

1 **Short title:** Balbina downstream impact

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

5  
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55 **Abstract**

56 1. The Balbina hydropower dam in the Central Amazon basin, established in the 1980s in  
57 the Uatumã River, is emblematic for its socioenvironmental disaster. However, its  
58 environmental impacts go far beyond the reservoir and dam, affecting the floodplain  
59 forests (igapó) in the downstream area (dam shadow), which were assessed by a  
60 transdisciplinary research approach, synthesized in this review.

61 2. Floodplain tree species are adapted to a regular and predictable flood pulse with a high  
62 and low water period during the year, which was severely affected by the operation of the  
63 Balbina dam, causing a suppression of the aquatic phase at higher floodplain elevations  
64 and the terrestrial phase at lower floodplain elevations ("sandwich-effect").

65 3. Already during the period of construction and reservoir fill, large-scale mortality occurred  
66 in the floodplains of the dam shadow, due to reduced streamflow in synergy with severe  
67 drought conditions induced by El Niño events causing hydraulic failure and turning  
68 floodplains vulnerable to wildfires.

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3 69 4. During the post-dam period, permanent flooding conditions at low topographical  
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5 70 elevations resulted in massive tree mortality. So far, 12% of the igapó forests died along  
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8 71 a downstream river stretch of more than 125 km. Because of the flood suppression at the  
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10 72 highest elevations, an encroachment of secondary tree species from upland (terra-firme)  
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12 73 forests occurred.

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15 74 5. More than 35 years after the Balbina dam implementation, the downstream impacts caused  
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17 75 massive losses of macrohabitats, ecosystem services, and diversity of flood-adapted tree  
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19 76 species, probably cascading down to the entire food web, which must be considered in  
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21 77 conservation management.

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24 78 6. These findings are critically discussed, emphasizing the urgent need for Brazilian  
25  
26 79 environmental regulatory agencies to incorporate downstream impacts in the  
27  
28 80 environmental assessments of the several dam projects, planned in the Amazon region.

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33  
34 82 **Keywords:** disturbance, flood pulse, hydropower dam, igapó, long term ecological research  
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36 83 (LTER), tree mortality, Uatumã River, wildfire.

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45 86 **Introduction**

46  
47 87 The Amazon River basin is one of the few remaining large networks of free-flowing rivers  
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49 88 on Earth (Grill et al., 2019). The largest hydrobasin of our planet, with about 16-18% of the  
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51 89 worldwide discharge of freshwater to the oceans (Latrubesse, 2008), is composed of a variety  
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54 90 of flood-pulsing rivers, creating vast floodplains of about 750,000 km<sup>2</sup>, mainly covered by  
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3 91 forests (Junk et al., 2011; Melack & Hess, 2010). The nutrient-rich várzea floodplains along  
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5 92 the geomorphological dynamic and sediment-loaded white-water rivers drain the Andean  
6  
7 93 forelands and constitute about 450,000 km<sup>2</sup> (Wittmann & Junk, 2016). Igapó floodplains  
8  
9 94 occur mainly along cratonic rivers draining the Precambrian and Archaic Guiana and  
10  
11 95 Brazilian shields in the northern and southern regions of the Amazon basin (Latrubesse,  
12  
13 96 Stevaux, & Sinha, 2005), covering a total area of about 300,000 km<sup>2</sup> (Junk et al., 2011).  
14  
15 97 Based on morphological and physiochemical parameters, Sioli (1965) classified cratonic  
16  
17 98 rivers into black- and clear-water rivers, as they show differences in pH, electric conductivity,  
18  
19 99 and floodplains with varying soil fertility and distinct vegetation (Junk et al., 2011; Wittmann  
20  
21 100 & Junk, 2016). In comparison to the várzea, igapós show a low tree species diversity and are  
22  
23 101 characterized by slow dynamical processes (e.g., Junk, Wittmann, Schöngart, & Piedade,  
24  
25 102 2015; Montero, Piedade, & Wittmann, 2014; Rosa et al., 2017; Schöngart, Wittmann,  
26  
27 103 Piedade, Junk, & Worbes, 2005; Wittmann, Schöngart, & Junk, 2010).  
28  
29 104 A common driver of geomorphological processes and biogeochemical cycles, as well as life  
30  
31 105 cycles and growth rhythms of the floodplain biota in várzea and igapó along large rivers is  
32  
33 106 the regular and predictable (monomodal) flood-pulse of high amplitude (Junk, Bayley, &  
34  
35 107 Sparks, 1989). Tree species have adapted to the hydrological cycles over evolutionary time  
36  
37 108 scales by developing and combining morpho-anatomic, physiological and biochemical  
38  
39 109 mechanisms to cope with anoxic conditions induced by flooding (e.g., De Simone et al.,  
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41 110 2002; Haase & Rättsch, 2010; Junk, 1989; Parolin et al., 2004; Piedade, Ferreira, Oliveira  
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43 111 Wittmann, Buckeride, & Parolin, 2010). This also holds for the aquatic fauna, such as fishes  
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45 112 (Val, 2019) and invertebrates (Adis, 2010).  
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3 113 Floodplains are key elements in the Amazonian landscape as they harbour an enormous  
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5 114 diversity of partially endemic flora and fauna and are important drivers for diversification  
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8 115 processes and speciation (Junk & Piedade, 1992; Wittmann et al., 2006; Wittmann et al.,  
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10 116 2013; Wittmann & Junk, 2016). Due to the seasonal change between terrestrial and aquatic  
11  
12 117 phases, floodplains further episodically offer habitats for plants, and food sources for  
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14  
15 118 numerous species of the aquatic and terrestrial fauna (Wittmann & Junk, 2016). In addition,  
16  
17 119 they provide fundamental ecosystem services to the society, such as storing water (essential  
18  
19 120 to buffer river discharge and to recharge groundwater), purifying water, sediment retention,  
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21  
22 121 and the regulation of microclimate as well as biogeochemical and nutrient cycles (Junk et al.,  
23  
24 122 2014). Amazonian floodplains have been settled and used by indigenous for thousands of  
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26 123 years and by post-Columbian riverine populations for centuries, providing them with natural  
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28 124 resources for subsistence and trade (Junk, Ohly, Piedade, & Soares, 2000; Junk, Piedade,  
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31 125 Wittmann, Schöngart, & Parolin, 2010) and contributing to their cultural safeguarding (Junk  
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33 126 et al., 2014).

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36 127 The integrity and functioning of Amazonian river-floodplain systems are endangered by an  
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38 128 unprecedented boom of hydropower plants, driven by long-term governmental plans to  
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40 129 enhance energy security and supply for increasing industrialization, population and living  
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43 130 standards of the countries sharing this continental-size region (Castello et al., 2013).  
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45 131 Downstream impacts of hydropower dams on floodplains have been studied in many regions  
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47 132 (e.g., Agostinho, Thomaz, & Gomes, 2004; Braatne, Rood, Goater, & Blair, 2008; Kingsford,  
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50 133 2000; Nilsson & Berggren, 2000). Although the complex and far-reaching consequences of  
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52 134 damming Amazonian rivers are by far not well understood, considerable alterations of river-  
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54 135 floodplain system can be expected (Castello & Macedo, 2016). More than 222 dams (>1

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3 136 megawatt – MW) exist and are planned or under construction in the Cratonic geotectonic  
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5 137 domain of Amazonian river-floodplain systems, while another bulk of up to 200 dams is  
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8 138 established and planned in the Andean headwaters and forelands, and a smaller fraction (8  
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10 139 dams) in the Amazonian lowlands (Anderson et al., 2018; Finer & Jenkins, 2012; Latrubesse  
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12 140 et al., 2017; Lees, Peres, Fearnside, Schneider, & Zuanon, 2016). From this total, large (30-  
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15 141 1,000 MW) and mega (>1,000 MW) dams account for 48% and 7%, respectively (Latrubesse  
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17 142 et al., 2017).

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20 143 This development is accompanied by an exponential increase in academic research of  
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22 144 transdisciplinary fields, associated with hydropower dams during the last two decades. Many  
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24 145 studies provide evidence of severe socio-environmental impacts of hydropower dams,  
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27 146 however, with focus on the areas of the dams and reservoirs, questioning the social,  
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29 147 economic, and environmental sustainability of these large infrastructural projects (e.g., Abril,  
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31 148 Parize, Pérez, & Filizola, 2013; Altahyde et al., 2019; Fearnside, 2015; Kemenes, Forsberg,  
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33 149 & Melack, 2011; Moser, Simon, Medeiros, Gontijo, & Costa, 2019; Rosenberg, Bodaly, &  
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36 150 Usher, 1995; Rufin, Gollnow, Müller, & Hostert, 2019). However, only few studies assess  
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38 151 the impacts on Amazonian floodplains downstream of dams (Assahira et al., 2017; Junk &  
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40 152 Nunes de Mello, 1990; Manyari & Carvalho, 2007; Timpe & Kaplan, 2017; Zuanon et al.,  
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43 153 2019). In this review a synthesis of a transdisciplinary research effort of downstream impacts  
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45 154 on black-water floodplain forests (igapó), caused by the Balbina dam, implemented in the  
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47 155 1980s in the cratonic Uatumã River (Central Amazonia) is provided. The overall aim is to  
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50 156 understand the complex spatiotemporal disturbances in the floodplain forests downstream of  
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52 157 an Amazonian hydropower dam operating for decades.

