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7 **POST-FIRE DYNAMICS OF WOODY VEGETATION IN SEASONALLY FLOODED**  
8 **FORESTS (*IMPUCAS*) IN THE CERRADO-AMAZONIAN FOREST TRANSITION ZONE**  
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30 **ABSTRACT**

31 Fire disturbance alters the structural complexity of forests, above-ground biomass stocks and  
32 patterns of growth, recruitment and mortality that determine community temporal dynamics.  
33 These changes may alter forest species composition, richness, and diversity. We compared  
34 changes in recruitment, mortality, and turnover time over three years between burned and

35 unburned sites of two *impucas* (seasonally flooded natural forest patches in a predominantly  
36 savanna landscape) to determine how fire alters forest dynamics and species composition. Within  
37 each *impuca*, 50 permanent plots (20 × 10 m) were established and all individuals  $\geq 5$  cm  
38 diameter at breast height (DBH) identified and measured in two censuses, the first in 2007 and  
39 the second in 2010. Unplanned fires burned 30 plots in *impuca* 1 and 35 in *impuca* 2 after the  
40 first census, which enabled the comparison between burned and unburned sites. The highest  
41 mortality (8.0 and 24.3% year<sup>-1</sup> for *impuca* 1 and 2) and turnover time (69 and 121.5 years) were  
42 observed in the burned sites, compared to 3.7 and 5.2% year<sup>-1</sup> (mortality), and 28.4 and 40.9  
43 years (turnover), respectively, for the unburned sites. Although these seasonally flooded forested  
44 *impucas* are embedded in a fire-adapted savanna landscape, the *impucas* vegetation appears to be  
45 sensitive to fire, with burned areas having higher mortality and turnover than unburned areas.  
46 This indicates that these forest islands are potentially at risk under increasing regional fire  
47 frequency.

48

49 **Keywords:** *impuca*, tropical forest fire, mortality, recruitment, southern Amazonia, Brazil.

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51

## 52 **Introduction**

53 The increase in global demand for grain, livestock, and biofuels driven by the rising price  
54 of oil, combined with episodic drought and fire have led to a rapid process of structural  
55 degradation and fragmentation of some Amazonian forests (Nepstad et al., 2008; Nogueira et al.,  
56 2008). Deforestation for the expansion of agriculture occurs mainly in the southern Amazonia  
57 “arc of deforestation,” transitional areas of between forest and savanna (Nogueira et al., 2008).  
58 These areas have had several intense droughts over the last two decades (Marengo et al., 2011).  
59 Deforestation and drought events not only induce tree mortality (Phillips et al., 2009), but also  
60 alter the forest microclimate, for example, by allowing sun-light to penetrate canopy openings  
61 and fragment edges, drying the forest floor, rendering it more flammable, and thereby favouring  
62 the spread and recurrence of fires (Nepstad et al., 2008; Davidson et al., 2012). In addition,  
63 frequent fires modify the structure, floristic composition and functioning of plant communities in  
64 the Amazon, favouring dry-forest and savanna species which are more adapted to the presence of  
65 fire (Nepstad et al., 2008). Fire is considered one of the major threats to Amazonian forest  
66 diversity (Cochrane and Schulze, 1999; Barlow and Peres, 2004, 2008). It is therefore important  
67 to understand the effects of fire on Amazonian forests, especially in vegetation types

68 representing the rapidly shrinking forest-savanna transition zone, to understand how plant  
69 community structure and composition changes through time.

70 The structure and dynamics of forests may be strongly influenced by natural or man-  
71 made disturbance and fire (Cochrane et al., 1999), especially due to the low resistance and  
72 resilience of forest species against such impacts (Hoffmann et al., 2000, 2003), which normally  
73 results in high mortality rates (Barlow and Peres, 2004, 2008; Balch et al., 2008). Small-scale  
74 disturbances, such as those originating from branch or tree fall, are responsible for an increase in  
75 forest structural and floristic complexity (Molino and Sabatier, 2001; Budke et al., 2010). On the  
76 other hand, large-scale disturbances such as selective logging, fragmentation and burning, may  
77 exert considerable effects on forest dynamics, causing a reduction in richness and diversity  
78 (Strasberg et al., 1995; Thonicke et al., 2001). Seasonal flooding and the saturation of soils may  
79 also affect vegetation structure and composition (Jirka et al., 2007). The effects of seasonal  
80 flooding (Guilherme et al., 2004) and fire (Nepstad et al., 2001; Balch et al., 2008) on tropical  
81 forest dynamics are known for some areas of Amazonia; however, there is currently a lack of  
82 information about how fire affects seasonally flooded forest located in the transition zone  
83 between the Amazon forest and the Cerrado biome. Moreover, the transitional forests between  
84 Cerrado and Amazon forest are very vulnerable to burning (Balch et al., 2008; Davidson et al.,  
85 2012), mainly when the occurrence of fire is related to episodes of severe droughts (Alencar et  
86 al., 2006; Balch et al., 2008; Aragão and Shimabukuro, 2010; Davidson et al., 2012).

87 The transition zone in Mato Grosso State in Brazil presents a wide physiognomic,  
88 structural, and floristic range because of the presence of three important biomes: Cerrado,  
89 Amazon Forest and Pantanal (Eiten, 1975, 1985; Ackerly et al., 1989; Alho, 2008). However,  
90 this region is highly threatened: almost 500.000 km<sup>2</sup> of original Cerrado vegetation were  
91 converted into pasture through mid-2000, an area equivalent to Spain (Klink and Machado,  
92 2005); and, according to Latrubesse et al. (2009), “no other biome in the world has been  
93 destroyed so quickly and thoroughly in human history.”

94 In the Araguaia Plain, or Araguaia Pantanal, in the transition between Cerrado and  
95 Amazon forest, there are flooded forests regionally known as *impucas* (Eiten, 1985; Marimon et  
96 al., 2008) occurring in natural depressions, which favour seasonal flooding for a longer period of  
97 time. On the plains, the Araguaia River forms a vast basin and maintains the most important  
98 wetlands of Central Brazil. Threats to the biodiversity of this area are enormous (Latrubesse et  
99 al., 2009), especially as a result of recurrent fires (Marimon et al., 2008). The few studies of  
100 *impucas* found in the literature provide only general descriptions of the vegetation structure and  
101 are based on only one inventory (Marimon and Lima, 2001; Martins et al., 2002; Brito et al.,

102 2006, 2008; Marimon et al., 2008; Barbosa et al., 2011). Seasonal flooding is a factor that  
103 restrains species richness and diversity in flooded forests (Ivanauskas et al., 1997) and in  
104 *impucas* (or *ipucas*) (Brito et al., 2008; Barbosa et al., 2011), since survival in flooded  
105 environments requires species having specific physiological and morphological adaptations (Joly  
106 and Crawford, 1982; Scarano et al., 1994; Toniato et al., 1998). In addition, flood-tolerance may  
107 present an important competitive advantage (Joly and Crawford, 1982; Parolin et al., 2004), with  
108 adapted species becoming very abundant. These flood-adapted species may also be exposed to  
109 fire, which enters from the surrounding grasslands and woody savanna. Despite the regional  
110 importance of fire, it is unclear how *impucas* vegetation responds to fire.

111 The aim of this study, therefore, was to analyse and compare the woody vegetation  
112 dynamics of burned and unburned sites of two seasonally flooded *impucas* in north-eastern State  
113 of Mato Grosso, Brazil. We tested the hypothesis that *impucas* are highly susceptible to fire,  
114 which significantly alters community dynamics and vegetation species composition in a  
115 relatively short period due to a strong increase in mortality rates and a decrease in basal area and  
116 recruitment rates.

