val and de Almeida-Val,1995; www.fishbase.org
17	*Acaronia nassa*		Indirect estimate; Ferreira da Costa, 2005; www.fishbase.org/	Indirect estimate; www.fishbase.org /	Indirect estimate; www.fishbase.org/	Mérona and Rankin-de-Mérona, 2004;Val and de Almeida-Val,1995 www.fishbase.org
18	*Satanoperca acuticeps*		Indirect estimate; Ferreira da Costa, 2005; Sá-Oliveira et al., 2014	Indirect estimate; Sá-Oliveira et al. 2014; www.fishbase.org /	Indirect estimate; Sá-Oliveira et al. 2014; www.fishbase.org/	Keppeler, F. (unpubblished data); www.fishbase.org

	Group name	Species aggregation	B	P/B	Q/B	Diet
19	*Acarichthys heckelii*		Indirect estimate; Ferreira da Costa, 2005; Bayley, P. 1988	Indirect estimate; Bayley, P. 1988; www.fishbase.org/	Indirect estimate; Bayley, P. 1988; www.fishbase.org/	Keppeler, F. (unpubblished data); www.fishbase.org
20	*Bryconops* spp.	*B. cephalus, B. insignis, B. pesu*	Indirect estimate; Ferreira da Costa, 2005; Giarrizzo et al., 2015	Indirect estimate; Giarrizzo et al., 2015; www.fishbase.org/	Indirect estimate; Giarrizzo et al., 2015; www.fishbase.org/	Keppeler, F. (unpubblished data); www.fishbase.org
21	*Pacu*	*Myleus* spp., *Metynnis* spp., *Mylossoma* spp.	Indirect estimate; Ferreira da Costa, 2005; Giarrizzo et al. 2015	Indirect estimate; Giarrizzo et al., 2015; www.fishbase.org/	Indirect estimate; Giarrizzo et al., 2015; www.fishbase.org/	Keppeler, F. (unpubblished data); Benedito-Cecilio et al.,2000; Mérona and Rankin-de-Mérona, 2004; www.fishbase.org
22	*Geophagus* spp.	*G.proximus, G.surinamensis*	Indirect estimate; Ferreira da Costa, 2005; Giarrizzo et al., 2015	Indirect estimate; Giarrizzo et al., 2015; www.fishbase.org	Indirect estimate; Giarrizzo et al., 2015; www.fishbase.org	Keppeler, F. (unpubblished data); Mérona and Rankin-de-Mérona, 2004; www.fishbase.org
23	*Hemiodus* spp.	*H.argenteus, H.atranalis, H.goeldii, H.gracilis, H.immaculatus, H. unimaculatus*	Indirect estimate; Ferreira da Costa, 2005; Giarrizzo et al., 2015	Indirect estimate; Giarrizzo et al., 2015; www.fishbase.org	Indirect estimate; Giarrizzo et al., 2015; www.fishbase.org	Keppeler, F. (unpubblished data); Mérona and Rankin-de-Mérona, 2004; www.fishbase.org
24	*Schizodon* spp.	*S. fasciatus, S. vittatus,*	Indirect estimate; Ferreira da Costa, 2005; Giarrizzo et al., 2015	Indirect estimate; Giarrizzo et al., 2015; www.fishbase.org	Indirect estimate; Giarrizzo et al., 2015; www.fishbase.org	Mérona and Rankin-de-Mérona, 2004; www.fishbase.org
