Annals of Forest Science (2019) 76:110
https://doi.org/10.1007/s13595-019-0901-4

RESEARCH PAPER

Decline of large-diameter trees in a bamboo-dominated forest following anthropogenic disturbances in southwestern Amazonia

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Received: 3 May 2019 / Accepted: 17 November 2019

Abstract

· ***Key message*** **Reduction in the aboveground biomass of larger trees is the main consequence of disturbances in open forests dominated by bamboo. Because these trees are of central importance both for ecosystem function and for the economic value of the forest for management, the impact on these trees due to the increase of bamboo abundance following anthropogenic disturbances is both an environmental and a commercial concern**.

· ***Context*** Bamboo-dominated forests in southwestern Amazonia are increasingly exposed to the combined impacts of fire and selective logging. Although the climbing bamboos (*Guadua* spp.) are considered native species of these forests, disturbances contribute to a discontinuous canopy, which is an ideal scenario for an increase in abundance of these opportunistic plants. The regeneration of tree biomass is limited in these cases, decreasing the carbon stock of the forest.

· ***Aims*** This study compares changes in bamboo abundance and forest structure in the face of forest fire and post-burn logging in the municipality (county) of Rio Branco, Acre state, Brazil.

· ***Methods*** The study was conducted on the Transacreana Highway (AC 090) in the eastern portion of Acre state, Brazil. We compared changes in bamboo abundance and aboveground biomass (AGB) of an area of forest with no known recent disturbances to areas in the same forest that had been disturbed by fire and post-burn logging, which are frequent sources of disturbance in this region. The live and dead AGB values were estimated by field inventory in 2016, which was 11 years after a fire and 9 years after selective logging. The AGB values for trees and palms were estimated by allometric equations in three 2-ha areas. Bamboo abundance was expressed both by bamboo biomass (Mg ha^{-1}) and culm density (culms ha^{-1}), sampled by direct measurements in three 200-m^2 areas.

· ***Results*** Bamboo abundance was over 20% higher in forest that had been burned but not logged, as compared to undisturbed forest. Compared to undisturbed plots, aboveground forest biomass (live + dead) was 34% lower in plots exposed to fire but not logging, and 36% lower if exposed to both. Live trees and palms represented 77% of the total forest biomass (live + dead), and almost a half of this contribution (41%) was in individuals in the largest diameter class (diameter at breast height > 50 cm).

· ***Conclusion*** Increase in the level of impact led to a reduction in aboveground carbon stock of the forest. One of the main consequences of disturbances in open forests dominated by bamboo is reduction of live trees and palms, especially in the diameter at breast height (DBH) class over 50 cm.

Keywords Brazil · Acre · Bamboo forest · *Guadua* spp. · Forest fires · Logging

Handling Editor: Paulo Fernandes

Contributions LGZ designed the study and conducted the fieldwork, data analysis and writing. PMLAG, EOF and PMF contributed to the project design, data interpretation and writing

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Published online: 11 December 2019

1 Introduction

Forest fires are not common natural events in the Amazon rainforest. The only known natural cause of forest fires is lightning strikes, and in humid tropical forests, burning is almost always limited to a single tree or a very small patch of vegetation (Fearnside 1990). In contrast, forest fires from human ignition are increasingly frequent sources of disturbance.

Fire occurrences are directly related to the vegetation type, climatic conditions and socioeconomic context of a given region. Even at different time scales, a strong relationship persists between the fire regime and the territorial dynamics (Molina and Galiana-Martín 2016). Logging is an example of human activity that determines forest-fire susceptibility. Logging roads and the gaps formed by felling trees promote the opening of the canopy, contributing to an increase in the probability of occurrence of forest fires (Nepstad et al. 1999).

An important reflection of anthropogenic disturbances can be observed in the open forests of southwestern Amazonia. These forests occupy an estimated area of at least 161,500 km^2 and are characterized by the dominance of native bamboo species of the genus *Guadua* in the understory. Although the occurrence of *Guadua* spp.in the Amazon is naturally associated with luvisols (Kandisols) and eutrophic cambisols (Inceptisols), disturbance in the forest can promote clearings favorable to *Guadua* spp., creating conditions for it to occur in areas where it would not otherwise exist (de Carvalho et al. 2013; Ferreira 2014). Forests of southwestern Amazonia subject to disturbances such as windthrows, logging, and fire are characterized by a discontinuous canopy that provides ideal conditions for invasion of aggressive pioneering plants, such as bamboo.