117

118

## 119 **Materials and methods**

### 120 ***Study sites***

121 The study was carried out in two seasonally flooded forests (*impucas*), in the Araguaia  
122 State Park (PEA) (*Impuca* 1: 12°09'4.2" S and 50°49'37" W and *Impuca* 2: 12°19'11.2" S and  
123 50°44'15.6" W), municipality of Novo Santo Antônio, eastern Mato Grosso State (Fig. 1). The  
124 PEA encompasses an area of 223,619 ha and is located in the flood plain formed by the  
125 confluence of the *Rio das Mortes* with the *Rio Araguaia*. It has a mean altitude of 200 m, and is  
126 part of the Sedimentary Plain of Bananal or, according to Marimon et al. (2008), in the Araguaia  
127 Pantanal. The topography of the PEA is generally flat, and waterlogged in the rainiest months.  
128 Soils are primarily composed of Plinthosols and Gleysols, both with drainage impediments and  
129 subject to seasonal flooding (Brasil, 1994). The regional climate is the Aw type (hot tropical  
130 continental), according to Köppen's classification, characterized by a dry season between April  
131 and September, and a rainy season between October and March (Silva et al., 2008).

132

### ***Insert Figure 1***

133 The Araguaia Plain, which extends across the States of Goiás, Tocantins and eastern  
134 Mato Grosso, within the area of the *Rio das Mortes* and *Rio Araguaia*, constitutes a region with  
135 high biodiversity (Marimon and Lima, 2001), as it occurs in the transition zone between the

136 Cerrado and Amazon Forest biomes (Ratter, 1987). This influences the floristic composition and  
137 creates a complex vegetation mosaic in its seasonally-flooded wide plain (Marimon and Lima,  
138 2001; Martins et al., 2008; Barbosa et al., 2011). The region has been classified by vegetation,  
139 animal and physical specialists as an area of “extremely high biological importance” (MMA,  
140 1999; Marimon and Lima, 2001). However, during the dry season, anthropogenic fire is  
141 becoming increasingly frequent, caused by local inhabitants, who burn the vegetation to promote  
142 the sprouting of native grasses and feed cattle, since ranching is the main activity within the park  
143 (Marimon et al., 2008).

144 Fires of varying sizes, intensities and frequencies occur in the Araguaia State Park (PEA)  
145 (Marimon et al., 2008). Sometimes, fire burns the surrounding matrix of the *impucas* (wet  
146 grasslands), but does not reach the forest (Marimon et al., 2008; Barbosa et al., 2011).  
147 Nevertheless, under conditions of low humidity and with the presence of the invasive species,  
148 *Scleria* sp. (Barbosa et al., 2011), the flames have penetrated the *impucas* and caused high tree  
149 mortality. In some cases, the *impucas* do not burn completely because, even in the dry season,  
150 they can be partially flooded.

151

### 152 ***Vegetation inventory***

153 In September 2007 we established five parallel transects in each *impuca*, 50 m apart.  
154 Each transect was subdivided into plots of 20 x 10 m, with its length depending on the form and  
155 size of each *impuca*, and ranging from 50 to 120 m (see Fig. 1). In each transect, all living and  
156 individuals with diameter at breast height (DBH)  $\geq 5$  cm were tagged identified, and their  
157 diameter measured (Barbosa et al., 2011). In 2010, all plots were re-surveyed, with all surviving  
158 and standing dead individuals re-measured. Individuals that reached 5 cm diameter were treated  
159 as recruits, tagged and identified. Species identifications were carried out through comparisons  
160 with the herbarium collections of the University of Mato Grosso State, Nova Xavantina *Campus*  
161 (Herbarium NX), the University of Brasilia (Herbarium UB), the Federal University of Mato  
162 Grosso (Herbarium UFMT), the Herbarium of Embrapa Amazonia Oriental (Herbarium IAN),  
163 and by consulting specialists. All herbarium specimens with flowers and/or fruits was  
164 incorporated into the collection of NX Herbarium.

165 Two fires occurred at the PEA after the first vegetation census. The first occurred in  
166 September 2007 soon after installation of the transects and reached 30 plots of *impuca* 1 and the  
167 second in September 2008, reaching 35 plots of *impuca* 2. In order to analyse the effects of the  
168 fires, the subplots were designated as either burned or unburned.

169

170 **Data analysis**

171 Based on the data collected in the 2007 and 2010 inventories, we calculated basal area for  
172 the community and for individual species (Mueller-Dombois and Elleberg, 1974), and from  
173 these values calculated several metrics to assess how dynamics and composition changed due to  
174 fire. First, based on the basal area, we calculated the average annual mortality rates (MO)  
175 (Equation 1),  
176

$$177 \quad MO = \left\{ 1 - [(AB_0 - AB_m) / AB_0]^{1/t} \right\} \times 100 \quad (\text{Equation 1})$$

178 where,  $AB_0$  is initial basal area, and  $AB_m$  is dead basal area.

179

180 Recruitment (RE) (Eq. 2) (Sheil et al. 1995; 2000) was calculated as,

$$181 \quad RE = [1 - (1 - AB_r / AB_t)^{1/t}] \times 100 \quad (\text{Eq. 2})$$

182 where,  $AB_r$  is recruits basal area,  $AB_t$  is final basal area, and  $t$  is the elapse of time in years.

183

184 Loss (L) (Eq. 3) and gain (G) (Eq. 4) in basal area (Guimarães et al., 2008), in addition to the  
185 basal area turnover time (TUR) (Eq. 5) (Korning and Balslev, 1994), were calculated as,

$$186 \quad L = \left\{ 1 - [(AB_0 - AB_m - AB_d) / AB_0]^{1/t} \right\} \times 100 \quad (\text{Eq. 3})$$

$$187 \quad G = \left\{ 1 - [1 - (AB_r + AB_g) / AB_t]^{1/t} \right\} \times 100 \quad (\text{Eq. 4})$$

$$188 \quad TUR = (T_{1/2} + T_2) / 2 \quad (\text{Eq. 5})$$

189 where,  $AB_0$  is initial basal area,  $AB_m$  is dead basal area,  $AB_d$  is basal area decrement,  $AB_r$  is  
190 recruits basal area,  $AB_g$  is basal area increment,  $AB_t$  is final basal area,  $t$  is the elapsed time in  
191 years,  $T_{1/2}$  is half-life time, and  $T_2$  is duplication time.

192

193 Based on the individuals occurring in both inventories, we calculated the average annual  
194 mortality rates (Mo) (Eq. 6) and recruitment rates (Re) (Eq. 7) (Sheil et al., 1995, 2000),

$$195 \quad Mo = \left\{ 1 - [(N_0 - N_m) / N_0]^{1/t} \right\} \times 100 \quad (\text{Eq. 6})$$

$$196 \quad Re = [1 - (1 - N_r / N_t)^{1/t}] \times 100 \quad (\text{Eq. 7})$$

197 where,  $N_0$  is initial number of individuals,  $N_m$  is the number of dead individuals,  $N_r$  is the number  
198 of recruits,  $N_t$  is the final number of individuals, and  $t$  is the elapse of time in years;

199

200 And, the half-life time ( $T_{1/2}$ ) (Eq. 8), i.e., the time necessary for a given population to decrease  
201 by 50% of its individuals from its current mortality rate, duplication time ( $T_2$ ) (Eq. 9), i.e., the

202 time necessary for a given population to duplicate its individuals from its current recruitment rate  
203 (Lieberman et al., 1985),

$$204 \quad T_{1/2} = \text{Ln}_{(1/2)} / \text{Ln}[(N_0 - N_m) / N_0 J^{1/t}] \text{ (Eq. 8)}$$

$$205 \quad T_2 = \text{Ln}_{(2)} / \text{Ln}[(N_0 + N_r) / N_0 J^{1/t}] \text{ (Eq. 9)}$$

206 stability (E) (Eq. 10), i.e., the values nearest to zero indicate that the community would be more  
207 stable, and turnover time (TUR) (Eq. 11), i.e., how much higher the turnover rate, higher  
208 mortality rates and/or recruitment (Korning and Balslev, 1994).

$$209 \quad E = (T_{1/2} - T_2) \text{ (Eq. 10)}$$

$$210 \quad \text{TUR} = ((T_{1/2} + T_2) / 2) \text{ (Eq. 11)}$$

211 where, Ln is the natural logarithm,  $N_0$  is the initial number of individuals,  $N_m$  is the number of  
212 dead individuals,  $N_r$  is the number of recruits,  $t$  is the elapse of time in years,  $T_{1/2}$  is the half-life  
213 time, and  $T_2$  is the duplication time.

