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

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Abstract

1. The Balbina hydropower dam in the Central Amazon basin, established in the Uatumã River in the 1980s, is emblematic for its socio-environmental disaster. Its environmental impacts go far beyond the reservoir and dam, however, affecting the floodplain forests (igapó) in the downstream area (dam shadow), which have been assessed using a transdisciplinary research approach, synthesized in this review.

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2. Floodplain tree species are adapted to a regular and predictable flood pulse, with high- and low-water periods occurring during the year. This was severely affected by the operation of the Balbina dam, which caused the suppression of both the aquatic phase at higher floodplain elevations and the terrestrial phase at lower floodplain elevations (termed the 'sandwich effect').
3. During the period of construction and reservoir fill, large-scale mortality already occurred in the floodplains of the dam shadow as a result of reduced stream flow, in synergy with severe drought conditions induced by El Niño events, causing hydraulic failure and making floodplains vulnerable to wildfires.
4. During the operational period of the dam, permanent flooding conditions at low topographical elevations resulted in massive tree mortality. So far, 12% of the igapó forests have died along a downstream river stretch of more than 125 km. As a result of 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 implementation of the Balbina dam, 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 discussed critically, emphasizing the urgent need for the Brazilian environmental regulatory agencies to incorporate downstream impacts in the environmental assessments of several dam projects planned for the Amazon region.

KEYWORDS

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

1 | 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 approximately 16–18% of the worldwide discharge of fresh water to the oceans (Latrubesse, 2008), is composed of a variety of flood-pulsing rivers, creating vast floodplains of approximately 750,000 km² that are mainly covered by forests (Junk et al., 2011; Melack & Hess, 2010). The nutrient-rich várzea floodplains occur along the geomorphologically dynamic and sediment-loaded white-water rivers draining the Andean forelands and constitute approximately 450,000 km² (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 approximately 300,000 km² (Junk et al., 2011). Based on morphological and physicochemical parameters, Sioli (1965) classified cratonic rivers into black- and clear-water rivers, as they show differences in pH and electric conductivity, and have floodplains with varying soil fertility hosting distinct vegetation (Junk et al., 2011; Wittmann & Junk, 2016). In comparison with the várzea, igapós

have low tree species diversity and are characterized by slow dynamic processes (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 the anoxic conditions induced by flooding (De Simone et al., 2002; Haase & Rättsch, 2010; Junk, 1989; Parolin et al., 2004; Piedade, Ferreira, Oliveira Wittmann, Buckeride, & Parolin, 2010). This also holds true 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, 2013; Wittmann & Junk, 2016). Owing to the seasonal change between terrestrial and

aquatic phases, floodplains 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 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 communities 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 the 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 (Agostinho, Tomaz, & Gomes, 2004; Braatne, Rood, Goater, & Blair, 2008; Kingsford, 2000; Nilsson & Berggren, 2000). Although the complex and far-reaching consequences of damming Amazonian rivers are not well understood, considerable alterations of river–floodplain systems can be expected (Castello & Macedo, 2016). More than 222 dams (>1 MW) exist, are planned, or are under construction in the cratonic geotectonic domain of Amazonian river–floodplain systems, whereas another tranche of up to 200 dams is established and planned in the Andean headwaters and forelands, with a smaller fraction (eight dams) sited 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% of the dams, respectively (Latrubesse et al., 2017).

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

2 | THE BALBINA DAM

The Balbina dam was planned in the 1970s during the petroleum crisis (Moran, 2016). It was built to provide energy for Manaus, the capital of the Amazonas State, which is a booming city with more than 2.2 million inhabitants. Driven by its expanding free-trade zone and associated sectors, nowadays Manaus consumes up to 1,800 MW. The hydropower plant is located 150 km directly north east 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 km², and drowning floodplain and upland (terra firme) forests on slopes and depressions (Feitosa, Graça, & Fearnside, 2007). Only the plateaux of the terra firme at higher elevations remained, forming a fragmented landscape of more than 3,500 islands isolated in a cemetery of millions of dead trees (Benchimol & Peres, 2015; Fearnside, 1990, 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 full capacity of 1,335 m³ s⁻¹. Since the start of its operation in February 1989, however, the average annual power generation attained was only 112.2 MW, with an average discharge of 657 m³ s⁻¹ (Fearnside, 2015). The creation of the reservoir produced large volumes of greenhouse gases (GHGs). Accounting for emissions from the reservoir and turbines, as well as diffusive emission in the downstream area (up to 30 km distance), Kemeses et al. (2011) estimated the annual emission to be in the order of $3,141 \times 10^9$ g C-CO₂eq yr⁻¹ (CO₂-equivalent C emissions, the relative contribution of CH₄ and CO₂ is 19% and 81%, respectively) corresponding to 2.9 Mg C-CO₂eq MWh⁻¹.

3 | STUDY REGION

The Uatumã River is a black-water river with a catchment area of approximately 69,500 km² 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 with low electric conductivity (7.8 μS cm⁻¹), and is poor in nutrients but rich in humic material (Lopes et al., 2019). As is typical for Central Amazonian black-water rivers, it shows low geomorphological dynamics and relatively stable river beds (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 approximately 17 m in a relatively entrenched river bed. The remaining stretch until the river mouth (of approximately 280 km) has a low slope of only approximately 5 m, characterized by vast igapós of 9,800 km² in extent 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 confluences approximately 161 and 228 km

downstream from Balbina dam in fluvial distance (thalweg), respectively (Figure 1).

The nutrient-poor alluvial soils of the Uatumã River have a clay-like texture at lower levels and an increase in the sand fraction towards higher elevations, whereas soils of the Abacate River have predominantly sandy soils with low clay fractions at all altitudes (Lobo, Wittmann, & Piedade, 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 approximately 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 and the cultural, socio-economic, and traditional lifestyle needs of the residents, the conservation unit is divided into zones: strict biodiversity protection and research (approx. 60% of the area); extensive land use (approx. 35% of the area); and intensive land use (approx. 5% of the area). Zones for the extensive exploration of timber and non-timber forest products and tourism are mainly located along the main stem and major tributaries of the Uatumã River and floodplains and adjacent palaeofluvial terraces, covered by dense forest and some campinarana patches. Intensive land use destined for agriculture, livestock, and residences occurs in floodplains and adjacent palaeofluvial terraces close to the communities. The residents of the USDR are also involved in scientific projects and programmes developing ecotourism and sport fishing as alternative economic activities (IDESAM, 2009).

