Short title: Balbina downstream impact

The shadow of the Balbina dam – a synthesis of over 35 years of downstream impacts on floodplain forests in Central Amazonia

Jochen Schöngart[1], Florian Wittmann[2], Angélica Faria de Resende[1,3], Cyro Assahira[1,3a], Guilherme de Sousa Lobo[1,4], Juliana Rocha Duarte Neves[1,5b], Maíra da Rocha[1,3], Gisele Biem Mori[1], Adriano Costa Quaresma[1], Layon Oreste Demarchi[1,3], Bianca Weiss Albuquerque[1,4], Yuri Oliveira Feitosa[1,3], Gilvan da Silva Costa[1,6], Gildo Vieira Feitoza[1], Flávia Machado Durgante[1,2], Aline Lopes[1,7], Susan E. Trumbore[8], Thiago Sanna Freire Silva[9c], Hans ter Steege[10,11], Adalberto Luis Val[12], Wolfgang J. Junk[13], & Maria Teresa Fernandez Piedade[1]

[1] Instituto Nacional de Pesquisas da Amazônia (INPA), Grupo de Pesquisa Ecologia, Monitoramento e uso Sustentável de Áreas Úmidas (MAUA), Manaus, Brazil

[2] Karlsruhe Institute for Technology (KIT), Institute of Geography and Geoecology, Department of Wetland Ecology, Rastatt, Germany

[3] Programa de Pós-graduação em Botânica, Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil

[4] Programa de Pós-graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil

[5] Programa de Pós-graduação em Clima e Ambiente, Instituto Nacional de Pesquisas da Amazônia (INPA)/Universidade do Estado do Amazonas (UEA), Manaus, Brazil

[6] Programa de Pós-graduação em Biologia de Água Doce e Pesca Interior, Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil

[7] Universidade de Brasília (UnB), Instituto de Ciências Biológicas, Departamento de Ecologia, Brasília, Brazil,

[8] Max-Planck-Institute for Biogeochemistry, Department of Biogeochemical Processes, Jena, Germany

[9] Universidade Estadual Paulista (Unesp), Instituto de Geociências e Ciências Exatas, Rio Claro, Brazil

[10] Naturalis Biodiversity Center, Leiden, the Netherlands

[11] Vrije Universiteit Amsterdam, Systems Ecology, Amsterdam, The Netherlands

[12] Instituto Nacional de Pesquisas da Amazônia (INPA), Laboratório de Ecofisiologia e Evolução Molecular (LEEM), Instituto Nacional de Ciência e Tecnologia em Adaptações da Biota Aquática da Amazônia (ADAPTA), Manaus, Brazil

[13] Instituto Nacional de Ciência e Tecnologia em Áreas Úmidas (INAU), Universidade Federal de Mato Grosso (UFMT), Cuiabá, Brazil

Corresponding author:

Dr. Jochen Schöngart

Postal address: Instituto Nacional de Pesquisas da Amazônia (INPA), Av. André Araújo 2936, 69011–970 Manaus-AM, Brazil.

E-mail: jochen.schongart@inpa.gov.br, Phone: +55 (0)92 3643–3266

Actual affiliations

[a] Universidade de São Paulo (USP), Programa de Ciências Ambientais (PROCAM), São Paulo, Brazil

[b] Universidade Federal do Sul da Bahia (UFSB), Centro de Formação em Ciências Agroflorestais, Ilhéus, Brazil

[c] University of Stirling, Faculty of Natural Sciences, Stirling, UK

Abstract

1. The Balbina hydropower dam in the Central Amazon basin, established in the 1980s in the Uatumã River, is emblematic for its socioenvironmental disaster. However, its environmental impacts go far beyond the reservoir and dam, affecting the floodplain forests (igapó) in the downstream area (dam shadow), which were assessed by a transdisciplinary research approach, synthesized in this review.
2. Floodplain tree species are adapted to a regular and predictable flood pulse with a high and low water period during the year, which was severely affected by the operation of the Balbina dam, causing a suppression of the aquatic phase at higher floodplain elevations and the terrestrial phase at lower floodplain elevations ("sandwich-effect").
3. Already during the period of construction and reservoir fill, large-scale mortality occurred in the floodplains of the dam shadow, due to reduced streamflow in synergy with severe drought conditions induced by El Niño events causing hydraulic failure and turning floodplains vulnerable to wildfires.

4. During the post-dam period, permanent flooding conditions at low topographical elevations resulted in massive tree mortality. So far, 12% of the igapó forests died along a downstream river stretch of more than 125 km. Because of the flood suppression at the highest elevations, an encroachment of secondary tree species from upland (terra-firme) forests occurred.

5. More than 35 years after the Balbina dam implementation, the downstream impacts caused massive losses of macrohabitats, ecosystem services, and diversity of flood-adapted tree species, probably cascading down to the entire food web, which must be considered in conservation management.

6. These findings are critically discussed, emphasizing the urgent need for Brazilian environmental regulatory agencies to incorporate downstream impacts in the environmental assessments of the several dam projects, planned in the Amazon region.

Keywords: disturbance, flood pulse, hydropower dam, igapó, long term ecological research (LTER), tree mortality, Uatumã River, wildfire.

Introduction

The Amazon River basin is one of the few remaining large networks of free-flowing rivers on Earth (Grill et al., 2019). The largest hydrobasin of our planet, with about 16-18% of the worldwide discharge of freshwater to the oceans (Latrubesse, 2008), is composed of a variety of flood-pulsing rivers, creating vast floodplains of about 750,000 km², mainly covered by forests (Junk et al., 2011; Melack & Hess, 2010). The nutrient-rich várzea floodplains along the geomorphological dynamic and sediment-loaded white-water rivers drain the Andean forelands and constitute about 450,000 km^2 (Wittmann & Junk, 2016). Igapó floodplains occur mainly along cratonic rivers draining the Precambrian and Archaic Guiana and Brazilian shields in the northern and southern regions of the Amazon basin (Latrubesse, Stevaux, & Sinha, 2005), covering a total area of about 300,000 km^2 (Junk et al., 2011). Based on morphological and physiochemical parameters, Sioli (1965) classified cratonic rivers into black- and clear-water rivers, as they show differences in pH, electric conductivity, and floodplains with varying soil fertility and distinct vegetation (Junk et al., 2011; Wittmann & Junk, 2016). In comparison to the várzea, igapós show a low tree species diversity and are characterized by slow dynamical processes (e.g., Junk, Wittmann, Schöngart, & Piedade, 2015; Montero, Piedade, & Wittmann, 2014; Rosa et al., 2017; Schöngart, Wittmann, Piedade, Junk, & Worbes, 2005; Wittmann, Schöngart, & Junk, 2010).

A common driver of geomorphological processes and biogeochemical cycles, as well as life cycles and growth rhythms of the floodplain biota in várzea and igapó along large rivers is the regular and predictable (monomodal) flood-pulse of high amplitude (Junk, Bayley, & Sparks, 1989). Tree species have adapted to the hydrological cycles over evolutionary time scales by developing and combining morpho-anatomic, physiological and biochemical mechanisms to cope with anoxic conditions induced by flooding (e.g., De Simone et al., 2002; Haase & Rätsch, 2010; Junk, 1989; Parolin et al., 2004; Piedade, Ferreira, Oliveira Wittmann, Buckeride, & Parolin, 2010). This also holds for the aquatic fauna, such as fishes (Val, 2019) and invertebrates (Adis, 2010).

Floodplains are key elements in the Amazonian landscape as they harbour an enormous diversity of partially endemic flora and fauna and are important drivers for diversification processes and speciation (Junk & Piedade, 1992; Wittmann et al., 2006; Wittmann et al., 2013; Wittmann & Junk, 2016). Due to the seasonal change between terrestrial and aquatic phases, floodplains further episodically offer habitats for plants, and food sources for numerous species of the aquatic and terrestrial fauna (Wittmann & Junk, 2016). In addition, they provide fundamental ecosystem services to the society, such as storing water (essential to buffer river discharge and to recharge groundwater), purifying water, sediment retention, and the regulation of microclimate as well as biogeochemical and nutrient cycles (Junk et al., 2014). Amazonian floodplains have been settled and used by indigenous for thousands of years and by post-Columbian riverine populations for centuries, providing them with natural resources for subsistence and trade (Junk, Ohly, Piedade, & Soares, 2000; Junk, Piedade, Wittmann, Schöngart, & Parolin, 2010) and contributing to their cultural safeguarding (Junk et al., 2014).