Open bamboo-dominated forests have a reduced number of trees in the largest diameter classes when compared to forests where bamboo does not occur, which promotes a reduction in total aboveground biomass, carbon stock, and, consequently, in the economic value of these forests (Oliveira 2000; Nelson et al. 2001). Avoiding degradation in these forests is essential for the continuity of important ecosystem services (ES), such as hydrological regulation, maintenance of biodiversity, and carbon stock (Daily 1997).

Logging is not likely to decrease in the near future in Brazil, given the new presidential administration's dramatic shift toward less environmental regulation and more promotion of extractive activities (Ferrante and Fearnside 2019). Logging has been shown to form gaps by removal of large trees from the forest. These gaps provide favorable conditions for native climbing bamboo, often starting a self-perpetuating disturbance cycle where these bamboos hang on the trees, causing physical damage to the their crowns and promoting greater canopy opening, which is a favorable scenario for the development of more ramets (Griscom and Ashton 2006). Thus, regeneration of tree species of commercial value becomes limited (D'Oliveira et al. 2013; Rockwell et al. 2014).

Occurrence of forest fires is critical under these circumstances, because an increase in tree mortality, in bamboo dominance, and in dead biomass (necromass) provides fuel for future fire events (Smith and Nelson 2011; Veldman and Putz 2011). Intensification of climate change, with effects such as more-frequent extreme droughts, and increases in other direct human impacts, such as selective logging, is consistent with the observed progressive increase in the number of forest fires and of the gaps that are left as a legacy of these disturbances killing trees and palms, enhancing bamboo density in these forests (Lewis et al. 2011; Ferreira 2014).

The increase in culm density per unit area may not necessarily reflect a direct increase in bamboo biomass. Culms tend to lose verticality in forests with reduced numbers of large trees, where bamboo becomes locally dominant and has diameter increments of ramets restricted by limited access to light (Yavit 2017). This scenario of bamboo dominance in a forest leads to alterations in the floristic composition, reducing the number of species in a single hectare by almost 40%, on average (Silveira 2005).

An important first step to reduce degradation effects in these forests is to better understand and quantify the impacts associated with the main sources of disturbance. This paper aims to help fill an important gap in knowledge of the effect of fire and post-burn logging on the structure and composition of forests dominated by *Guadua* spp. in the understory. Here, we investigate how these disturbances affect the dominance of bamboo, aboveground forest biomass, and abundance of large trees in southwestern Amazon forests.

2 Materials and methods

2.1 Study area

The study area is located in the eastern portion of Acre State on the Transacreana Highway (AC 090), 45 km from the city of Rio Branco (9° 59′ 10″ S; 68° 11′ 33″ W). The municipality (county) of Rio Branco has an area of 8835.5 km^2 and an estimated population of 383,443 (Brazil, IBGE, 2017). The region has an annual average temperature of 25.6 °C and receives mean annual precipitation of approximately 2200 mm (Sombroek 2001). The rainy season usually begins in October and lasts until May. The rainiest quarter comprises the months of January, February, and March, while the driest quarter corresponds to June, July, and August (Acre, Governo do Estado 2000).

Two areas were selected in the same forest remnant, both disturbed by the same forest fire in 2005. One of the areas was further disturbed by logging in 2007 (logging intensity 16.82 m^3 ha^{-1}). Based on the 0.54 g cm^{-3} average wood density value in this part of Amazonia (Nogueira et al.

