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## 1 Forest Fires Facilitate Growth of Herbaceous Bamboos in Central Amazonia

2  
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21

### 22 Abstract

23 Severe droughts in Amazonia caused by El Niño and Atlantic dipole events are expected to  
24 become more frequent due to anthropogenic climate change. These droughts lead the tropical  
25 forests of central Amazonia to become increasingly exposed to fire. Forest-fire disturbances  
26 can create ideal scenarios for opportunistic plants, such as some bamboos. In this study, we  
27 investigate the influence of forest fires, canopy openness, and vertical distance to channel  
28 network (VDCN – a proxy for soil moisture availability) on the growth and expansion of  
29 *Olyra latifolia* and *Taquara micrantha* in the municipality of Autazes, Amazonas, Brazil. The  
30 density of these herbaceous bamboos was represented by the density of clumps (clumps ha<sup>-1</sup>)  
31 and of culms (culms ha<sup>-1</sup>), while bamboo growth was expressed as culms per clump and the  
32 average height of clumps. Principal component analysis (PCA) was used to evaluate bamboo  
33 density and growth together as a proxy for bamboo abundance in the understory. Forest  
34 disturbed by fire had a density of culms 116% higher than the value found in the control  
35 treatment. Plots affected by fire, which were at lower VDCN, showed evidence of higher  
36 potential for fire ignition in the low areas. The average number of culms per clump was  
37 significantly higher in post-burn forests. While canopy opening revealed a significant positive  
38 linear relationship with the abundance of herbaceous bamboo in our study area, VDCN had a  
39 negative effect on bamboo growth, suggesting that, in addition to fire, light in the understory  
40 and access to the water table are limiting factors for these two species in the upland forests of  
41 central Amazonia.

42  
43 **Keywords:** Amazonia; Brazil; biological invasion; fire; forest degradation; Olyreae; *Olyra*  
44 *latifolia*; *Taquara micrantha*; tropical forest  
45  
46

### 47 INTRODUCTION

48

49 Bamboos, which are popularly known as “*tabocas*” or “*taquaras*” in Brazilian Amazonia,  
 50 are members of the family Poaceae, subfamily Bambusoideae. Bamboos have almost 1700  
 51 described species grouped into approximately 127 genera, and are classified into three tribes  
 52 (Clark & Oliveira, 2018). The woody bamboo species are grouped into the tribes  
 53 Arundinarieae and Bambuseae, which are, respectively, composed of 581 species primarily in  
 54 the temperate zone and 976 species primarily in the tropics. Herbaceous bamboos are  
 55 included in the tribe Olyreae, which is currently composed of 124 species in 24 genera  
 56 (Vorontsova et al., 2016; Soreng et al., 2017; Lima et al., 2020). Herbaceous bamboos  
 57 usually occur in the understory in tropical forests (Clark et al., 2015), but a few species (i.e.  
 58 *Olyra* spp. and *Taquara* spp.) commonly occur along forest edges or in gaps (Oliveira et al.,  
 59 2020a; Soderstrom & Zuloaga, 1989).

60 Previous studies have shown that multiple disturbances can accelerate the growth of  
 61 potentially dominant bamboo species (Gagnon & Platt, 2008). This phenomenon was  
 62 observed for *Melocanna baccifera* in northeastern India (Lalnunmawia, 2008), Bangladesh,  
 63 Myanmar and Thailand (Platt et al., 2010), where some areas are also dominated by bamboos  
 64 in the genus *Thyrsostachys* (Ramyarangsi, 1985). In Vietnam, *Schizostachyum* species  
 65 dominate secondary vegetation areas where tropical forests have been degraded by fire,  
 66 logging, and deforestation for cattle ranching and by the impacts of war (Banik, 2015). In  
 67 Amazonian forests, it is likely that *Guadua* spp. have benefitted from natural disturbances  
 68 such as strong wind-throws (Griscom & Ashton, 2003) and anthropogenic disturbances such  
 69 as fire and logging (Keeley & Bond, 1999; Veldman et al., 2009). Because of their strong  
 70 underground rhizome system and the climbing nature of these woody bamboos promoting  
 71 damage to trees, clearings can also trigger a self-perpetuating bamboo disturbance cycle in  
 72 the forest over time, even in undisturbed areas (Griscom & Ashton, 2006; Medeiros et al.,  
 73 2013). Bona et al. (2020) point out that *Guadua weberbaueri* Pilg. acts as a filter for the  
 74 establishment of trees in the understory, reducing the number of species dispersed via seed  
 75 rain and affecting forest dynamics.

76 The intense dry periods caused by El Niño make the forests in central Amazonia  
 77 susceptible to forest fires (Aragão et al., 2007). These fires are responsible for the mortality  
 78 of many trees, leading to changes in forest structure and increasing the probability of  
 79 subsequent fires (Nepstad et al., 1999; Barlow & Peres, 2004). Fire spreads easily through  
 80 seasonally flooded forests, where it also causes extensive damage (de Resende et al., 2014).  
 81 Forest fires have become more frequent and widespread in many regions of Amazonia in  
 82 recent years (Alencar et al., 2015), impacting the entirety of the Amazon Basin in 2019  
 83 (Lizundia-Loiola et al., 2020; Kelley et al., 2020). In upland forests of central Amazonia,  
 84 wildfires are likely to become more frequent and widespread with the shift of Brazil’s current  
 85 presidential administration toward less environmental regulation (Ferrante & Fearnside,  
 86 2019). Although herbaceous bamboos are not likely to have additional traits that confer fire  
 87 resistance, their growth may be favored by the gaps resulting from the death of trees  
 88 following a forest fire (Banik, 2015).

89 In addition to canopy gaps, the water table depth is another key parameter that is  
 90 recognized for conditioning vegetation composition in central Amazonia (Schietti et al.,  
 91 2014). In general, soil moisture and water dynamics on the floor of a tropical forest are  
 92 mainly controlled by local topography and net rainfall rates (Maass & Burgos, 2011; Malhi et  
 93 al., 2002; Marin et al., 2000). Poulsen & Balslev (1991) showed that topography is a key  
 94 environmental factor for the distribution patterns of many herbaceous species in Amazonia.  
 95 In central Amazonia, fluctuations of local soil draining potential are associated with the  
 96 vertical height above the nearest drainage channel (Nobre et al., 2011), which also reflects the  
 97 horizontal distance from a stream (Broedel et al., 2017; Hodnett et al., 1997; Tomasella et al.,  
 98 2008).

