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Forest Fires Facilitate Growth of Herbaceous Bamboos in Central Amazonia

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Abstract

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

Keywords: Amazonia; Brazil; biological invasion; fire; forest degradation; Olyreae; *Olyra latifolia*; *Taquara micrantha*; tropical forest

INTRODUCTION

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

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

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

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

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

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

METHODS

Study area

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

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

Herbaceous bamboo sampling

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

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

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

Environmental variables

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

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

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

Data analysis

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

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

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

Where:
β_0: Intercept;
β_1 to β_4: Estimated coefficients (Figure 6);
VDCN: Vertical distance to channel network (m);
CO: Canopy openness (%);
Treatment: Dummy variable with two levels (control & fire).

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

RESULTS

While the clump density in the control plots (3511 clumps ha^{-1}) was higher than in the fire-affected plots (2844 clumps ha^{-1}), the culm density in the fire-affected plots (40,644 culms ha^{-}

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

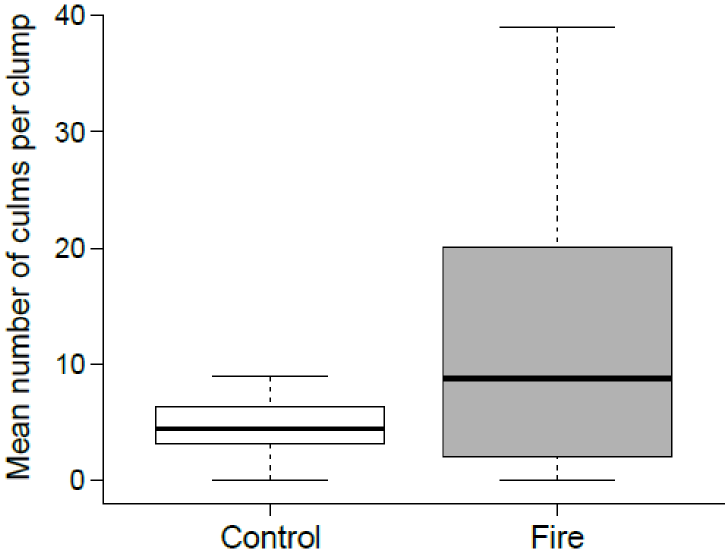

Figure 1. Mean number of culms per clump in the studied treatments. Boxplots show the median (horizontal lines), the interquartile range for the first (25th) and third (75th) percentiles (boxes), and the minimum and maximum values (whiskers).

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

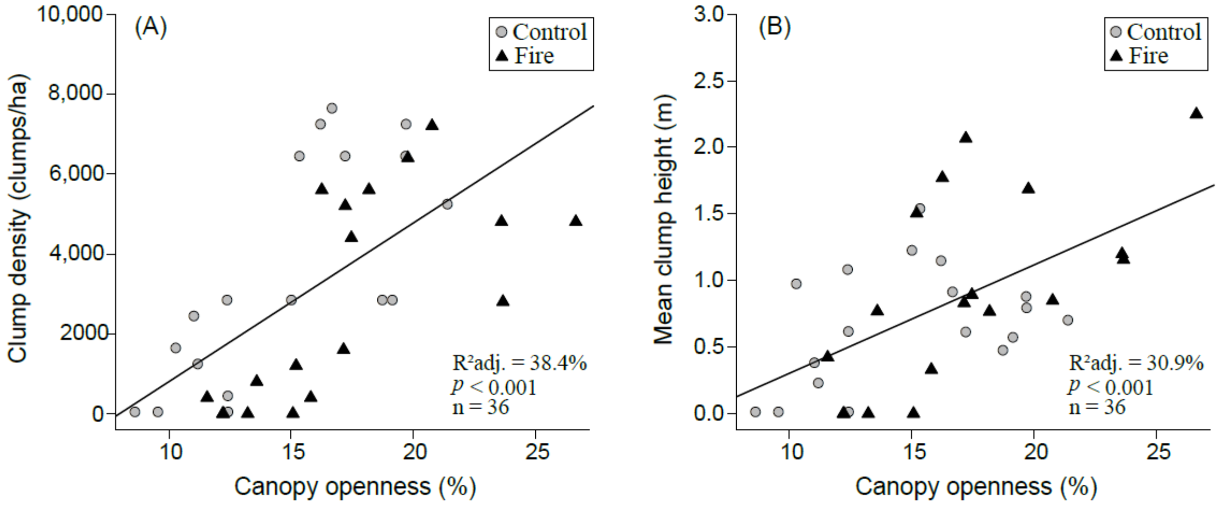

Figure 2. Relationships between the density of clumps (A) and average height of clumps (B) with the canopy opening. R²adj. = adjusted coefficient of determination.