The integrity and functioning of Amazonian river-floodplain systems are endangered by an unprecedented boom of hydropower plants, driven by long-term governmental plans to enhance energy security and supply for increasing industrialization, population and living standards of the countries sharing this continental-size region (Castello et al., 2013). Downstream impacts of hydropower dams on floodplains have been studied in many regions (e.g., Agostinho, Thomaz, & Gomes, 2004; Braatne, Rood, Goater, & Blair, 2008; Kingsford, 2000; Nilsson & Berggren, 2000). Although the complex and far-reaching consequences of damming Amazonian rivers are by far not well understood, considerable alterations of river-floodplain system can be expected (Castello & Macedo, 2016). More than 222 dams (>1 megawatt – MW) exist and are planned or under construction in the Cratonic geotectonic domain of Amazonian river-floodplain systems, while another bulk of up to 200 dams is established and planned in the Andean headwaters and forelands, and a smaller fraction (8 dams) in the Amazonian lowlands (Anderson et al., 2018; Finer & Jenkins, 2012; Latrubesse et al., 2017; Lees, Peres, Fearnside, Schneider, & Zuanon, 2016). From this total, large (30-1,000 MW) and mega (>1,000 MW) dams account for 48% and 7%, respectively (Latrubesse et al., 2017).

This development is accompanied by an exponential increase in academic research of transdisciplinary fields, associated with hydropower dams during the last two decades. Many studies provide evidence of severe socio-environmental impacts of hydropower dams, however, with focus on the areas of the dams and reservoirs, questioning the social, economic, and environmental sustainability of these large infrastructural projects (e.g., Abril, Parize, Pérez, & Filizola, 2013; Altahyde et al., 2019; Fearnside, 2015; Kemenes, Forsberg, & Melack, 2011; Moser, Simon, Medeiros, Gontijo, & Costa, 2019; Rosenberg, Bodaly, & Usher, 1995; Rufin, Gollnow, Müller, & Hostert, 2019). However, only few studies assess the impacts on Amazonian floodplains downstream of dams (Assahira et al., 2017; Junk & Nunes de Mello, 1990; Manyari & Carvalho, 2007; Timpe & Kaplan, 2017; Zuanon et al., 2019). In this review a synthesis of a transdisciplinary research effort of downstream impacts on black-water floodplain forests (igapó), caused by the Balbina dam, implemented in the 1980s in the cratonic Uatumã River (Central Amazonia) is provided. The overall aim is to understand the complex spatiotemporal disturbances in the floodplain forests downstream of an Amazonian hydropower dam operating for decades.

The Balbina dam

The Balbina dam was planned in the decade of 1970, during the petroleum crisis (Moran 2016), to provide energy for Manaus, the capital of the Amazonas State, a booming city with meanwhile more than 2.2 million inhabitants, driven by its expanding free-trade zone and associated sectors consuming nowadays up to 1,800 MW. The hydropower plant is located 150 km in direct line northeast of the city of Manaus and was implemented in the middle reach of the Uatumã River at the Balbina cataracts. The construction started in 1983 and the dam was closed in October 1987, creating a vast reservoir of almost 3,000 km^2, drowning floodplain and upland (terra-firme) forests on slopes and depressions (Feitosa, Graça, & Fearnside, 2007). Only the plateaus of the terra-firme at higher elevations remained, forming a fragmented landscape of more than 3,500 islands inserted in a cemetery of millions of dead trees (Benchimol & Peres, 2015; Fearnside, 1990; Fearnside, 2015; Jones, Peres, Benchimol, Bunnefeld, & Dent, 2019). Originally, the Balbina dam was planned to have a nominal installed capacity of 250 MW, provided by five turbines with an estimated maximum discharge at a full capacity of 1,335 $m^3\ s^{-1}$. However, since the start of its operation in February 1989, the average annual power generation attained only 112.2 MW, with an average discharge of 657 $m^3\ s^{-1}$ (Fearnside, 2015). The creation of the reservoir produces large amounts of greenhouse gases (GHG). Accounting for emissions from the reservoir and turbines, as well as diffusive emission in the downstream area (up to 30 km distance), Kemenes et al. (2011) estimated the annual emission in the order of $3{,}141 \times 10^9$ g C-CO_2eq $year^{-1}$ (CO_2 equivalent C-emissions, the relative contribution of CH_4 and CO_2 is 19% and 81%, respectively) corresponding to 2.9 Mg C-CO_2eq MWh^{-1}.

Study region

The Uatumã River is a black-water river with a catchment area of approximately 69,500 km^2 situated on the Precambrian formation of the Guiana Shield (Junk et al., 2011; Melack & Hess, 2010), covered mainly by terra-firme forests and podzolic white-sand ecosystems (campinarana) (IDESAM, 2009). Consequently, the water is characterized by low pH-values (5.3), with almost no sediment load and a low conductivity (7.8 $\mu S\ cm^{-1}$), is poor in nutrients, but rich in humic material (Lopes et al., 2019). As typical for Central Amazonian black-water rivers, it shows low geomorphic dynamics and relatively stable riverbeds (Junk et al., 2015). Along the first 35 km downstream of the Balbina dam until the Morena rapids the Uatumã River has a steeper slope of about 17 m in a relatively entrenched riverbed. The remaining stretch until the river mouth (about 280 km) has a low slope of only about 5 m, characterized by vast igapós with 9,800 km^2 extension along the Uatumã River and its major tributaries, mainly covered by forests (Resende et al., 2019). The Abacate and Jatapú rivers are the two major tributaries of the Uatumã River, draining the Guiana Shield in the North with its confluences about 161 km and 228 km downstream from the Balbina dam in fluvial distance (thalweg), respectively (Figure 1).

The nutrient-poor alluvial soils of the Uatumã River have clayey textures at the lower topography and an increase in sand fraction towards higher elevations, while those of the Abacate River have predominantly sandy soils with low clay fractions at all topographies (Lobo et al., 2019; Targhetta, Kesselmeier, & Wittmann, 2015). The climate in the region is characterized by an average annual rainfall of 2,077 mm (standard deviation of ±438 mm) (1975–2005), with a distinct rainy season from December to May and an annual mean temperature of 27°C (Carneiro & Trancoso, 2007).

The study sites are in the Uatumã Sustainable Development Reserve (USDR), a state conservation unit since June 2004 (Law 24,295). The USDR has an area of about 4,244 km² (Figure 1) and accommodates approximately 2,100 residents, distributed over 20 communities situated along the Uatumã and Jatapú rivers (demographic census 2017; FAS, 2017). In accordance with Brazilian environmental laws, as well as cultural aspects, socioeconomic activities and traditional lifestyle of the residents, the conservation unit is divided into zones for strict biodiversity protection and research (about 60% of the area), extensive (~35%) and intensive (~5%) land-uses. Zones for the extensive exploration of timber and non-timber forest products and tourism are mainly located along the mainstem and major tributaries of the Uatumã River and floodplains, adjacent paleofluvial terraces, covered by dense forest and some campinarana patches. Intensive land-use destined for agriculture, livestock and residences occurs in floodplains and adjacent paleofluvial terraces close to the communities. The residents of the USDR are also involved in scientific projects and programs developing ecotourism and sport-fishing as alternative economic activities (IDESAM, 2009).

First visits by the research team to the USDR occurred in August 2009 at the beginning of the ATTO-project (Amazon Tall Tower Observatory) implementation, a 325-m tall tower system monitoring local and large-scale fluxes between the biosphere and atmosphere (Andreae et al., 2015). On this occasion, dead forests on the lowest floodplain topographies of the igapó along the Uatumã River downstream of the Balbina dam were observed, which raised the hypothesis that the massive tree mortality was caused by changes in the hydrological regime due to the operation of the hydropower dam. To obtain first information on the igapó forests of the USDR, Targhetta et al. (2015) performed floristic inventories in the impacted igapó during the dry season 2010/2011 to relate floristic composition, diversity, forest structure and biomass stocks to environmental factors (hydrological regime and soil conditions). The recorded species richness of 26–49 spp. ha^{-1} (>10 cm diameter at breast height–DBH) and aboveground wood biomass stocks of 126–173 Mg ha^{-1} of the igapó were relatively low in comparison to other black-water igapós along the Negro River and its tributaries (57–79 species ha^{-1}; 170–260 Mg ha^{-1}) (Aguiar, 2015; Batista, 2015; Corrêa, 2017; Montero et al., 2014) giving first hints of potential downstream impacts on the igapó flora.