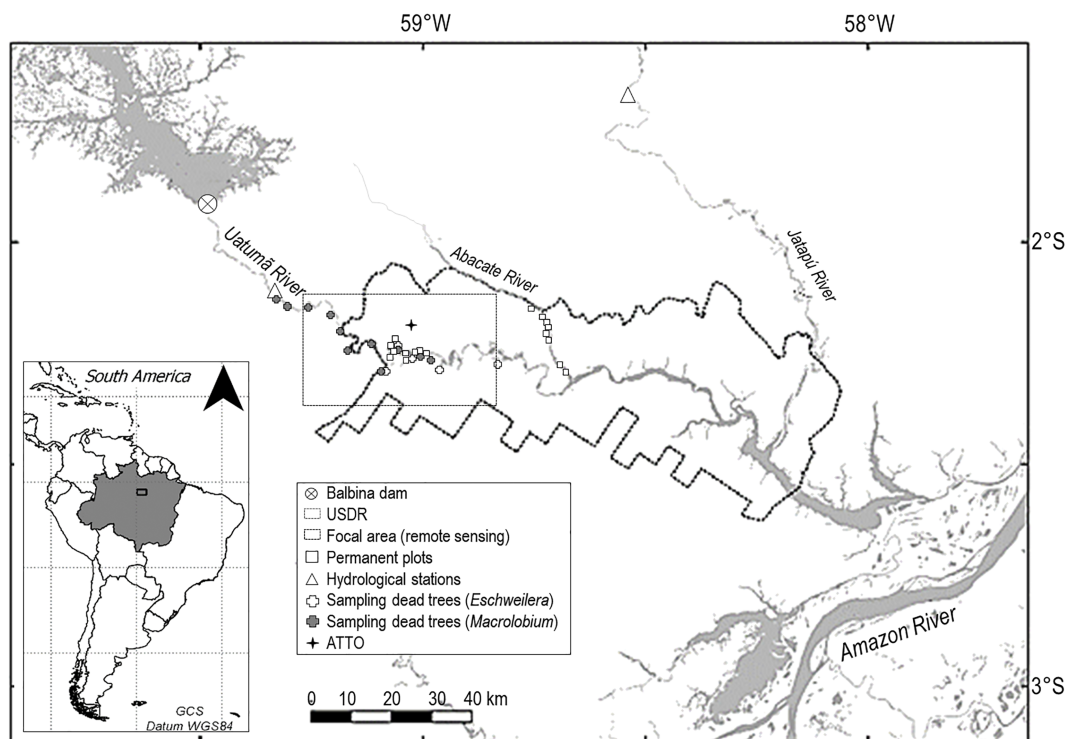


FIGURE 1 Location of the study region in the Central Brazilian Amazon, indicating the Uatumã Sustainable Development Reserve (USDR), the Balbina dam, the Uatumã River and its major tributaries (Abacate and Jatapú rivers), the hydrological stations analysed (Morena and Siderma Jusante), the location of the permanent plots in the igapó, the sample sites of dead trees, the focal area for remote-sensing analysis and the ATTO (Amazon Tall Tower Observatory) site. Photos (from left to right) show: an aerial view of the igapó floodplains of the Uatumã River (July 2009) approximately 100 km downstream of the Balbina dam (photo: Florian Wittmann); dead tree population of *Eschweilera tenuifolia* in a floodplain lake (October 2015) at the lowest topographical elevations of the igapó, approximately 105 km downstream of the Balbina dam (photo: Jochen Schöngart); and disturbed forests in the focal area at the medium topography of the igapó of the Uatumã River (April 2018), dominated by the tree species *Nectandra amazonum* and the palm species *Astrocaryum jauari* (photo: Jochen Schöngart)

The first visits of the research team to the USDR occurred in August 2009, at the beginning of the implementation of the Amazon Tall Tower Observatory (ATTO) project, 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 levels of the igapó along the Uatumã River downstream of the Balbina dam were observed, which raised the hypothesis that this massive tree mortality was caused by changes in the hydrological regime resulting from the operation of the hydro-power dam. To obtain the first information on the igapó forests of the USDR, Targhetta et al. (2015) performed floristic inventories in the affected 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 above-ground wood biomass stocks of 126–173 Mg ha⁻¹ of the igapó were relatively low in comparison with other black-water igapós along the Negro River and its tributaries (57–79 spp. ha⁻¹ and 170–260 Mg ha⁻¹; Aguiar, 2015; Batista, 2015; Corrêa, 2017; Montero et al., 2014), giving the first hints of potential downstream impacts on the igapó flora.

4 | MATERIAL AND METHODS

The assessment of spatiotemporal disturbances along a 35-year time line 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 characteristics of dominant tree species (Lobo et al., 2019; Neves, Piedade, Resende, Feitosa, & Schöngart, 2019; Rocha et al., 2019, 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 in order to highlight the extent of change. For this study, the IHA and RVA analyses of the post-dam period have been expanded (1991–2018) and compared with 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, 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://www.snirh.gov.br/hidroweb/serieshistoricas>).

The impacts of the Balbina dam implementation and operation at a landscape level were assessed, applying remote-sensing techniques. The igapó floodplains and dead forests were mapped by Resende et al. (2019) 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). A total of 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, and object-based image analysis (OBIA) and random forests using a supervised classification algorithm with an overall accuracy of 87.2% were performed. 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) images from different months of those years were processed and compared (Gorelick et al., 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. *Macaranga 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 yr⁻¹ (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 yr⁻¹ (Junk et al., 2015; Resende et al., 2020). Both species can live for up to 500 years in the case of *M. acaciifolium* (Schöngart et al., 2005) and more than 800 years in the case of *E. tenuifolia* (Resende et al., 2020), and are therefore excellent long-term indicators of environmental conditions in floodplains (Junk, Piedade, Nunes da Cunha, Wittmann, & Schöngart, 2018).