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### 159 **The Balbina dam**

160 The Balbina dam was planned in the decade of 1970, during the petroleum crisis (Moran  
161 2016), to provide energy for Manaus, the capital of the Amazonas State, a booming city with  
162 meanwhile more than 2.2 million inhabitants, driven by its expanding free-trade zone and  
163 associated sectors consuming nowadays up to 1,800 MW. The hydropower plant is located  
164 150 km in direct line northeast of the city of Manaus and was implemented in the middle  
165 reach of the Uatumã River at the Balbina cataracts. The construction started in 1983 and the  
166 dam was closed in October 1987, creating a vast reservoir of almost 3,000 km<sup>2</sup>, drowning  
167 floodplain and upland (terra-firme) forests on slopes and depressions (Feitosa, Graça, &  
168 Fearnside, 2007). Only the plateaus of the terra-firme at higher elevations remained, forming  
169 a fragmented landscape of more than 3,500 islands inserted in a cemetery of millions of dead  
170 trees (Benchimol & Peres, 2015; Fearnside, 1990; Fearnside, 2015; Jones, Peres, Benchimol,  
171 Bunnefeld, & Dent, 2019). Originally, the Balbina dam was planned to have a nominal  
172 installed capacity of 250 MW, provided by five turbines with an estimated maximum  
173 discharge at a full capacity of 1,335 m<sup>3</sup> s<sup>-1</sup>. However, since the start of its operation in  
174 February 1989, the average annual power generation attained only 112.2 MW, with an  
175 average discharge of 657 m<sup>3</sup> s<sup>-1</sup> (Fearnside, 2015). The creation of the reservoir produces  
176 large amounts of greenhouse gases (GHG). Accounting for emissions from the reservoir and  
177 turbines, as well as diffusive emission in the downstream area (up to 30 km distance),  
178 Kemenes et al. (2011) estimated the annual emission in the order of  $3,141 \times 10^9$  g C-CO<sub>2</sub>eq  
179 year<sup>-1</sup> (CO<sub>2</sub> equivalent C-emissions, the relative contribution of CH<sub>4</sub> and CO<sub>2</sub> is 19% and  
180 81%, respectively) corresponding to 2.9 Mg C-CO<sub>2</sub>eq MWh<sup>-1</sup>.

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3 182 **Study region**  
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6 183 The Uatumã River is a black-water river with a catchment area of approximately 69,500 km<sup>2</sup>  
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8 184 situated on the Precambrian formation of the Guiana Shield (Junk et al., 2011; Melack &  
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10 185 Hess, 2010), covered mainly by terra-firme forests and podzolic white-sand ecosystems  
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12 186 (campinarana) (IDESAM, 2009). Consequently, the water is characterized by low pH-values  
13  
14 187 (5.3), with almost no sediment load and a low conductivity (7.8 µS cm<sup>-1</sup>), is poor in nutrients,  
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16 188 but rich in humic material (Lopes et al., 2019). As typical for Central Amazonian black-water  
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18 189 rivers, it shows low geomorphic dynamics and relatively stable riverbeds (Junk et al., 2015).  
19  
20 190 Along the first 35 km downstream of the Balbina dam until the Morena rapids the Uatumã  
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22 191 River has a steeper slope of about 17 m in a relatively entrenched riverbed. The remaining  
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24 192 stretch until the river mouth (about 280 km) has a low slope of only about 5 m, characterized  
25  
26 193 by vast igapós with 9,800 km<sup>2</sup> extension along the Uatumã River and its major tributaries,  
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28 194 mainly covered by forests (Resende et al., 2019). The Abacate and Jatapú rivers are the two  
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30 195 major tributaries of the Uatumã River, draining the Guiana Shield in the North with its  
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32 196 confluences about 161 km and 228 km downstream from the Balbina dam in fluvial distance  
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34 197 (thalweg), respectively (Figure 1).  
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41 198 The nutrient-poor alluvial soils of the Uatumã River have clayey textures at the lower  
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43 199 topography and an increase in sand fraction towards higher elevations, while those of the  
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45 200 Abacate River have predominantly sandy soils with low clay fractions at all topographies  
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47 201 (Lobo et al., 2019; Targhetta, Kesselmeier, & Wittmann, 2015). The climate in the region is  
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49 202 characterized by an average annual rainfall of 2,077 mm (standard deviation of ±438 mm)  
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51 203 (1975–2005), with a distinct rainy season from December to May and an annual mean  
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53 204 temperature of 27°C (Carneiro & Trancoso, 2007).  
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3 205 The study sites are in the Uatumã Sustainable Development Reserve (USDR), a state  
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5 206 conservation unit since June 2004 (Law 24,295). The USDR has an area of about 4,244 km<sup>2</sup>  
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8 207 (Figure 1) and accommodates approximately 2,100 residents, distributed over 20  
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10 208 communities situated along the Uatumã and Jatapú rivers (demographic census 2017; FAS,  
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12 209 2017). In accordance with Brazilian environmental laws, as well as cultural aspects,  
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15 210 socioeconomic activities and traditional lifestyle of the residents, the conservation unit is  
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17 211 divided into zones for strict biodiversity protection and research (about 60% of the area),  
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19 212 extensive (~35%) and intensive (~5%) land-uses. Zones for the extensive exploration of  
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21 213 timber and non-timber forest products and tourism are mainly located along the mainstem  
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23 214 and major tributaries of the Uatumã River and floodplains, adjacent paleofluvial terraces,  
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25 215 covered by dense forest and some campinarana patches. Intensive land-use destined for  
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28 216 agriculture, livestock and residences occurs in floodplains and adjacent paleofluvial terraces  
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31 217 close to the communities. The residents of the USDR are also involved in scientific projects  
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33 218 and programs developing ecotourism and sport-fishing as alternative economic activities  
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35 219 (IDESAM, 2009).

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38 220 First visits by the research team to the USDR occurred in August 2009 at the beginning of  
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40 221 the ATTO-project (Amazon Tall Tower Observatory) implementation, a 325-m tall tower  
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43 222 system monitoring local and large-scale fluxes between the biosphere and atmosphere  
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45 223 (Andreae et al., 2015). On this occasion, dead forests on the lowest floodplain topographies  
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47 224 of the igapó along the Uatumã River downstream of the Balbina dam were observed, which  
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50 225 raised the hypothesis that the massive tree mortality was caused by changes in the  
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52 226 hydrological regime due to the operation of the hydropower dam. To obtain first information  
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54 227 on the igapó forests of the USDR, Targhetta et al. (2015) performed floristic inventories in  
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3 228 the impacted igapó during the dry season 2010/2011 to relate floristic composition, diversity,  
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5 229 forest structure and biomass stocks to environmental factors (hydrological regime and soil  
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8 230 conditions). The recorded species richness of 26–49 spp. ha<sup>-1</sup> (>10 cm diameter at breast  
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10 231 height–DBH) and aboveground wood biomass stocks of 126–173 Mg ha<sup>-1</sup> of the igapó were  
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12 232 relatively low in comparison to other black-water igapós along the Negro River and its  
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15 233 tributaries (57–79 species ha<sup>-1</sup>; 170–260 Mg ha<sup>-1</sup>) (Aguiar, 2015; Batista, 2015; Corrêa,  
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17 234 2017; Montero et al., 2014) giving first hints of potential downstream impacts on the igapó  
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19 235 flora.

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## 23 24 25 237 **Material and methods**

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28 238 The assessment of spatiotemporal disturbances along a 35-year timeline combines  
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30 239 hydrological alterations of the Uatumã River during the post-dam period (Assahira et al.,  
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32 240 2017) with mortality patterns based on remote-sensing-analyses (Resende et al., 2019),  
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34 241 radiocarbon-dating and dendrochronology (Assahira et al., 2017; Resende et al., 2020), as  
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37 242 well as data on tree species diversity and ecological characteristic from dominant tree species  
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39 243 (Lobo, Wittmann, & Piedade, 2019; Neves, Piedade, Resende, Feitosa, & Schöngart, 2019;  
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41 244 Rocha et al., 2019; Rocha et al. 2020). Using water level records from the Cachoeira Morena  
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44 245 station, approximately 35 km downstream of the dam (Figure 1), Assahira et al. (2017)  
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46 246 analysed the changes in the hydrological regime (1973–2012), applying the method of  
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48 247 Indicators of Hydrologic Alteration (IHA) and Range of Variability Approach (RVA)  
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51 248 (Richter, Baumgartner, Powell, & Braun, 1996; Richter, Baumgartner, Wigington, & Braun  
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53 249 1997). The IHA method considers a set of biologically relevant hydrological indicators (33  
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55 250 parameters classified into five groups) derived from daily water level data considering the  
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3 251 magnitude, timing, frequency, duration and rate of changes of hydrological conditions (see  
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5 252 also Timpe & Kaplan, 2017). The RVA compares the variation of each IHA parameter  
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8 253 between the pre- and post-dam periods to highlight its extent of change. For this study, the  
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10 254 IHA and RVA analyses of the post-dam period have been expanded (1991–2018) and  
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12 255 compared to the pristine conditions (1973–1982) (the period of dam construction and closure  
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15 256 was not considered). The hydrological regime of the Uatumã River was contrasted with its  
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17 257 major affluent (Jatapú River) by linear regression models (Figure 1), considering the periods  
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19 258 of pristine conditions (1973–1982), dam construction and reservoir fill (1983–1989) and dam  
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21 259 operation (1989–2018). Daily water level records were obtained from the HidroWeb database  
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24 260 of the Brazilian National Agency of Waters (ANA) (<http://hidroweb.ana.gov.br>).