Material and methods

The assessment of spatiotemporal disturbances along a 35-year timeline combines hydrological alterations of the Uatumã River during the post-dam period (Assahira et al., 2017) with mortality patterns based on remote-sensing-analyses (Resende et al., 2019), radiocarbon-dating and dendrochronology (Assahira et al., 2017; Resende et al., 2020), as well as data on tree species diversity and ecological characteristic from dominant tree species (Lobo, Wittmann, & Piedade, 2019; Neves, Piedade, Resende, Feitosa, & Schöngart, 2019; Rocha et al., 2019; Rocha et al. 2020). Using water level records from the Cachoeira Morena station, approximately 35 km downstream of the dam (Figure 1), Assahira et al. (2017) analysed the changes in the hydrological regime (1973–2012), applying the method of Indicators of Hydrologic Alteration (IHA) and Range of Variability Approach (RVA) (Richter, Baumgartner, Powell, & Braun, 1996; Richter, Baumgartner, Wigington, & Braun 1997). The IHA method considers a set of biologically relevant hydrological indicators (33 parameters classified into five groups) derived from daily water level data considering the magnitude, timing, frequency, duration and rate of changes of hydrological conditions (see also Timpe & Kaplan, 2017). The RVA compares the variation of each IHA parameter between the pre- and post-dam periods to highlight its extent of change. For this study, the IHA and RVA analyses of the post-dam period have been expanded (1991–2018) and compared to the pristine conditions (1973–1982) (the period of dam construction and closure was not considered). The hydrological regime of the Uatumã River was contrasted with its major affluent (Jatapú River) by linear regression models (Figure 1), considering the periods of pristine conditions (1973–1982), dam construction and reservoir fill (1983–1989) and dam operation (1989–2018). Daily water level records were obtained from the HidroWeb database of the Brazilian National Agency of Waters (ANA) (http://hidroweb.ana.gov.br).

The impacts of the Balbina dam implementation and operation on a landscape level were assessed, applying remote-sensing techniques. Considering an 80-km stretch (focal area) along the Uatumã River after the Morena rapids, located between 43 and 123 km downstream of the reservoir (Figure 1), the igapó floodplains and dead forests were mapped by Resende et al. (2019). For this, 56 ALOS-1/PALSAR (Advanced Land Observing Satellite-1/Phased Array Type L-band Synthetic Aperture Radar Sensor) images at different flood levels during the post-dam period (2006-2011) were acquired, performing object-based image analysis (OBIA) and random forests to a supervised classification algorithm with an overall accuracy of 87.2%. To demonstrate the hydrological changes imposed by the Balbina dam construction (1985), reservoir fill (1988) and dam operation (2009) in the downstream areas, Landsat 4-5 Thematic Mapper (TM) imageries from different months of these years were processed and composed (Gorelick, Hancher, Dixon, Ilyushchenko, Thau, & Moore, 2017).

To assess the causes of tree mortality in the igapó floodplains downstream of Balbina dam, Assahira et al. (2017) and Resende et al. (2020) dated the year of death from two dominant tree species growing at the low topographic elevations in the igapó of the Uatumã River. *Macrolobium acaciifolium* (Benth.) Benth. (Fabaceae) is one of the so-called hyperdominant tree species (ter Steege et al., 2013), frequently occurring in high abundances at low elevations in Amazonian floodplain forests along white-water, clear-water and black-water rivers in the Amazon basin with inundations lasting up to 240 days (Wittmann et al., 2010). This brevi-deciduous species shows complex physiological adaptations to prolonged inundations, switching its metabolism to anaerobic pathways (Schlüter & Furch, 1992; Schöngart, Piedade, Ludwigshausen, Horna, & Worbes, 2002). *Eschweilera tenuifolia* (O. Berg) Miers (Lecythidaceae) is an evergreen tree species in the igapó, growing mainly in monodominant formations (Maia & Piedade, 2002; ter Steege et al., 2019) with open canopies on the lowest topographies, annually flooded for up to 300 days year^{-1} (Junk et al., 2015; Resende et al., 2020). Both species can achieve a high age of up to 500 years in the case of *M. acaciifolium* (Schöngart et al., 2005) and more than 800 years in *E. tenuifolia* (Resende et al., 2020) and are therefore excellent long-term indicators for environmental conditions in floodplains (Junk, Piedade, Nunes da Cunha, Wittmann & Schöngart, 2018). The sampling of dead trees occurred within fluvial distances between 35 km and 125 km downstream of the Balbina dam (Figure 1). Cross-sections of 17 dead *M. acaciifolium* and 29 dead *E. tenuifolia* trees were sampled during the terrestrial phases of 2012 and 2015/2016, respectively. The last formed tree ring, indicative for the year of death, was dated by radiocarbon (^{14}C) (26 of the ^{14}C-dated samples of *E. tenuifolia* fell into the post-bomb period, Resende et al., 2020) and for *M. acaciifolium*, using additional cross-dating techniques (dendrochronology). Mortality patterns of both species were related to the annual duration of the terrestrial phases (non-flooded period), during pristine conditions and the post-dam period. For more detailed information on sampling and dating techniques, see Assahira et al. (2017) and Resende et al. (2020).

The detection of dead forests in the downstream igapó through remote-sensing analyses was limited to low topographical elevations (Resende et al., 2019). The impacts of the hydrological alterations on tree species diversity and dominant tree species was assessed by comparison of forests along the Uatumã River with those of an adjacent, undammed affluent (Abacate River) (Figure 1). Available floristic data for igapó forests comprised 6 ha in the focal area of the Uatumã River and 3.75 ha of the Abacate River (for more details see Lobo et al., 2019; Rocha et al., 2019; Rocha et al., 2020; Targhetta et al., 2015) (Figure 1). Floristic data were also available for adjacent terra-firme forests in both areas (total of 1 ha) (Lobo et al., 2019). All plots were divided into 25 x 25 m (625 m²) sub-plots, where all trees ≥10 cm DBH, including palms, were tagged and identified and the mean duration of the aquatic phase for each subplot was calculated (for more details see Lobo et al., 2019). Rocha et al. (2019, 2020) selected four subplots (625-m² plots) at the low, medium and high topographies of the igapó in the Uatumã and Abacate rivers (12 cross-transects of 25 × 1 m in each system), to study the species composition of tree seedlings (15–100 cm height). Based on this floristic data, tree species diversity for each plot (individuals >10 cm DBH), was estimated by Fisher's alpha (Fisher, Corbet, & Williams, 1943), which was then correlated with the corresponding duration of the aquatic phase by non-linear regression models. Lobo et al. (2019) and Rocha et al. (2019) calculated the importance value index (IVI) summing the relative values of each tree species' frequency, abundance, and dominance (basal area). In this study, the relative IVIs of the five most important species ($IVI_{\Sigma 1-5}$) of trees >10 cm DBH and seedlings (15–100 cm height) was determined, considering three distinct topographic inundation classes (low, medium, and high). Estimated tree ages and mean diameter increment (MDI) rates of the dominant tree species have been provided by Neves et al. (2019) analysing a total of 589 trees at different topographies of the Uatumã and Abacate rivers. Further, basic wood density of the dominant tree species was considered in the comparison of the pristine and disturbed river stretches (Mori, Schietti, Poorter, & Piedade, 2019; Neves, 2018).

Results

Hydrological changes of the Uatumã River

The IHA parameters in Figure 2 reflect the drastic changes in the streamflow regime of the Uatumã River, caused by the Balbina power plant. As the management of the hydropower dam aims at a year-round uniform power generation, it tends to store more water in the reservoir during the rainy season, which is then released during the dry season. Therefore, both the high-water and low-water regimes are affected. The RVA indicated a decrease of maximum (April-June) and an increase in the minimum (October-December) water level, reflected by the increase in the low and high RVA categories, respectively (Figure 2a). For the low-water regime, especially the period 2000-2008 was crucial when the minimum water levels were, on average, more than 1 m higher than those during the pristine period (Assahira et al., 2017), which is indicated by the enhanced baseflow index (7-day minimum water level divided by mean water level) during this period (Figure 2b). Simultaneously, the high-water regime declined especially in the periods 2003–2007 and after 2011, when the maximum water levels remained below the 25th percentile of the pre-dam period. The dam-induced increasing flooding conditions at the lowest topographic elevations and simultaneously decreasing of maximum water levels affecting the higher topographies of the floodplains was characterized as the "sandwich-effect" (Wittmann, Damm, & Schöngart, 2019). The water level further showed a more than twofold increase in the fall and raise rates and a threefold increase in the number of reversals between fall and rise rates, compared to pristine conditions (Figures 2c-e). Also, significant changes were observed in the timing of annual minimum and maximum water levels. During pristine conditions, the annual minimum water level regularly occurred in the period between the end of September and mid-December around Julian days (J.D.) 273–346 (25–75th percentiles; median: J.D. 332), while maximum water levels occurred between the end of April and the beginning of June at Julian days 114–156 (25–75th percentiles; median: J.D. 128). This scenario changed dramatically during the operational period of the Balbina dam showing a remarkably high temporal variation at both extreme conditions (Figures 2f, g).