99 Our re-measurement of permanent plots in a forest in the municipality (county) of  
 100 Autazes suggests that populations of two herbaceous bamboos [*Olyra latifolia* L. and  
 101 *Taquara micrantha* (Kunth) I.L.C. Oliveira & R.P. Oliveira] might be expanding following  
 102 forest fire. While a high abundance of large, well-developed clumps was observed in an area  
 103 affected by fire, few smaller clumps were observed in an adjacent unburned area in the same  
 104 forest remnant (Supplementary Material, Fig. S1). The present study was undertaken to verify  
 105 this observation, investigating whether forest fire favors the increase in density and growth of  
 106 herbaceous bamboo species in central Amazonia. It is worth mentioning that both these  
 107 species are in need of ecological studies. While a considerable number of observational  
 108 studies have been done for the Olyreae group (i.e., Soderstrom, 1981, 1982; Soderstrom et  
 109 al., 1988; Soderstrom & Zuloaga, 1989; Clark, 1990; Oliveira & Longhi-Wagner, 2001;  
 110 Oliveira et al., 2020b), there is a lack of field measurements to quantify the specific growth  
 111 responses of *O. latifolia* and *T. micrantha* after fire disturbances in Amazonian forests.

112 Disturbances such as forest fires reduce forest canopy cover, which increases the incidence  
 113 of light in the understory (Almeida et al., 2016; Brando et al., 2014; Morton et al., 2011). In  
 114 recent decades, invasions of herbaceous species after fire events were reported in different  
 115 parts of Amazonia (Brando et al., 2014; Flores et al., 2016). Because the herbaceous ground  
 116 cover has an influence on tree seed germination by imposing a physical barrier for seeds  
 117 dispersed to the forest floor (George & Bazzaz, 2003), increased densities of herbaceous  
 118 species in the understory may play an important role in forest dynamics, acting as a filter for  
 119 tree regeneration over time. Here we hypothesize that forest fires promote an increase in  
 120 growth and abundance of *Olyra latifolia* and *Taquara micrantha* in upland forests of central  
 121 Amazonia. Because the occurrence of these species is common along forest edges or in gaps  
 122 (Oliveira et al., 2020a; Soderstrom & Zuloaga, 1989), and because herbaceous bamboos often  
 123 have shallow roots to access soil water, we also hypothesize that the growth of these  
 124 widespread species is favored by canopy openness and is constrained by water-table depth,  
 125 regardless of disturbance by fire. To test these hypotheses, we compared growth and  
 126 abundance of *O. latifolia* and *T. micrantha* between burned and unburned areas. We also  
 127 evaluated relationships between canopy openness, vertical distance to channel network  
 128 (VDCN) and growth of these species.

## 131 METHODS

### 133 Study area

135 The study was carried out in an area of upland (*terra firme*) forest (3°32'S, 59°16'W)  
 136 located in the northern portion of the Purus-Madeira interfluvium (3°32'S, 59°16'W) in the  
 137 municipality of Autazes (Amazonas, Brazil), approximately 100 km southeast of Manaus and  
 138 with a total area of 763.226 ha. Surrounded by the Lower Amazon (Amazonas), Madeira,  
 139 Upper Amazon (Solimões) and Lower Purus Rivers, the annual precipitation in Autazes  
 140 varies between 2000 and 2400 mm (Sombroek, 2001). Highway AM-254, which connects the  
 141 municipality to Highway BR-319, is the main access to the study area, which is an upland  
 142 forest area adjacent to small farms, flooded forests (*igapós*) and private properties.

143 Large-scale forest fires affected the region during the 2015 dry season peak, between  
 144 September and October (Supplementary Material, Fig. S2). This was a period of prolonged  
 145 precipitation deficits and a marked increase in temperatures due to the occurrence of a strong  
 146 El Niño (Aragão et al., 2018; Panisset et al., 2017).

### 148 Herbaceous bamboo sampling

149

150 In December 2015, twelve rectangular permanent plots ( $250 \times 10$  m) were installed in the  
 151 study area two months after the end of the forest fire. Each permanent plot is divided into ten  
 152  $25 \times 10$ -m sections. Six of the 12 plots are located in areas affected by the 2015 forest fire  
 153 (fire treatment) and 6 plots in areas with no known recent impacts (control treatment). The  
 154 minimum distance between adjacent plots is 250 m. Size and abundance of herbaceous  
 155 bamboos were sampled in November 2017, in three subplots ( $5 \times 5$  m) systematically  
 156 allocated 95 m apart within their respective permanent plots. We thus sampled 18 subplots in  
 157 each treatment, totaling 885 culms and 303 clumps measured in  $900 \text{ m}^2$  (Supplementary  
 158 Material, Figs. S2 and S3).

159 Samples of herbaceous bamboos were collected in the field and identified in the herbarium  
 160 of the National Institute for Research in Amazonia (INPA) (Supplementary Material, Fig.  
 161 S1). These are two species in the family Poaceae, subfamily Bambusoideae, tribe Olyreae: *O.*  
 162 *latifolia* and *T. micrantha*. However, we did not distinguish between these species in our  
 163 analyses. Both are native to tropical American forests (Longhi-Wagner, 2012), being the  
 164 tallest and most-robust species among herbaceous bamboos that commonly occur near forest  
 165 edges and in gaps (Thompson et al., 1998; Lima et al., 2015).

166 To address the abundance and growth of these herbaceous bamboos in the understory, we  
 167 sampled density of clumps (clumps  $\text{ha}^{-1}$ ), density of culms (culms  $\text{ha}^{-1}$ ), number of culms per  
 168 clump and the average height of clumps. We estimated the height variable from the direct  
 169 measurement of at least three culms per clump: the highest culm, the lowest culm and one of  
 170 intermediate size. This sampling is justified by field observations, indicating that the height  
 171 of the culms of the same clump showed little variation. Individual clumps were visually  
 172 defined in the field. Although we did not follow any specific rules during our data collection  
 173 in 2017, in order to increase the representation and visibility of bamboo in forest surveys, a  
 174 recently published protocol provides guidelines for sampling and monitoring bamboo in  
 175 tropical forests (Fadrique et al., 2020).

176

## 177 Environmental variables

178

179 Canopy openness is an indicator of light availability in the understory, and openness is  
 180 increased in fire-affected areas (de Almeida et al. 2016). To calculate the canopy-opening  
 181 fraction, we recorded the canopy at the central point of each subplot using a hemispherical  
 182 lens (Soligor fisheye,  $0.25 \times 52$  mm) coupled to a digital camera (Nikon D60 10.2  
 183 megapixel). All images were taken under uniform diffuse light conditions on the same days  
 184 that the herbaceous bamboos were sampled. The camera was always placed at a height of  
 185 1.10 m, plumbed and facing north, with its view aimed directly upward ( $90^\circ$  from the  
 186 horizontal). Images were processed using Gap Light Analyzer (GLA v2.0) free software, with  
 187 thresholds visually defined in each image for the binary conversion step. A similar  
 188 methodology has been adopted in other studies (Galvão et al., 2011; Bispo et al., 2016).  
 189 Besides canopy openness, we also sampled the number of trees with fire marks and the  
 190 maximum height of these marks on the trees.