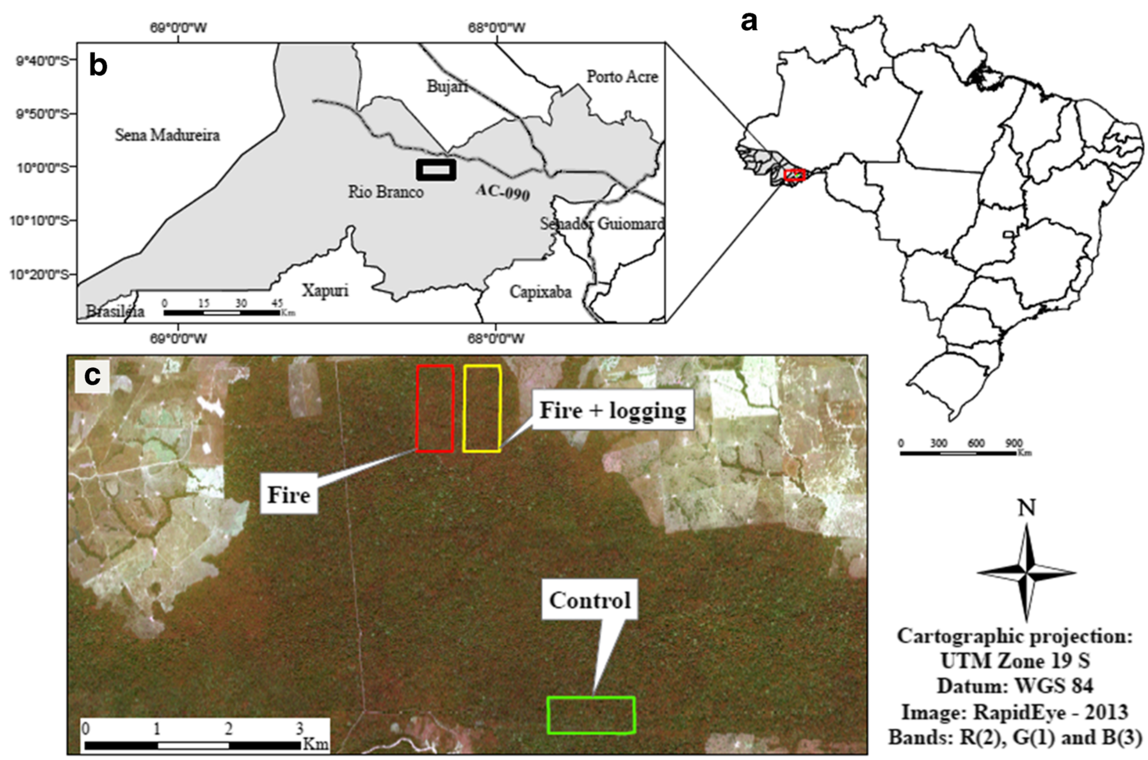

Fig. 1 Location map of study areas (**c**) in the municipality of Rio Branco (**b**), Brazil (**a**)

2007), the loss of wood biomass after logging was 10.16 Mg ha^{-1}. In this same remnant, approximately 4 km to the south of the first two areas, we selected an area used as reference (control) that was not affected by fires or by recent extractive processes (Fig. 1).

According to local residents, most of the forests in the region were disturbed by forest fires in 2005. A major drought occurred in 2005 in this part of Amazonia (da Silva et al. 2018; Vasconcelos et al. 2013), and the many cattle ranches along the AC-90 Highway probably also contributed to the widespread fires. The increase of the density of bamboo in the forest was subsequent to these fires.

2.2 Sampling design

The study was carried out along three transects, each 1100 m in length (one for each treatment). Placement of transects respected a minimum distance of 100 m from the edge of the forest. Along each transect, 8 plots of 50 × 50 m were systematically placed at 100-m intervals, summing 2 ha as the sample area for estimating aboveground biomass in each treatment (Fig. 2).

Bamboo biomass was obtained directly in 8 subplots of 5 × 5 m (25 m^2), installed systematically, totaling a sample area of 200 m^2 for each treatment.

2.3 Aboveground biomass

Aboveground biomass was estimated by summing live and dead biomass (necromass) classes. All values referring to estimates of live and dead biomass of trees and palms were obtained by allometric equations developed for the Amazon region. Bamboo biomass was obtained by direct weighing. Woody residues were estimated by line-intercept transects (Van Wagner 1968) (Table 1).