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

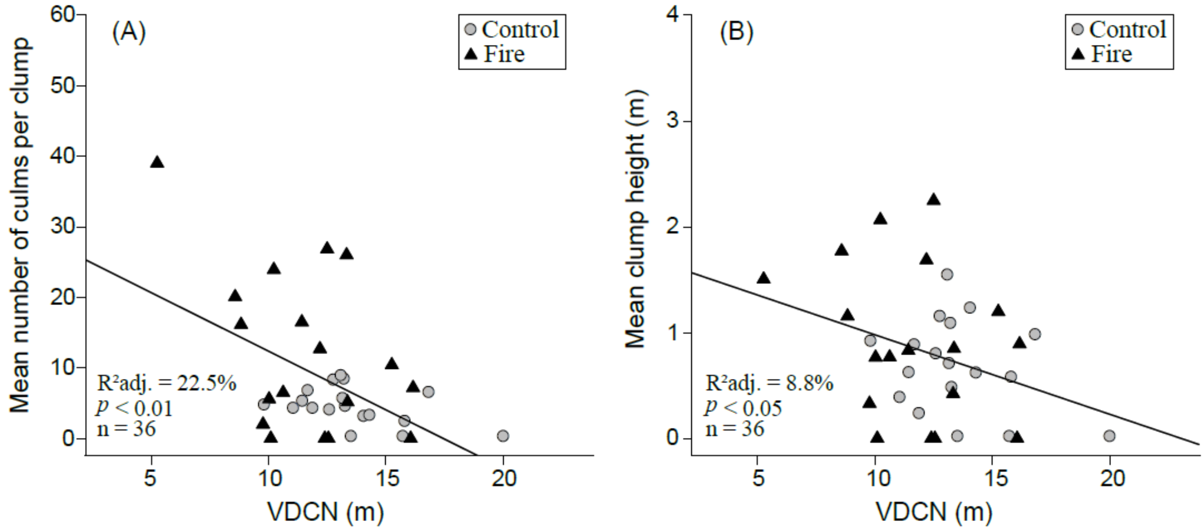

Figure 3. Relationships between the mean number of culms per clump (A) and mean clump height (B) with the vertical distance to channel network (VDCN). R^2adj. = adjusted coefficient of determination.

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

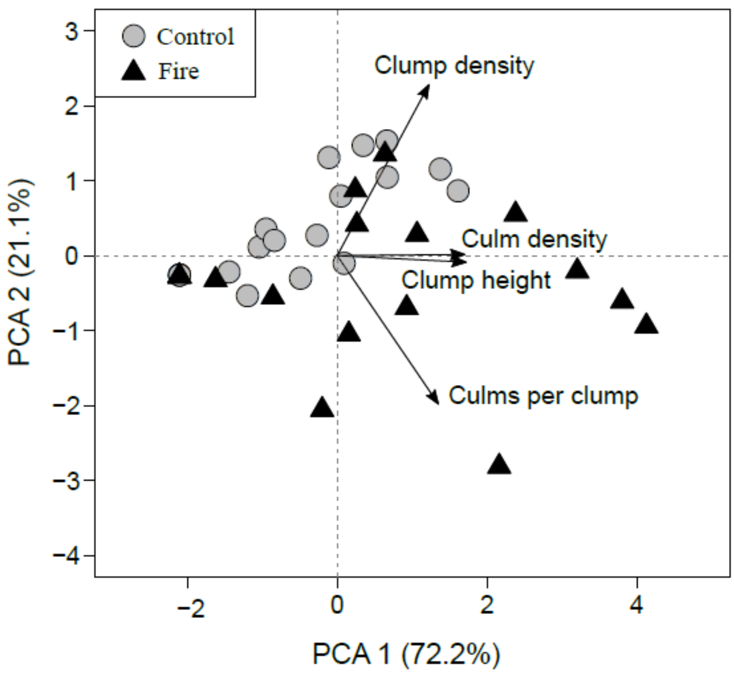

Figure 4. First two principal components from PCA analysis of bamboo abundance data, plotted for individual subplots. Symbols indicate different treatments.