The sampling of dead trees occurred within fluvial distances 35–125 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 of year of death, was dated by radiocarbon (26 of the ¹⁴C-dated samples of *E. tenuifolia* provided reliable radiocarbon determinations; Resende et al., 2020), with additional cross-dating techniques (dendrochronology) used for *M. acaciifolium* (Assahira et al., 2017). 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 impacts of the hydrological alterations on tree species diversity and dominant tree species were assessed by comparing the forests along the Uatumã River with those of an adjacent, undammed affluent (Abacate River) (Figure 1). The floristic data available for igapó forests comprised 6 ha in the focal area of the Uatumã River and 3.75 ha of the Abacate River (for further details, see Lobo et al., 2019; Rocha et al., 2019, 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-m × 25-m subplots (625 m²), 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 further details, see Lobo et al., 2019). In four subplots (625-m² plots) at low, medium, and high elevations of the igapó in the Uatumã and Abacate rivers, Rocha et al. (2019, 2020) established cross transects of 25 m × 1 m (12 transects at each site) to study the species composition of tree seedlings (15–100 cm in height). Based on this floristic data, the 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 the frequency, abundance, and dominance (basal area) of each tree species. In this study, the relative IVIs of the five most important species (IVI_{Σ1-5}) 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 elevations of the Uatumã and Abacate rivers. In addition, basic wood density of the dominant tree species was considered in the comparison of pristine and disturbed river stretches (Mori et al., 2019; Neves, 2018).

5 | RESULTS

5.1 | Hydrological changes of the Uatumã River

The IHA parameters in Figure 2 reflect the drastic changes in the stream-flow 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 in the maximum water level (April–June) and an increase in the minimum water level (October–December), reflected by an increase in the low and high RVA categories, respectively (Figure 2a). For the low-water regime, the period from 2000 to 2008 was especially crucial, when the minimum water levels were, on average, more than 1 m higher than the minimum water levels of 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) (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 increased flooding conditions at the lowest topographic elevations and simultaneously decreased 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 two-fold increase in the fall and rise rates and a three-fold increase in the number of reversals between fall and rise rates, compared with pristine conditions (Figures 2c–e). Also, significant changes were observed in the timing of the 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 (JDs) 273–346 (25–75th percentiles; median JD 332), with maximum water levels occurring between the end of April and the beginning of June at JDs 114–156 (25–75th percentiles; median JD 128). This scenario changed dramatically during the operational period of the Balbina dam, showing a remarkably high temporal variation for 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). This relationship weakened during the period of dam construction ($R^2 = 0.44$, $P < 0.001$), indicating the first disturbance 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 ($R^2 = 0.12$, $P < 0.001$). Compared with 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, owing to the extreme low stream flow of only 4.7–19.7 m³ s⁻¹ in this period (Fearnside, 1989), whereas 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, and 2015/2016), which affected the rainfall and stream-flow regimes, especially in the northern, central, and eastern sections of the Amazon basin (Aragão et al., 2018; Marengo et al., 2018), resulted in remarkably low water levels in the Uatumã and Jatapú rivers (Figure 3a).

5.2 | Tree mortality

Massive tree mortality was detected in the focal area across approximately 90 km² of floodplain forests, affecting 12% (approx. 11 km²) of the igapó (Figure 4). Dead forests were observed at lower topographical elevations, mainly close to lakes and inner convex banks of the geomorphologically stable fluvial meanders (slip-off slopes). Of the dead trees analysed in the igapó downstream of the dam, 98% had