191 In recent decades, calculations of water storage and movements on land have been possible  
 192 using Digital Elevation Models (DEMs) that represent the spatial variation of elevations in a  
 193 given landscape (Moore et al., 1992). In this study we compared burned and unburned plots  
 194 using the VDCN terrain model (Conrad et al., 2015). One advantage of using VDCN and  
 195 similar algorithms to assess soil water is that DEMs are normalized according to distributed  
 196 vertical distances relative to the outflow channels (Nobre et al., 2011). Using the open-source  
 197 software SAGA (version 2.3.2), we processed the local DEM with 12.5-m resolution derived  
 198 from the Radiometric Terrain Correction (RTC) products from the Advanced Land Observing

199 Satellite (ALOS) Phased Array type L-band Synthetic Aperture Radar (PALSAR) data to  
 200 obtain the channel network and to determine the VDCN for the study area. VDCN values for  
 201 each subplot were extracted using the GPS coordinates previously collected in the field.

202

### 203 **Data analysis**

204

205 The non-parametric Mann-Whitney *U*-test was applied to compare treatments (Mann &  
 206 Whitney, 1947). PCA was performed to summarize bamboo abundance based on a  
 207 correlation matrix of variables related to growth and development of herbaceous bamboo in  
 208 the understory: Mean clump height (m), clump density (clumps ha<sup>-1</sup>), mean of culms per  
 209 clump and culm density (culms ha<sup>-1</sup>). Histograms were examined to assess the distribution of  
 210 each variable, and transformations were done by centering (subtracting means) and scaling  
 211 the dataset (dividing centered values by their standard deviations). Finally, the first PCA axis  
 212 (PC1) was correlated with canopy openness and VDCN to evaluate the relationship between  
 213 environmental drivers and bamboo abundance (as indicated by a measure combining the  
 214 number and the height of bamboo clumps).

215 In order to assess the relative effect of each environmental variable (and the interactions  
 216 among variable effects) on bamboo abundance, we used an automated model-selection  
 217 feature from the “glmulti” package in R (Calcagno & de Mazancourt, 2010) with bamboo  
 218 abundance (PC1) as the dependent variable. The best model was selected by testing all  
 219 predictor variables together: VDCN (m), canopy openness (%), number of trees with fire  
 220 marks, height of fire marks, and treatment (as a dummy variable). Through an exhaustive  
 221 screening of the candidate models using the main effects and pairwise interactions of the  
 222 predictors, the possible models were indicated based on the Delta Akaike Information  
 223 Criterion ( $\Delta$  AIC) ranking. To select the best model among all the possibilities, we chose the  
 224 highest adjusted coefficient of determination ( $R^2$ adj.) as a secondary criterion. More  
 225 precisely, all models having  $\Delta$  AIC < 2 were considered as having substantial support, but of  
 226 the models meeting this criterion we preferred the model with highest  $R^2$  adj. Our selected  
 227 model included three predictor variables and one interaction:

228

$$229 \quad PC1 = \beta_0 + (\beta_1 \times VDCN) + (\beta_2 \times CO) + (\beta_3 \times Treatment) + (\beta_4 \times CO \times Treatment) \quad (Eq. 1)$$

230

231 Where:

232  $\beta_0$ : Intercept;233  $\beta_1$  to  $\beta_4$ : Estimated coefficients (Figure 6);

234 VDCN: Vertical distance to channel network (m);

235 CO: Canopy openness (%);

236 Treatment: Dummy variable with two levels (control &amp; fire).

237

238 The geographical coordinates (latitude and longitude) of the central point of each plot were  
 239 collected with a navigation GPS device (Garmin 64ST). These coordinates were used to  
 240 control spatial autocorrelation in the model through a generalized least-squares function from  
 241 the “nlme” package in R (Pinheiro et al., 2015). The strength of each variable in the model  
 242 was assessed by both the standardized coefficients and the *p* value. We conducted all of the  
 243 analyses in R software (R Core Team, 2018).