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27 261 The impacts of the Balbina dam implementation and operation on a landscape level were  
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29 262 assessed, applying remote-sensing techniques. Considering an 80-km stretch (focal area)  
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31 263 along the Uatumã River after the Morena rapids, located between 43 and 123 km downstream  
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33 264 of the reservoir (Figure 1), the igapó floodplains and dead forests were mapped by Resende  
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35 265 et al. (2019). For this, 56 ALOS-1/PALSAR (Advanced Land Observing Satellite-1/Phased  
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37 266 Array Type L-band Synthetic Aperture Radar Sensor) images at different flood levels during  
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40 267 the post-dam period (2006-2011) were acquired, performing object-based image analysis  
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43 268 (OBIA) and random forests to a supervised classification algorithm with an overall accuracy  
44  
45 269 of 87.2%. To demonstrate the hydrological changes imposed by the Balbina dam construction  
46  
47 270 (1985), reservoir fill (1988) and dam operation (2009) in the downstream areas, Landsat 4-5  
48  
49  
50 271 Thematic Mapper (TM) imageries from different months of these years were processed and  
51  
52 272 composed (Gorelick, Hancher, Dixon, Ilyushchenko, Thau, & Moore, 2017).  
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3 273 To assess the causes of tree mortality in the igapó floodplains downstream of Balbina dam,  
4  
5 274 Assahira et al. (2017) and Resende et al. (2020) dated the year of death from two dominant  
6  
7  
8 275 tree species growing at the low topographic elevations in the igapó of the Uatumã River.  
9  
10 276 *Macrobium acaciifolium* (Benth.) Benth. (Fabaceae) is one of the so-called hyperdominant  
11  
12 277 tree species (ter Steege et al., 2013), frequently occurring in high abundances at low  
13  
14  
15 278 elevations in Amazonian floodplain forests along white-water, clear-water and black-water  
16  
17 279 rivers in the Amazon basin with inundations lasting up to 240 days (Wittmann et al., 2010).  
18  
19 280 This brevi-deciduous species shows complex physiological adaptations to prolonged  
20  
21 281 inundations, switching its metabolism to anaerobic pathways (Schlüter & Furch, 1992;  
22  
23 282 Schöngart, Piedade, Ludwigshausen, Horna, & Worbes, 2002). *Eschweilera tenuifolia* (O.  
24  
25 283 Berg) Miers (Lecythidaceae) is an evergreen tree species in the igapó, growing mainly in  
26  
27  
28 284 monodominant formations (Maia & Piedade, 2002; ter Steege et al., 2019) with open  
29  
30  
31 285 canopies on the lowest topographies, annually flooded for up to 300 days year<sup>-1</sup> (Junk et al.,  
32  
33 286 2015; Resende et al., 2020). Both species can achieve a high age of up to 500 years in the  
34  
35 287 case of *M. acaciifolium* (Schöngart et al., 2005) and more than 800 years in *E. tenuifolia*  
36  
37  
38 288 (Resende et al., 2020) and are therefore excellent long-term indicators for environmental  
39  
40 289 conditions in floodplains (Junk, Piedade, Nunes da Cunha, Wittmann & Schöngart, 2018).  
41  
42 290 The sampling of dead trees occurred within fluvial distances between 35 km and 125 km  
43  
44 291 downstream of the Balbina dam (Figure 1). Cross-sections of 17 dead *M. acaciifolium* and  
45  
46 292 29 dead *E. tenuifolia* trees were sampled during the terrestrial phases of 2012 and 2015/2016,  
47  
48 293 respectively. The last formed tree ring, indicative for the year of death, was dated by  
49  
50  
51 294 radiocarbon (<sup>14</sup>C) (26 of the <sup>14</sup>C-dated samples of *E. tenuifolia* fell into the post-bomb period,  
52  
53  
54 295 Resende et al., 2020) and for *M. acaciifolium*, using additional cross-dating techniques  
55  
56 296 (dendrochronology). Mortality patterns of both species were related to the annual duration of  
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3 297 the terrestrial phases (non-flooded period), during pristine conditions and the post-dam  
4  
5 298 period. For more detailed information on sampling and dating techniques, see Assahira et al.  
6  
7  
8 299 (2017) and Resende et al. (2020).

9  
10 300 The detection of dead forests in the downstream igapó through remote-sensing analyses was  
11  
12 301 limited to low topographical elevations (Resende et al., 2019). The impacts of the  
13  
14 302 hydrological alterations on tree species diversity and dominant tree species was assessed by  
15  
16  
17 303 comparison of forests along the Uatumã River with those of an adjacent, undammed affluent  
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19  
20 304 (Abacate River) (Figure 1). Available floristic data for igapó forests comprised 6 ha in the  
21  
22 305 focal area of the Uatumã River and 3.75 ha of the Abacate River (for more details see Lobo  
23  
24 306 et al., 2019; Rocha et al., 2019; Rocha et al., 2020; Targhetta et al., 2015) (Figure 1). Floristic  
25  
26  
27 307 data were also available for adjacent terra-firme forests in both areas (total of 1 ha) (Lobo et  
28  
29 308 al., 2019). All plots were divided into 25 x 25 m (625 m<sup>2</sup>) sub-plots, where all trees ≥10 cm  
30  
31 309 DBH, including palms, were tagged and identified and the mean duration of the aquatic phase  
32  
33  
34 310 for each subplot was calculated (for more details see Lobo et al., 2019). Rocha et al. (2019,  
35  
36 311 2020) selected four subplots (625-m<sup>2</sup> plots) at the low, medium and high topographies of the  
37  
38 312 igapó in the Uatumã and Abacate rivers (12 cross-transects of 25 × 1 m in each system), to  
39  
40 313 study the species composition of tree seedlings (15–100 cm height). Based on this floristic  
41  
42  
43 314 data, tree species diversity for each plot (individuals >10 cm DBH), was estimated by  
44  
45 315 Fisher's alpha (Fisher, Corbet, & Williams, 1943), which was then correlated with the  
46  
47 316 corresponding duration of the aquatic phase by non-linear regression models. Lobo et al.  
48  
49  
50 317 (2019) and Rocha et al. (2019) calculated the importance value index (IVI) summing the  
51  
52 318 relative values of each tree species' frequency, abundance, and dominance (basal area). In  
53  
54 319 this study, the relative IVIs of the five most important species (IVI<sub>Σ1-5</sub>) of trees >10 cm DBH

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3 320 and seedlings (15–100 cm height) was determined, considering three distinct topographic  
4  
5 321 inundation classes (low, medium, and high). Estimated tree ages and mean diameter  
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7 322 increment (MDI) rates of the dominant tree species have been provided by Neves et al. (2019)  
8  
9 323 analysing a total of 589 trees at different topographies of the Uatumã and Abacate rivers.  
10  
11 324 Further, basic wood density of the dominant tree species was considered in the comparison  
12  
13 325 of the pristine and disturbed river stretches (Mori, Schietti, Poorter, & Piedade, 2019; Neves,  
14  
15 326 2018).  
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## 23 328 **Results**

### 24 25 329 *Hydrological changes of the Uatumã River*

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27 330 The IHA parameters in Figure 2 reflect the drastic changes in the streamflow regime of the  
28  
29 331 Uatumã River, caused by the Balbina power plant. As the management of the hydropower  
30  
31 332 dam aims at a year-round uniform power generation, it tends to store more water in the  
32  
33 333 reservoir during the rainy season, which is then released during the dry season. Therefore,  
34  
35 334 both the high-water and low-water regimes are affected. The RVA indicated a decrease of  
36  
37 335 maximum (April-June) and an increase in the minimum (October-December) water level,  
38  
39 336 reflected by the increase in the low and high RVA categories, respectively (Figure 2a). For  
40  
41 337 the low-water regime, especially the period 2000-2008 was crucial when the minimum water  
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43 338 levels were, on average, more than 1 m higher than those during the pristine period (Assahira  
44  
45 339 et al., 2017), which is indicated by the enhanced baseflow index (7-day minimum water level  
46  
47 340 divided by mean water level) during this period (Figure 2b). Simultaneously, the high-water  
48  
49 341 regime declined especially in the periods 2003–2007 and after 2011, when the maximum  
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51 342 water levels remained below the 25<sup>th</sup> percentile of the pre-dam period. The dam-induced  
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3 343 increasing flooding conditions at the lowest topographic elevations and simultaneously  
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5 344 decreasing of maximum water levels affecting the higher topographies of the floodplains was  
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7  
8 345 characterized as the "sandwich-effect" (Wittmann, Damm, & Schöngart, 2019). The water  
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10 346 level further showed a more than twofold increase in the fall and raise rates and a threefold  
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12 347 increase in the number of reversals between fall and rise rates, compared to pristine  
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14  
15 348 conditions (Figures 2c-e). Also, significant changes were observed in the timing of annual  
16  
17 349 minimum and maximum water levels. During pristine conditions, the annual minimum water  
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19 350 level regularly occurred in the period between the end of September and mid-December  
20  
21 351 around Julian days (J.D.) 273–346 (25–75th percentiles; median: J.D. 332), while maximum  
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23 352 water levels occurred between the end of April and the beginning of June at Julian days 114–  
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25 353 156 (25–75th percentiles; median: J.D. 128). This scenario changed dramatically during the  
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27  
28 354 operational period of the Balbina dam showing a remarkably high temporal variation at both  
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30  
31 355 extreme conditions (Figures 2f, g).

32  
33 356 During the pristine period, the hydrological regimes of the Uatumã and Jatapú rivers showed  
34  
35 357 the typical monomodal flood-pulse pattern (Junk et al., 1989). Consequently, 79% of the  
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37 358 variability of the water level oscillations were shared between both rivers ( $R^2 = 0.79$ ;  $p$   
38  
39 359  $<0.001$ ) (Figure 3a). The relation weakened during the period of dam construction ( $R^2 = 0.44$ ;  
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41 360  $p <0.001$ ), indicating first disturbances in the hydrological regime of the Uatumã River. The  
42  
43 361 post-dam period is characterized by a loss of the flood-pulse pattern in the Uatumã River,  
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45 362 resulting in 88% of unexplained variation of its hydrological regime with reference to the  
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48  
49 363 regular flood-pulsing pattern of the Jatapú River ( $R^2 = 0.12$ ;  $p <0.001$ ). In comparison to the  
50  
51 364 period of dam construction (1985), the damming of the Uatumã River to fill the Balbina  
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53 365 reservoir (1988) caused severe dry conditions in the focal area, due to the extreme low  
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3 366 streamflow of only 4.7–19.7 m<sup>3</sup> s<sup>-1</sup> in this period (Fearnside, 1989), while the period of dam  
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5 367 operation (2009) showed an increased low-water regime (Figure 3b). The three strongest El  
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8 368 Niño events on record (1982/1983, 1997/1998, 2015/2016), which affected the rainfall and  
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10 369 streamflow regimes especially in the northern, central and eastern section of the Amazon  
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12 370 basin (Aragão et al., 2018; Marengo et al., 2018) resulted in remarkably low water levels of  
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15 371 the Uatumã and Jatapú rivers (Figure 3a).  
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20 373 *Tree mortality*