2.3.1 Live trees and palms

For aboveground biomass estimation of live trees, we used the equation developed for forests located in the "arc of deforesta-

Fig. 2 Schematic of the sampling design in each transect of 1100 m in length

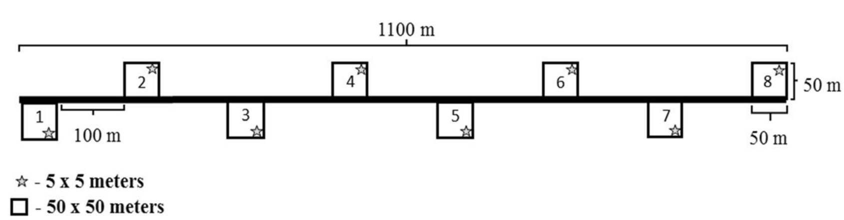

Table 1 Allometric equations and methods used to estimate biomass in each compartment

Compartment	Equation/method	Author
Live trees (DBH ≥ 10 cm)	[ln (AGB) = −1.716 + 2.413 × ln (DBH)] × c	Adapted from (Nogueira et al. 2008a)
Live palms (DBH ≥ 10 cm)	[ln (AGB) = −3.3488 + 2.748 × [ln (DBH)] × p	Adapted from (Goodman et al. 2013)
Standing dead trees (DBH ≥ 10 cm)	AGB = G × H × *β0* × d × 0.1	Brown et al. 1995
Crownless trees and dead palms (DBH ≥ 10 cm)	AGB = G × H × F × d	Graça et al. 1999
Woody debris (DBH ≥ 10 cm)	Line-intercept transects	Van Wagner 1968
Bamboo (live and dead)	Direct weighing	–

AGB aboveground biomass (dry weight in kg); *DBH* diameter at breast height, measured 1.30 m above the ground or above any buttresses (cm); *c* species wood density correction coefficient for trees (wood density of the species divided by the mean wood density in the area, which for this part of Amazonia is 0.540 g cm^{-3}) (Nogueira et al. 2008a); *p* density correction coefficient for palms. Mean wood density = 0.488 g cm^{-3} (Chave et al. 2006); *G* cross-sectional area (cm^2); *H* total height (m); *β0* regression coefficient (0.62); *d* density attributed to the decomposition phase (g cm^{-3}); *F* form factor, or the ratio of the volume of a bole to the volume of a cylinder with the length of the bole and diameter of the DBH (0.78)

tion" along the southern edge of the Amazon forest (Nogueira et al. 2008a), incorporating a density correction coefficient based on the ratio between the species wood density (Zanne et al. 2009) and the average value of 0.54 g cm^{-3} for wood density in this region (Nogueira et al. 2007). The same density correction coefficient was used to calculate the ratio between the palms species wood density and the average value of 0.488 g cm^{-3} for the family Arecaceae (Chave et al. 2006).

For species that did not have densities in the database, we used the mean density of the genus. In cases lacking a value for the genus, we used the average value for the family (Chave et al. 2006). The estimated dry biomass of each tree and palm individual was multiplied by the carbon concentrations of 50% and 49.4%, respectively, in order to estimate carbon stock (Malhi et al. 2004; Goodman et al. 2013).

2.3.2 Dead biomass (necromass)

For each class of dead biomass, it was necessary to determine density values for the different phases of decomposition. The decomposition category was assigned in the field based on the classification proposed by Silva et al. (2016) (Appendix, Table 4).

After classification of the samples as a function of the decomposition phase, they were separated and weighed and their individual wet volumes were determined by the water-displacement method (Archimedes principle). Samples were in the form of cross-sectional disks in order to represent the radial variability in wood anatomy. The dry weights of the samples were obtained after air drying for a period of 15 days and the mean values for density of the samples in each of the three decomposition classes were used for estimating the biomass of standing dead trees, crownless trees, dead palms, and woody debris.