25	*Leporinus* spp.	*L. falcipinnis, L. friderici, L. trifasciatus*	Indirect estimate; Ferreira da Costa, 2005; Giarrizzo et al., 2015	Indirect estimate; Giarrizzo et al., 2015; www.fishbase.org	Indirect estimate; Giarrizzo et al., 2015; www.fishbase.org	Keppeler, F. (unpubblished data); Mérona and Rankin-de-Mérona, 2004; www.fishbase.org
26	*Laemolyta* spp.	*L. proxima, L.taeniata*	Indirect estimate; Ferreira da Costa, 2005; Giarrizzo et al., 2015	Indirect estimate; Giarrizzo et al., 2015; www.fishbase.org	Indirect estimate; Giarrizzo et al., 2015; www.fishbase.org	Keppeler, F. (unpubblished data); Mérona and Rankin-de-Mérona, 2004; www.fishbase.org
27	*Loricariichthys* spp.		Indirect estimate; Ferreira da Costa, 2005; www.fishbase.org	From Angelini et al., 2013 Ecopath model	From Angelini et al., 2013 Ecopath model	Keppeler, F. (unpubblished data); www.fishbase.org
28	*Semaprochilodus* spp.	*S.insignis, S.taeniurus*	Indirect estimate; Ferreira da Costa, 2005; Giarrizzo et al. 2015	Indirect estimate; Giarrizzo et al. 2015; www.fishbase.org/	Indirect estimate; Giarrizzo et al. 2015; www.fishbase.org	Keppeler, F. (unpubblished data); Benedito-Cecilio et al.,2000; www.fishbase.org
29	Terrestrial invertebrates	Arachnida, Diptera, Ephemeroptera, Hemiptera, Hymenoptera, Isoptera, Odonata. *Dytiscidae, Elmidae, Eremobelbidae, Formicidae, Fuhrmannodesmidae, Hydrophilidae, Hypochthoniidae, Leptoceridae, Noteridae, Paradoxomatidae, Pseudonannolenidae, Pyrgodesmidae, Tipulidae*	Fittkau. and Klinge, 1973; Junk, 1997	Slansky and Scriber,1982	Slansky and Scriber,1982	Magnusson et al., 1999
30	Aquatic invertebrates	Arachnida, Bivalvia, Hemiptera, Clitellata, Nematoda. *Ampullariidae, Atyidae, Chaoboridae* (larvae), *Chironomidae* (larvae), *Ceratopogonidae, Corixidae, Mesoveliidae, Palaemonidae, Polymitarcyidae, Polycentropodidae, Physidae*	Rio Xingu's Ecopath model (Camargo, 2009)	Angelini et al., 2013 (Ecopath model)	Angelini et al., 2013 (Ecopath model)	Hamilton et al., 1992
31	Zooplankton	Classes: *Branchiopoda, Conchostraca, Copepoda, Digononta, Monogononta*	Trevisan and Forsberg, 2007	McClain et al., 2001; Junk, 1997	Caete´ Mangrove Estuary Ecopath model (Wolff et al., 2000)	Junk, 1997
32	Igapo Forest	Families: *Arecaceae, Euphorbiaceae, Fabaceae, Malpighiaceae, Myrtaceae, Rubiaceae, Sapindaceae*	Malhi et al., 2006	Malhi et al., 2006		
33	Periphyton	Classes: *Bacillariophyceae, Chlorophyceae, Conjugatophyceae, Cyanophyta, Euglenophyta, Pyrrophyta, Rhodophyta*	McClain et al., 2001; Junk, 1997	McClain et al., 2001; Junk, 1997		
34	Phytoplankton	Classes: *Bacillariophyceae, Chlorophyceae, Chrysophyceae, Cryptophyceae Cyanobacteria,, Zygnemaphyceae,*	Freitas da Silva, 2012	McClain et al., 2001, Junk, 1997		
35	Detritus		Christensen and Pauly, 1993; Cebrian, 1999			