During the pristine period, the hydrological regimes of the Uatumã and Jatapú rivers showed the typical monomodal flood-pulse pattern (Junk et al., 1989). Consequently, 79% of the variability of the water level oscillations were shared between both rivers ($R^2 = 0.79$; $p < 0.001$) (Figure 3a). The relation weakened during the period of dam construction ($R^2 = 0.44$; $p < 0.001$), indicating first disturbances in the hydrological regime of the Uatumã River. The post-dam period is characterized by a loss of the flood-pulse pattern in the Uatumã River, resulting in 88% of unexplained variation of its hydrological regime with reference to the regular flood-pulsing pattern of the Jatapú River ($R^2 = 0.12$; $p < 0.001$). In comparison to the period of dam construction (1985), the damming of the Uatumã River to fill the Balbina reservoir (1988) caused severe dry conditions in the focal area, due to the extreme low streamflow of only 4.7–19.7 $m^3 s^{-1}$ in this period (Fearnside, 1989), while the period of dam operation (2009) showed an increased low-water regime (Figure 3b). The three strongest El Niño events on record (1982/1983, 1997/1998, 2015/2016), which affected the rainfall and streamflow regimes especially in the northern, central and eastern section of the Amazon basin (Aragão et al., 2018; Marengo et al., 2018) resulted in remarkably low water levels of the Uatumã and Jatapú rivers (Figure 3a).

Tree mortality

Massive tree mortality was detected in the focal area, with about 90 km^2 of floodplain forests, affecting 12% (about 11 km^2) of the igapó (Figure 4). Dead forests were observed at lower topographical elevations, mainly close to lakes and inner, convex banks of the geomorphic stable fluvial meanders (slip-off slopes). Ninety-eight percent of the analysed dead trees in the igapó downstream of the dam died after its implementation. However, both studied tree species revealed distinct mortality patterns (Figure 5). Increased mortality of *E. tenuifolia* already occurred in the period of dam construction (1983–1987) and closure (October 1987–February 1989). A second peak of mortality of this species was observed during the period of 1994-1997, with rising low-water regime (Figure 2b) and subsequent loss of the terrestrial phase. The strong El Niño event in 1997/1998 caused a low streamflow (Figure 3a) and resulted in a terrestrial phase of about two (*E. tenuifolia*) to three (*M. acaciifolium*) months. Conversely, permanent flooding conditions of these trees started in 2000 and lasted for over eight consecutive years as a consequence of the increase in the minimum water level (Figures 2, 3), causing further tree mortality, especially for *M. acaciifolium* (Assahira et al., 2017).

Tree species diversity and ecological characteristics of dominant tree species in disturbed igapó floodplains

In the pristine and disturbed igapó, 90% and 76% of the variation of tree species diversity can be explained by the duration of the aquatic phase, respectively (Figure 6). With increasing duration of the flooding period, a decrease in tree species diversity can be observed in both igapós, similar to other studies performed in Amazonian floodplains (i.e., Assis, Wittmann, Piedade, & Haugaasen, 2015; Montero et al., 2014; Wittmann, Junk & Piedade, 2004; Wittmann et al., 2006; Wittmann et al., 2010). However, species diversity decreases continuously with increasing flood duration in the pristine igapó, while in the disturbed system it shows an exponential decay suggesting a massive loss of tree species (Figure 6).

The $IVI_{\Sigma 1–5}$ and corresponding tree ages, MDIs, and wood densities (tree species >10 cm DBH) are shown in Table 1 for the distinct topographies of the pristine and disturbed igapó. The high-igapó showed similar $IVI_{\Sigma 1–5}$ in the disturbed (31.9%) and pristine (33.7%) floodplain, however, the dominant tree species of the disturbed igapó are mainly secondary tree species from adjacent terra-firme forests (Lobo et al., 2019; Rocha et al., 2019) with higher MDI rates (1.8–3.9 mm year $^{-1}$), lower wood densities (0.50–0.67 g cm^{-3}) and lower tree ages (52–77 years) compared to the pristine igapó. The oldest trees with similar MDIs and wood densities occurred at the low-igapó at both sites (Table 1), however, composed of different species, which are likely the result of different grain-sized substrates (Lobo et al., 2019). Dominant tree species had, however, higher $IVI_{\Sigma 1–5}$ at the disturbed site (61.8%), compared to the pristine one (36.6%). The most significant differences were observed at the medium-igapó, where the $IVI_{\Sigma 1–5}$ of the pristine system (26.3%) was much lower compared to the disturbed igapó (61.8%). The palm *Astrocaryum jauari* Mart. (Arecaceae) is the dominating species together with tree species showing low mean tree ages (28-66 years) and wood densities (0.42–0.58 g cm^{-3}) and high MDI rates of 3.2–4.8 mm $year^{-1}$, which differed significantly from all other elevations (Neves et al., 2019). At this topography, Neves et al. (2019) identified an age-cohort of young and almost even-aged trees, mainly composed of *Nectandra amazonum* Nees (Lauraceae) (28±4 years).

At the level of seedlings, Rocha et al. (2019, 2020) observed even higher IVIs for dominant tree species. At the disturbed low-igapó, 55% of the total IVI in the seedling stratum was represented by *Pouteria elegans* (A. DC.) Baehni (Sapotaceae), while at the disturbed high-igapó the arborescent palm *Attalea maripa* (Aubl.) Mart. (Arecaceae) dominated the seedling stratum (22.5% of the total IVI). This species is a well-known indicator for disturbance in terra-firme forests (Salm, 2005). At the disturbed site of the medium-igapó, the flood-adapted palm species *A. jauari* (IVI of 48.4%) dominated the seedling stratum. Overall, the results indicated an increasing dominance of secondary tree species in the impacted igapó, suggesting disturbance along the entire topographical gradient. More detailed analyses of floristic patterns are available in the studies of Lobo et al. (2019) and Rocha et al. (2019, 2020), indicating distinct patterns in the composition of tree species and genera between the disturbed and pristine igapó.

Discussion

The novel assessment of long-term ecological impacts downstream of the Balbina hydropower dam revealed a broad range of major structural and functional changes in floodplain vegetation, providing a unique opportunity to understand these effects, as summarized schematically in Figure 7, and to propose a preliminary framework. Observed disturbances in the studied igapó forests are discussed in light of fundamental theory that can be used to test further hypotheses. The extent to which such findings can be extrapolated to other hydropower dams within, and even outside, the Amazon basin is discussed, and recommendations regarding the operation of existing and the implementation of future hydropower plants are provided.

Spatiotemporal disturbances in floodplains of the downstream area

Large-scale disturbances in the igapós of the Uatumã River associated with the Balbina dam already started in the period of dam construction (1983-1987) and the reservoir fill (1987-1989). During this period, the water discharge was strongly reduced exposing the entire igapó floodplains to severe dry conditions (Figure 3), which were intensified by El Niño events (1982/1983 and 1986–1988), which increased temperature and reduced rainfall and humidity (Aragão et al., 2018; Marengo et al., 2018). The generated extreme dry hydroclimatic conditions (Figure 7) are the most plausible cause for the mortality of *E. tenuifolia* trees during this period (Figure 5), causing hydraulic failure, carbon starvation or both, as carbon and water dynamics are interrelated by stomatal conductance and vascular transport (Cailleret et al., 2017; Gessler et al., 2018; Hartmann et al., 2018). Fontes et al. (2020) observed for *E. tenuifolia* in the study region a high vulnerability to xylem embolism based on measured P_{50} values (water potential causing 50% loss of hydraulic conductivity). Dead forests dominated by this species occurred mainly around floodplain lakes and slip-off slopes of fluvial meanders (Figures 4). Likely, the drying of the fine-grained alluvial soils caused soil cracking, physically damaging the superficial fine roots, contributing even further to hydraulic failure. Interestingly, no tree mortality of this species was observed during this period for the same macrohabitats in the igapó of the Jaú River, an affluent of the Negro River in Central Amazonia with an undisturbed flood-pulse regime (Resende et al., 2020). The severe dry conditions, caused by the synergetic effects of dam implementation and climate conditions, possibly also increased the vulnerability of igapós to wildfires (Flores, Piedade, & Nelson, 2014; Flores et al., 2017; Schöngart, Wittmann, Junk, & Piedade, 2017). Igapó forests have lower canopy heights and lack a dense understory compared to well-stratified terra-firme forests, and consequently, air humidity in igapó forests is much lower (Almeida et al., 2016; Resende, Nelson, Flores, & Almeida, 2014). Due to the long flooding, litter slowly decomposes and accumulates on the forest floor, which is covered by dense root mats at or near the ground surface (dos Santos & Nelson, 2013), providing a large amount of combustion material. The presence of an approximately 30-year old age-cohort of *Nectandra amazonum* (Neves et al., 2019) and low tree species diversity (Table 1, Figure 6) suggest massive disturbances on the medium elevation in the igapó along the Uatumã River, originating from wildfires occurring during the implementation of the Balbina dam (Figure 7). This species has been characterised as a secondary species of the nutrient-rich and highly dynamic white-water floodplains (várzea) (Wittmann, Anhuf & Junk, 2002), where it shows low maximum tree age (44 years) and comparatively high MDIs (4.8–14.8 mm year^{-1}) (Schöngart, 2003; Worbes, Klinge, Revilla, & Martius, 1992). The hypothesis is that this pioneer species established in opened igapó areas, that originated from wildfires (Figure 7). The high solar radiation and enhanced nutrient supply in the burnt areas created similar environmental conditions as in early successional stages of the várzea (Wittmann et al., 2004; Worbes et al., 1992), favouring its establishment and resulting in species-poor floodplain forests with high dominance of secondary species (Figure 7). Seeds possibly reached these sites from nearby igapós or from the várzea floodplains of the Amazon River dispersed by animals, especially fishes since the plant is referred as an ichthyochoric species (Weiss, Zuanon, & Piedade, 2016).