214  
215 In addition, for the ten main species in terms of importance value (VI *sensu* Curtis and  
216 McIntosh, 1950) measured in the 2007 inventory, we calculated the average annual mortality and  
217 recruitment rates, and the half-life and duplication times based on the number of individuals  
218 between 2007 and 2010. For the same period, and based on the individual basal area, we  
219 calculated the average annual rates of loss (Eq. 3) and gain in basal area (Eq. 4).

220 The average annual rates of mortality, recruitment, loss, gain and turnover (based on the  
221 number of individuals and the individual basal area), and the half-life and duplication times for  
222 each plot were used to compare the dynamics of burned and unburned sites within each *impuca*.  
223 For these comparisons, we used the non-parametric analysis of Mann-Whitney (Sokal and Rohlf,  
224 1995). Histograms were plotted of individual and basal area distribution in diameter classes,  
225 where the equation for the calculation of the class intervals was based on Spiegel (1976). For  
226 each diameter classes. To compare the distributions of both inventories within the same sites of  
227 each *impuca*, we performed Kolmogorov-Smirnov tests. To determine the relationship between  
228 mortality (number of dead individuals and their basal area) and the diameter classes, we used  
229 simple linear regressions. All analyses were conducted using the R software statistical platform  
230 (R Development Core Team, 2011).

231

232

## 233 **Results**

234 Between 2007 and 2010, there was a reduction in basal area and absolute density of  
235 individuals in both burned and unburned sites of the *impucas* (Table 1). For the unburned sites,  
236 there was little reduction in *impuca* 1 (2.8% on a basal area-basis), while in *impuca* 2 the  
237 reduction was 8%, for a basal area-basis. In the burned sites, the reduction in basal area was  
238 greater for both *impuca* 1 (10.1%, basal area-basis) and for *impuca* 2 (39.3%, for basal area-  
239 basis) (Table 1). The higher basal area loss due to mortality compared to basal area gain due to  
240 recruitment resulted in an average net loss of basal area for all of the sites (Table 2).

241 ***Insert Table 1***

242 In comparing the effect of fire, there were high average annual mortality rates (8% year<sup>-1</sup>  
243 in *impuca* 1 and 24.3 in *impuca* 2) compared to recruitment in the burned sites (0.68% yr<sup>-1</sup> in  
244 *impuca* 1 and 0.66 in *impuca* 2), and also compared to mortality in the unburned sites of both  
245 *impucas* (Table 2). Due to the high mortality rates observed in the burned sites, there was a  
246 significant difference with respect to basal area loss between burned and unburned sites in both  
247 *impucas* (Table 2). For the gain rate of basal area, there was only a significant difference  
248 between the burned and unburned sites of *impuca* 1, with a greater gain for the unburned sites. In  
249 contrast, despite the burned sites of *impuca* 2 having higher gain rates of basal area than the  
250 unburned sites, their rate of loss of individuals was nearly four times higher, compared to  
251 unburned sites (Table 2). The recruitment rates of all sites (burned and unburned) were low  
252 (between 0.7% yr<sup>-1</sup> in *impuca* 1 and 2% yr<sup>-1</sup> in *impuca* 2) (Table 2). Even the unburned sites had  
253 lower recruitment than mortality rates. The individual- and basal area-based mortality rates in the  
254 burned sites were higher than the rates observed in the unburned sites of both *impucas*. In  
255 contrast, the recruitment rates in the burned sites were higher than in the unburned sites of both  
256 *impucas* (Tables 1 and 2).

257 ***Insert Table 2***

258 For all studied sites (burned and unburned), the values of half-life time were lower than  
259 the duplication time, on both an individual- and basal area-basis (Table 2). The values turnover  
260 time, on both an individual- and basal area-basis, were higher for the burned than for the  
261 unburned sites in both *impucas* (Table 2). There was a reduction in the number of individuals in  
262 most of the diameter classes after fire occurrence, and changes within and between the diameter  
263 classes (Fig. 3). The distribution of individuals among diameter classes did not differ between  
264 inventories for unburned sites (KS,  $\chi^2 = 0.0319$ ,  $P > 0.05$ ) and burned sites (KS,  $\chi^2 = 0.0537$ ,  
265  $p > 0.05$ ) for *impuca* 1 and unburned sites of *impuca* 2 (KS,  $\chi^2 = 0.0301$ ,  $P > 0.05$ ). There was  
266 only a reduction in the frequency of individuals of burned sites in *impuca* 2 (KS,  $\chi^2 = 0.1818$ ,  $P$   
267  $< 0.001$ ).



268

### *Insert Figure 2 and 3*

269 For mortality, on an individual-basis, there was a negative relationship with increasing  
270 diameter class for the burned sites of *impuca* 1 ( $R^2 = 0.79$ ;  $F = 27.42$ ;  $P = 0.002$ ) and *impuca* 2  
271 ( $R^2 = 0.90$ ;  $F = 66.76$ ;  $P = 0.001$ ) (Fig. 4A, B). Mortality on a basal area-basis was negatively  
272 related with diameter class only for the burned sites of *impuca* 2 ( $R^2 = 0.60$ ;  $F = 11.54$ ;  $P =$   
273  $0.01$ ), with no significant relationship in *impuca* 1 ( $R^2 = 0.17$ ;  $F = 2.43$ ;  $P = 0.16$ ) (Fig. 4C, D).  
274 Even with most of the dead individuals concentrated in the smaller diameter classes (Fig. 4), the  
275 highest mortality rates were observed for the larger diameter classes for the unburned sites of  
276 *impuca* 1 (>35 to 40 cm) and *impuca* 2 (>30 to 35 cm) (Fig. 2A and C), while for the burned  
277 sites of these *impucas*, the highest mortality rates were observed in the first diameter class 5 to  
278 10 cm (Fig. 2A, C). The highest recruitment rates, on both an individual- and basal area-basis,  
279 were found in the smallest diameter classes of the burned and unburned sites of both *impucas*  
280 (Fig. 2B, D). Considering both individual- and basal area-basis, the rates of change were  
281 negative for most of the classes of all the burned and unburned sites, except for the larger  
282 diameter classes (Fig. 4).