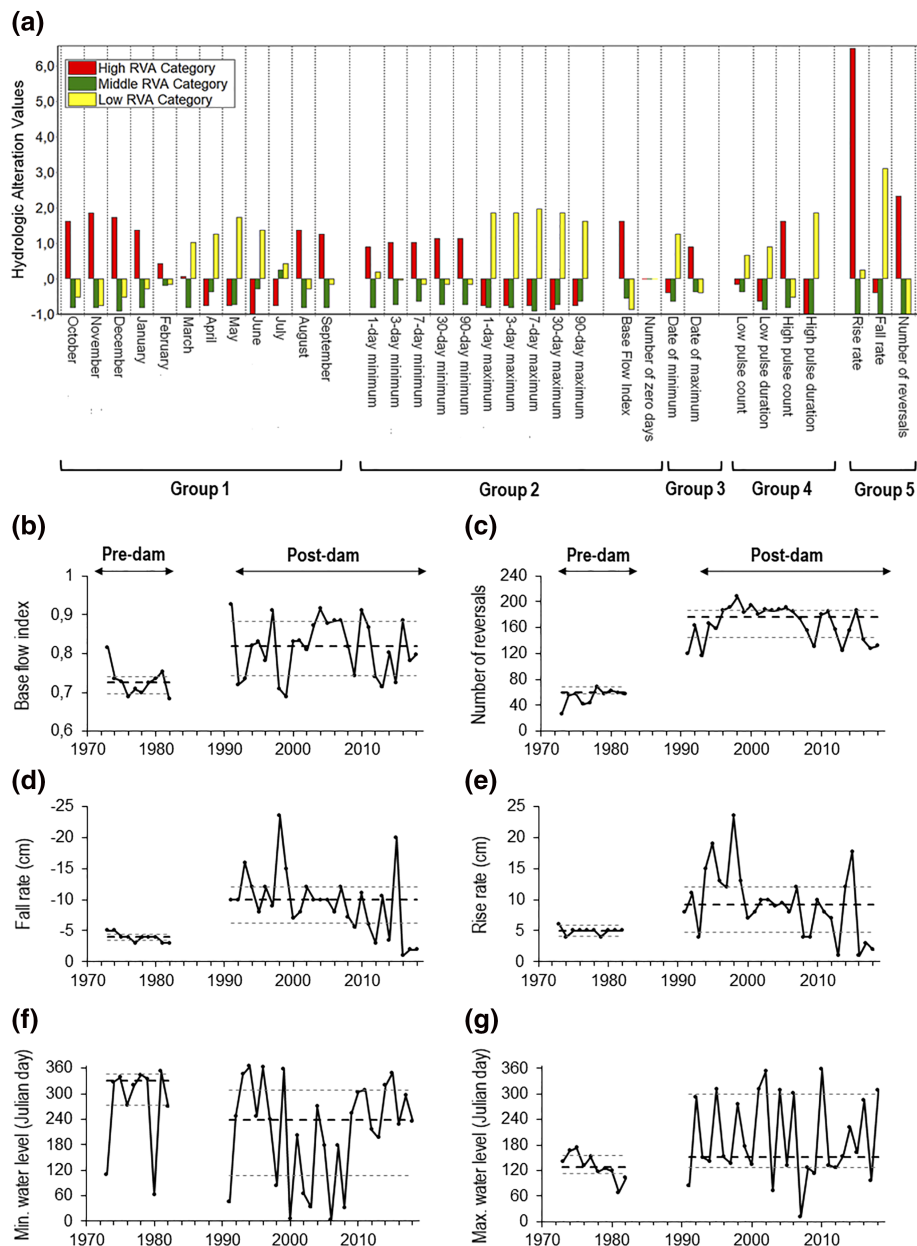


FIGURE 2 Analyses of indicators of hydrologic alteration (IHA) of the Uatumã River downstream of the Balbina dam and range of variability approach (RVA) (Richter et al., 1996, 1997), comparing pristine conditions (1973–1982) with the period of dam operation (1991–2018). IHA parameters were calculated based on daily water level data (hydrological year from October to September) using nonparametric statistics (median, and 25th and 75th percentiles) for the pre-dam and post-dam periods by software IHA 7.1. (a) RVA evidencing changes from the pre-dam to the post-dam period in the monthly median water levels from October to September (group 1); magnitude, duration (group 2), and timing of annual extreme water conditions (group 3); frequency and duration of high and low pulses (group 4); rate and frequency of water condition changes (group 5). The three RVA categories are based on percentile values of equal size (low, <34th percentile; middle, 34–67th percentile; high, >67th percentile). For each category the hydrologic alteration factor is computed, which quantifies the degree of alteration of each IHA parameter. Positive values indicate that the frequency of values in the category has increased from the pristine to the post-dam period, whereas negative values represent a decrease in frequency. The lower panels 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 rates; (e) rise rates; (f) timing of minimum water level; and (g) timing of maximum water level (black horizontal dashed lines are the medians; grey dashed lines represent the 25th and 75th 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://www.snirh.gov.br/hidroweb/serieshistoricas>)

died during dam installation and operation; however, both of the tree species studied revealed distinct mortality patterns (Figure 5). An increased mortality of *E. tenuifolia* had 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 a rising low-water

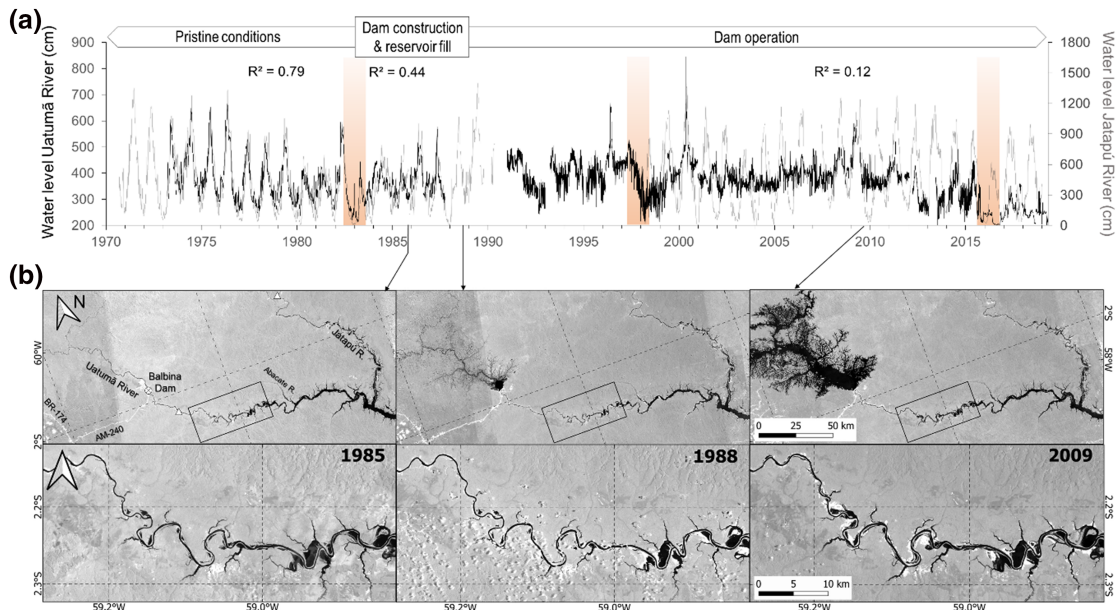


FIGURE 3 (a) Daily water levels from the Uatumã River, downstream of the Balbina dam (black), and its major tributary, the Jatapú River (grey). Both hydrological regimes show high congruence during the period of pristine conditions (until 1983), which weakened during the period installing the Balbina dam (1983–1987) and is reduced for the post-dam period (1998–2018) (data from Brazilian National Agency of Waters, ANA; <http://www.snirh.gov.br/hidroweb/serieshistoricas>). No data were available for the Uatumã River (Cachoeira Morena station, ID code 16100000) between 1 October, 1987 and 31 December, 1990 (period of reservoir fill and the start of dam operation); for the Jatapú River (Siderma-Jusante station, ID code 16205000) data are available from 13 September, 1970 to 27 April, 1990 and from 1 May, 1998 to 31 December, 2018. Vertical reddish bars indicate the occurrence of strong El Niño events in the periods 1982/1983, 1997/1998, and 2015/2016, leading to extremely low water levels in both rivers. (b) Composition of Landsat Thematic Mapper (TM) images for the years 1985 (dam construction), 1988 (reservoir fill), and 2009 (dam operation), and the downstream impacts of the dam on the floodplains of the focal area (black rectangle) along the Uatumã River during the low-water period (September–November). The locations of the Balbina dam (circle) and the hydrological stations of the Uatumã and Jatapú rivers (triangles) are indicated. Note the differences of flooding conditions (black areas) in the focal area between the periods of reservoir fill and dam operation (data from Landsat 4–5 TM; imagery reproduced courtesy of the US Geological Survey EROS Archive; doi: 10.5066/F7N015TQ)