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23 374 Massive tree mortality was detected in the focal area, with about 90 km<sup>2</sup> of floodplain forests,  
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25 375 affecting 12% (about 11 km<sup>2</sup>) of the igapó (Figure 4). Dead forests were observed at lower  
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28 376 topographical elevations, mainly close to lakes and inner, convex banks of the geomorphic  
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30 377 stable fluvial meanders (slip-off slopes). Ninety-eight percent of the analysed dead trees in  
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32 378 the igapó downstream of the dam died after its implementation. However, both studied tree  
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34 379 species revealed distinct mortality patterns (Figure 5). Increased mortality of *E. tenuifolia*  
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36 380 already occurred in the period of dam construction (1983–1987) and closure (October 1987–  
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38 381 February 1989). A second peak of mortality of this species was observed during the period  
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41 382 of 1994–1997, with rising low-water regime (Figure 2b) and subsequent loss of the terrestrial  
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43  
44 383 phase. The strong El Niño event in 1997/1998 caused a low streamflow (Figure 3a) and  
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46 384 resulted in a terrestrial phase of about two (*E. tenuifolia*) to three (*M. acaciifolium*) months.  
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48 385 Conversely, permanent flooding conditions of these trees started in 2000 and lasted for over  
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50  
51 386 eight consecutive years as a consequence of the increase in the minimum water level (Figures  
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53 387 2, 3), causing further tree mortality, especially for *M. acaciifolium* (Assahira et al., 2017).  
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389 *Tree species diversity and ecological characteristics of dominant tree species in disturbed*  
390 *igapó floodplains*

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

399 The  $IVI_{\Sigma 1-5}$  and corresponding tree ages, MDIs, and wood densities (tree species >10 cm  
400 DBH) are shown in Table 1 for the distinct topographies of the pristine and disturbed igapó.  
401 The high-igapó showed similar  $IVI_{\Sigma 1-5}$  in the disturbed (31.9%) and pristine (33.7%)  
402 floodplain, however, the dominant tree species of the disturbed igapó are mainly secondary  
403 tree species from adjacent terra-firme forests (Lobo et al., 2019; Rocha et al., 2019) with  
404 higher MDI rates (1.8–3.9 mm year<sup>-1</sup>), lower wood densities (0.50–0.67 g cm<sup>-3</sup>) and lower  
405 tree ages (52–77 years) compared to the pristine igapó. The oldest trees with similar MDIs  
406 and wood densities occurred at the low-igapó at both sites (Table 1), however, composed of  
407 different species, which are likely the result of different grain-sized substrates (Lobo et al.,  
408 2019). Dominant tree species had, however, higher  $IVI_{\Sigma 1-5}$  at the disturbed site (61.8%),  
409 compared to the pristine one (36.6%). The most significant differences were observed at the  
410 medium-igapó, where the  $IVI_{\Sigma 1-5}$  of the pristine system (26.3%) was much lower compared  
411 to the disturbed igapó (61.8%). The palm *Astrocaryum jauari* Mart. (Arecaceae) is the

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3 412 dominating species together with tree species showing low mean tree ages (28-66 years) and  
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5 413 wood densities ( $0.42\text{--}0.58\text{ g cm}^{-3}$ ) and high MDI rates of  $3.2\text{--}4.8\text{ mm year}^{-1}$ , which differed  
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7  
8 414 significantly from all other elevations (Neves et al., 2019). At this topography, Neves et al.  
9  
10 415 (2019) identified an age-cohort of young and almost even-aged trees, mainly composed of  
11  
12 416 *Nectandra amazonum* Nees (Lauraceae) ( $28\pm 4$  years).

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14  
15 417 At the level of seedlings, Rocha et al. (2019, 2020) observed even higher IVIs for dominant  
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17 418 tree species. At the disturbed low-igapó, 55% of the total IVI in the seedling stratum was  
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19  
20 419 represented by *Pouteria elegans* (A. DC.) Baehni (Sapotaceae), while at the disturbed high-  
21  
22 420 igapó the arborescent palm *Attalea maripa* (Aubl.) Mart. (Arecaceae) dominated the seedling  
23  
24 421 stratum (22.5% of the total IVI). This species is a well-known indicator for disturbance in  
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26  
27 422 terra-firme forests (Salm, 2005). At the disturbed site of the medium-igapó, the flood-adapted  
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29 423 palm species *A. jauari* (IVI of 48.4%) dominated the seedling stratum. Overall, the results  
30  
31 424 indicated an increasing dominance of secondary tree species in the impacted igapó,  
32  
33 425 suggesting disturbance along the entire topographical gradient. More detailed analyses of  
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35 426 floristic patterns are available in the studies of Lobo et al. (2019) and Rocha et al. (2019,  
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37 427 2020), indicating distinct patterns in the composition of tree species and genera between the  
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40 428 disturbed and pristine igapó.

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## 44 45 46 430 **Discussion**

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49 431 The novel assessment of long-term ecological impacts downstream of the Balbina  
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51 432 hydropower dam revealed a broad range of major structural and functional changes in  
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53 433 floodplain vegetation, providing a unique opportunity to understand these effects, as  
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56 434 summarized schematically in Figure 7, and to propose a preliminary framework. Observed

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3 435 disturbances in the studied igapó forests are discussed in light of fundamental theory that can  
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5 436 be used to test further hypotheses. The extent to which such findings can be extrapolated to  
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8 437 other hydropower dams within, and even outside, the Amazon basin is discussed, and  
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10 438 recommendations regarding the operation of existing and the implementation of future  
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12 439 hydropower plants are provided.

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18 441 *Spatiotemporal disturbances in floodplains of the downstream area*

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21 442 Large-scale disturbances in the igapós of the Uatumã River associated with the Balbina dam  
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23 443 already started in the period of dam construction (1983-1987) and the reservoir fill (1987-  
24  
25 444 1989). During this period, the water discharge was strongly reduced exposing the entire igapó  
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28 445 floodplains to severe dry conditions (Figure 3), which were intensified by El Niño events  
29  
30 446 (1982/1983 and 1986–1988), which increased temperature and reduced rainfall and humidity  
31  
32 447 (Aragão et al., 2018; Marengo et al., 2018). The generated extreme dry hydroclimatic  
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34 448 conditions (Figure 7) are the most plausible cause for the mortality of *E. tenuifolia* trees  
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36 449 during this period (Figure 5), causing hydraulic failure, carbon starvation or both, as carbon  
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38 450 and water dynamics are interrelated by stomatal conductance and vascular transport (Cailleret  
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41 451 et al., 2017; Gessler et al., 2018; Hartmann et al., 2018). Fontes et al. (2020) observed for *E.*  
42  
43 452 *tenuifolia* in the study region a high vulnerability to xylem embolism based on measured P<sub>50</sub>  
44  
45 453 values (water potential causing 50% loss of hydraulic conductivity). Dead forests dominated  
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47 454 by this species occurred mainly around floodplain lakes and slip-off slopes of fluvial  
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51 455 meanders (Figures 4). Likely, the drying of the fine-grained alluvial soils caused soil  
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53 456 cracking, physically damaging the superficial fine roots, contributing even further to  
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55 457 hydraulic failure. Interestingly, no tree mortality of this species was observed during this  
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3 458 period for the same macrohabitats in the igapó of the Jaú River, an affluent of the Negro  
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5 459 River in Central Amazonia with an undisturbed flood-pulse regime (Resende et al., 2020).  
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8 460 The severe dry conditions, caused by the synergetic effects of dam implementation and  
9  
10 461 climate conditions, possibly also increased the vulnerability of igapós to wildfires (Flores,  
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12 462 Piedade, & Nelson, 2014; Flores et al., 2017; Schöngart, Wittmann, Junk, & Piedade, 2017).  
13  
14 463 Igapó forests have lower canopy heights and lack a dense understory compared to well-  
15  
16 464 stratified terra-firme forests, and consequently, air humidity in igapó forests is much lower  
17  
18 465 (Almeida et al., 2016; Resende, Nelson, Flores, & Almeida, 2014). Due to the long flooding,  
19  
20 466 litter slowly decomposes and accumulates on the forest floor, which is covered by dense root  
21  
22 467 mats at or near the ground surface (dos Santos & Nelson, 2013), providing a large amount of  
23  
24 468 combustion material. The presence of an approximately 30-year old age-cohort of *Nectandra*  
25  
26 469 *amazonum* (Neves et al., 2019) and low tree species diversity (Table 1, Figure 6) suggest  
27  
28 470 massive disturbances on the medium elevation in the igapó along the Uatumã River,  
29  
30 471 originating from wildfires occurring during the implementation of the Balbina dam (Figure  
31  
32 472 7). This species has been characterised as a secondary species of the nutrient-rich and highly  
33  
34 473 dynamic white-water floodplains (várzea) (Wittmann, Anhuf & Junk, 2002), where it shows  
35  
36 474 low maximum tree age (44 years) and comparatively high MDIs (4.8–14.8 mm year<sup>-1</sup>)  
37  
38 475 (Schöngart, 2003; Worbes, Klinge, Revilla, & Martius, 1992). The hypothesis is that this  
39  
40 476 pioneer species established in opened igapó areas, that originated from wildfires (Figure 7).  
41  
42 477 The high solar radiation and enhanced nutrient supply in the burnt areas created similar  
43  
44 478 environmental conditions as in early successional stages of the várzea (Wittmann et al., 2004;  
45  
46 479 Worbes et al., 1992), favouring its establishment and resulting in species-poor floodplain  
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48 480 forests with high dominance of secondary species (Figure 7). Seeds possibly reached these  
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3 481 sites from nearby igapós or from the várzea floodplains of the Amazon River dispersed by  
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5 482 animals, especially fishes since the plant is referred as an ichthyochoric species (Weiss,  
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7  
8 483 Zuanon, & Piedade, 2016).

9  
10 484 The high dominance of the palm *Astrocaryum jauari* at the medium-igapó of the Uatumã site  
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12 485 (see also Rocha et al., 2020; Targhetta et al., 2015) also suggests disturbance through  
13  
14 486 wildfires. This species is a typical floodplain palm occurring in várzea and igapó forests  
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16  
17 487 (Piedade et al., 2016). Besides ichthyochory, barochory (dispersal by gravity alone) with  
18  
19 488 subsequent vegetative propagation is an important dispersal mode leading to the formation  
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21 489 of dense populations of up to 2.000 stems ha<sup>-1</sup> in the fluvial archipelagos Anavilhanas and  
22  
23 490 Mariuá of the Negro River (Piedade, Parolin, & Junk, 2006). Several Amazonian terra-firme  
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25 491 palm species are fire-resistant, such as *Attalea maripa*, *Astrocaryum aculeatum* G. Mey.,  
26  
27 492 *Astrocaryum vulgare* Mart. and *Acrocomia aculeata* (Jacq.) Lodd. ex Mart., as well as  
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29 493 *Copernicia alba* Morong occurring in seasonally flooded savannas in the Bolivian Amazon  
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33 494 and also in the Pantanal (Carvalho, Ferreira, & Lima, 2010; Araújo, Oliveira Júnior, Assis  
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35 495 Oliveira, Gama, Gonçalves, & Almeida, 2012; Smith, 2015) and may benefit from fire by  
36  
37 496 increasing their dominance. Palms do not have a cambial tissue and many species have  
38  
39 497 diaspores with morpho-physiological dormancy (Baskin & Baskin, 2014). Seedlings of some  
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41 498 palm species like *Attalea* spp. have sprouting tips growing down into the soil before emerging  
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43 499 above ground (cryptogeal germination), making them resistant to surface fires (Smith, 2015).  
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46 500 Some older inhabitants of the USDR indicated the occurrence of wildfires in the igapós,  
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48  
49 501 during the period of dam implementation. Remote-sensing analyses, that map out fire-scars  
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51 502 overtime series since the period of dam construction, should bring evidence of the magnitude  
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3 503 of wildfire activity during this period, as applied by Carvalho (2019) for the igapós of the Jaú  
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5 504 National Park.