283

### *Insert Figure 4*

284 For the ten main species in terms of importance value in all sites, seven had higher  
285 mortality than recruitment rates. Only three species in the unburned sites of *impuca* 1 had  
286 recruitment rates equal or higher than mortality rates (*Licania apetala*, *Ormosia excelsa* and  
287 *Diospyros poeppigiana*) (Table 3). For basal area in the burned sites, all species had higher rates  
288 of loss than gain. However, in the unburned sites, the rates of basal area gain were higher than  
289 basal area loss for six species of *impuca* 1 (*L. apetala*, *Mabea paniculata*, *O. excelsa*,  
290 *Calophyllum brasiliense*, *Diospyros tetrandra*, and *D. poeppigiana*) and three species of *impuca*  
291 2 (*Ternstroemia candolleana*, *Symmeria paniculata*, and *Roupala montana*) (Table 3).

292

### *Insert Table 3*

293

294

## **Discussion**

296

297 The results of this study, the first of our knowledge examining the response of *impucas*  
298 fire, indicate that these seasonally flooded forests are generally not fire-resistant. Mortality rates  
299 and basal area loss were high, while recruitment was outpaced by mortality. Some species have  
300 adaptations to fire, e.g. thicker bark (*Calophyllum brasiliense*, *Licania apetala*, *Roupala*  
301 *montana* and *Vochysia divergens*). This unique vegetation type in the Cerrado-Amazon forest

302 transition appears to be highly dynamic (both unburned and burned plots), responding to the dual  
303 stress of seasonally saturated soil environment of the roots and infrequent, but over the years  
304 increasing fire events.

305

306

### 307 ***Community-level patterns***

308 The mortality rates from the unburned *impucas* of our study were higher than those in an  
309 experimental study in a burned Amazonian transition forest (4.8% per year) (Balch et al. 2008).  
310 Furthermore, annual mortality rates in the burned *impucas* of our study were two to six times this  
311 rate. Mortality rates commonly reported for protected tropical forests are approximately 1 to 2%  
312 per year (Condit et al., 1995; Stephenson and van Mantgem, 2005), much lower than the rates  
313 observed for the burned and unburned *impucas* sites, suggesting that unburned sites may also be  
314 affected by additional factors with negative influence (e.g. drought). On the other hand, the high  
315 mortality rates measured in the burned sites of our study show that fire has a negative effect on  
316 *impuca* vegetation and that areas that are seasonally inundated are still susceptible to fire  
317 intrusion despite the long period with saturated soil and likely proximity of the water table to the  
318 surface (Brito et al., 2008).

319 The high number of dead individuals and reduced basal area in burned compared to  
320 unburned sites is consistent with our hypothesis that the *impucas* are highly susceptible to fire.  
321 However, since a reduction in individual density and in basal area was also measured in the  
322 unburned forest, it is also possible that the 2010 drought-- which reduced rainfall in this region  
323 compared to the long-term average (Marengo et al., 2011)-- may have been a factor influencing  
324 negatively the sites. The reduction in individuals in the unburned sites in our study may also be a  
325 result in a time-lag in mortality from previous fires, since some *impucas* in the region may have  
326 previously burned (Barbosa et al., 2011). It is also important to emphasise that the losses due to  
327 fire may go beyond the direct effects observed immediately after the burning, since fire increases  
328 the probability and susceptibility to future burning (Cochrane et al., 1999).

329

### 330 ***Effects of tree size***

331 We found contrasting patterns of tree mortality by diameter class, with the larger classes  
332 having the highest mortality rates in unburned plots, but the smallest classes having the highest  
333 mortality rates in burned plots. Losses from the smaller size-classes may affect future  
334 regeneration, while losses from the larger diameter classes results in a large reduction in basal  
335 area and may affect seed sources, and increase irradiance. In forests, the highest numbers of dead

336 individuals are commonly measured in the smaller diameter classes. This pattern could be  
337 attributed to the low capacity of smaller individuals to compete with canopy trees (Felfili, 1995),  
338 and higher vulnerability to disturbance, such as fire. In the present study, this pattern was  
339 observed in both the burned and unburned sites. Therefore, it is probable that the higher  
340 mortality in the smaller size classes is related to the higher proportion of individuals in these  
341 smaller size classes (Fig. 2), and their low tolerance to fire (Hoffmann and Solbrig, 2003;  
342 Medeiros and Miranda, 2005). Barlow et al. (2003) reported significant loss of individuals in the  
343 Amazon Forest after fire disturbance, and observed that even large trees, which seem to be  
344 initially fire resist, died nearly three years after fire occurrence. In the unburned sites of the  
345 *impucas* of our study, the high mortality rates observed in the larger diameter classes may be  
346 related to the presence of older, senescent individuals or a delayed response to fire occurrence  
347 before 2007 (Herson Lima, PEA Administrator, pers. communication). However, the low  
348 number of individuals in the larger classes could be overestimating the mortality rates, because  
349 of the high stochasticity in the data due to small sample sizes. Sampling and evaluation of the  
350 plot data for a longer period will give a still more realistic picture of the effects of fire on  
351 individuals with different diameters.

352 Fire also appears to have exerted a strong effect on the smaller individuals in the burned  
353 sites and did reduce recruitment. Generally, recruitment rates exhibited by the vegetation in the  
354 *impuca* forests were low, when compared to other forest studies where values ranged from 3.5 to  
355 4.5% year<sup>-1</sup> (Gomes et al., 2003; Paiva et al., 2007; Silva and Araújo, 2009). It is important to  
356 note that even the unburned sites had on average lower recruitment rates than those reported for  
357 other forests.

358

### 359 **Populations**

360 Species that had higher recruitment and gain rates than mortality and basal area loss, such  
361 as *Calophyllum brasiliense* and *Symmeria paniculata*, have thicker bark (Barbosa et al., 2011)  
362 and were distributed in a more central position in the forests, more distant from the border and  
363 from the fire, respectively. The liana *Combretum laxum* had the highest mortality rate among the  
364 burned and unburned sites for species of *impuca* 2, as well as high basal area loss relative to gain  
365 for the burned sites, consistent with the idea that lianas are very sensitive to fire (Gerwing, 2002;  
366 Nepstad et al., 2007; Balch et al., 2011).

367

### 368 **Climate**

369 In a flooded forest plain in the Peruvian Amazon, Nebel et al. (2001) reported low  
370 mortality rates (between 2.2 and 3.2% year<sup>-1</sup>), and the recruitment rates (between 3.0 and 4.6%  
371 year<sup>-1</sup>) were higher than the mortality rates. In contrast, in the present study, even the unburned  
372 sites had recruitment rates lower than mortality rates. One explanation for the differences  
373 between the results of Nebel et al. (2001) and ours may be that their sites are located in a more  
374 central area of the Amazonian biome and are under more stable climatic conditions. The *impucas*  
375 of our study, besides being under a seasonal climate with lower annual rainfall, are surrounded  
376 by grassland and herbaceous fields (Martins et al., 2002, 2006; Marimon et al., 2008; Barbosa et  
377 al., 2011) favouring the development and passage of fire into the forest during the dry season,  
378 especially at the margins of the stands (Oliveira-Filho et al., 1997, 2007). Therefore, it is likely  
379 that local climatic conditions, including drought, and the border effect may have contributed to  
380 the observed difference in mortality and recruitment.

381

### 382 ***Root system***

383 The soils of the forests of our study have a thick layer of organic matter and are streaked  
384 by a mesh of fine roots (Barbosa et al., 2011). During the month when burnings occurred  
385 (September), the litter layer and the mesh of roots that covers the soil became dry and susceptible  
386 to fire. After fire had entered the forests, root systems of several trees were completely burned,  
387 resulting in the trunks of some large trees remaining suspended in the air supported by their  
388 canopies locked into those of neighbouring trees. This observation reinforces other studies  
389 indicating that creeping fires on the forest floor causes major impacts in Amazonian forests, and  
390 in the case of our study, higher mortality rates.