The high dominance of the palm *Astrocaryum jauari* at the medium-igapó of the Uatumã site (see also Rocha et al., 2020; Targhetta et al., 2015) also suggests disturbance through wildfires. This species is a typical floodplain palm occurring in várzea and igapó forests (Piedade et al., 2016). Besides ichthyochory, barochory (dispersal by gravity alone) with subsequent vegetative propagation is an important dispersal mode leading to the formation of dense populations of up to 2.000 stems ha^{-1} in the fluvial archipelagos Anavilhanas and Mariuá of the Negro River (Piedade, Parolin, & Junk, 2006). Several Amazonian terra-firme palm species are fire-resistant, such as *Attalea maripa*, *Astrocaryum aculeatum* G. Mey., *Astrocaryum vulgare* Mart. and *Acrocomia aculeata* (Jacq.) Lodd. ex Mart., as well as *Copernicia alba* Morong occurring in seasonally flooded savannas in the Bolivian Amazon and also in the Pantanal (Carvalho, Ferreira, & Lima, 2010; Araújo, Oliveira Júnior, Assis Oliveira, Gama, Gonçalves, & Almeida, 2012; Smith, 2015) and may benefit from fire by increasing their dominance. Palms do not have a cambial tissue and many species have diaspores with morpho-physiological dormancy (Baskin & Baskin, 2014). Seedlings of some palm species like *Attalea* spp. have sprouting tips growing down into the soil before emerging above ground (cryptogeal germination), making them resistant to surface fires (Smith, 2015). Some older inhabitants of the USDR indicated the occurrence of wildfires in the igapós, during the period of dam implementation. Remote-sensing analyses, that map out fire-scars overtime series since the period of dam construction, should bring evidence of the magnitude of wildfire activity during this period, as applied by Carvalho (2019) for the igapós of the Jaú National Park.

During the period of dam operation, the "sandwich-effect" (Wittmann et al., 2019) occurred, characterized by the suppression of the aquatic phase at high topographies and the loss of the terrestrial phase at the low topographies over a period of 30 years (Figure 7). Periods with permanent flooding conditions affected first the lowest topographical elevations, dominated by *E. tenuifolia*, and in subsequent periods the population of *M. acaciifolium,* growing on higher elevations (Figure 5). Although both tree species are well adapted to regular, seasonal inundations, pluriannual permanent flooding seems to be the major trigger of tree mortality for these and other highly flood-adapted tree species, as the prolonged anoxic conditions exceed the capacities of adaptations developed by these species to tolerate seasonal inundations (Assahira et al., 2017; Piedade et al., 2013; Resende et al., 2020).

Tree mortality along the upstream courses is usually faster than in the dam shadow, because it affects mainly vegetation not or less adapted to flooding (Cochrane, Matricardi, Numata, & Lefebvre, 2017; Moser et al., 2019). Downstream disturbances of recently installed power plants tend to be hidden over years and even decades as floodplain tree species developed sophisticated adaptations to seasonal flooding which can extend mortality-inducing processes over long periods (Resende et al., 2020). So far, the Balbina dam resulted in 12% of dead igapó forests at the low topographical elevations (Figure 4), which expands to more than 125 km downstream of the hydropower plant (Assahira et al., 2017; Resende et al., 2019; Resende et al., 2020). If in future the dam operation continues to enhance the low-water regime, additionally 18% of the igapó forests, classified by Resende et al. (2019) as threatened (Figure 4), will probably suffer massive mortality as disturbances expand further downstream and achieve also higher topographies. The slow decompositions of dead biomass (about 129 ± 14 × 10^9 g C) under almost constant anaerobic conditions (Resende et al., 2019) is likely to result in increasing GHG emissions, especially CH_4. By long-term monitoring of atmospheric CH_4 mixing ratios at the nearby ATTO site (Figure 1), Botia et al. (2020) detected night-time CH_4 increases, which most likely originated from the dead igapó forests. However, so far GHG emissions (CO_2, CH_4) have only been measured in the Balbina reservoir, at the dam (turbine discharge and outflow) and in the first 30 km downstream of the power plant (Kemenes et al., 2011). To give a whole picture of GHG emission related to the Balbina dam, these measurements should be extended to the affected igapó floodplains by future studies and monitoring.

At high topographical elevations of the igapó, the loss of flooding favoured the encroachment of mainly secondary species from adjacent terra-firme forests (Figure 7), especially dominating in the establishment stratum such as *Tapirira guianensis* Aubl. (Anacardiaceae), *Attalea maripa*, *Trichilia micrantha* Benth. (Meliaceae) and *Rinorea racemosa* (Mart.) Kunze (Violaceae) (Lobo et al., 2019; Rocha et al., 2019). These species are probably better adapted to the changed environmental conditions and more competitive as the former igapó tree species, as indicated by the higher observed MDI rates (Table 1).

The IHA and RVA analyses further indicated changes in the timing (parameter group 3) of the highest and lowest water levels (Figures 2f, g). Many floodplain tree species produce fruits during the aquatic phase (Kubitzki & Ziburski, 1994; Schöngart et al., 2002) and are mainly dispersed by water (hydrochory) and/or fish (ichthyochory) (Ayres, 1993; Goulding, 1980; Parolin, Waldhoff, & Piedade, 2010; Van den Broek, van Diggelen, & Bobbink, 2005; Weiss et al., 2016). Although germination of some floodplain tree species may occur when seeds still float upon the water (Kubitzki & Ziburski, 1994; Melo, Franco, Silva, Piedade, & Ferreira, 2015; Oliveira Wittmann, Piedade, Wittmann, & Parolin, 2007), seedlings need the contact with the alluvial substrate in the subsequent terrestrial phase for successful establishment (Parolin, 2001; Waldhoff, Saint-Paul, & Furch, 1996). The high temporal variability of the maximum and minimum water level (Figures 2 f, g), during the post-dam period, probably results in an asynchrony of phenology patterns, dispersal mechanisms, and establishment processes for many tree species occurring at topographies, which still are seasonally flooded. As the low-igapós are under near-permanent aquatic conditions and floods have been suppressed at the high-igapós, the hypothesis is postulated, that tree species relying on water and fish for dispersal no longer get established at these topographies in the long term (Figure 7). Consequently, fish populations lose this important food source which may reduce populations regionally.

The frequency and duration of high and low pulses (group 4) and rate and frequency of changing water condition (group 5) changed considerably during the post-dam period (Figure 2), which possibly has strong impacts on the physiology of igapó tree species. Mori et al. (2019) observed that igapó species, in general, have functional traits related to the carbon and nitrogen metabolism associated with high resource conservation and persistence, leading to slow growth, as shown by Neves et al. (2019) (see also Table 1). However, the changes in the frequency and magnitude of water deficit or hypoxic/anoxic conditions may affect many of these species, setting up new environmental filters and inducing new trade-offs. This may explain the observed decrease of tree species diversity (Figure 6) and simultaneously increasing dominance of tree species (Table 1), which possess a higher resilience and functional traits to adapt to the changed environmental conditions (Figure 7).

Overall, the described hydrological alterations impact several processes in the floodplain system relevant for tree species (Figure 7). It alters habitat and soil moisture availability as well as anaerobic conditions, and affects the synchrony between the flooding regime with phenological patterns, growth rhythms, dispersal mechanisms and processes of establishment for which floodplain trees adapted over evolutionary periods (Junk, 1989; Parolin et al., 2004; Schöngart et al., 2002; Wittmann et al., 2010). These disturbances are likely to cascade down through the entire food web by similarly affecting terrestrial and aquatic species, ultimately leading to a considerable loss in biodiversity. Further impacts on biodiversity are expected from damming the Uatumã River, which blocks migrations and cut population connectivity of fish and changes their habitats by modifying physical and chemical conditions (e.g., Agostinho et al., 2004; Castello & Machado, 2016; Costa-Pereira et al., 2018; Val, Fearnside & Almeida-Val, 2016; Winemiller et al., 2016).