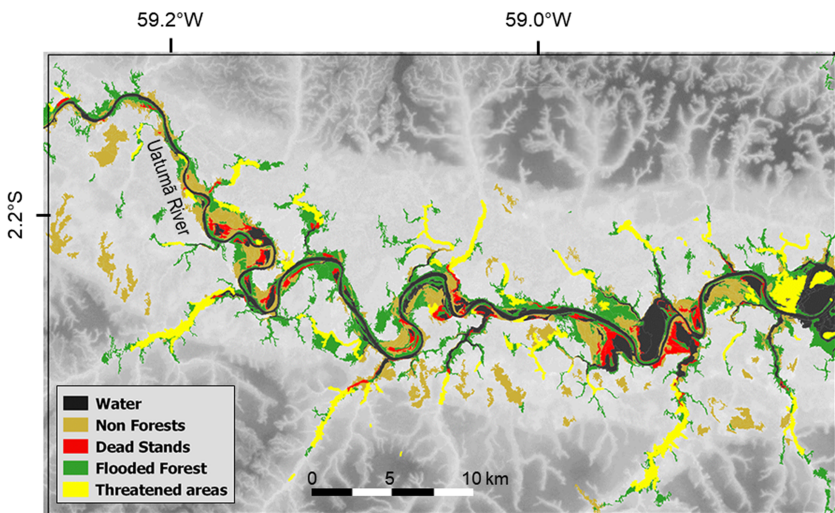


FIGURE 4 Mapped dead forests and potentially threatened forests in the focal area of the igapó floodplains along the Uatumã River downstream of the Balbina dam (background: shaded relief derived from the Shuttle Radar Topography Mission–SRTM digital elevation model; Resende et al., 2019)

regime (Figure 2b) and subsequent loss of the terrestrial phase. The strong El Niño event in 1997/1998 caused low stream flow (Figure 3a) and resulted in a terrestrial phase lasting

approximately 2 months (*E. tenuifolia*) or 3 months (*M. acaciifolium*). Conversely, the permanent flooding conditions of these trees started in 2000 and lasted for more than 8 consecutive years as a

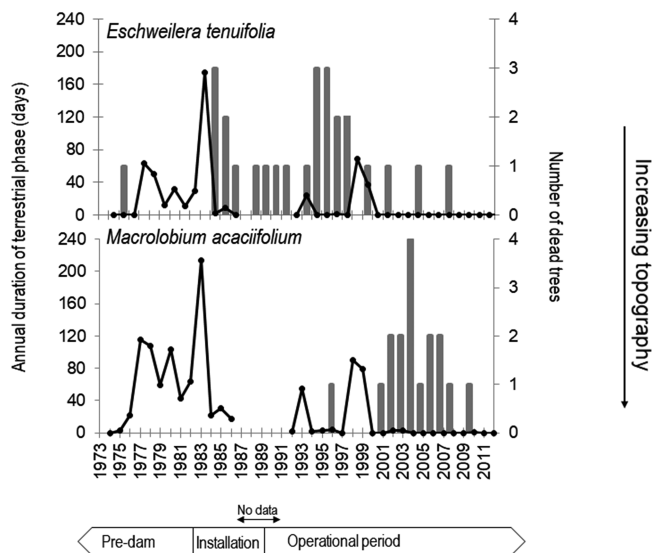


FIGURE 5 Mortality patterns for *Macrolobium acaciifolium* (Fabaceae) and *Eschweilera tenuifolia* (Lecythidaceae) based on cross dating and radiocarbon dating to estimate the year of death in the igapó floodplains downstream of the Balbina dam. The mortality patterns are related to the duration of the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

consequence of the increase in the minimum water level (Figures 2 and 3), causing further tree mortality, especially for *M. acaciifolium* (Assahira et al., 2017).

5.3 | 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 the 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 (Assis et al., 2015; Montero et al., 2014; Wittmann, Junk, & Piedade, 2004; Wittmann et al., 2006, 2010). However, species diversity decreases continuously with increasing flood duration in the pristine igapó, whereas 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 inundation classes of the pristine and disturbed igapó. The high igapó showed similar $IVI_{\Sigma 1-5}$ values in the disturbed (31.9%)

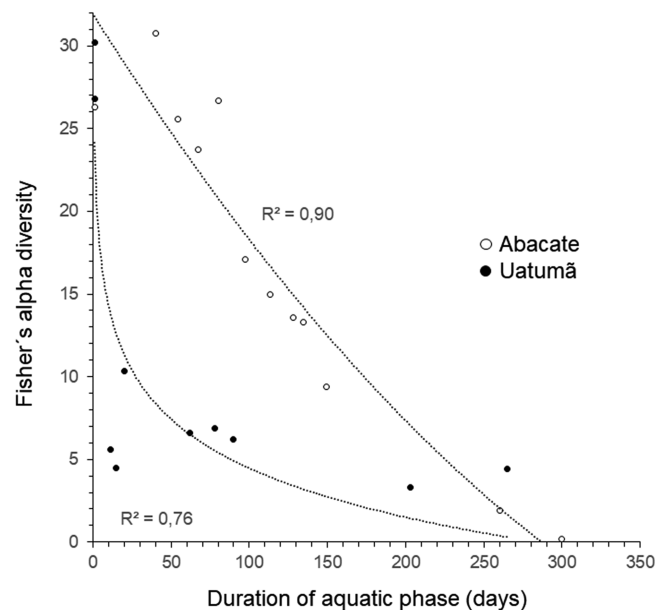


FIGURE 6 Relationship between Fisher's alpha diversity and the duration of the aquatic phase comparing the pristine igapó forests (Abacate) with the disturbed system downstream of the Balbina dam (Uatumã). Fisher's alpha diversity from adjacent terra firme forests (Lobo et al., 2019) are included in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

and pristine (33.7%) floodplains; 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 yr⁻¹), lower wood densities (0.50–0.67 g cm⁻³), and lower tree ages (52–77 yr), compared with the pristine igapó. The oldest trees with similar MDIs and wood densities occurred in the low igapó at both sites (Table 1); however, they were composed of different species, probably as a result of the different grain-sized substrates (Lobo et al., 2019). The dominant tree species had a higher $IVI_{\Sigma 1-5}$ value at the disturbed site (61.8%) compared with the pristine site (36.6%). The most significant differences were observed in the medium igapó, where the $IVI_{\Sigma 1-5}$ value of the pristine system (26.3%) was much lower compared with the $IVI_{\Sigma 1-5}$ value of the disturbed igapó (61.8%). The palm *Astrocaryum jauari* Mart. (Arecaceae) is the dominant 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 yr⁻¹, which differed significantly from all other elevations (Neves et al., 2019). At this elevation, 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. In the disturbed low igapó, 55% of the total IVI in the seedling stratum was represented by *Pouteria elegans* (A. DC.) Baehni (Sapotaceae), whereas in the disturbed high igapó the arborescent palm *Attalea maripa* (Aubl.) Mart. (Arecaceae)