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8 505 During the period of dam operation, the "sandwich-effect" (Wittmann et al., 2019) occurred,  
9  
10 506 characterized by the suppression of the aquatic phase at high topographies and the loss of the  
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12 507 terrestrial phase at the low topographies over a period of 30 years (Figure 7). Periods with  
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14 508 permanent flooding conditions affected first the lowest topographical elevations, dominated  
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16 509 by *E. tenuifolia*, and in subsequent periods the population of *M. acaciifolium*, growing on  
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18 510 higher elevations (Figure 5). Although both tree species are well adapted to regular, seasonal  
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20 511 inundations, pluriannual permanent flooding seems to be the major trigger of tree mortality  
21  
22 512 for these and other highly flood-adapted tree species, as the prolonged anoxic conditions  
23  
24 513 exceed the capacities of adaptations developed by these species to tolerate seasonal  
25  
26 514 inundations (Assahira et al., 2017; Piedade et al., 2013; Resende et al., 2020).

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29 515 Tree mortality along the upstream courses is usually faster than in the dam shadow, because  
30  
31 516 it affects mainly vegetation not or less adapted to flooding (Cochrane, Matricardi, Numata,  
32  
33 517 & Lefebvre, 2017; Moser et al., 2019). Downstream disturbances of recently installed power  
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35 518 plants tend to be hidden over years and even decades as floodplain tree species developed  
36  
37 519 sophisticated adaptations to seasonal flooding which can extend mortality-inducing  
38  
39 520 processes over long periods (Resende et al., 2020). So far, the Balbina dam resulted in 12%  
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41 521 of dead igapó forests at the low topographical elevations (Figure 4), which expands to more  
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43 522 than 125 km downstream of the hydropower plant (Assahira et al., 2017; Resende et al., 2019;  
44  
45 523 Resende et al., 2020). If in future the dam operation continues to enhance the low-water  
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47 524 regime, additionally 18% of the igapó forests, classified by Resende et al. (2019) as  
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49 525 threatened (Figure 4), will probably suffer massive mortality as disturbances expand further  
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3 526 downstream and achieve also higher topographies. The slow decompositions of dead biomass  
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5 527 (about  $129 \pm 14 \times 10^9$  g C) under almost constant anaerobic conditions (Resende et al., 2019)  
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7  
8 528 is likely to result in increasing GHG emissions, especially CH<sub>4</sub>. By long-term monitoring of  
9  
10 529 atmospheric CH<sub>4</sub> mixing ratios at the nearby ATTO site (Figure 1), Botia et al. (2020)  
11  
12 530 detected night-time CH<sub>4</sub> increases, which most likely originated from the dead igapó forests.  
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14  
15 531 However, so far GHG emissions (CO<sub>2</sub>, CH<sub>4</sub>) have only been measured in the Balbina  
16  
17 532 reservoir, at the dam (turbine discharge and outflow) and in the first 30 km downstream of  
18  
19 533 the power plant (Kemenes et al., 2011). To give a whole picture of GHG emission related to  
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21 534 the Balbina dam, these measurements should be extended to the affected igapó floodplains  
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23  
24 535 by future studies and monitoring.

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26  
27 536 At high topographical elevations of the igapó, the loss of flooding favoured the encroachment  
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29 537 of mainly secondary species from adjacent terra-firme forests (Figure 7), especially  
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31 538 dominating in the establishment stratum such as *Tapirira guianensis* Aubl. (Anacardiaceae),  
32  
33 539 *Attalea maripa*, *Trichilia micrantha* Benth. (Meliaceae) and *Rinorea racemosa* (Mart.)  
34  
35 540 Kunze (Violaceae) (Lobo et al., 2019; Rocha et al., 2019). These species are probably better  
36  
37 541 adapted to the changed environmental conditions and more competitive as the former igapó  
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39 542 tree species, as indicated by the higher observed MDI rates (Table 1).

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43 543 The IHA and RVA analyses further indicated changes in the timing (parameter group 3) of  
44  
45 544 the highest and lowest water levels (Figures 2f, g). Many floodplain tree species produce  
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47 545 fruits during the aquatic phase (Kubitzki & Ziburski, 1994; Schöngart et al., 2002) and are  
48  
49 546 mainly dispersed by water (hydrochory) and/or fish (ichthyochory) (Ayres, 1993; Goulding,  
50  
51 547 1980; Parolin, Waldhoff, & Piedade, 2010; Van den Broek, van Diggelen, & Bobbink, 2005;  
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53 548 Weiss et al., 2016). Although germination of some floodplain tree species may occur when  
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3 549 seeds still float upon the water (Kubitzki & Ziburski, 1994; Melo, Franco, Silva, Piedade, &  
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5 550 Ferreira, 2015; Oliveira Wittmann, Piedade, Wittmann, & Parolin, 2007), seedlings need the  
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8 551 contact with the alluvial substrate in the subsequent terrestrial phase for successful  
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10 552 establishment (Parolin, 2001; Waldhoff, Saint-Paul, & Furch, 1996). The high temporal  
11  
12 553 variability of the maximum and minimum water level (Figures 2 f, g), during the post-dam  
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14  
15 554 period, probably results in an asynchrony of phenology patterns, dispersal mechanisms, and  
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17 555 establishment processes for many tree species occurring at topographies, which still are  
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19 556 seasonally flooded. As the low-igapós are under near-permanent aquatic conditions and  
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21  
22 557 floods have been suppressed at the high-igapós, the hypothesis is postulated, that tree species  
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24 558 relying on water and fish for dispersal no longer get established at these topographies in the  
25  
26 559 long term (Figure 7). Consequently, fish populations lose this important food source which  
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28 560 may reduce populations regionally.

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31 561 The frequency and duration of high and low pulses (group 4) and rate and frequency of  
32  
33 562 changing water condition (group 5) changed considerably during the post-dam period (Figure  
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35 563 2), which possibly has strong impacts on the physiology of igapó tree species. Mori et al.  
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37 564 (2019) observed that igapó species, in general, have functional traits related to the carbon  
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39  
40 565 and nitrogen metabolism associated with high resource conservation and persistence, leading  
41  
42 566 to slow growth, as shown by Neves et al. (2019) (see also Table 1). However, the changes in  
43  
44 567 the frequency and magnitude of water deficit or hypoxic/anoxic conditions may affect many  
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46 568 of these species, setting up new environmental filters and inducing new trade-offs. This may  
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49 569 explain the observed decrease of tree species diversity (Figure 6) and simultaneously  
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51 570 increasing dominance of tree species (Table 1), which possess a higher resilience and  
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53 571 functional traits to adapt to the changed environmental conditions (Figure 7).  
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3 572 Overall, the described hydrological alterations impact several processes in the floodplain  
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5 573 system relevant for tree species (Figure 7). It alters habitat and soil moisture availability as  
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8 574 well as anaerobic conditions, and affects the synchrony between the flooding regime with  
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10 575 phenological patterns, growth rhythms, dispersal mechanisms and processes of establishment  
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12 576 for which floodplain trees adapted over evolutionary periods (Junk, 1989; Parolin et al., 2004;  
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14  
15 577 Schöngart et al., 2002; Wittmann et al., 2010). These disturbances are likely to cascade down  
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17 578 through the entire food web by similarly affecting terrestrial and aquatic species, ultimately  
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19 579 leading to a considerable loss in biodiversity. Further impacts on biodiversity are expected  
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21  
22 580 from damming the Uatumã River, which blocks migrations and cut population connectivity  
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24 581 of fish and changes their habitats by modifying physical and chemical conditions (e.g.,  
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26 582 Agostinho et al., 2004; Castello & Machado, 2016; Costa-Pereira et al., 2018; Val, Fearnside  
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28 583 & Almeida-Val, 2016; Winemiller et al., 2016).