Table S2. Conversion factors used in this study

Functional group	Ratio	Source
Phytoplankton		
Chlorophyll a to Carbon	1 to 40	O'Reilly and Dow, 1998 from Strickland, 1966
Carbon to dry organic matter	1 to 2	O'Reilly and Dow, 1998 from Strickland, 1966
Carbon to Wet weight	1 to 10	O'Reilly and Dow, 1998 from Strickland, 1966
Zooplankton		
Dry Mass to Wet Mass	1 to 0.451	Brey, 2001
Terrestrial and aquatic invertebrates		
Carbon to dry organic matter (Benthic macrofauna)	1 to 10	Mackinson and Daskalov 2007
Dry to wet weight (Benthic macrofauna)	1 to 7.5	Mackinson and Daskalov 2007

Table S3. Criteria included in Ecopath for definition of 'pedigree' for Biomass, P/B, Q/B and Diet composition input data. The index value is used for calculation of a pedigree index. The confidence intervals (CI) are used to describe parameter uncertainty in the balanced ecosystem model using the Monte Carlos routine in Ecosim simulations. Index values and confidence intervals are defaults that can be changed by users.

Option	Index	CI (%)
Estimated by Ecopath (other model)	0.0	±80
Guesstimate	0.1	±70
From other model	0.2	±60
Empirical relationship	0.5	±50
Similar group/species, similar system	0.6	±40
Similar group/species, same system	0.7	±30
Same group/species, similar system	0.8	±20
Same group/species, same system	1.0	±10

Table S4 Data quality ranking used to assign coefficient of variation values (CVs) for biomass (for fish and river dolphins separately), production to biomass (P/B) values, and consumption to biomass (Q/B) values and Diet composition values.

Data quality ranking criteria	
Biomass CV	
0.15	Recent (2000–2016) stock assessment for the whole model domain (lower Tapajós River)
0.2	Recent (2000–2016) stock assessment for a fraction of the model domain
0.25	Survey not assessment or assessment but incomplete info or multiple sources
0.3	Any stock assessment before 2000
0.35	Information from before 2000 and not a stock assessment
0.4	Value taken from another Ecopath ecosystem model
0.5	Value estimated by Ecopath software
River dolphin biomass CV	
0.05	Estimates for the entire domain (lower Tapajós River) are from 2000 or later
0.1	Majority (>75% and <100%) of estimates are from 2000 or later
0.15	Most estimates from 2000 or later but adjusted amount for biomass outside of the model domain or scaled for regions without estimates
0.2	All estimates from 1990–2000
0.25	Estimates from before 1990
P/B CV	
0.05	Data used is from a recent source (recent stock assessment or research study) or is a well established estimate (natural mortality used in stock assessment is old but has been used for multiple years/assessments)
0.1	Data from before 1990 OR estimated/calculated by Camargo and collaborators (2015) with older information (past stock assessments) OR mortality is an average for different ages/sexes
0.15	Wrong region, but correct species OR similar species, correct region
0.2	Generalization/assumption for large/multi-species functional group OR value taken form other Ecopath ecosystem model
Q/B CV	
0.05	Uses recent data and uses established methods to calculate QB—a.k.a. uses numbers at age data and Essington et al. (2001) to calculate Q/B
0.1	Calculated based on older data (before 1990) OR certain information was estimated but based on real data
0.15	Wrong region, but correct species OR similar species, correct region OR wrong life history stage
0.2	Generalization/assumption for large/multi-species functional group OR assumed growth efficiency OR value taken form other Ecopath ecosystem model
Diet quality ranking	
0 (worst)	Generalization/assumption
0.2	From a similar system (outside domain) OR for a similar species not in the functional group OR values taken form other Ecopath ecosystem model
0.4	All studies have sample sizes <25 OR qualitative diet composition studies
0.6	Majority (>50%) of data is older (1920s–1980s)
0.8	Recent (2000-2016) quantitative data of diet composition but only for one region or one year
1 (best)	Recent (2000-2016) quantitative data of diet composition for multiple regions and majority have good sample sizes

Table S5. Fishing mortality, predation mortality and natural mortality for the functional groups of the Tapajós River Ecopath model