391

### 392 ***Factors causing instability in Amazonian transition forests***

393 Disturbances such as flooding, burning, droughts, and human activity may cause forest  
394 instability. Alencar et al. (2004) emphasized that the Amazonian transitional forests, besides  
395 suffering strong deforestation pressure (Nogueira et al., 2008), have been suffering major  
396 damage caused by fire. This is partially a result of having a more open canopy structure  
397 compared to the dense forests of central Amazonia, making transitional forests more prone to  
398 drying, and increasing vulnerability to fire. Moreover, several studies have reported  
399 disequilibrium between mortality and recruitment in seasonal forests (Appolinário et al., 2005;  
400 Enquist and Enquist, 2011) and gallery forests (Braga and Rezende, 2007; Miguel et al., 2011).  
401 Additionally, the ground fires are passing rather quickly a certain location so that extreme  
402 temperatures are measured there only for few minutes (e.g. Northern Conifer Forests). Whereas,

403 crown-fires remain for a longer period of time at a particular site, thus increasing the extreme  
404 temperature situation and making inefficient all plant adaptations against quickly passing fire  
405 fronts, as observed in the *impucas*. Although in the current study it appears that fire and/or  
406 drought may be the main causative agent of this disequilibrium, natural flooding, or changes in  
407 the flood regime must also be evaluated as a potential driver in future studies, since some studies  
408 have reported that the flood period is one of the most important factors that influence growth,  
409 distribution and richness of species in flooded forests in the Amazon (Wittmann et al., 2002,  
410 2004).

411

### 412 ***Turnover***

413 The high turnover time, duplication time, as well as the low half-life time observed in the  
414 burned sites reinforce that effects of fire on the *impuca* communities are quite deleterious, as  
415 they reduce the number of individuals by half within a short period of time (< 7 years), so that it  
416 would take substantial time (> 130 years) to duplicate the number of individuals, if the high rates  
417 of mortality and low rates of recruitment found in this study continued. For some forests not  
418 subjected to seasonal flooding, there is a reported pattern of balance between half-life and  
419 duplication times (Oliveira-Filho et al., 1997; Paiva et al., 2007; Silva and Araújo, 2009). The  
420 disequilibrium between such parameters reported in our study may be attributed to the imbalance  
421 between the mortality and recruitment rates. In the burned sites, fire may have been the key-  
422 factor for this increase in disequilibrium, since in these sites we observed low recruitment and  
423 high mortality of individuals. A forest community, in order to be balanced, requires stability in  
424 mortality, recruitment, half-life and duplication times (Korning and Balslev, 1994). The lack of  
425 stability in these rates raises concerns about the maintenance of these forests in the short and  
426 medium term.

427 The values of half-life time of the unburned sites were similar to the 17.2 and 16.9 years  
428 in a semi-deciduous forest of Minas Gerais State, Brazil, reported by Paiva et al. (2007) and  
429 Silva and Araújo (2009). In a disturbed forest in the Peruvian Amazon, Nebel et al. (2001)  
430 reported higher half-life times (between 22 and 32 years) and lower duplication times (between  
431 16 and 24 years). Other studies in Amazonia reported higher half-life times (between 24 and 99  
432 years) and lower duplication times (between 25 and 86 years) (Uhl et al., 1988; Rankin-de-  
433 Mérona et al., 1990; Gentry and Terborgh, 1990; Phillips et al., 1994; Phillips and Gentry, 1994)  
434 compared to those observed in the burned *impuca* sites, emphasizing the high rates of  
435 disturbance observed in both forests of our study. The turnover times of our study were high  
436 when compared with those non-seasonally flooded forests (Oliveira-Filho et al., 1997; Paiva et

437 al., 2007; Silva and Araújo, 2009), indicating that *impucas*, both burned and unburned, are  
438 extremely dynamic compared to other forests.

439

440

441

442

## 443 **Conclusions**

444 Here we provided new information on the impacts of fire on seasonally flooded forests of  
445 the Cerrado-Amazon Forest transition. However, due to spatial and temporal limitations of our  
446 study, care should be taken when extrapolating our findings to other regions of Amazonia.  
447 Future studies should increase the number of sampling units, the monitoring period, and extend  
448 sampling to other physiognomies in the Amazon transitional zone. In summary, our results  
449 support the hypothesis that greater structural changes occurred in the burned sites of both forests.  
450 The high rates of mortality and loss in basal area and the relatively low rates of recruitment and  
451 gain in basal area observed in the burned sites may be attributed to fire entering the forests.  
452 However, the high level of dynamism observed for the unburned sites indicate that these forests  
453 are also being affected by other factors in addition to fire. Humans have been responsible for the  
454 increased frequency of fire in *impucas*, and if these forests are to remain, it may be necessary to  
455 adopt fire prevention measures. Long-term studies that also examine the effects of flooding and  
456 drought on forest dynamism and productivity of *impucas* will help to separate the effect of fire  
457 from climatic drivers of productivity in this unique vegetation community of the Amazon Forest  
458 – Cerrado Biome transition.

459

460

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## List of tables

Table 1. Number of individuals ( $\text{ha}^{-1}$ ) and basal area ( $\text{m}^2 \text{ha}^{-1}$ ) of the woody vegetation sampled in two *impucas* (seasonally flooded forests) for burned and unburned plots, and your respective percentage of change between years (2007 and 2010). The fire occurred in 2007 following the 2007 census.

	Impuca 1						Impuca 2					
	unburned			burned			unburned			burned		
	2007	2010	% change	2007	2010	% change	2007	2010	% change	2007	2010	% change
Number of individuals	650	616	5.2	688	546	20.6	620	548	11.6	1,382	611	55.8
Basal area	10.08	9.8	2.8	15.1	13.5	10.6	12.63	11.6	8.2	22.7	13.8	39.2

Table 2. Parameters of the woody vegetation dynamics of burned and unburned sites of two seasonally flooded forests (*impucas*).  $W$  = test of Mann-Whitney. \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ , n.s. = not significant.

PARAMETERS	<i>IMPUCA 1</i>			<i>IMPUCA 2</i>		
	Unburned	Burned	$W$	Unburned	Burned	$W$
Average annual mortality rates (individual-basis, % year <sup>-1</sup> )	3.7	8.0	149.00**	5.2	24.3	22.00***
Average annual recruitment rates (individual -basis, % year <sup>-1</sup> )	2.0	0.7	431.50**	1.2	0.7	349.50*
Average annual rates of gain (basal area-basis, % year <sup>-1</sup> )	0.6	0.2	398.00*	1.9	2.3	n.s.
Average annual rates of loss (basal area-basis, % year <sup>-1</sup> )	3.9	4.9	181.00**	4.3	16.0	46.00***
Average annual mortality rates (basal area-basis, % year <sup>-1</sup> )	1.4	3.6	170.00**	2.9	15.4	51.00***
Average annual recruitment rates (basal area-basis, % year <sup>-1</sup> )	0.4	0.1		0.2	0.1	
Half-life time (individual-basis, years)	18.3	6.8	333.00**	13.0	2.5	468.00***
Duplication time (individual-basis, years)	38.6	131.1	469.50***	68.9	240.5	361.50**
Turnover rate (individual-basis, years)	28.4	69.0	424.50**	40.9	121.5	366.00**
Turnover rate (basal area-basis, years)	91.2	428.2	390.00*	203.8	644.9	359.00**
Half-life time (basal area-basis, years)	17.3	14.2		17.1	4.1	
Duplication time (basal area-basis, years)	165.0	842.1		390.6	1,285.6	
Stability (individual-basis, years)	20.3	124.3		55.9	238.0	
Stability (basal area-basis, years)	147.6	827.9		373.6	1,281.5	
Recruits basal area (m <sup>2</sup> ha <sup>-1</sup> )	0.13	0.04		0.07	0.04	
Dead basal area	1.14	2.05		1.45	9.02	

Table 3. Parameters for vegetation dynamics of the 10 highest IV species (importance value) in 2007 for the burned and unburned sites of two seasonally flooded forests (*impucas*). The species are ordered according to the IV in 2007. M= mortality (% year<sup>-1</sup>), R= recruitment (% year<sup>-1</sup>), t<sub>1/2</sub>= half-life time (years), t<sub>2</sub>= duplication time (years), RBA= recruits basal area (m<sup>2</sup> ha<sup>-1</sup>), IBA= basal area increment (m<sup>2</sup> ha<sup>-1</sup>), DBA= decrement in basal area (m<sup>2</sup> ha<sup>-1</sup>), GBA= gain in basal area (%year<sup>-1</sup>), LBA= loss in basal area (%year<sup>-1</sup>).