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31 584 The observed massive loss and degradation of macrohabitats in the disturbed igapó  
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33 585 floodplains caused by the Balbina dam with severe impacts on ecosystem functioning, loss  
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35 586 of biodiversity and environmental services has relevant implications for conservation.  
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37 587 Floodplains in the USDR are excluded from the permanent protection zones and destined for  
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40 588 extensive and intensive land-use (IDESAM, 2009). Igapós of the Uatumã River until its  
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43 589 confluence with the Abacate River (Figure 1) are likely to suffer from the complex and  
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45 590 persistent disturbance regime, which affects both, the economic activities (e.g., fishery,  
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47 591 ecotourism) and welfare of the local inhabitants. Dead forests are additionally a risk for large  
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50 592 wildfires during extreme El Niño conditions, when huge amounts of flammable materials are  
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52 593 exposed to severe dry conditions, due to extremely low water levels, such as during  
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3 594 2015/2016 (Figure 3a). These are relevant aspects for the conservation management of the  
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5 595 USDR.  
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11 597 *Implications of the findings for other Amazonian dams*  
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14 598 Downstream impacts on floodplains differ strongly among hydropower plants depending on  
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16 599 many factors, such as the geomorphology, hydrochemical conditions, sediment load,  
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18 600 biogeography, diversity and dynamics of the vegetation as well as size and elevation of the  
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21 601 reservoir, time since dam construction, technical aspects of the impoundment and synergies  
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23 602 with other land-use forms and intensities (Altahyde et al., 2019; Rufin et al., 2019; Timpe &  
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25 603 Kaplan, 2017). These differences limit the extrapolation of the findings of this study to  
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28 604 hundreds of other operating hydropower plants and those under construction or planning as  
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30 605 no comparable studies on downstream impacts are available for the Amazon basin. Timpe &  
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32 606 Kaplan (2017) analysed IHA parameters for upstream and downstream hydrological data of  
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34 607 33 dams across the Brazilian Amazon (including Balbina) and Cerrado (Central Brazilian  
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36 608 savannah biome) integrating a large range of the factors mentioned above. Despite  
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38 609 identifying limitations of this approach, they observed that the magnitude and duration of  
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41 610 annual extreme water conditions (IHA group 2) ("sandwich-effect") was positively correlated  
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44 611 with the reservoir area and negatively related to the elevation of impoundment. Increased  
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46 612 elevation of dams resulted further in a decrease of frequency and duration of high and low  
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48 613 pulses (IHA group 4) and the rate and frequency of water condition changes (IHA group 5)  
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51 614 (see also Figure 3). Therefore, it is not surprising that the intense hydrological alteration  
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53 615 (Figures 2 and 3), associated with the large Balbina reservoir at a low elevation caused the  
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55 616 massive observed disturbances (Figure 7) on the integral functioning of the downstream  
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3 617 floodplains, which is adapted to a monomodal flood pulse regime. At higher elevations in the  
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5 618 region of the headwaters, rivers in general show lower and less regular flood-pulses due to  
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8 619 the smaller catchment area (Junk et al., 2011) and tree species adapted to these regimes  
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10 620 probably suffer less impacts by dam-induced hydrological alterations. Timpe & Kaplan  
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12 621 (2017) further observe that multiple dams in rivers have cumulative and cascading effects,  
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15 622 affecting especially IHA parameters of groups 4 and 5, which is of high relevance for many  
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17 623 cratonic rivers in the Brazilian Amazon (Fearnside, 2019; Latrubesse et al., 2017), but also  
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19 624 in the Cerrado (savanna belt) (Latrubesse et al., 2019).

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22 625 Downstream impacts also may vary according to geomorphological and hydrochemical  
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24 626 characteristics of floodplain ecosystems. Black-water floodplain tree species are likely more  
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27 627 vulnerable to dams than their white-water counterparts, because the latter have adaptations  
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29 628 to dynamic hydrogeomorphic processes, such as erosion and burial through sediment  
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31 629 deposition, which are lacking in igapó tree species (Peixoto, Nelson, & Wittmann, 2009;  
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33 630 Wittmann et al., 2004; Wittmann & Parolin, 2005; Worbes et al., 1992). Planned mega-dams  
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36 631 in the upper Negro River (São Gabriel and Santa Isabel-Uaupés/Negro, with a total of 4,000  
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38 632 MW planned capacity; Fearnside, 2019), possibly will have stronger downstream impacts  
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41 633 than those of the Madeira River (Santo Antônio and Jirau with 3,150 MW and 3,750 MW  
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43 634 installed capacity, respectively; Latrubesse et al., 2017) and the several dams planned at  
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45 635 higher altitudes in the Andean catchments and forelands (Anderson et al., 2018; Finer &  
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47 636 Jenkins, 2012; Forsberg et al., 2017).

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50 637 The provided synthesis on impacts of Amazonian river dams on downstream river hydrology  
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52 638 and floodplain forests in time and space (Figure 7) is a first compilation demonstrating that  
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55 639 hydropower plants have much wider impact than previously reported. At this stage, the

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3 640 proposed framework is still restricted to central Amazonian black-water river-floodplain  
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5 641 systems with monomodal flood-pulses. Yet, studies on the downstream impact of river dams  
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8 642 in other Amazonian river types, such as clear-water rivers draining the cratonic Guiana and  
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10 643 Central Brazilian shields, are not available for comparison. Many of these rivers have already  
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12 644 been dammed, and in others, dams are under construction or planned in the near future  
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15 645 (Latrubesse et al., 2017; Lees et al., 2016). There is an urgent need for further  
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17 646 transdisciplinary studies to reveal dam-induced downstream impacts on floodplain forests in  
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19 647 other river types of the Amazon basin, but also in other tropical regions. This is a major  
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22 648 challenge for science due to the wide range of factors that must be considered in this  
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24 649 approach.

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### 30 651 **Recommendations and concluding remarks**

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32 652 The "sandwich-effect" in the dam shadow is a threat for floodplains controlled by regular and  
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34 653 predictable flood pulses, which is the dominant pattern across large tropical rivers (Junk et  
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36 654 al., 1989). Hydrological changes downstream of dams are already evident for the river basins  
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39 655 of the Paraná and São Francisco in Brazil, where the implementation of many hydropower  
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42 656 plants started several decades ago (Agostinho et al., 2004; Bustamante et al., 2019). Tropical  
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44 657 floodplains along large flood-pulsing rivers such as the Araguaia-Tocantins, Orinoco,  
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46 658 Magdalena, Congo, Mekong and many others are likely to suffer drastic hydrological  
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49 659 alterations due to already installed and planned large hydropower dams (Latrubesse et al.,  
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51 660 2017; Latrubesse et al., 2019; Winemiller et al., 2016). This threatens the integrity of tropical  
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53 661 river-floodplain systems over thousands of square kilometres in the Amazon and other  
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3 662 tropical regions, which host the last remaining large networks of free-flowing rivers (Grill et  
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5 663 al., 2019).

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8 664 The novel insights on the potential scale of downstream impacts on floodplains caused by  
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10 665 hydropower dams allows to draw recommendations which should be considered in  
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12 666 environmental impact assessments and associated reports (EIA/RIMA), in the Amazon and  
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14 667 elsewhere. For dams under construction and during the reservoir fill, severe dry conditions  
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17 668 should be avoided in the downstream floodplains, as it arguably will provoke tree mortality  
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20 669 and wildfires. Already operating hydropower dams should adapt a power generation,  
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22 670 simulating the natural flood-pulse and maintaining annually the pre-dam baseflow index of  
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24 671 the river to mitigate the downstream impacts in the floodplains. This should be also a  
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27 672 guideline for planned hydropower dams. Therefore, the environmental impact assessment  
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29 673 must integrate floodplains downstream of the planned hydropower dams at least until the  
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31 674 confluence of a major undisturbed affluent of the same river order (Strahler, 1957) or until  
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33 675 the area affected by backwater effects from rivers with higher ranked orders (Meade, Rayol,  
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35 676 Conceição, & Natividade, 1991), which are likely to buffer the dam-induced hydrological  
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37 677 alterations. The downstream assessment should provide inventories of major macrohabitats  
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40 678 (Junk et al., 2018) in the potentially affected floodplains on ground and landscape levels with  
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43 679 associated hydrogeomorphic data. Simulation models relating river discharge, potential  
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45 680 power generation and water level, should allow an assessment and evaluation of mitigated  
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47 681 downstream impacts and monetary losses for power generation maintaining the pre-dam  
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50 682 baseflow index and flood-pulse regime. This would contribute to a critical evaluation of  
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52 683 hydropower options by a consortium involving government, scientists, stakeholders from  
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54 684 civil society, industry, and financial agencies. Massive losses of macrohabitats, biodiversity,  
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3 685 and environmental services in floodplains caused by hydropower dams must be avoided or  
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5 686 at least mitigated, to maintain ecosystem functioning, food security and the welfare of the  
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8 687 present and future generations of traditional and indigenous populations. This is of essential  
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10 688 importance, as synergetic effects of climate and land-use changes are expected to cause a  
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12 689 serious imbalance of floodplain ecosystems in future.  
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45 1110 **Figure legends**

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48 1111 **Figure 1:** Location of the study region in the Central Brazilian Amazon indicating the  
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50 1112 Uatumã Sustainable Development Reserve (USDR), the Balbina dam, the Uatumã River and  
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52 1113 its major tributaries (Abacate and Jatapú rivers), the analysed hydrological stations (Morena  
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54 1114 and Siderma Jusante), the location of the permanent plots in the igapó, sample sites of dead  
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3 1115 trees and the focal area for remote sensing analysis. Photos (from left to right) show an aerial  
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5 1116 view of the igapó floodplains of the Uatumã River (July 2009) about 100 km downstream of  
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7 1117 the Balbina dam (photo: Florian Wittmann); dead tree population of *Eschweilera tenuifolia*  
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9 1118 in a floodplain lake (October 2015) at the lowest topographical elevations of the igapó, about  
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11 1119 105 km downstream of the Balbina dam (photo: Jochen Schöngart); disturbed forests in the  
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13 1120 focal area at the medium topography of the igapó of the Uatumã River (April 2018)  
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15 1121 dominated by the tree species *Nectandra amazonum* and the palm species *Astrocaryum jauari*  
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17 1122 (photo: Jochen Schöngart).