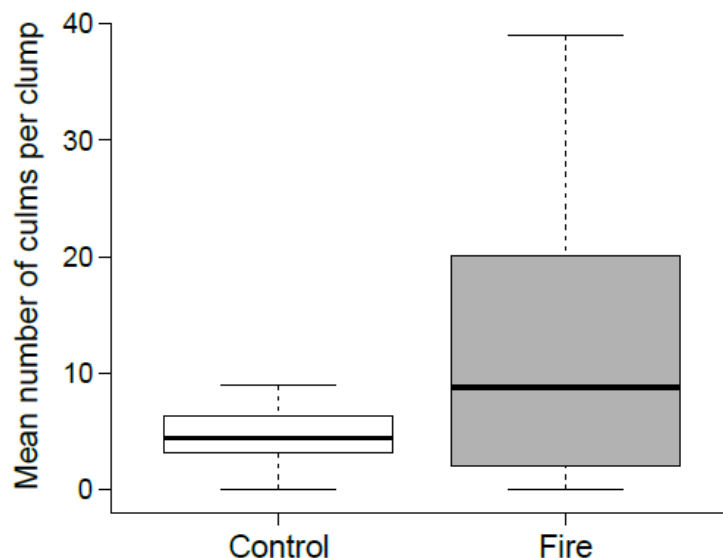
244

## 245 **RESULTS**

246

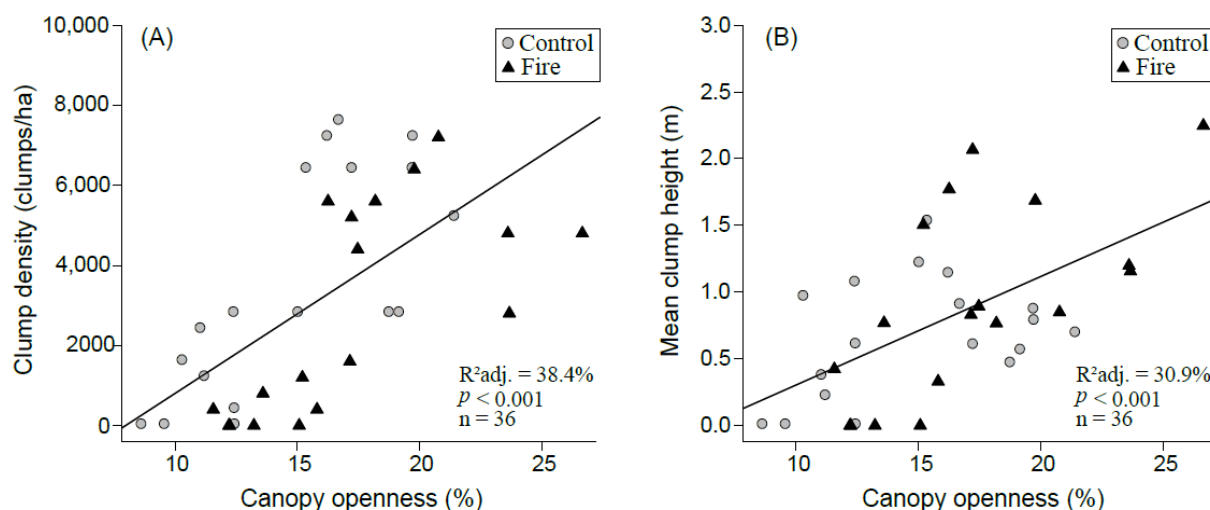
247 While the clump density in the control plots (3511 clumps ha<sup>-1</sup>) was higher than in the fire-  
 248 affected plots (2844 clumps ha<sup>-1</sup>), the culm density in the fire-affected plots (40,644 culms ha<sup>-1</sup>)

249 <sup>1</sup>) was more than twice that observed in control plots (18,777 culms ha<sup>-1</sup>). The average height  
 250 of clumps in the burned area (0.92 m) was 28% higher than the value observed in the control  
 251 treatment (0.66 m). However, no significant differences between treatments were observed  
 252 for the densities of clumps ( $U = 190$ ;  $p = 0.38$ ) and of culms ( $U = 126$ ;  $p = 0.26$ ), or for the  
 253 average height of clumps ( $U = 134$ ;  $p = 0.38$ ). We found a significant difference for the  
 254 average number of culms per clump ( $U = 98.5$ ;  $p < 0.05$ ) between the two treatments (Fig. 1).



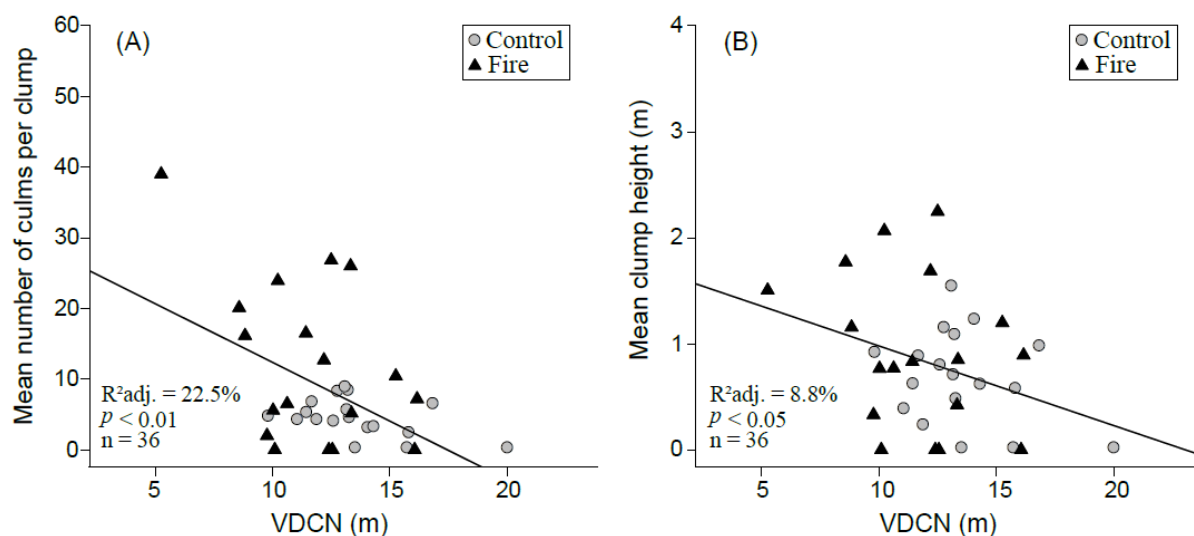
255 **Figure 1.** Mean number of culms per clump in the studied treatments. Boxplots show the median  
 256 (horizontal lines), the interquartile range for the first (25<sup>th</sup>) and third (75<sup>th</sup>) percentiles (boxes), and  
 257 the minimum and maximum values (whiskers).  
 258  
 259

260 Canopy openness was significantly positively related to culm density and mean clump  
 261 height (Fig. 2). The average canopy openness in the fire affected plots (17.2%) was not  
 262 significant different from the control treatment (14.8%;  $U=114.5$ ;  $p = 0.137$ ).



263 **Figure 2.** Relationships between the density of clumps (A) and average height of clumps  
 264 (B) with the canopy opening.  $R^2_{adj.}$  = adjusted coefficient of determination.  
 265  
 266

267 In contrast to the positive effect of canopy opening on the growth of herbaceous bamboo,  
 268 VDCN was significantly negatively related to the mean number of culms per clump and mean  
 269 clump height (Fig. 3).

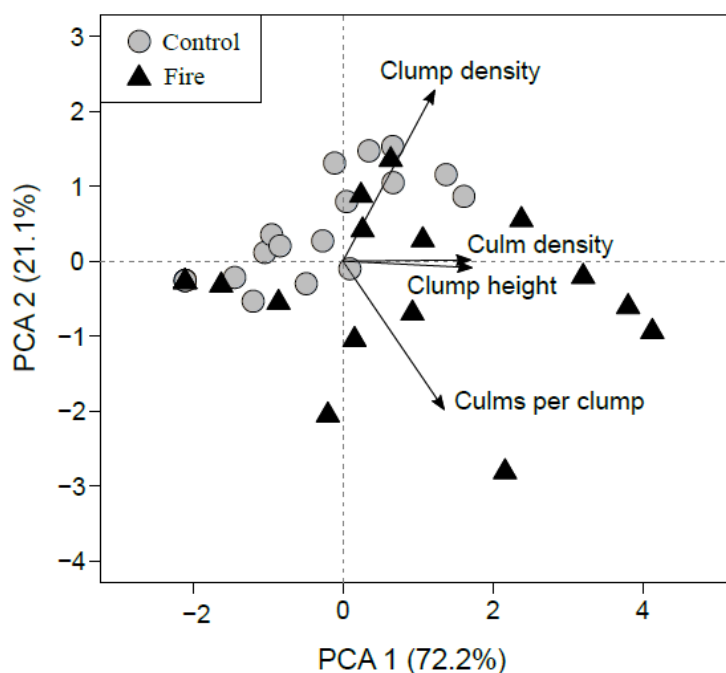


270

271 **Figure 3.** Relationships between the mean number of culms per clump (A) and mean clump  
 272 height (B) with the vertical distance to channel network (VDCN).  $R^2_{adj.}$  = adjusted  
 273 coefficient of determination.