The observed massive loss and degradation of macrohabitats in the disturbed igapó floodplains caused by the Balbina dam with severe impacts on ecosystem functioning, loss of biodiversity and environmental services has relevant implications for conservation. Floodplains in the USDR are excluded from the permanent protection zones and destined for extensive and intensive land-use (IDESAM, 2009). Igapós of the Uatumã River until its confluence with the Abacate River (Figure 1) are likely to suffer from the complex and persistent disturbance regime, which affects both, the economic activities (e.g., fishery, ecotourism) and welfare of the local inhabitants. Dead forests are additionally a risk for large wildfires during extreme El Niño conditions, when huge amounts of flammable materials are exposed to severe dry conditions, due to extremely low water levels, such as during

2015/2016 (Figure 3a). These are relevant aspects for the conservation management of the USDR.

Implications of the findings for other Amazonian dams

Downstream impacts on floodplains differ strongly among hydropower plants depending on many factors, such as the geomorphology, hydrochemical conditions, sediment load, biogeography, diversity and dynamics of the vegetation as well as size and elevation of the reservoir, time since dam construction, technical aspects of the impoundment and synergies with other land-use forms and intensities (Altahyde et al., 2019; Rufin et al., 2019; Timpe & Kaplan, 2017). These differences limit the extrapolation of the findings of this study to hundreds of other operating hydropower plants and those under construction or planning as no comparable studies on downstream impacts are available for the Amazon basin. Timpe & Kaplan (2017) analysed IHA parameters for upstream and downstream hydrological data of 33 dams across the Brazilian Amazon (including Balbina) and Cerrado (Central Brazilian savannah biome) integrating a large range of the factors mentioned above. Despite identifying limitations of this approach, they observed that the magnitude and duration of annual extreme water conditions (IHA group 2) ("sandwich-effect") was positively correlated with the reservoir area and negatively related to the elevation of impoundment. Increased elevation of dams resulted further in a decrease of frequency and duration of high and low pulses (IHA group 4) and the rate and frequency of water condition changes (IHA group 5) (see also Figure 3). Therefore, it is not surprising that the intense hydrological alteration (Figures 2 and 3), associated with the large Balbina reservoir at a low elevation caused the massive observed disturbances (Figure 7) on the integral functioning of the downstream floodplains, which is adapted to a monomodal flood pulse regime. At higher elevations in the region of the headwaters, rivers in general show lower and less regular flood-pulses due to the smaller catchment area (Junk et al., 2011) and tree species adapted to these regimes probably suffer less impacts by dam-induced hydrological alterations. Timpe & Kaplan (2017) further observe that multiple dams in rivers have cumulative and cascading effects, affecting especially IHA parameters of groups 4 and 5, which is of high relevance for many cratonic rivers in the Brazilian Amazon (Fearnside, 2019; Latrubesse et al., 2017), but also in the Cerrado (savanna belt) (Latrubesse et al., 2019).

Downstream impacts also may vary according to geomorphological and hydrochemical characteristics of floodplain ecosystems. Black-water floodplain tree species are likely more vulnerable to dams than their white-water counterparts, because the latter have adaptations to dynamic hydrogeomorphic processes, such as erosion and burial through sediment deposition, which are lacking in igapó tree species (Peixoto, Nelson, & Wittmann, 2009; Wittmann et al., 2004; Wittmann & Parolin, 2005; Worbes et al., 1992). Planned mega-dams in the upper Negro River (São Gabriel and Santa Isabel-Uaupés/Negro, with a total of 4,000 MW planned capacity; Fearnside, 2019), possibly will have stronger downstream impacts than those of the Madeira River (Santo Antônio and Jirau with 3,150 MW and 3,750 MW installed capacity, respectively; Latrubesse et al., 2017) and the several dams planned at higher altitudes in the Andean catchments and forelands (Anderson et al., 2018; Finer & Jenkins, 2012; Forsberg et al., 2017).

The provided synthesis on impacts of Amazonian river dams on downstream river hydrology and floodplain forests in time and space (Figure 7) is a first compilation demonstrating that hydropower plants have much wider impact than previously reported. At this stage, the proposed framework is still restricted to central Amazonian black-water river-floodplain systems with monomodal flood-pulses. Yet, studies on the downstream impact of river dams in other Amazonian river types, such as clear-water rivers draining the cratonic Guiana and Central Brazilian shields, are not available for comparison. Many of these rivers have already been dammed, and in others, dams are under construction or planned in the near future (Latrubesse et al., 2017; Lees et al., 2016). There is an urgent need for further transdisciplinary studies to reveal dam-induced downstream impacts on floodplain forests in other river types of the Amazon basin, but also in other tropical regions. This is a major challenge for science due to the wide range of factors that must be considered in this approach.

Recommendations and concluding remarks

The "sandwich-effect" in the dam shadow is a threat for floodplains controlled by regular and predictable flood pulses, which is the dominant pattern across large tropical rivers (Junk et al., 1989). Hydrological changes downstream of dams are already evident for the river basins of the Paraná and São Francisco in Brazil, where the implementation of many hydropower plants started several decades ago (Agostinho et al., 2004; Bustamante et al., 2019). Tropical floodplains along large flood-pulsing rivers such as the Araguaia-Tocantins, Orinoco, Magdalena, Congo, Mekong and many others are likely to suffer drastic hydrological alterations due to already installed and planned large hydropower dams (Latrubesse et al., 2017; Latrubesse et al., 2019; Winemiller et al., 2016). This threatens the integrity of tropical river-floodplain systems over thousands of square kilometres in the Amazon and other tropical regions, which host the last remaining large networks of free-flowing rivers (Grill et al., 2019).

The novel insights on the potential scale of downstream impacts on floodplains caused by hydropower dams allows to draw recommendations which should be considered in environmental impact assessments and associated reports (EIA/RIMA), in the Amazon and elsewhere. For dams under construction and during the reservoir fill, severe dry conditions should be avoided in the downstream floodplains, as it arguably will provoke tree mortality and wildfires. Already operating hydropower dams should adapt a power generation, simulating the natural flood-pulse and maintaining annually the pre-dam baseflow index of the river to mitigate the downstream impacts in the floodplains. This should be also a guideline for planned hydropower dams. Therefore, the environmental impact assessment must integrate floodplains downstream of the planned hydropower dams at least until the confluence of a major undisturbed affluent of the same river order (Strahler, 1957) or until the area affected by backwater effects from rivers with higher ranked orders (Meade, Rayol, Conceição, & Natividade, 1991), which are likely to buffer the dam-induced hydrological alterations. The downstream assessment should provide inventories of major macrohabitats (Junk et al., 2018) in the potentially affected floodplains on ground and landscape levels with associated hydrogeomorphic data. Simulation models relating river discharge, potential power generation and water level, should allow an assessment and evaluation of mitigated downstream impacts and monetary losses for power generation maintaining the pre-dam baseflow index and flood-pulse regime. This would contribute to a critical evaluation of hydropower options by a consortium involving government, scientists, stakeholders from civil society, industry, and financial agencies. Massive losses of macrohabitats, biodiversity, and environmental services in floodplains caused by hydropower dams must be avoided or at least mitigated, to maintain ecosystem functioning, food security and the welfare of the present and future generations of traditional and indigenous populations. This is of essential importance, as synergetic effects of climate and land-use changes are expected to cause a serious imbalance of floodplain ecosystems in future.

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Figure legends

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indicate temporal changes between pre-dam and post-dam conditions of the IHA parameters: b) baseflow index (7-day minimum water level divided by mean annual value), c) number of reversals, d) fall and, e) rise rates, f) timing of minimum and g) maximum water level (black horizontal dashed lines are the medians, the grey dashed lines represents the 25^{th} and 75^{th} percentiles). Data were obtained from Cachoeira Morena station (id code: 16100000), available at the HidroWeb database of the Brazilian National Agency of Waters (ANA; http://hidroweb.ana.gov.br).

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Figure 5: Mortality patterns for *Macrolobium acaciifolium* (Fabaceae) and *Eschweilera tenuifolia* (Lecythidaceae) based on cross-dating and radiocarbon-dating to estimate the year of death in the igapó floodplains downstream of the Balbina dam. The mortality patterns are related to the duration of the terrestrial phase (black line) calculated for the mean topography of each species based on the daily water levels from the Cachoeira Morena station (id code: 16100000, data: Agência Nacional de Águas–ANA). Note that *Macrolobium* grows on slightly higher elevations compared to *Eschweilera* resulting in prolonged periods of terrestrial phases (Assahira et al., 2017; Resende et al., 2020).