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22 1123 **Figure 2:** Analyses of Indicators of Hydrologic Alteration (IHA) of the Uatumã River  
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24 1124 downstream of the Balbina dam and Range of Variability Approach (RVA) (Richter et al.,  
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26 1125 1996, 1997) comparing pristine conditions (1973-1982) with the period of dam operation  
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28 1126 (1991-2018). IHA parameters were calculated based on daily water level data (hydrological  
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30 1127 year from October-September) using non-parametric statistics (median, 25th and 75th  
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32 1128 percentiles) for the pre-dam and post-dam periods by the IHA software (version 7.1). a) RVA  
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34 1129 evidencing changes from the pre-dam to the post-dam period in the monthly median water  
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36 1130 levels from October to September (group 1), magnitude, duration (group 2) and timing of  
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38 1131 annual extreme water conditions (group 3), frequency and duration of high and low pulses  
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40 1132 (group 4) as well as rate and frequency of water condition changes (group 5). The three RVA  
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42 1133 categories are based on percentile values of equal size (low: <34<sup>th</sup> percentile; middle 34–67<sup>th</sup>  
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44 1134 percentile; high: >67<sup>th</sup> percentile). For each category the Hydrologic Alteration Factor is  
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46 1135 computed, which quantifies the degree of alteration of each IHA parameter. Positive values  
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48 1136 indicate that the frequency of values in the category has increased from the pristine to the  
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50 1137 post-dam period, while negative values represent a decreasing frequency. The lower panels  
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3 1161 of reservoir fill and dam operation (data: Landsat 4-5 Thematic Mapper; imagery courtesy of  
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5 1162 the U.S. Geological Survey EROS Archive; doi: 10.5066/F7N015TQ).  
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8 1163 **Figure 4:** Mapped dead forests and potentially threatened forests in the focal area of the  
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10 1164 igapó floodplains along the Uatumã River downstream of the Balbina dam (background:  
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12 1165 shaded relief derived from the Shuttle Radar Topography Mission–SRTM digital elevation  
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14 1166 model) (Resende et al., 2019).  
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18 1167 **Figure 5:** Mortality patterns for *Macrolobium acaciifolium* (Fabaceae) and *Eschweilera*  
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20 1168 *tenuifolia* (Lecythidaceae) based on cross-dating and radiocarbon-dating to estimate the year  
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22 1169 of death in the igapó floodplains downstream of the Balbina dam. The mortality patterns are  
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24 1170 related to the duration of the terrestrial phase (black line) calculated for the mean topography  
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26 1171 of each species based on the daily water levels from the Cachoeira Morena station (id code:  
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28 1172 16100000, data: Agência Nacional de Águas–ANA). Note that *Macrolobium* grows on  
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30 1173 slightly higher elevations compared to *Eschweilera* resulting in prolonged periods of  
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32 1174 terrestrial phases (Assahira et al., 2017; Resende et al., 2020).  
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37 1175 **Figure 6:** Relationship between Fisher’s alpha diversity and the duration of the aquatic phase  
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39 1176 comparing the pristine igapó forests (Abacate) with the disturbed system downstream of the  
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41 1177 Balbina dam (Uatumã). Fisher’s alfa diversity from adjacent terra-firme forests (Lobo et al.,  
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43 1178 2019) are included in the analyses.  
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47 1179 **Figure 7:** Spatiotemporal disturbances in the igapó floodplains downstream of the Balbina  
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49 1180 dam over a 35-year period dramatically impacted this ecosystem resulting into a loss of  
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51 1181 macrohabitats, massive tree mortality and tree species diversity affecting the functioning and  
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53 1182 provision of ecosystem services of a conservation unit. During the installation of the Balbina  
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55 1183 dam and the reservoir fill in synergy with El Niño conditions (1982/1983 and 1986-1988)  
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3 1184 severe dry conditions were generated in the downstream floodplains (Figure 3) leading to  
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5 1185 hydraulic failure and tree mortality at the lowest topographies and caused possibly wildfires  
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8 1186 affecting mainly the medium topographies resulting into forest succession and the  
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10 1187 establishment of pioneer tree species. Hydrological alterations during the post-dam period  
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12 1188 caused the typical "sandwich-effect" (red arrows) characterized by the suppression of the  
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15 1189 terrestrial phase at the lower topographies and of the aquatic phase at the higher topographies  
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17 1190 in consequence of higher minimum and lower maximum water levels, respectively. The  
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19 1191 temporal asynchrony between the hydrological regime and phenology, growth rhythms,  
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21 1192 hydrochoric and ichthyochoric seed dispersal of tree species and increasing alternations  
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24 1193 between water deficit and anoxic conditions is hypothesized to favour the dominance of tree  
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26 1194 species adapted to this disturbance regime.

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32 1196 **Table 1:** Dominant tree species (>10 cm DBH) of the studied igapó forests at three distinct  
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34 1197 topographic inundation classes (low, medium and high) of the Uatumã River (impacted area)  
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36 1198 and the Abacate River (natural conditions) indicating the relative importance value index  
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39 1199 (IVI%), mean and standard deviation of tree age (years) and mean annual diameter increment  
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41 1200 (MDI; mm) as well as wood density ( $\rho$ ; g cm<sup>-3</sup>) (data: Lobo et al., 2019; Mori et al., 2019;  
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43 1201 Neves, 2018; Neves et al., 2019; Rocha et al., 2019).

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Uatumã					Abacate				
High-igapó					High-igapó				
Tree species	IVI%	Age	MDI	$\rho$	Tree species	IVI%	Age	MDI	$\rho$
<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 macroleoba</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
<b>Medium-igapó</b>					<b>Medium-igapó</b>				
<b>Tree species</b>	<b>IVI%</b>	<b>Age</b>	<b>MDI</b>	<b><math>\rho</math></b>	<b>Tree species</b>	<b>IVI%</b>	<b>Age</b>	<b>MDI</b>	<b><math>\rho</math></b>
<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>Guatteria guianensis</i>	3.7	64±25	2.2±0.9	0.43
<b>Low-igapó</b>					<b>Low-igapó</b>				
<b>Tree species</b>	<b>IVI%</b>	<b>Age</b>	<b>MDI</b>	<b><math>\rho</math></b>	<b>Tree species</b>	<b>IVI%</b>	<b>Age</b>	<b>MDI</b>	<b><math>\rho</math></b>
<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 laevicarpa</i>	5.5	190±21	1.4±0.6	0.55

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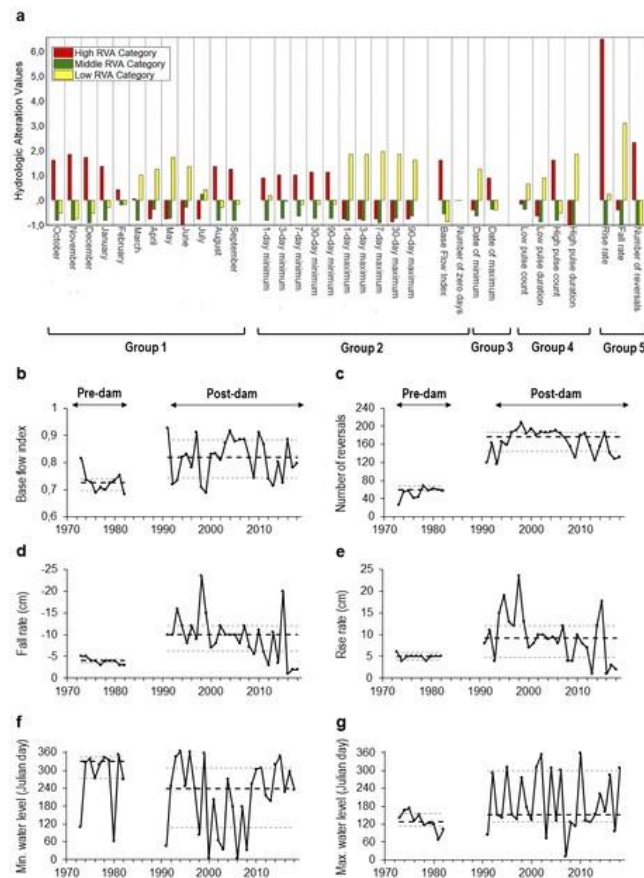
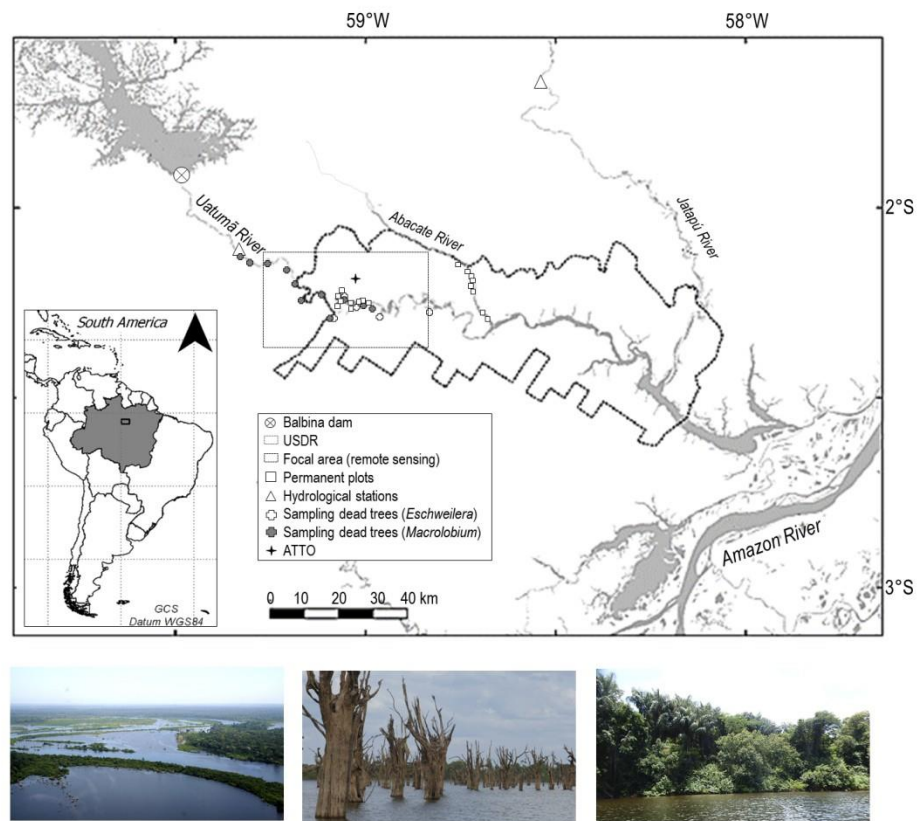


Figure 2: Analyses of Indicators of Hydrologic Alteration (IHA) of the Uatumã River downstream of the Balbina dam and Range of Variability Approach (RVA) (Richter et al., 1996, 1997) comparing pristine conditions (1973-1982) with the period of dam operation (1991-2018). IHA parameters were calculated based on daily water level data (hydrological year from October-September) using non-parametric statistics (median, 25th and 75th percentiles) for the pre-dam and post-dam periods by the IHA software (version 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) as well as 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, while negative values represent a decreasing frequency. The lower panels indicate temporal changes between pre-dam and post-dam conditions of the IHA parameters: b) baseflow



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3 index (7-day minimum water level divided by mean annual value), c) number of reversals, d) fall and, e)  
4 rise rates, f) timing of minimum and g) maximum water level (black horizontal dashed lines are the  
5 medians, the grey dashed lines represents the 25th and 75th percentiles). Data were obtained from  
6 Cachoeira Morena station (id code: 16100000), available at the HidroWeb database of the Brazilian National  
7 Agency of Waters (ANA; <http://hidroweb.ana.gov.br>).