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

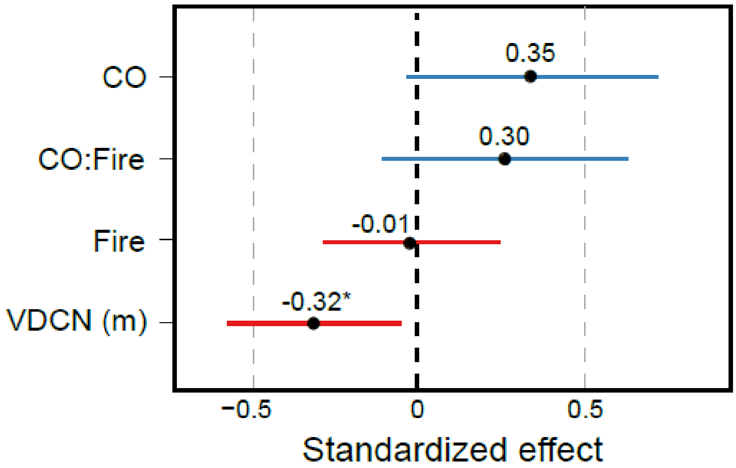

Figure 5: Standardized coefficients and confidence intervals of predictor variables (Eq. 1). The red and blue colors represent negative and positive values, respectively (* $p < 0.05$). The effect of fire was observed by taking the control treatment as the reference.

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

DISCUSSION

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

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

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

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

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

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

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

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

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

CONCLUSION

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

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

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SUPPORTING INFORMATION

DATA AVAILABILITY STATEMENT

LITERATURE CITED

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SUPPLEMENTARY MATERIAL

Forest Fires Facilitate Growth of Herbaceous Bamboos in Central Amazonia

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FIGURE S1

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

FIGURE S2

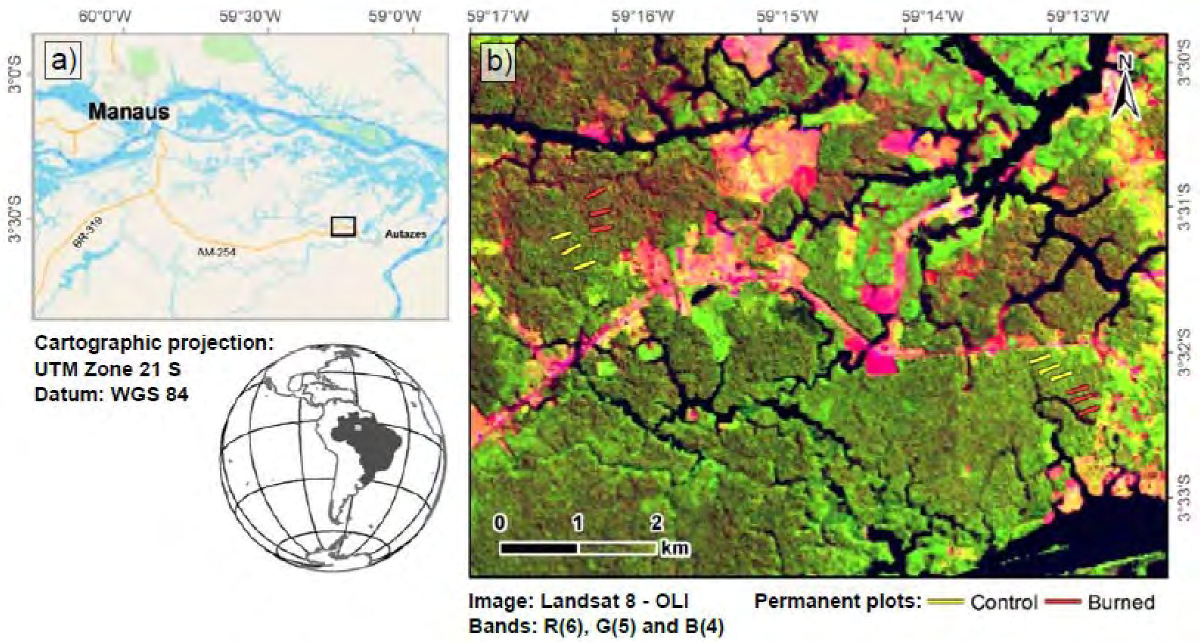

Figure S2. Location map of plots with indication of the burned area (b) in the municipality of Autazes (a). The image acquired on July 7, 2017 is courtesy of the United States Geological Survey (USGS).