	Group name	Fishing mortality (%)	Predation mortality (%)	Natural mortality (%)
1	River dolphins	0	0	1.00
2	Otters	0	0	1.00
3	Turtles	95.2	0	4.76
4	Others piscivores	12.5	85.00	2.53
5	Others invertivores	0.4	76.30	23.31
6	Others frugivores	0.5	77.30	22.24
7	Others algivores/detritivores	1.5	87.75	10.72
8	*Arapaima gigas*	95.0	0.00	5.00
9	*Brachyplatystoma filamentosum*	67.9	27.09	5.00
10	*Brachyplatystoma rousseauxii*	69.0	26.03	5.00
11	*Pellona castelnaeana*	28.5	66.51	5.00
12	*Cichla* spp.	21.5	76.94	1.58
13	*Hypophthalmus marginatus*	6.8	88.21	5.00
14	*Plagioscion squamosissimus*	45.9	49.11	5.00
15	*Colossoma macropomum*	5.0	90.03	5.00
16	*Mesonauta festivus*	0.1	92.85	7.10
17	*Acaronia nassa*	0.0	95.84	4.14
18	*Satanoperca acuticeps*	0.6	93.04	6.41
19	*Acarichthys heckelii*	0.3	74.31	25.36
20	*Bryconops* spp.	0.1	95.32	4.55
21	*Pacu*	6.7	88.42	4.90
22	*Geophagus* spp.	7.1	86.66	6.26
23	*Hemiodus* spp.	6.3	86.77	6.92
24	*Schizodon* spp.	1.1	78.49	20.45
25	*Leporinus* spp.	3.6	85.30	11.12
26	*Laemolyta* spp.	8.8	81.31	9.92
27	*Loricariichthys* spp.	0.0	95.55	4.45
28	*Semaprochilodus* spp.	25.0	68.42	6.60
29	Terrestrial invertebrates	0.0	95.33	4.67
30	Aquatic invertebrates	0.0	59.82	40.18
31	Zooplankton	0.0	52.64	47.36
32	Igapo Forest	0.0	25.81	74.19
33	Periphyton	0.0	25.60	74.40
34	Phytoplankton	0.0	43.45	56.55

PREBAL Diagnostics

Pre-balance (PREBAL) diagnostics for lower Tapajós River.