TABLE 1 Dominant tree species (>10 cm DBH) of the igapó forests studied in 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)

Uatumã					Abacate				
High igapó					High igapó				
Tree species	IVI%	Age	MDI	ρ	Tree species	IVI%	Age	MDI	ρ
<i>Tapirira guianensis</i>	12.8	71 ± 3	3.9 ± 0.1	0.50	<i>Licania macrophylla</i>	16.3	71 ± 23	1.5 ± 0.4	0.82
<i>Pentaclethra macroloba</i>	7.0	77 ± 6	2.6 ± 0.1	0.65	<i>Myrcia fallax</i>	5.9	76 ± 32	1.1 ± 0.2	0.82
<i>Attalea maripa</i>	4.2	-	-	-	<i>Eschweilera cf. albiflora</i>	4.2	90 ± 41	1.6 ± 0.4	0.83
<i>Trichilia micrantha</i>	4.2	74 ± 17	1.8 ± 0.2	0.67	<i>Ocotea aciphylla</i>	3.8	95 ± 42	1.4 ± 0.6	0.64
<i>Naucleopsis glabra</i>	3.7	52 ± 26	1.8 ± 0.7	0.62	<i>Crudia amazonica</i>	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
<i>Astrocaryum jauari</i>	17.0	-	-	-	<i>Eschweilera cf. albiflora</i>	6.5	67 ± 28	1.2 ± 0.1	0.83
<i>Nectandra amazonum</i>	13.5	28 ± 4	4.8 ± 1.2	0.42	<i>Licania macrophylla</i>	5.9	106 ± 43	1.7 ± 0.2	0.82
<i>Alchornea discolor</i>	13.0	79 ± 27	3.2 ± 0.6	0.46	<i>Ouratea discophora</i>	4.1	67 ± 22	1.9 ± 0.5	0.79
<i>Mabea nitida</i>	9.7	47 ± 16	4.7 ± 0.6	0.55	<i>Pouteria pachyphylla</i>	3.8	107 ± 57	1.6 ± 0.1	0.75
<i>Inga sp.</i>	8.7	66 ± 15	3.7 ± 0.3	0.58	<i>Gutteria guianensis</i>	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
<i>Pouteria elegans</i>	22.8	98 ± 29	1.9 ± 0.2	0.73	<i>Pouteria pachyphylla</i>	9.0	102 ± 47	1.7 ± 0.3	0.75
<i>Amanoa oblongifolia</i>	19.9	126 ± 12	1.7 ± 0.3	0.76	<i>Elvasia calophyllea</i>	8.6	122 ± 59	1.7 ± 0.4	0.80
<i>Mabea nitida</i>	6.6	65	1.0	0.55	<i>Couratari cf. tenuicarpa</i>	7.2	106 ± 41	2.2 ± 0.6	0.43
<i>Handroanthus barbatus</i>	6.5	90 ± 25	2.1 ± 0.2	0.87	<i>Manilkara bidentata</i>	6.4	84 ± 31	1.8 ± 0.8	0.92
<i>Leptolobium nitens</i>	6.0	173 ± 89	1.6 ± 0.3	0.72	<i>Swartzia laeviscarpa</i>	5.5	190 ± 21	1.4 ± 0.6	0.55

Note: Data taken from: Lobo et al. (2019); Mori et al. (2019); Neves (2018); Neves et al. (2019); Rocha et al. (2019).

dominated the seedling stratum (22.5% of the total IVI). This species is a well-known indicator of 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 disturbed 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 igapós.

6 | 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. The disturbances observed in the igapó forests studied 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 hydropower plants and the implementation of future hydropower plants are provided.

6.1 | Spatiotemporal disturbances in floodplains of the downstream area

Large-scale disturbances in the igapós of the Uatumã River associated with the Balbina dam had already begun in the period of dam construction (1983–1987) and reservoir fill (1987–1989). During these periods, 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) that increased the temperature and reduced the rainfall and humidity (Aragão et al., 2018; Marengo et al., 2018). The extreme dry hydroclimatic conditions generated (Figure 7) is 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 through stomatal conductance and vascular