274

275 PCA of the combined dataset revealed that the effects of fire were associated with  
 276 variation in clump height and number of culms per clump (Fig. 4), where the first two  
 277 principal components accounted for 93.3 % of the variation in herbaceous bamboo abundance  
 278 (PC1: 72.2%; PC2: 21.1%).

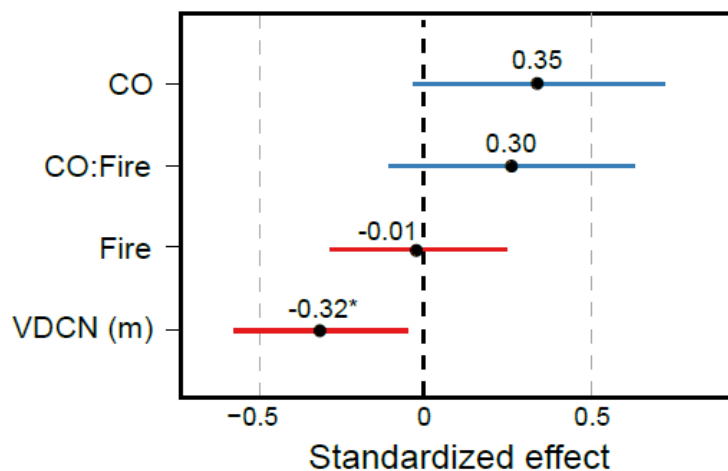


279

280 **Figure 4.** First two principal components from PCA analysis of bamboo abundance data,  
 281 plotted for individual subplots. Symbols indicate different treatments.

282

283 Bamboo abundance and growth expressed by PC1 showed a significant positive linear  
 284 relationship with canopy openness and a significant negative linear relationship with VDCN  
 285 (Fig. S4). The model selected to predict bamboo abundance (PC1) included three variables  
 286 and one interaction, and explained 49% ( $R^2_{adj.} = 0.489$ ,  $p < 0.001$ ) of the variance in PC1  
 287 (Fig. S5). The relative importance of each predictor in the model was addressed by both the  $p$   
 288 value and the standardized coefficients. VDCN had the highest relative importance in  
 289 predicting bamboo abundance, followed by canopy openness and fire (Figures 5 and S6).



290  
 291 **Figure 5:** Standardized coefficients and confidence intervals of predictor variables (Eq. 1).  
 292 The red and blue colors represent negative and positive values, respectively (\*  $p < 0.05$ ). The  
 293 effect of fire was observed by taking the control treatment as the reference.

294  
 295 Although VDCN has a negative effect on bamboo abundance, a significant difference ( $U =$   
 296  $226$ ;  $p = 0.043$ ) was observed for VDCN between burned and unburned plots, showing that  
 297 the plots affected by fire were located closer to drainage channels. The average VDCN found  
 298 for the control treatment was 13.45 m (SD = 2.37 m), a value higher than the 11.58 m  
 299 observed for the fire treatment (SD = 2.77 m).

## 300 301 DISCUSSION

302  
 303 In contrast to most herbaceous bamboo species found in Brazil, which are restricted to  
 304 small populations and are becoming increasingly rare due to the loss of habitats through  
 305 deforestation (Oliveira et al., 2020b), *O. latifolia* and *T. micrantha* occur widely in Brazilian  
 306 forests (Oliveira & Longhi-Wagner, 2001; Oliveira et al., 2011; Dórea et al., 2018). The  
 307 absence of significant differences for density-related variables indicates that, independent of  
 308 fire, these two species of herbaceous bamboo are common in the understory of the study area.  
 309 However, for the northern portion of the Purus-Madeira interfluvium, we found only one report  
 310 of *O. latifolia* (Medina et al., 1999) and no reports of *T. micrantha* (e.g., Junk & Piedade,  
 311 1993). The occurrence of these species is reported only on the other side of the Amazon  
 312 River: *O. latifolia* in a forest plantation at the Experimental Station of Tropical Forestry, 50  
 313 km north of Manaus (Lima & Vieira, 2013); and *T. micrantha* in a plot located in an upland  
 314 area with low slope in the Ducke Reserve, adjacent to Manaus (Drucker et al., 2005). In both  
 315 cases, the species were reported as occurring at extremely low absolute densities ( $< 15$   
 316 clumps  $ha^{-1}$ ), while we found a mean of 3178 clumps  $ha^{-1}$  in the studied areas. In addition to  
 317 these records, two species of the genus *Olyra* were reported in the *igapó* (black-water  
 318 swamp) forests of the middle Rio Negro region (Lopes et al., 2014).

319 Here we show that the growth of the two species can be favored by forest fire, since the  
 320 clumps in the fire affected plots had higher numbers of culms (Fig. 1). No other study in  
 321 Amazonia has indicated that these species are favored after a forest-fire disturbance. We  
 322 found only one record of numerous individuals of *O. latifolia*, this being in a fragment of  
 323 Open Ombrophilous Forest in southeastern Mato Grosso state (Brazil) 15 years after a forest  
 324 fire (Coelho et al., 2015). Therefore, dominant populations of *T. micrantha* have been found  
 325 to be related to forest degradation processes (e.g., Maciel et al., 2011; Coelho et al., 2015).  
 326 Fire has been found to promote invasion of herbaceous species in southeastern Amazonian  
 327 forest (Brando et al., 2014) and in Amazonian blackwater floodplain forests (Flores et al.,  
 328 2016).

329 We also showed that increased canopy openness favored the growth of the herbaceous  
 330 bamboos (Fig. 2), indicating that light in the understory is a limiting factor for the occurrence  
 331 and growth of these species in upland forests of central Amazonia. A similar relationship  
 332 between canopy opening and an increase of both an alien grass (*Urochloa maxima*) and a  
 333 native bamboo (*Guadua paniculata*) was found 1-5 years after logging in a deciduous  
 334 tropical forest, in Bolivia (Veldman et al., 2009). However, while this behavior is well known  
 335 for alien grasses and woody bamboos (i.e., *Guadua* spp.), most herbaceous bamboos are  
 336 vulnerable to disturbances (Oliveira et al., 2006; Pohl, 1977), and many species are currently  
 337 threatened with extinction (Oliveira et al., 2020b).