Figure 6: Relationship between Fisher's alpha diversity and the duration of the aquatic phase comparing the pristine igapó forests (Abacate) with the disturbed system downstream of the Balbina dam (Uatumã). Fisher's alfa diversity from adjacent terra-firme forests (Lobo et al., 2019) are included in the analyses.

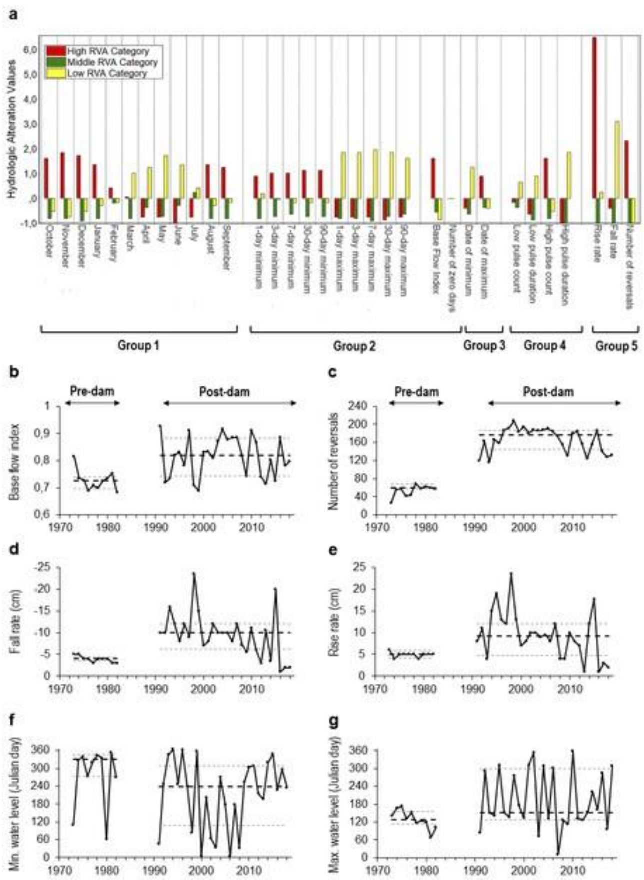
Figure 7: Spatiotemporal disturbances in the igapó floodplains downstream of the Balbina dam over a 35-year period dramatically impacted this ecosystem resulting into a loss of macrohabitats, massive tree mortality and tree species diversity affecting the functioning and provision of ecosystem services of a conservation unit. During the installation of the Balbina dam and the reservoir fill in synergy with El Niño conditions (1982/1983 and 1986-1988)

severe dry conditions were generated in the downstream floodplains (Figure 3) leading to hydraulic failure and tree mortality at the lowest topographies and caused possibly wildfires affecting mainly the medium topographies resulting into forest succession and the establishment of pioneer tree species. Hydrological alterations during the post-dam period caused the typical "sandwich-effect" (red arrows) characterized by the suppression of the terrestrial phase at the lower topographies and of the aquatic phase at the higher topographies in consequence of higher minimum and lower maximum water levels, respectively. The temporal asynchrony between the hydrological regime and phenology, growth rhythms, hydrochoric and ichthyochoric seed dispersal of tree species and increasing alternations between water deficit and anoxic conditions is hypothesized to favour the dominance of tree species adapted to this disturbance regime.

Table 1: Dominant tree species (>10 cm DBH) of the studied igapó forests at three distinct topographic inundation classes (low, medium and high) of the Uatumã River (impacted area) and the Abacate River (natural conditions) indicating the relative importance value index (IVI%), mean and standard deviation of tree age (years) and mean annual diameter increment (MDI; mm) as well as wood density (ρ; g cm^{-3}) (data: Lobo et al., 2019; Mori et al., 2019; Neves, 2018; Neves et al., 2019; Rocha et al., 2019).

Uatumã					**Abacate**				
High-igapó					**High-igapó**				
Tree species	**IVI%**	**Age**	**MDI**	**ρ**	**Tree species**	**IVI%**	**Age**	**MDI**	**ρ**
Tapirira guianensis	12.8	71±3	3.9±0.1	0.50	*Licania macrophylla*	16.3	71±23	1.5±0.4	0.82

Pentaclethra macroloba	7.0	77±6	2.6±0.1	0.65	*Myrcia fallax*	5.9	76±32	1.1±0.2	0.82
Attalea maripa	4.2	-	-	-	*Eschweilera* cf. *albiflora*	4.2	90±41	1.6±0.4	0.83
Trichilia micrantha	4.2	74±17	1.8±0.2	0.67	*Ocotea aciphylla*	3.8	95±42	1.4±0.6	0.64
Naucleopsis glabra	3.7	52±26	1.8±0.7	0.62	*Crudia amazonica*	3.5	57±21	1.9±0.3	0.87
Medium-igapó					**Medium-igapó**				
Tree species	**IVI%**	**Age**	**MDI**	***ρ***	**Tree species**	**IVI%**	**Age**	**MDI**	***ρ***
Astrocaryum jauari	17.0	-	-	-	*Eschweilera* cf. *albiflora*	6.5	67±28	1.2±0.1	0.83
Nectandra amazonum	13.5	28±4	4.8±1.2	0.42	*Licania macrophylla*	5.9	106±43	1.7±0.2	0.82
Alchornea discolor	13.0	79±27	3.2±0.6	0.46	*Ouratea discophora*	4.1	67±22	1.9±0.5	0.79
Mabea nitida	9.7	47±16	4.7±0.6	0.55	*Pouteria pachyphylla*	3.8	107±57	1.6±0.1	0.75
Inga sp.	8.7	66±15	3.7±0.3	0.58	*Guatteria guianensis*	3.7	64±25	2.2±0.9	0.43
Low-igapó					**Low-igapó**				
Tree species	**IVI%**	**Age**	**MDI**	***ρ***	**Tree species**	**IVI%**	**Age**	**MDI**	***ρ***
Pouteria elegans	22.8	98±29	1.9±0.2	0.73	*Pouteria pachyphylla*	9.0	102±47	1.7±0.3	0.75
Amanoa oblongifolia	19.9	126±12	1.7±0.3	0.76	*Elvasia calophyllea*	8.6	122±59	1.7±0.4	0.80
Mabea nitida	6.6	65	1.0	0.55	*Couratari* cf. *tenuicarpa*	7.2	106±41	2.2±0.6	0.43
Handroanthus barbatus	6.5	90±25	2.1±0.2	0.87	*Manilkara bidentata*	6.4	84±31	1.8±0.8	0.92
Leptolobium nitens	6.0	173±89	1.6±0.3	0.72	*Swartzia laevicarpa*	5.5	190±21	1.4±0.6	0.55



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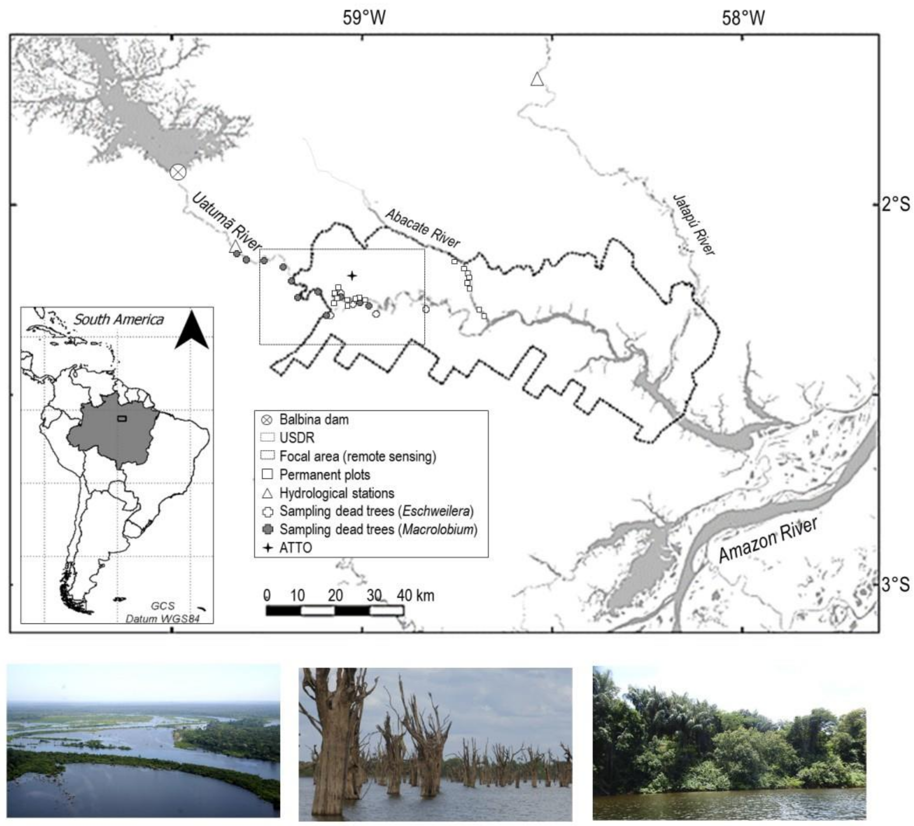