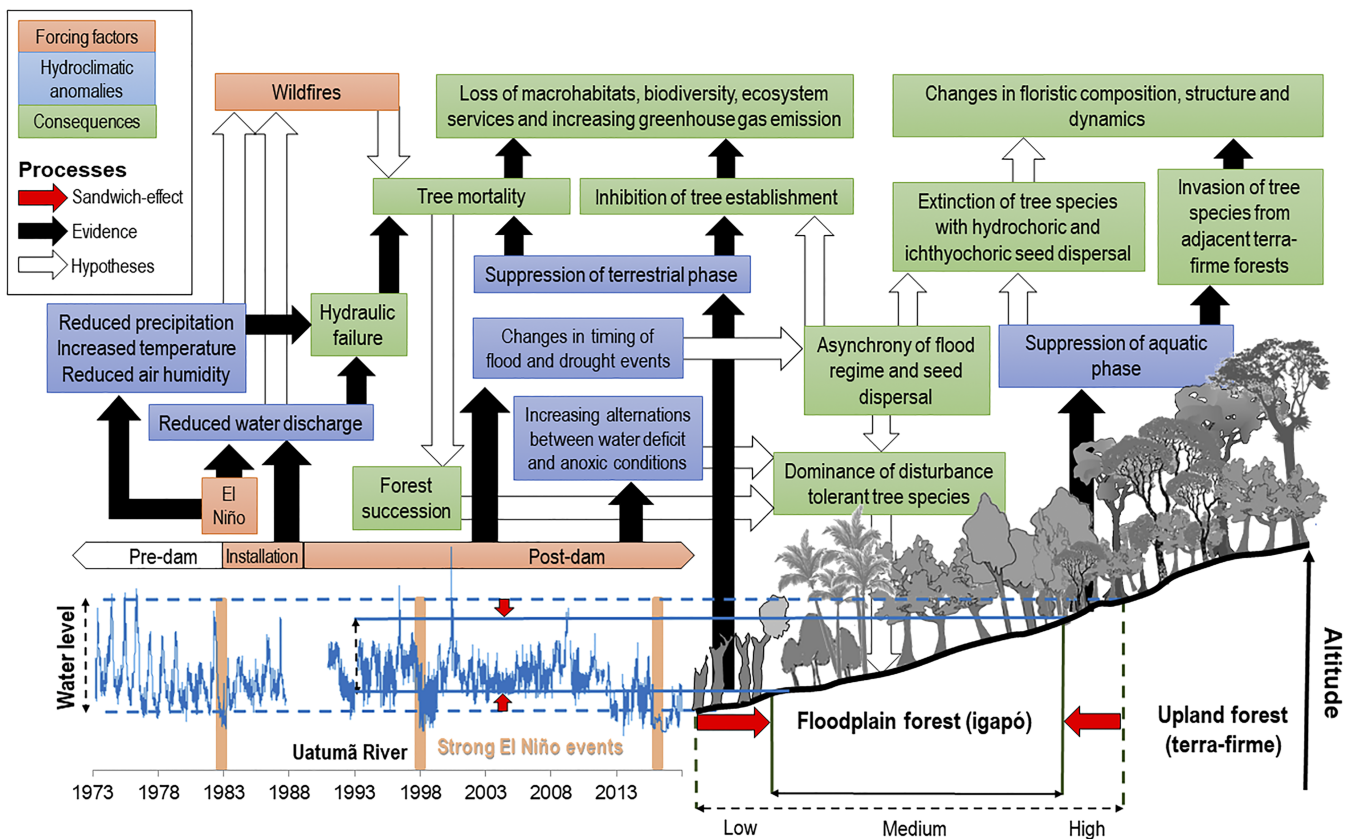


FIGURE 7 Spatiotemporal disturbances in the igapó floodplains downstream of the Balbina dam over a 35-year period had severe impacts on this ecosystem, resulting in a loss of macrohabitats, massive tree mortality, and altered tree species diversity, affecting the functioning and provision of ecosystem services of a conservation unit. During the installation of the Balbina dam and the reservoir fill, in combination with El Niño conditions (in 1982/1983 and 1986–1988), severe dry conditions were generated in the downstream floodplains (Figure 3). This led to hydraulic failure and tree mortality at the lowest elevations, and possibly caused wildfires affecting mainly the medium elevations, resulting in 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 lower elevations and suppression of the aquatic phase at higher elevations as a consequence of higher minimum and lower maximum water levels, respectively. The temporal asynchrony between the hydrological regime and phenology, growth rhythms, and 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

transport (Cailleret et al., 2017; Gessler et al., 2018; Hartmann et al., 2018). Fontes et al. (2020) observed a high vulnerability of *E. tenuifolia* to xylem embolism in the study region, 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). It is likely that the drying of the fine-grained alluvial soils caused soil cracking, physically damaging the superficial fine roots, and 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 combined effects of dam operation 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 understorey, compared with the well-stratified terra firme forests, and consequently the humidity of the air in igapó forests is much lower (Almeida et al., 2016; Resende, Nelson, Flores, & Almeida, 2014). Owing to the long periods of flooding, litter decomposes slowly 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 volume of combustible material. The presence of an approximately 30-year old age cohort of *N. amazonum* (Neves et al., 2019) and low tree species diversity (Figure 6; Table 1) suggests 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 characterized as a secondary species of the nutrient-rich and highly dynamic white-water floodplains (várzea) (Wittmann, Anhof, & 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 the 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 a 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, as the plant is described as an 'ichthyochoric' species (Weiss et al., 2016).

The high dominance of the palm *Astrocaryum jauari* in 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 of Anavilhanas and Mariuá in the Negro River (Piedade, Parolin, & Junk, 2006). Several Amazonian terra firme palm species are fire resistant, such as *Acrocomia aculeata* (Jacq.) Lodd. ex Mart., *Astrocaryum aculeatum* G. Mey., *Astrocaryum vulgare* Mart., and *Attalea maripa*, as well as *Copernicia alba* Morong, occurring in seasonally flooded savannas in the Bolivian Amazon and also in the Pantanal (Araújo et al., 2012; Carvalho, Ferreira, & Lima, 2010; Smith, 2015), and may benefit from fire by increasing their dominance. Palms do not have cambial tissue and many species have diaspores with morpho-physiological dormancy (Baskin & Baskin, 2014). Seedlings of some palm species, such as *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 over time series since the period of dam construction should provide evidence of the magnitude of wildfire activity during this period, as used 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 elevations and the loss of the terrestrial phase at low elevations 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 affected the population of *M. acaciifolium*, growing at higher elevations (Figure 5). Although both tree species are well adapted to regular seasonal inundations, pluri-annual 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 the adaptations developed by these species to tolerate seasonal inundations (Assahira et al., 2017; Piedade, Schöngart, Wittmann, Parolin, & Junk, 2013; Resende et al., 2020).

Tree mortality along the upstream courses is usually faster than in the dam shadow, because it mainly affects 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 have developed sophisticated adaptations to seasonal flooding, which can extend mortality-inducing processes over long periods (Resende et al., 2020). So far, the Balbina dam has resulted in 12% of dead igapó forests at the low topographical elevations (Figure 4), increasing to more than 125 km downstream of the hydropower plant (Assahira et al., 2017; Resende et al., 2019, 2020). If in future the dam operation continues to enhance the low-water regime, a further 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 also reach higher elevations. The slow decomposition of dead biomass (approx. $129 \pm 14 \times 10^9$ g C) under almost constant anaerobic conditions (Resende et al., 2019) is likely to result in increasing GHG emissions, especially of CH₄. The long-term monitoring of atmospheric CH₄ mixing ratios at the nearby ATTO site (Figure 1) by Botía et al. (2020) detected night-time CH₄ increases, which most likely originated from the dead igapó forests; however, so far GHG emissions (CO₂ and CH₄) 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 the whole picture of GHG emission related to the Balbina dam, these measurements should be extended to the affected igapó floodplains in future studies and monitoring.