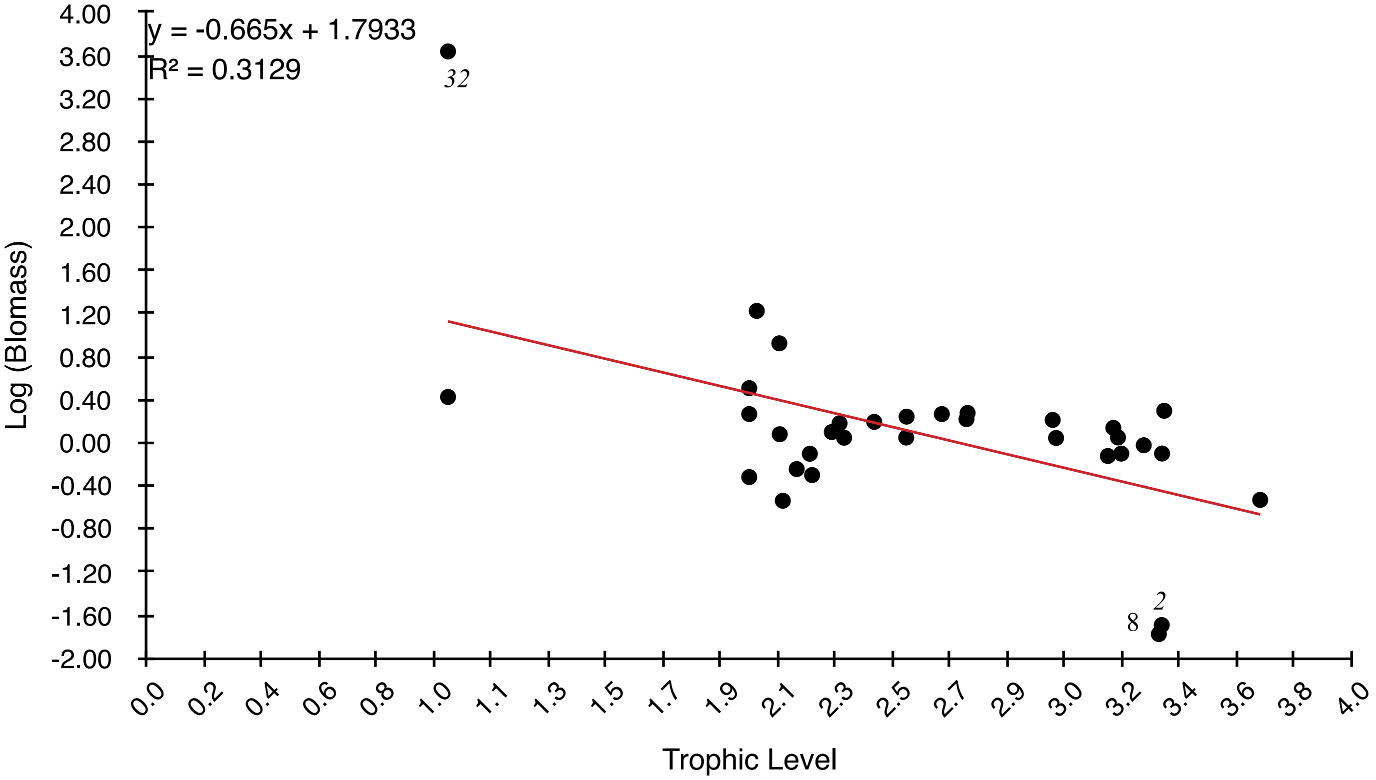

Fig. S1 Biomass estimates (t/km^2), on a log scale vs trophic level, from lowest to highest trophic level, of each species/functional group. Numbers indicates functional groups that are considerably below or above the trend line of biomass allocation across trophic levels. Numbers refer to functional group codes (Table 1). 2: Otters; 8: *Arapaima gigas;* 32: Igapó forest.