338 The first PCA axis (PC1) of our model explained 72.2% of the variation in parameters  
 339 related to abundance and growth of the herbaceous bamboos. Opposing relationships were  
 340 observed between PC1 and canopy openness and between PC1 and VDCN, suggesting that  
 341 these variables have opposite effects on the presence of herbaceous bamboo in the understory  
 342 of the study site (Figures 2, 3 and S4). The lower VDCN observed for the burned plots (Fig.  
 343 7) suggests that most of the fires at the study site were ignited in the valleys and spread to  
 344 adjacent forests, corroborating other studies in central Amazonia (de Almeida et al., 2016;  
 345 Flores et al., 2016). Along with promoting a decrease in forest cover and an increase in  
 346 canopy openness, fire in lowland forests can also facilitate the invasion of herbaceous species  
 347 (Flores et al., 2016). Although VDCN was the most important variable in our model for  
 348 predicting bamboo abundance, the interaction between canopy openness and fire showed a  
 349 positive effect on the growth of herbaceous bamboo species in the understory (Fig. 5 and  
 350 Supplementary Material, Fig. S7). This suggests that new gaps formed by fallen trees after  
 351 fire events may facilitate bamboo growth, especially in forests located at low VDCN.

352 Fires in Amazonian forests have been shown to spread more easily and promote greater  
 353 damage (i.e., tree mortality and delayed natural regeneration) in lowland rather than in upland  
 354 forests (Flores et al., 2014; Resende et al., 2014). As our sample took place 2 years after the  
 355 fire, the absence of a significant difference in canopy openness between the treatments can be  
 356 related to a rapid colonization of the canopy by fast-growing species in the burnt area  
 357 (Barlow & Peres, 2008; Cochrane & Schulze 1999; Numata et al., 2017), or to insufficient  
 358 sampling area. We stress that a better insight into the assessment of the effects of fire on  
 359 canopy structure can be achieved using other techniques that cover more extensive areas (i.e.  
 360 laser scanning and photogrammetry). Barlow et al. (2003) showed that the mortality of large  
 361 trees in Amazonian forests is intensified three years after fire, which would continue to create  
 362 gaps and provide conditions for the establishment and growth of herbaceous bamboo several  
 363 years after a fire.

364 The presence of dense populations of bamboos and other grasses also increases the  
 365 flammability of the understory (D'Antônio & Vitousek, 1992), in addition to covering the soil  
 366 and thus hindering natural regeneration and causing loss of the economic value of the forest  
 367 over time (Bona et al., 2020; Edwards-Widmer, 1999; Griscom & Ashton, 2003). This may  
 368 be a trigger for the system to be trapped in either a grass-dominated vegetation (Veldman &

369 Putz, 2011) or in a fire-dominated savanna state (Bond, 2008; Hoffman et al., 2009; Flores et  
 370 al., 2016). The increased number of culms per clump of *O. latifolia* and *T. micrantha*  
 371 observed after fire can contribute to increasing the density of the herbaceous layer in the  
 372 understory. Studies have shown that increased densities of herbaceous species in the  
 373 understory can impose a barrier for the germination of seeds on the forest floor, influencing  
 374 the dynamics of tree regeneration over time (George & Bazzaz, 2003; Royo & Carson, 2006;  
 375 Thrippleton et al., 2016). However, unlike many woody bamboos, herbaceous bamboos do  
 376 not have mechanisms to lean on trees and access the forest canopy, causing physical damage  
 377 and even the death of individual trees (Griscom & Ashton, 2006).

378 The municipality of Autazes has one of the highest frequencies of forest fire in the state of  
 379 Amazonas (White, 2018). Considering a 31-year time series (1985-2015), the area affected  
 380 by forest fires in this municipality was larger than the area impacted by deforestation, with  
 381 the occurrence of these fires being mainly in El Niño years (Reis, 2020). With the largest  
 382 herd of water buffaloes and the ninth largest herd of bovine cattle, the municipality leads  
 383 dairy production in the state of Amazonas (Almundi & Pinheiro, 2015). Repeated forest fires  
 384 in years of strong seasonal drought can contribute significantly to an increase in the mortality  
 385 of large trees and, consequently, to the abundance of herbaceous bamboo in the region. In  
 386 addition to the local reduction in biodiversity and loss of economic value of the forest for  
 387 timber management, the long-term degradation caused by repeated fires can contribute to the  
 388 expansion of cattle ranching in the region, compromising the resilience of important  
 389 ecosystem services maintained by the forest.

390 The negative relationship between bamboo abundance and VDCN suggests that, in  
 391 addition to light, access to the water table might be another limiting factor for the  
 392 development of herbaceous bamboo in the understory. However, as VDCN is not a direct  
 393 measurement of soil water storage, and our burned plots were located at lower VDCN, further  
 394 studies are needed to confirm the patterns observed between bamboo abundance and water  
 395 availability. We also stress that further research is needed on: (1) the occurrence and ecology  
 396 of *O. latifolia* and *T. micrantha* in central Amazonia, (2) the extent of areas of forest with  
 397 understories dominated by herbaceous bamboos, (3) the role of fire in the possible increase of  
 398 these bamboo areas, (4) the temporal dynamics of herbaceous bamboo populations, and (5)  
 399 the impact of bamboo on natural regeneration and on the floristic compositions of these  
 400 forests.

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## 403 CONCLUSION

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405 Although *Olyra latifolia* and *Taquara micrantha* are common in the understory of the  
 406 study area independent of fire disturbance, these herbaceous bamboos have higher numbers  
 407 of culms per clump following forest fire. While this effect is believed to be linked to greater  
 408 canopy openness due to the death of large trees, this behavior is atypical for the vast majority  
 409 of species in the Olyreae group. However, we showed that access to the water table is a  
 410 possible limiting factor for the growth and development of these species in central Amazon  
 411 forests.

412 The effect of forest fire on populations of herbaceous bamboos was observed two years  
 413 after the disturbance. This is the first study indicating that these species are favored after a  
 414 forest-fire disturbance in the upland forests of central Amazonia. Our results are not  
 415 representative of all herbaceous bamboos and further information is needed to better  
 416 understand the impacts of the increased growth of these two most-widespread herbaceous-  
 417 bamboo species on the regeneration and diversity of trees and palms in the understories of  
 418 these forests.