8 40x72mm (300 x 300 DPI)



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

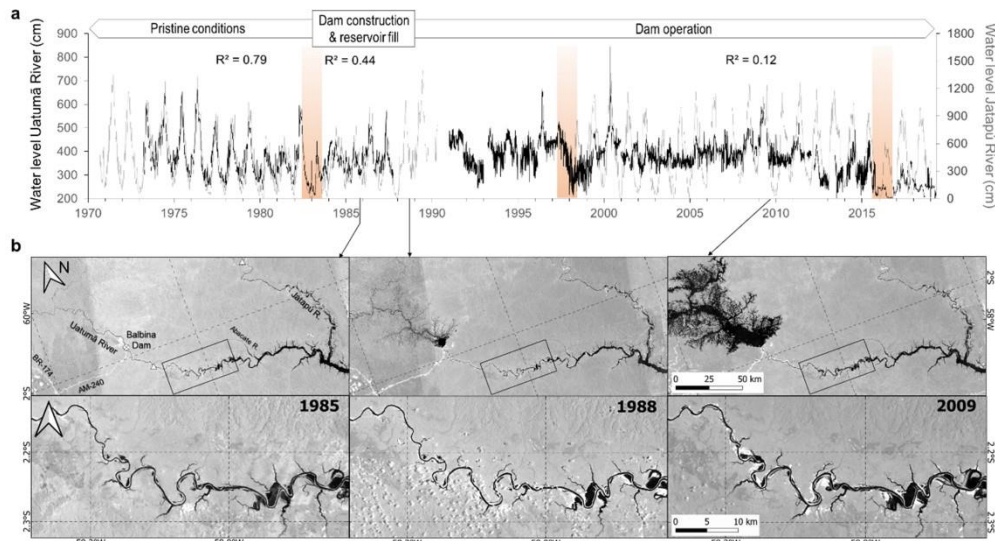
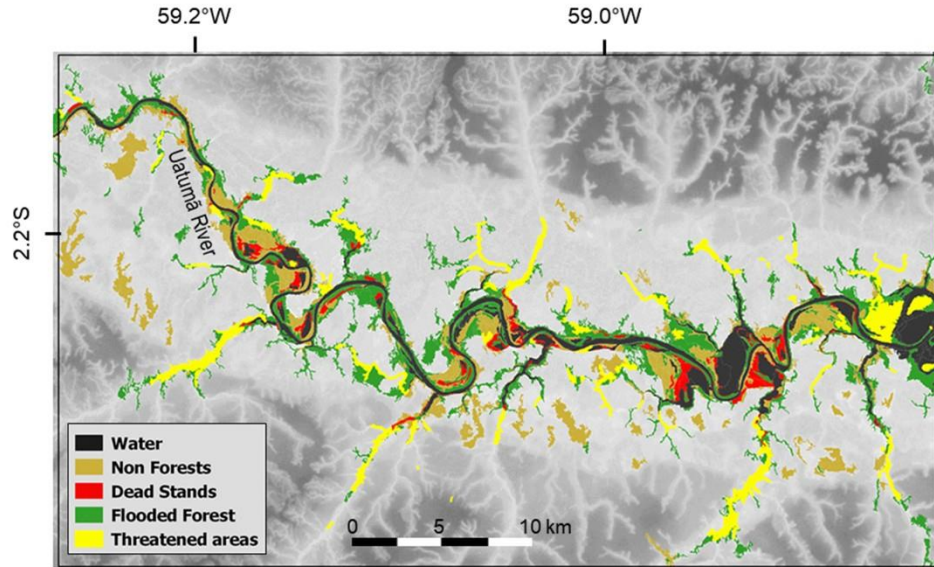


Figure 3: a) Daily water levels from the Uatumã River, downstream of the Balbina dam (black) and its major tributary, the Jatapú River (grey). Both hydrological regimes show high congruence during the period of pristine conditions (until 1983) which weakened during the period installing the Balbina dam (1983-1987) and is low for the post-dam period (1998-2018) (data: Brazilian National Agency of Waters-ANA; <http://hidroweb.ana.gov.br>). No data were available for the Uatumã River (Cachoeira Morena station; id code: 16100000) between 01/10/1987 and 31/12/1990 (period of reservoir fill and begin of dam operation); for the Jatapú River (Siderma-Jusante station; id code: 16205000) data are available from 13/09/1970–27/04/1990 and 01/05/1998–31/12/2018). 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 of both rivers. b) Composition of Landsat TM images for the years 1985 (dam construction), 1988 (reservoir fill) and 2009 (dam operation) and its downstream impacts in 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 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: Landsat 4-5 Thematic Mapper; imagery courtesy of the U.S. Geological Survey EROS Archive; doi: 10.5066/F7N015TQ).

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31 Figure 4: Mapped dead forests and potentially threatened forests in the focal of the igapó floodplains along  
32 the Uatumã River area downstream of the Balbina dam (background: shaded relief derived from the Shuttle  
33 Radar Topography Mission–SRTM digital elevation model) (Resende et al., 2019). In the focal area we show  
34 potentially threatened areas.

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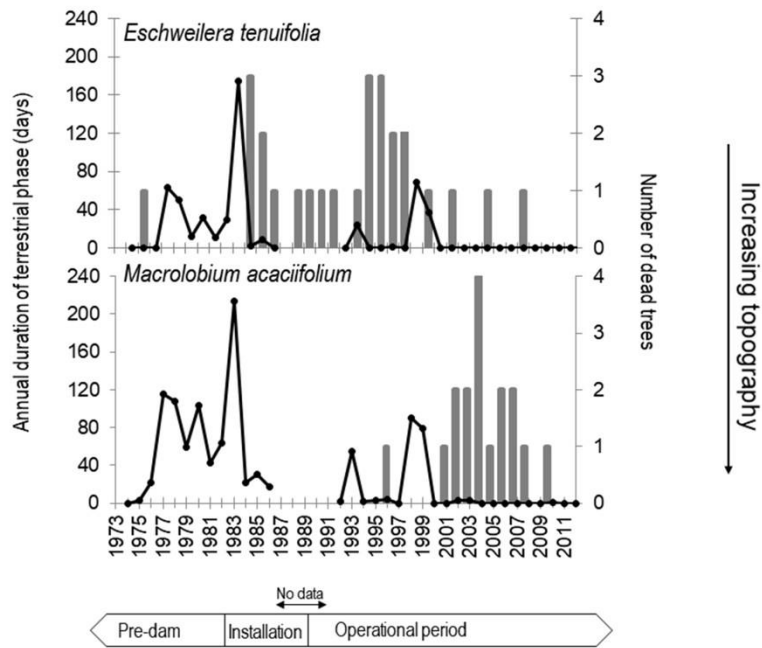


Figure 5: Mortality patterns for *Macrolobium acaciifolium* (Fabaceae) and *Eschweilera tenuifolia* (Lecythidaceae) based on cross-dating and radiocarbon-dating to estimate the year of death in the igapó floodplains downstream of the Balbina dam. The mortality patterns are related to the duration of 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).

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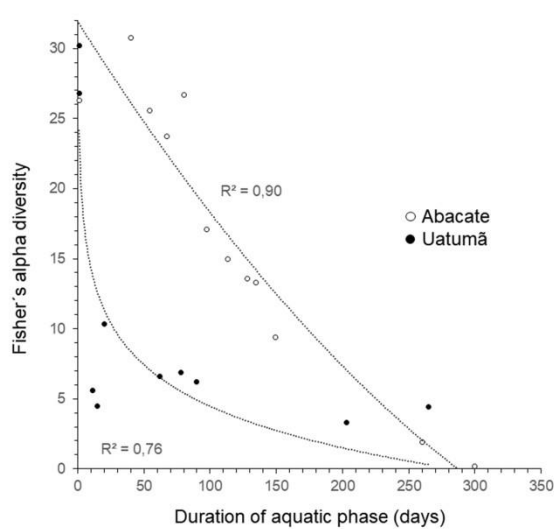


Figure 6: Relationship between Fisher's alpha diversity and the duration of the aquatic phase comparing the pristine igapó forests (Abacate) with the disturbed system downstream of the Balbina dam (Uatumã). Fisher's alpha diversity from adjacent terra-firme forests (Lobo et al., 2019) are included in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

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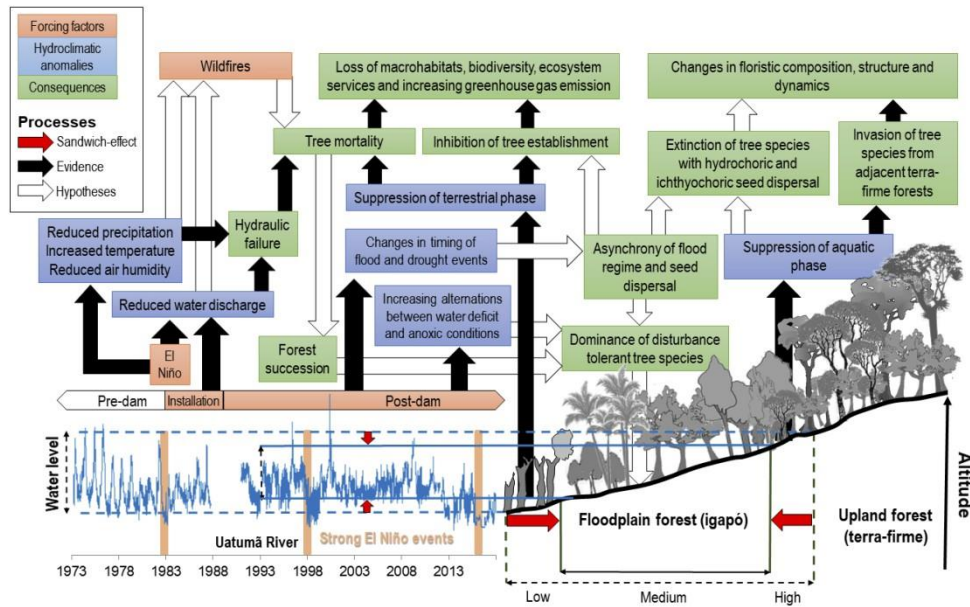


Figure 7: Spatiotemporal disturbances in the igapó floodplains downstream of the Balbina dam over a 35-year period dramatically impacted this ecosystem resulting into a loss of macrohabitats, massive tree mortality and tree species diversity affecting the functioning and provision of ecosystem services 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.