At high elevations of the igapós the loss of flooding has favoured the encroachment of mainly secondary species from adjacent terra firme forests (Figure 7), with species such as *Attalea maripa*, *Rinorea racemosa* (Mart.) Kunze (Violaceae), *Tapirira guianensis* Aubl. (Anacardiaceae), and *Trichilia micrantha* Benth. (Meliaceae) dominating the establishment stratum in particular (Lobo et al., 2019; Rocha et al., 2019). These species are probably better adapted to the changed environmental conditions and are more competitive than 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) that are mainly dispersed by water (hydrochory) 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 on the water (Kubitzki & Ziburski, 1994; Melo, Franco, Silva, Piedade, & Ferreira, 2015; Oliveira Wittmann, Piedade, Wittmann, & Parolin, 2007), seedlings need 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 levels during the post-dam period probably results in an asynchrony of phenology patterns, dispersal mechanisms, and establishment processes for many tree species occurring at levels that are still seasonally flooded (Figures 2f, g). As the low

igapós are under near-permanent aquatic conditions and floods have been suppressed in the high igapós, the hypothesis is postulated that tree species relying on water and fish for dispersal no longer become established at these elevations in the long term (Figure 7). Consequently, fish populations lose this important food source, which may reduce fish populations regionally.

The frequency and duration of high and low pulses (group 4) and the rate and frequency of changing water conditions (group 5) shifted considerably during the post-dam period (Figure 2), which possibly has profound 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 the increasing dominance of tree species (Table 1) with higher resilience and functional traits to adapt to the changed environmental conditions (Figure 7).

Overall, the hydrological alterations described have impacts on several processes in the floodplain system that are relevant for tree species (Figure 7): they alter habitat and soil moisture availability, as well as anaerobic conditions, and affect the synchrony between the flooding regime and the phenological patterns, growth rhythms, dispersal mechanisms, and processes of establishment that floodplain trees had adapted to 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 cuts the population connectivity of fish, and changes their habitats by modifying the physical and chemical conditions (Agostinho et al., 2004; Castello & Macedo, 2016; Costa-Pereira et al., 2018; Val et al., 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, and loss of biodiversity and environmental services, has relevant implications for conservation. Floodplains in the USDR are excluded from the permanent protection zones and are destined for extensive and intensive land use (IDESAM, 2009). Igapós of the Uatumã River to its confluence with the Abacate River (Figure 1) are likely to suffer from the complex and persistent disturbance regime, which affects both economic activities (e.g. fisheries and ecotourism) and the welfare of the local inhabitants. In addition, dead forests constitute a risk for large wildfires during extreme El Niño conditions, when huge volumes of flammable materials are exposed to severe dry conditions caused by extremely low water levels, such as during 2015/2016 (Figure 3a). These are relevant aspects for the conservation management of the USDR.

6.2 | Implications of the findings for other Amazonian dams

Downstream impacts on floodplains differ greatly among hydropower plants depending on many factors, such as the geomorphology, hydrochemical conditions, sediment load, biogeography, and 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 hydropower plants under operation, construction or being planned, as no comparable studies on downstream impacts are available for the Amazon basin. Timpe and 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 in 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 correlated with the elevation of the impoundment. The authors further observed that increasing elevation of dams resulted in a decrease in the frequency and duration of high and low pulses (IHA group 4) and in 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 disturbances observed in the integral functioning of the downstream floodplains (Figure 7), which are 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 owing to the smaller catchment areas (Junk et al., 2011), and tree species adapted to these regimes probably suffer fewer impacts by dam-induced hydrological alterations. Timpe and Kaplan (2017) further observed that multiple dams in rivers have cumulative and cascading impacts, affecting the IHA parameters of groups 4 and 5, in particular, which is highly relevant for many cratonic rivers in the Brazilian Amazon (Fearnside, 2019; Latrubesse et al., 2017), and also in the Cerrado (savanna belt) (Latrubesse et al., 2019).

Downstream impacts may also vary according to the geomorphological and hydrochemical characteristics of floodplain ecosystems. Black-water floodplain tree species are likely to be more vulnerable to dams than their white-water counterparts, because várzea tree species have adaptations to dynamic hydrogeomorphological processes, such as erosion and burial through sediment deposition, which are lacking in igapó tree species (Peixoto et al., 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 planned total capacity of 4,000 MW; Fearnside, 2019) will possibly have stronger downstream impacts than those of the Madeira River (Santo Antônio and Jirau with installed capacities 3,150

and 3,750 MW, 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 synthesis provided 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 impacts 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 other rivers dams are under construction or are 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 because of the wide range of factors that must be considered in this approach.

7 | 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, and Mekong, and many others, are likely to suffer drastic hydrological alterations resulting from already installed and planned large hydropower dams (Latrubesse et al., 2017, 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 recommendations to be made that should be considered in environmental impact assessments and associated reports (EIAs/RIMAs) in the Amazon and elsewhere.

1. For dams under construction and during the reservoir fill, severe dry conditions should be avoided in the downstream floodplains, as these are likely to provoke tree mortality and wildfires.
2. Hydropower dams that are already operating should adapt power generation to simulate the natural flood pulse and maintain annually the pre-dam baseflow index of the river to mitigate the

downstream impacts in the floodplains. This should also be a guideline for hydropower dams that are at the planning stage.

3. The environmental impact assessment must include floodplains downstream of the planned hydropower dams, at least until the river reaches the confluence of a major undisturbed affluent of the same river order (Strahler, 1957) or until it reaches the area influenced by backwater effects from rivers with higher ranked orders (Meade, Rayol, Da Conceicao, & Natividade, 1991), which are likely to buffer the dam-induced hydrological alterations.
4. The downstream assessment should provide inventories of major macrohabitats (Junk et al., 2018) in the potentially affected floodplains at site and landscape levels, with associated hydro-morphological data.
5. Models simulating the relationships between river discharge, potential power generation, and water level should allow an assessment and evaluation of mitigated downstream impacts and monetary losses for power generation that maintain 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 the combined effects of climate and land-use changes are expected to cause a serious imbalance of floodplain ecosystems in the future.

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CONFLICT OF INTEREST

The authors declare that they have no competing financial interests and have no other potential sources of conflict to disclose.

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