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## SUPPORTING INFORMATION

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## DATA AVAILABILITY STATEMENT

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1 **SUPPLEMENTARY MATERIAL**

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3 **Forest Fires Facilitate Growth of Herbaceous Bamboos in Central Amazonia**

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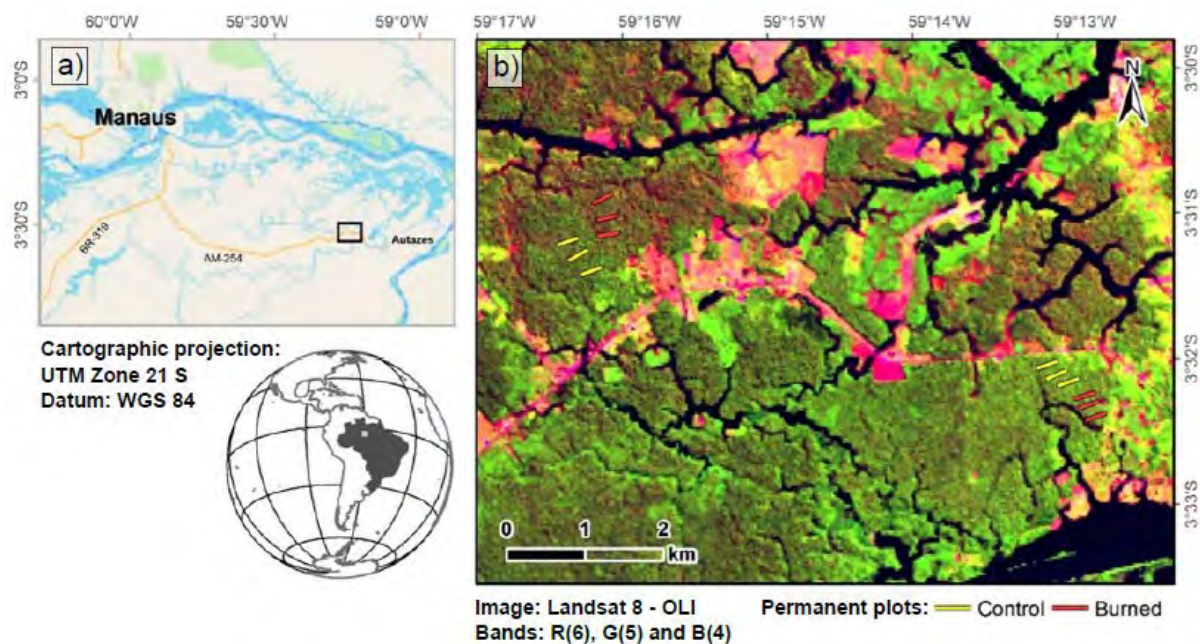
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FIGURE S1



28 Figure S1. (A) Moderate occurrence of herbaceous bamboo in the understory of an unburned  
29 forest area. Location [3°31'02" S, 59°16'09" W], 7 November 2016. (B) Strong occurrence of  
30 herbaceous bamboo in the understory of a burned forest area. Location [3°33'42" S,  
31 59°12'80" W], 11 November 2016. Voucher specimens of (C) *Olyra latifolia* (herbarium no.  
32 5108) and (D) *Taquara micrantha* (herbarium no. 27187), which are deposited at the INPA  
33 Herbarium (Manaus, Amazonas, Brazil).  
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## 35 FIGURE S2



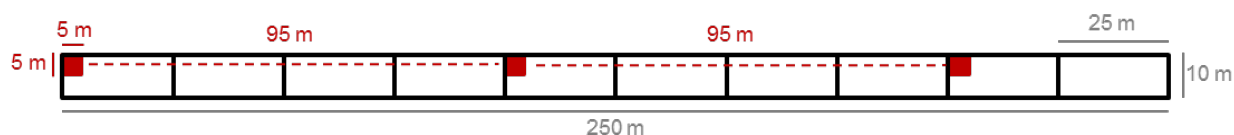
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37 Figure S2. Location map of plots with indication of the burned area (b) in the municipality of  
38 Autazes (a). The image acquired on July 7, 2017 is courtesy of the United States Geological  
39 Survey (USGS).

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## 42 FIGURE S3

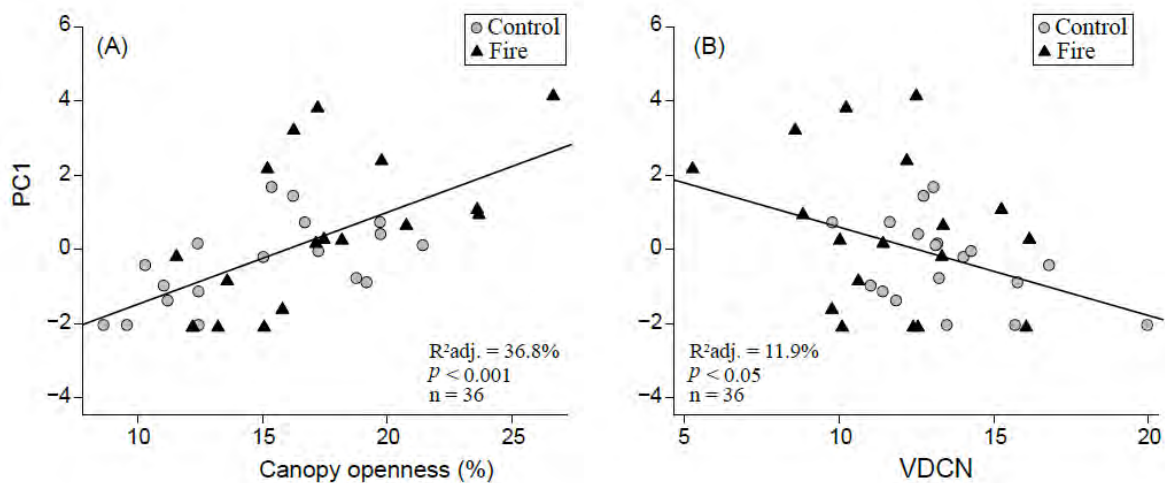
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45 Figure S3. Sampling design within each permanent plot. The black lines represent the  
46 borders of a  $250 \times 10$ -m permanent plot from the Fire-Associated Transient Emissions in  
47 Amazonia Project (FATE-Amazonian Project), which is divided into ten  $25 \times 10$ -m sections.  
48 The  $5 \times 5$ -m red rectangles represent the sub-plots for sampling the herbaceous bamboos.  
49 Distance between adjacent subplots within a permanent plot is 95 m (dashed line).