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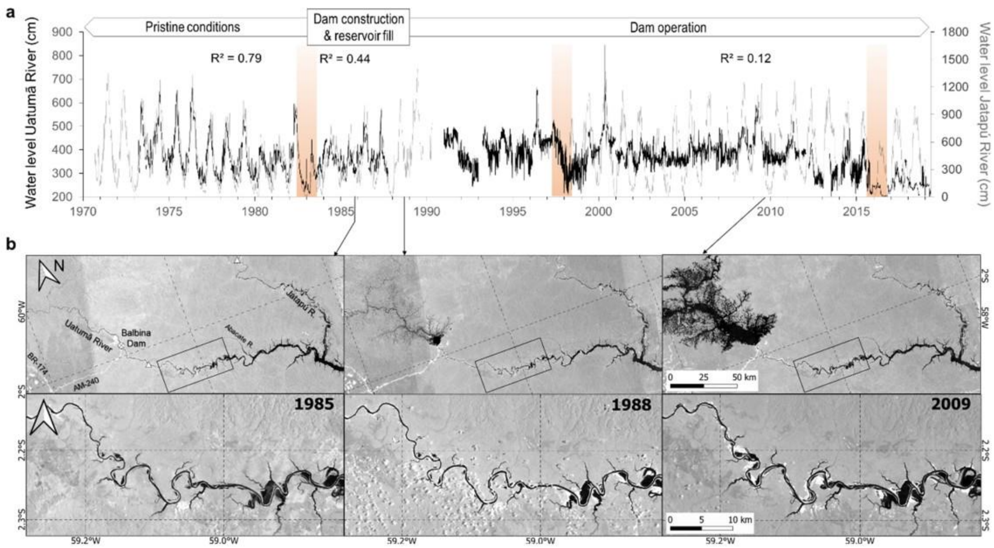

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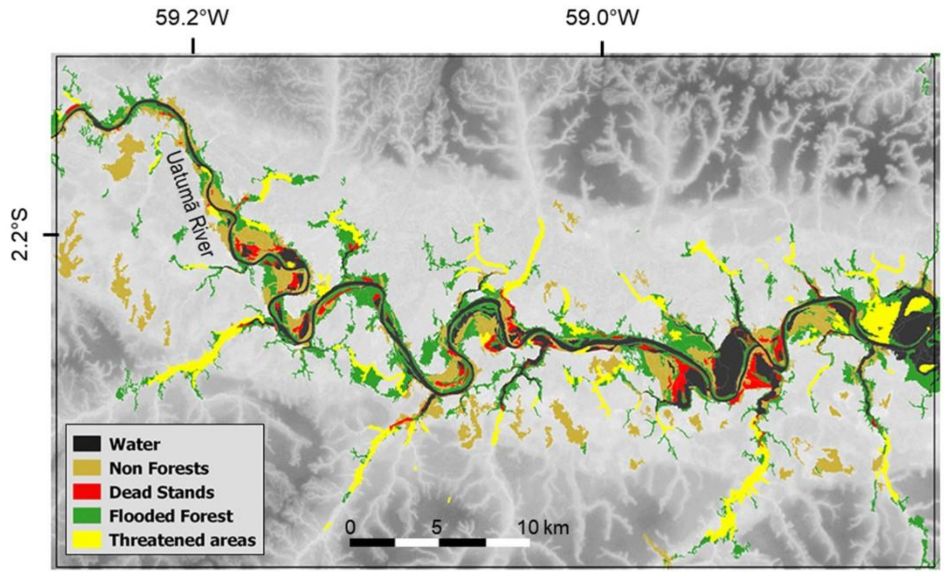

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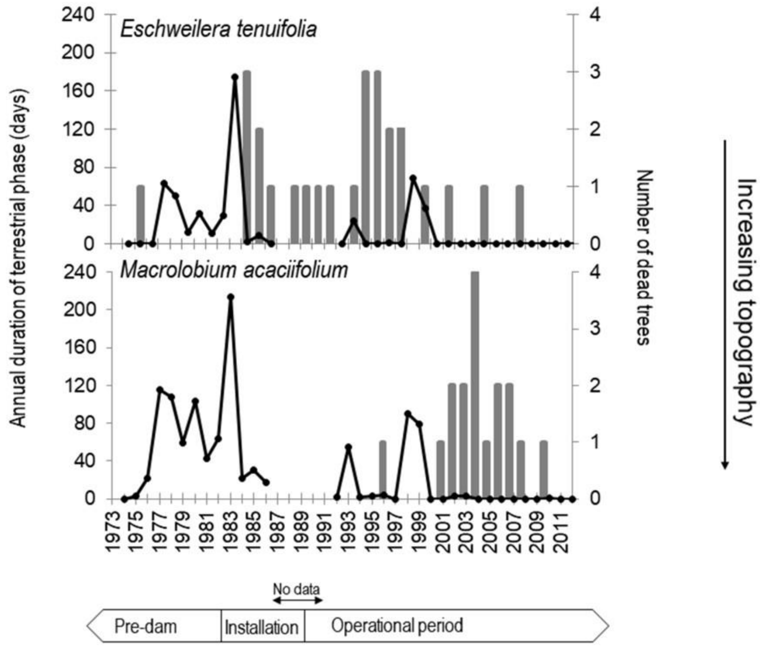

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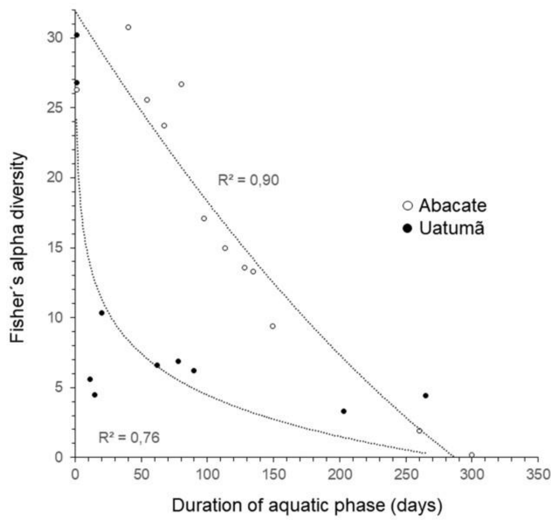

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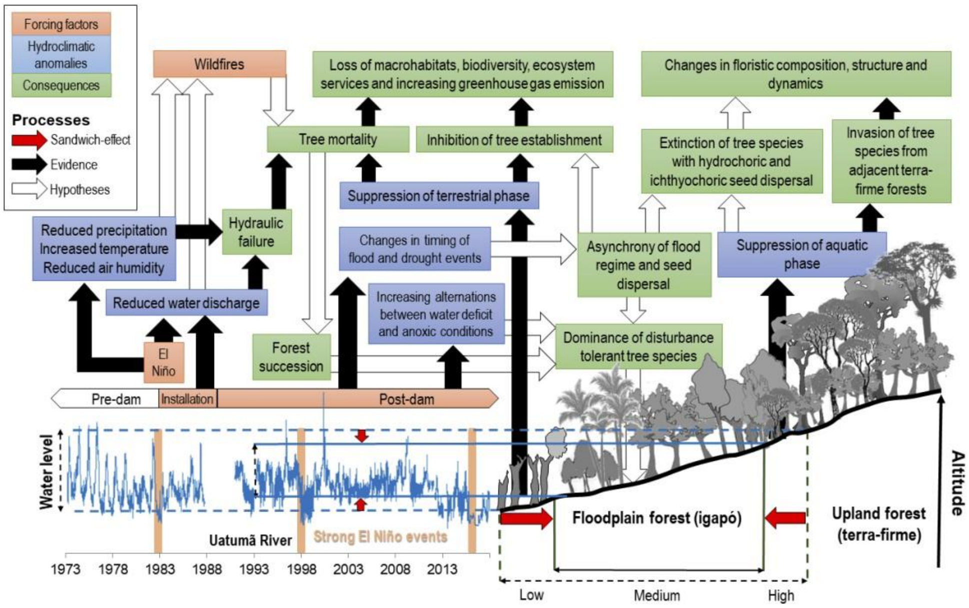

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