FIGURE S3

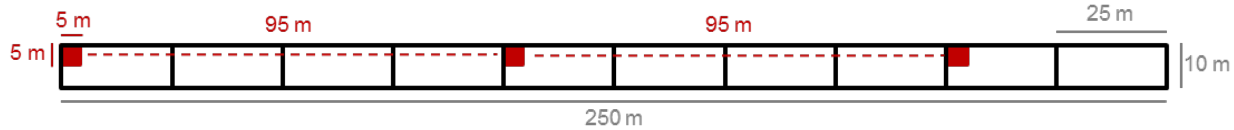

Figure S3. Sampling design within each permanent plot. The black lines represent the borders of a 250 × 10-m permanent plot from the Fire-Associated Transient Emissions in Amazonia Project (FATE-Amazonian Project), which is divided into ten 25 × 10-m sections. The 5 × 5-m red rectangles represent the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

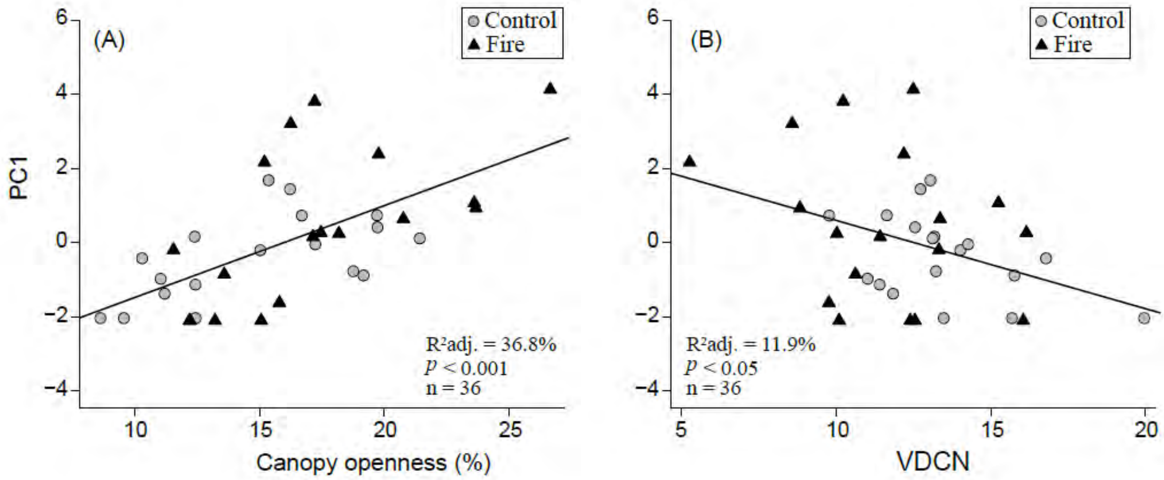

Figure S4. Relationships between canopy openness (%) and VDCN (m) with the first component of PCA (PC1). R²adj. = adjusted coefficient of determination.

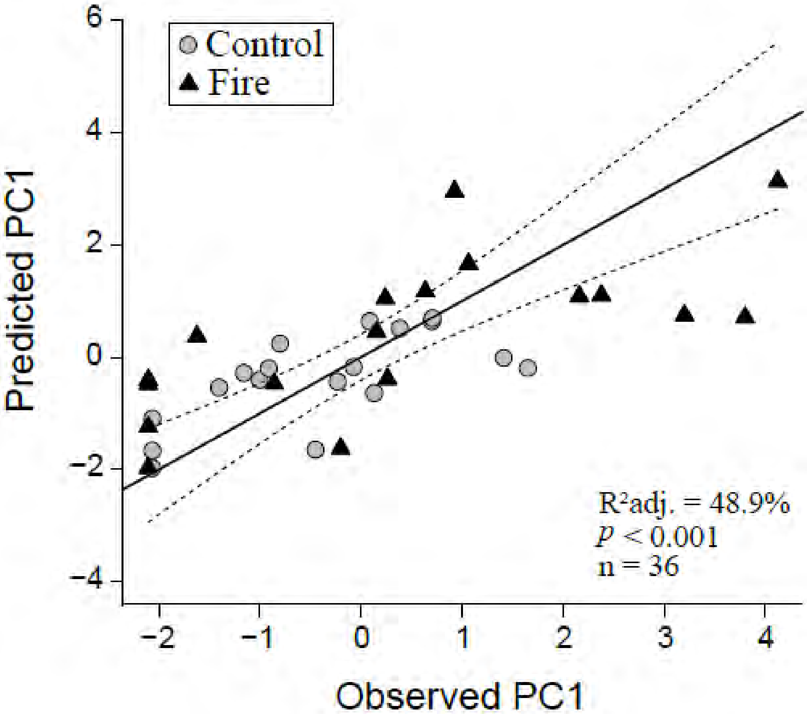

Figure S5: Relationship between predicted and observed PC1. Dashed lines represent the 95% confidence interval. The residuals are shown in Figure S5.