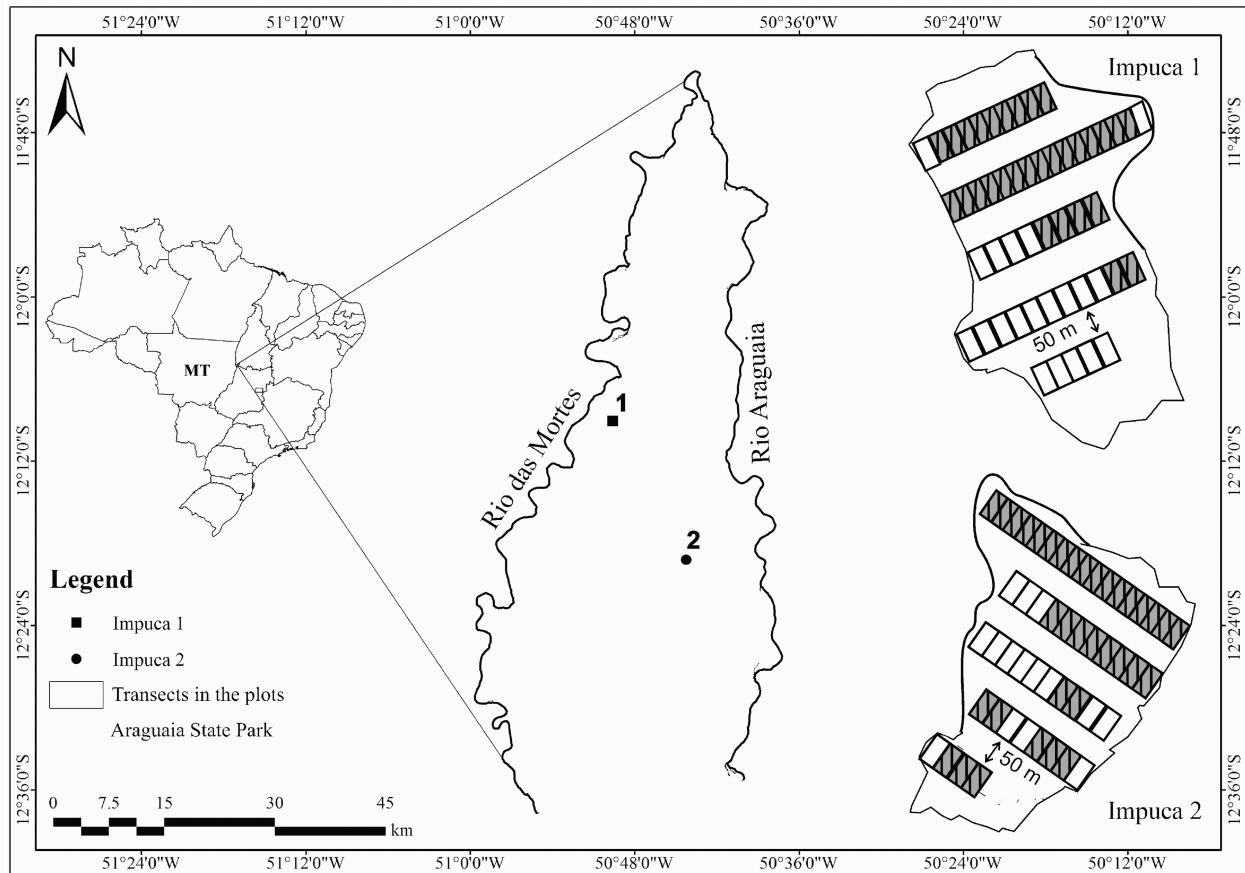
SPECIES	M	R	RBA	IBA	DBA	GBA	LBA
<b>IMPUCA 1 – unburned</b>							
<i>Occhthocosmus multiflorus</i> Ducke (Ixonanthaceae)	3.4	2.0	0.02	0.07	0.03	1.4	2.1
<i>Xylopia calophylla</i> R.E.Fr. (Annonaceae)	4.8	0.4	0.01	0.13	0	4.0	5.2
<i>Tachigali bracteosa</i> (Harms) Zarucchi & Pipoly (Fabaceae)	13.2	2.8	0.01	0.20	0.01	6.1	15.5
<i>Licania apetala</i> (E. Mey.) Fritsch (Chrysobalanaceae)	1.1	1.1	0.01	0.03	0.02	1.2	1.0
<i>Leptolobium nitens</i> Vogel (Fabaceae)	3.1	0	0	0.03	0.01	1.0	2.5
<i>Mabea paniculata</i> Spruce ex Benth.(Euphorbiaceae)	5.1	3.5	0.01	0.02	0.01	4.6	3.8
<i>Ormosia excelsa</i> Benth. (Fabaceae)	0	0	0	0.05	0	3.0	0
<i>Calophyllum brasiliense</i> Cambess. (Calophyllaceae)	5.0	1.8	0.01	0.05	0	4.9	1.0
<i>Diospyros tetrandra</i> Hiern (Ebenaceae)	1.7	0	0	0.04	0.01	2.5	0.3
<i>Diospyros poeppigiana</i> A. DC. (Ebenaceae)	0	4.0	0.02	0.04	0	7.0	0
<b>IMPUCA 1 – burned</b>							
<i>Licania apetala</i> (E. Mey.) Fritsch (Chrysobalanaceae)	2.2	0.3	0.01	0.08	0.01	0.5	1.1
<i>Tachigali bracteosa</i> (Harms) Zarucchi & Pipoly (Fabaceae)	22.1	0	0	0.25	0.01	4.5	9.1
<i>Duroia prancei</i> Steyerm. (Rubiaceae)	8.12	0.7	0.01	0.03	0.03	1.9	6.4
<i>Leptolobium nitens</i> Vogel (Fabaceae)	3.3	0	0	0.08	0.01	2.7	2.8
<i>Mabea paniculata</i> Spruce ex Benth. (Euphorbiaceae)	7.2	0.8	0.01	0.02	0.05	1.9	8.7
<i>Ormosia excelsa</i> Benth. (Fabaceae)	5.2	1.1	0.01	0.08	0.02	2.5	4.1
<i>Occhthocosmus multiflorus</i> Ducke (Ixonanthaceae)	9.5	3.1	0.01	0.02	0.01	5.2	14.6
<i>Calophyllum brasiliense</i> Cambess. (Calophyllaceae)	19.1	0	0	0.08	0.01	4.3	8.9
<i>Mauritiella armata</i> (Mart.) Burret (Arecaceae)	15.3	3.6	0.01	0.01	0.03	2.8	18.5
<i>Pera schomburgkiana</i> (Klotzsch) Müll. Arg. (Peraceae)	3.1	0	0	0.01	0.03	0.5	3.1