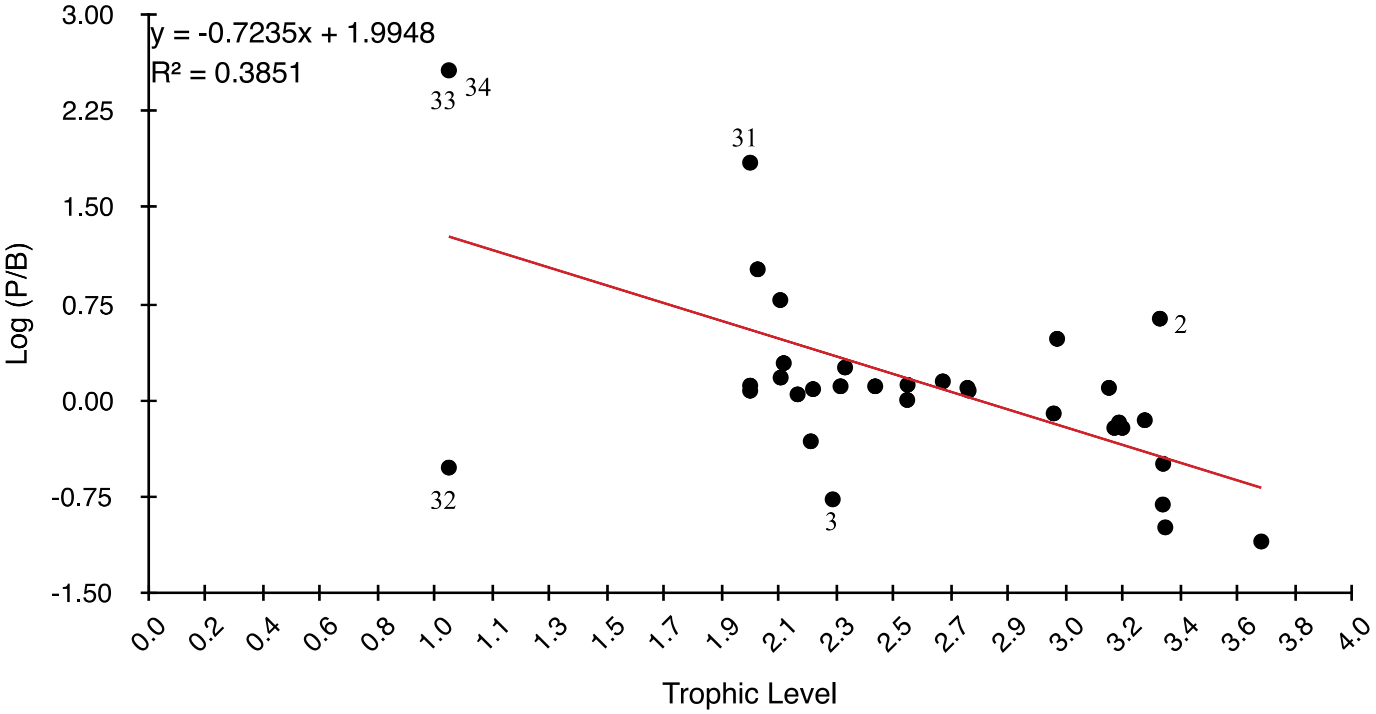

Fig. S2 Production/biomass ratio (per year) on a log scale vs trophic level, from lowest to highest trophic level, of each species/functional group. Numbers indicates functional groups that are considerably below or above the trend line. Numbers refer to functional group codes (Table 1). 2: Otters; 3: Turtles; 31: Zooplankton; 32: Igapó forest; 33: Periphyton; 34:Phytoplankton.

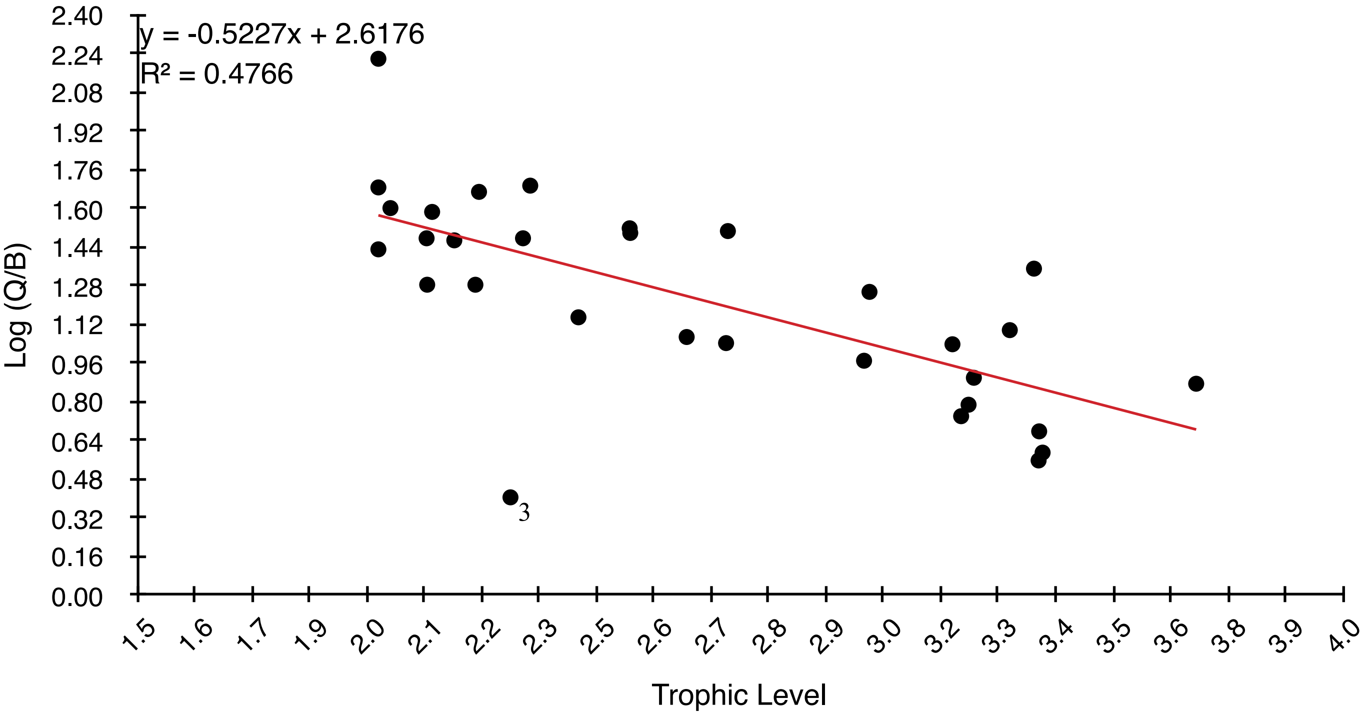

Fig. S3 Consumption/biomass (per year) on a log scale vs trophic level, from lowest to highest trophic level, of each species/functional group. Numbers indicates functional groups that are considerably below or above the trend line. Numbers refer to functional group codes (Table 1). 3: Turtles.