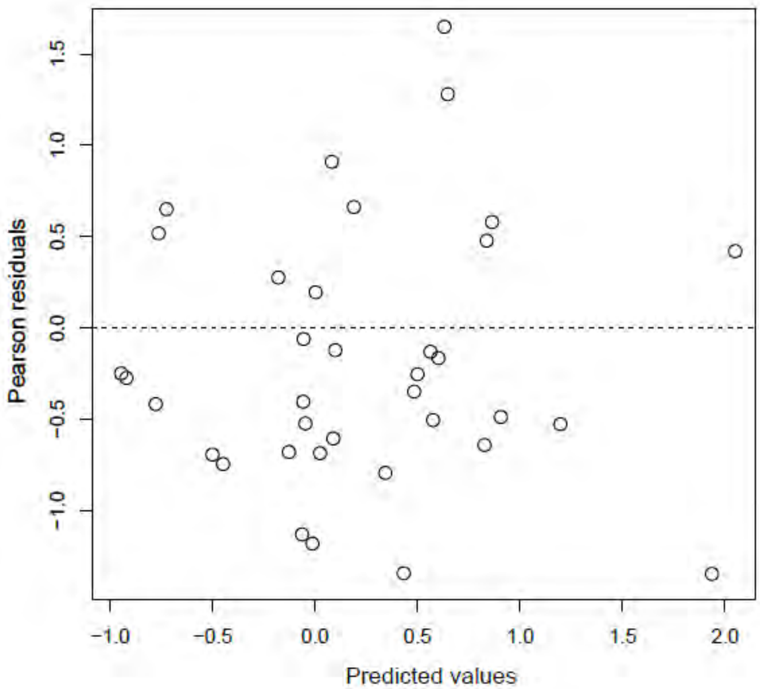

Figure S6: Pearson residuals of predicted PC1 by the model.

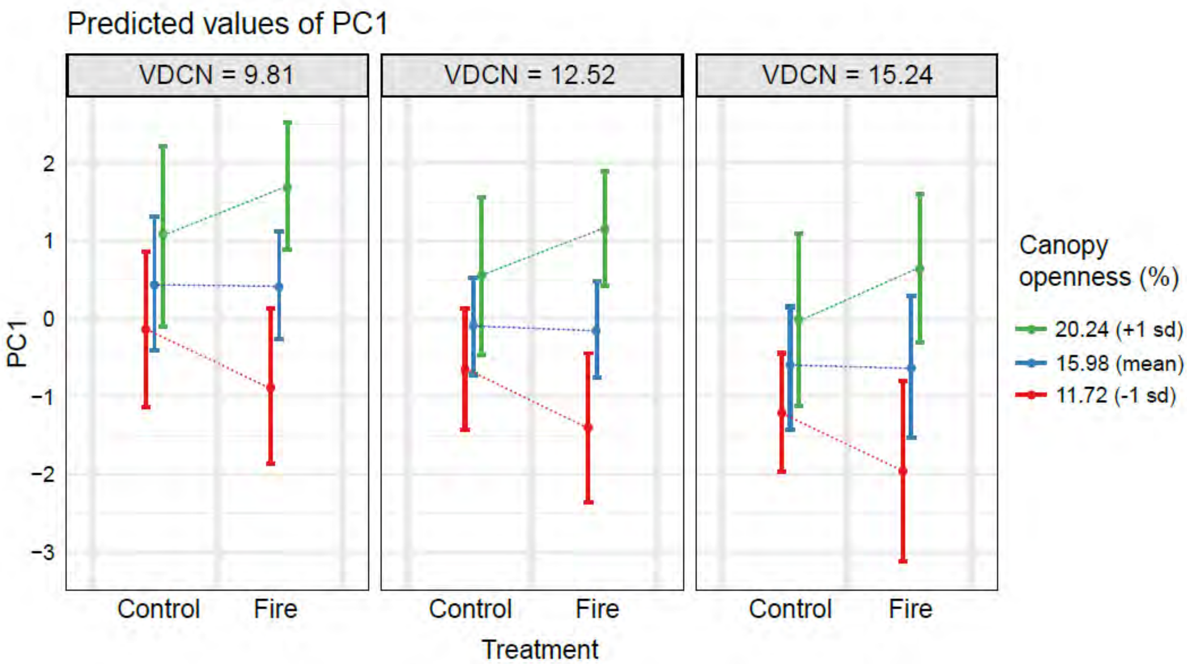

Figure S7: Marginal effects of interaction between variables in the model. The different colors and boxes represent the mean (± 1 standard deviation) for canopy openness (%) and VDCN (m), respectively.