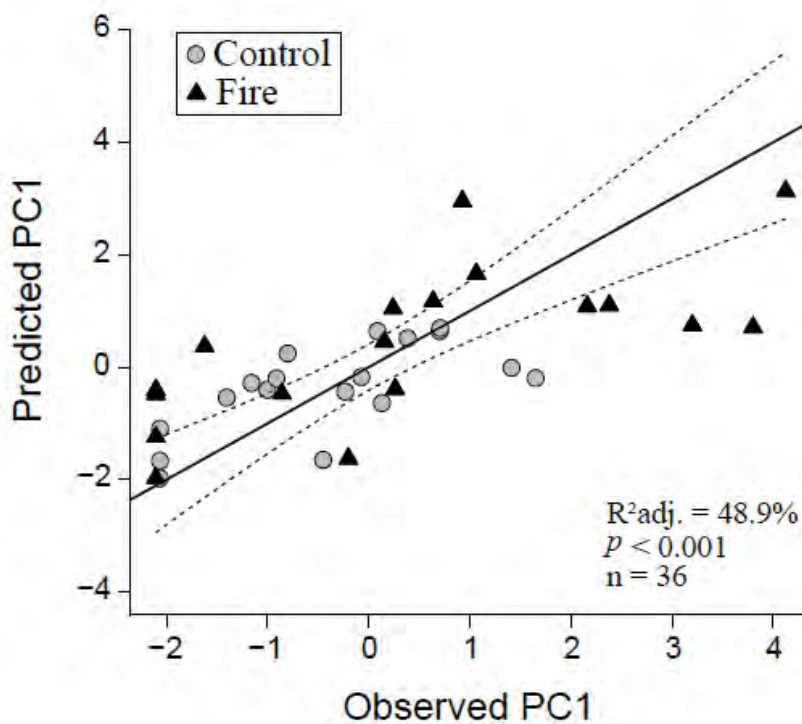
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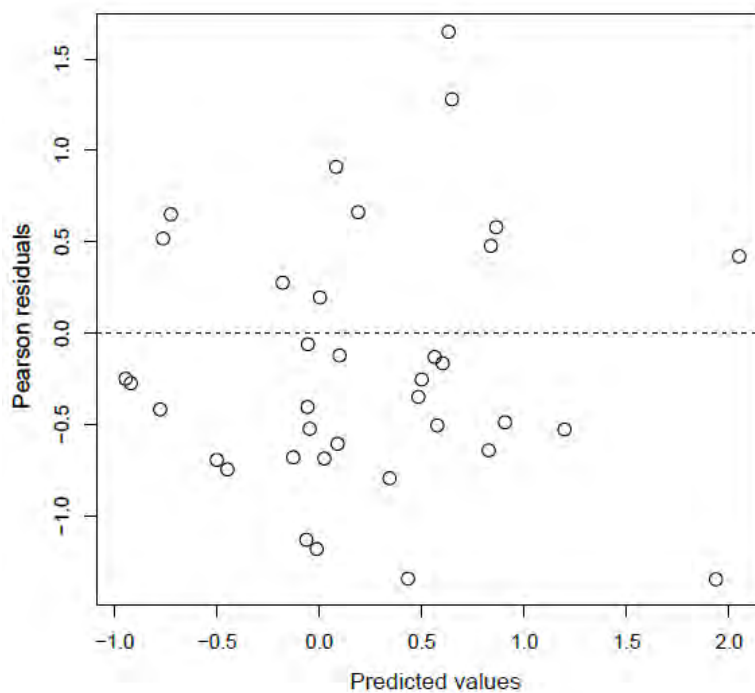
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Figure S4. Relationships between canopy openness (%) and VDCN (m) with the first component of PCA (PC1).  $R^2_{adj.}$  = adjusted coefficient of determination.



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Figure S5: Relationship between predicted and observed PC1. Dashed lines represent the 95% confidence interval. The residuals are shown in Figure S5.



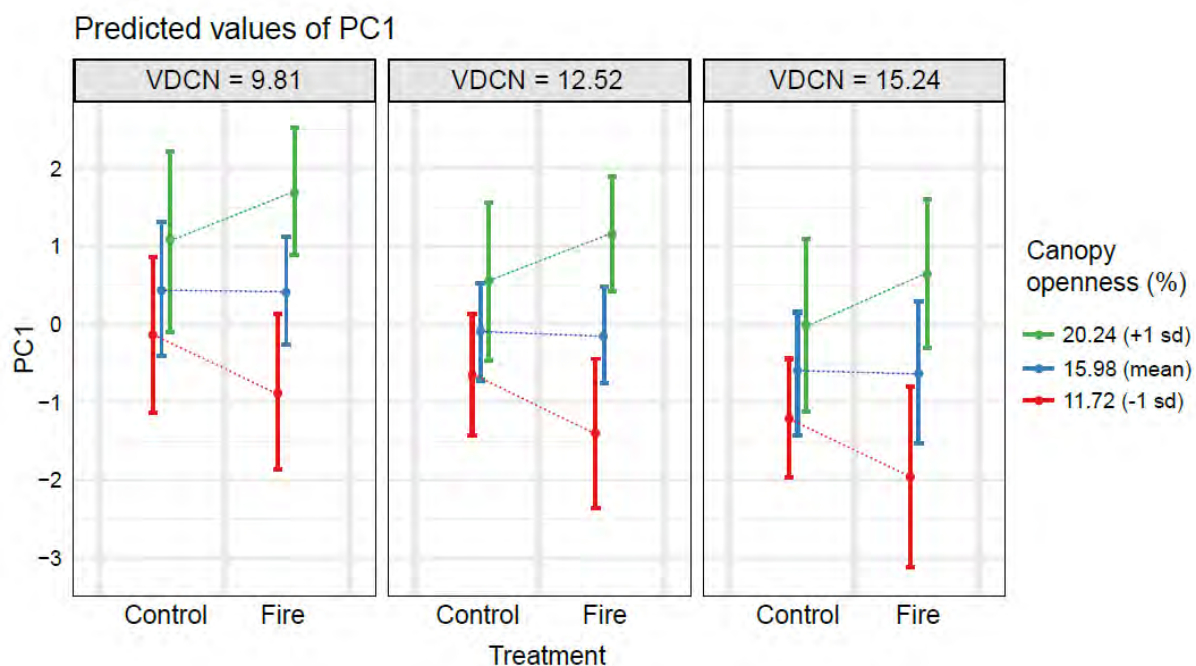
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Figure S6: Pearson residuals of predicted PC1 by the model.



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Figure S7: Marginal effects of interaction between variables in the model. The different colors and boxes represent the mean ( $\pm 1$  standard deviation) for canopy openness (%) and VDCN (m), respectively.

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