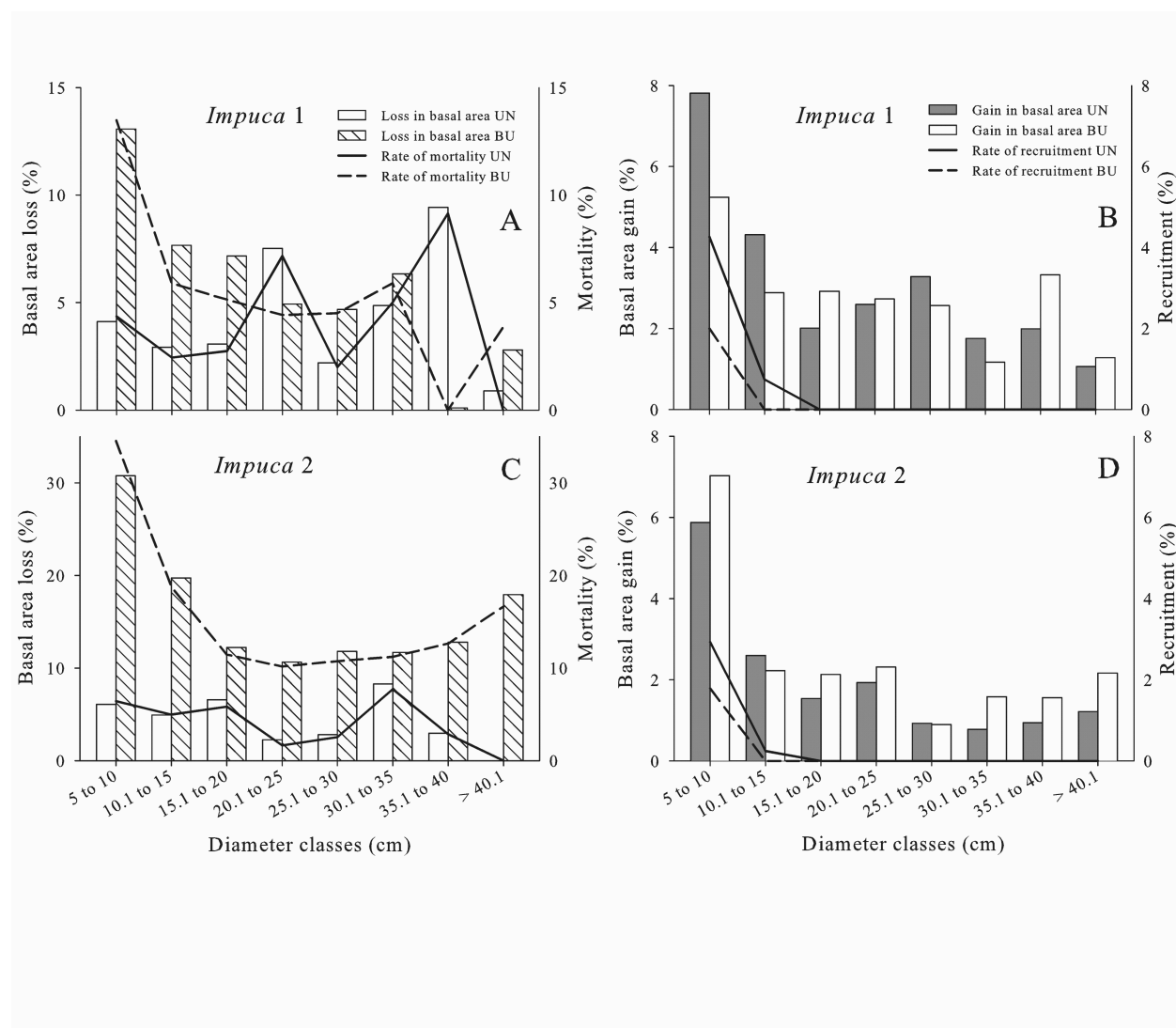
<b>IMPUCA 2 – unburned</b>							
<i>Micropholis gardneriana</i> (A. DC.) Pierre (Sapotaceae)	5.1	0.9	0.01	0.13	0.01	1.6	5.4
<i>Licania kunthiana</i> Hook. f. (Fabaceae)	4.3	0	0	0.05	0.01	1.3	4.5
<i>Licania apetala</i> (E. Mey.) Fritsch (Fabaceae)	1.8	0	0	0.02	0.01	0.5	0.6
<i>Diospyros tetrandra</i> Hiern (Ebenaceae)	4.6	0	0	0.07	0.04	1.8	3.3
<i>Ternstroemia candolleana</i> Wawra (Pentaphylacaceae)	1.5	0	0	0.02	0.01	1.5	0.5
<i>Symmeria paniculata</i> Benth. (Poligonaceae)	7.9	5.0	0.02	0.03	0.01	7.0	4.7
<i>Ochthocosmus multiflorus</i> Ducke (Ixonanthaceae)	2.2	1.1	0.01	0.01	0.01	1.1	1.9
<i>Roupala montana</i> Aubl. (Proteaceae)	3.3	0	0	0.02	0.01	1.6	1.4
<i>Eschweilera ovata</i> (Cambess.) Miers (Lecythidaceae)	8.4	0	0	0.02	0	2.0	5.3
<i>Combretum laxum</i> Jacq. (Combretaceae)	9.1	0	0	0.01	0.01	2.4	4.3
<b>IMPUCA 2 – burned</b>							
<i>Micropholis gardneriana</i> (A. DC.) Pierre (Sapotaceae)	25.5	0.7	0.01	0.16	0.01	1.9	13.6
<i>Calophyllum brasiliense</i> Cambess. (Calophyllaceae)	18.6	0	0	0.17	0	3.0	18.7
<i>Licania kunthiana</i> Hook. f. (Fabaceae)	13.9	0	0	0.09	0.01	2.2	8.3
<i>Ochthocosmus multiflorus</i> Ducke (Ixonanthaceae)	20.8	1.0	0.01	0.03	0.01	2.1	13.8
<i>Combretum laxum</i> Jacq. (Combretaceae)	67.2	7.2	0.01	0.01	0.01	4.9	47.1
<i>Diospyros poeppigiana</i> A. DC. (Ebenaceae)	27.5	0	0	0.02	0.01	1.5	21.5
<i>Roupala montana</i> Aubl. (Proteaceae)	24.4	0	0	0.03	0.01	1.9	17.7
<i>Ternstroemia candolleana</i> Wawra (Pentaphylacaceae)	25.3	0	0	0.02	0.01	1.5	24.2
<i>Sloanea garckeana</i> K. Schum. (Elaeocarpaceae)	13.9	0	0	0.04	0.03	1.4	6.4
<i>Eschweilera ovata</i> (Cambess.) Miers (Lecythidaceae)	18.1	0	0	0.06	0.01	3.9	10.1

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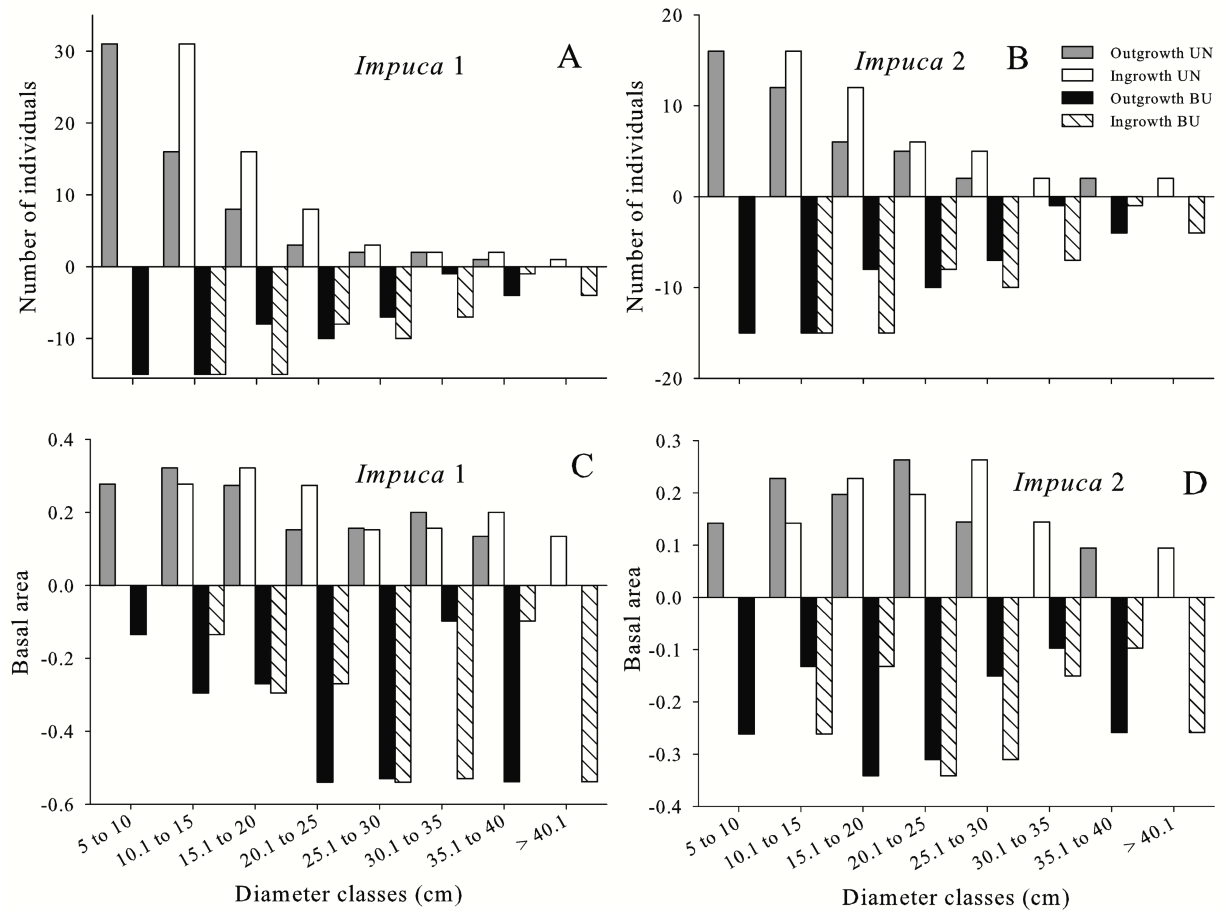
**Fig. 1.** Location of the seasonally flooded forests (*impucas*) sampled in the Araguaia State Park (PEA), State of Mato Grosso, and arrangement of the plots in the transects established in each *impuca*. ■ = burned subplots and □ = unburned subplots.



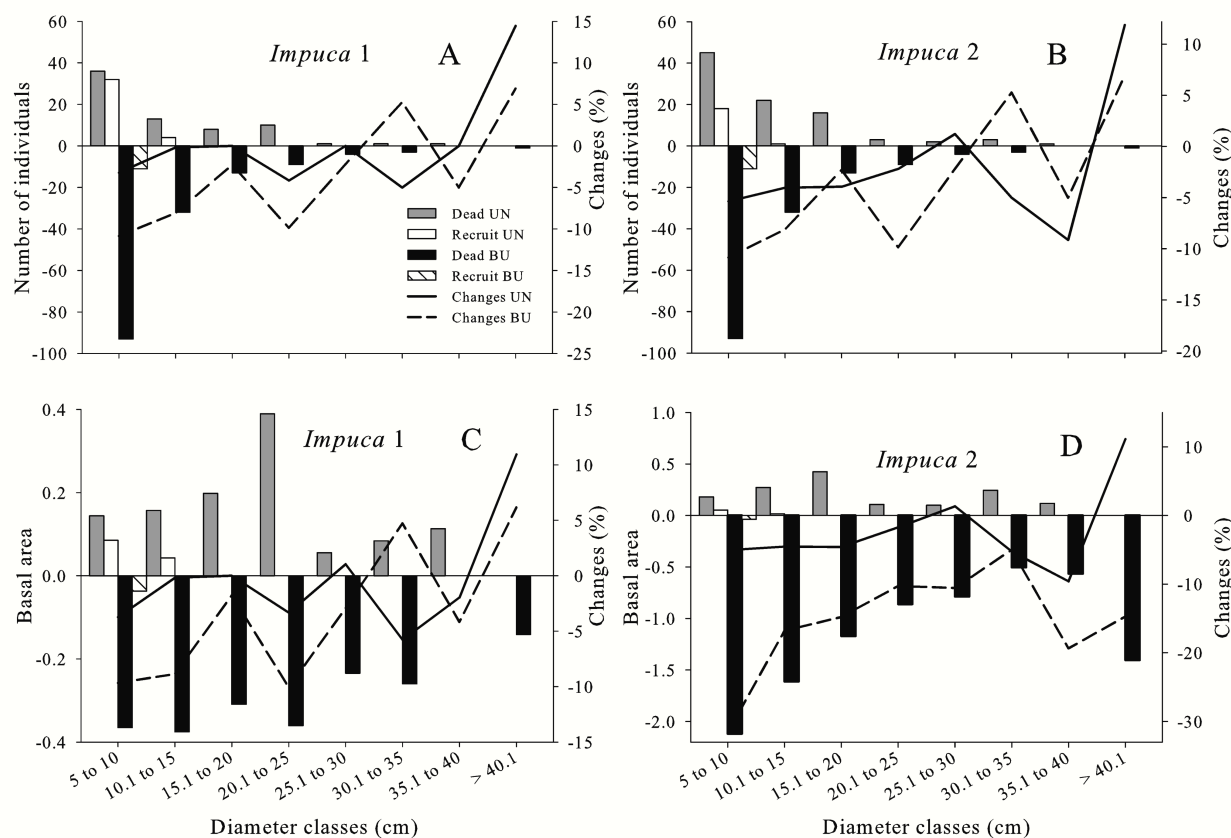
**Fig. 2.** Structural changes and dynamics of the woody vegetation between the years 2007 and 2010 by diameter classes of the burned and unburned sites of a seasonally flooded forest (*impucas* 1 and 2). A and C = Average annual rate of loss in basal area and average annual rate of mortality; B and D= Average annual rate of gain in basal area and average annual rate of recruitment; UN = unburned site and BU = burned site.



**Fig. 3.** Structural changes and dynamics of the woody vegetation by diameter classes of the burned and unburned sites of a seasonally flooded forest (*Impuca* 1 and 2). Number of the ingrowth (given by the entry of trees into a class by recruitment and growth) and outgrowth (given by the output of trees of a class by growth) considering both individual- and basal area-basis; UN = unburned site and BU = burned site.



**Fig. 4.** Changing parameters of the woody vegetation by diameter classes of the burned and unburned sites of seasonally flooded forests (*Impuca 1* and 2). A and B = Changing parameters in number of individuals and C and D = Changing parameters in basal area; UN = unburned site and BU = burned site.



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