2.3.3 Standing dead trees and palms

Biomass of standing dead trees was quantified using the equation fit by Brown et al. (1995) at the Samuel ecological station (Rondônia) and adapted by Nascimento and Laurance (2006) when considering wood density. We discounted 10% of the calculated value due to the absence of leaves and branches (Delaney et al. 1998**).** Biomass of crownless trees and dead palms was estimated by the equation proposed by Graça et al. (1999), adopting a form factor of 0.78 (Fearnside 1992).

2.3.4 Woody debris

For estimation dead biomass in woody debris, we adapted the line-intercept method described by Van Wagner (1968). Three 20-m lines were placed in each plot and all pieces of woody debris with diameter above 10 cm that intercepted the line were sampled, with the exception of bamboo. The diameter of each piece was recorded at the point it intercepted the line. A water content of 0.416 was considered for woody debris (Nogueira et al. 2008b). To estimate the carbon stored by the woody debris, we adopted a carbon content of 46.4% (Graça et al. 1999).

2.3.5 *Guadua* spp. biomass

Biomass of bamboo was estimated by directly weighing all of the ramets found in each sampled subplot. After recording the number of established stems, all bamboo ramets were sectioned using the lateral ends of the subplots as cutting limits. Weighing was done in the field using a spring balance with a maximum capacity of 200 kg and precision of 1 kg.

Samples of stems (live and dead) and of leaves (live and dead) were collected for determination of water content and density. The leaves were weighed separately from the culms, and live ramets were weighed separately from dead ones. The dry weight of each weighing was calculated by deducting the water content of each sampled compartment. For conversion of bamboo biomass to carbon stock, a carbon content of 50% was adopted as a default value for vegetation in general (Brown 1997).

2.3.6 Data analysis

Parametric statistical tests were applied to the analysis of variance (ANOVA) with 95% confidence for determination of possible effects of the impact levels on the different biomass compartments. Evaluations of the homoscedasticity and the normality of the data were performed by the F-max of Hartley and Shapiro-Wilk tests, respectively (Hartley 1950; Shapiro and Wilk 1965). We conducted all of the analyses in R software (R Core Team 2018).

In cases of absence of homoscedasticity or normality in the data, transformation techniques (i.e., logarithmic transformation) were used in order to comply with the assumptions of ANOVA. The Kruskal-Wallis non-parametric statistical test was applied in cases where the data did not fit the ANOVA assumptions (Fig. 3).

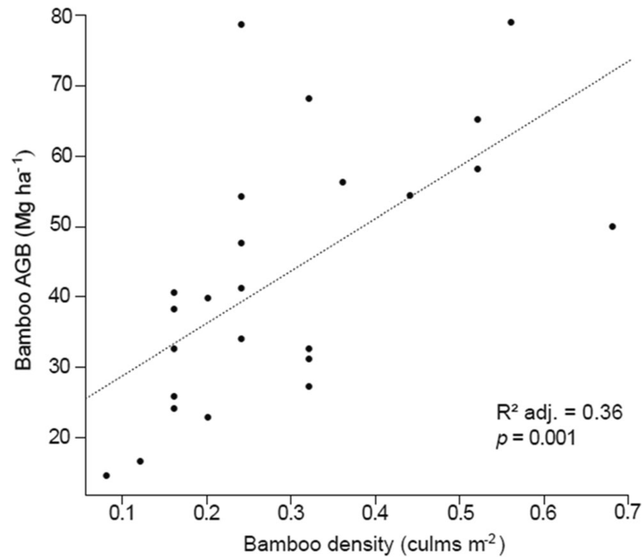

Fig. 4 Linear regression ($R^2 = 0.36$, $p = 0.001$) between aboveground biomass (Mg ha^{-1}) of bamboo and culm density for all sample units in the study

3 Results

3.1 *Guadua* spp. abundance

Two measures of bamboo abundance were evaluated: aboveground biomass (Mg ha^{-1}) and culm density per unit area (culms m^{-2}). The relationship between these two variables was observed through a significant linear regression ($R^2 = 0.36$; $p = 0.001$) (Fig. 4).

The average dry aboveground biomass (live + dead) of *Guadua* spp. was 27% higher in the treatment affected by fire when compared to the control (Table 2).

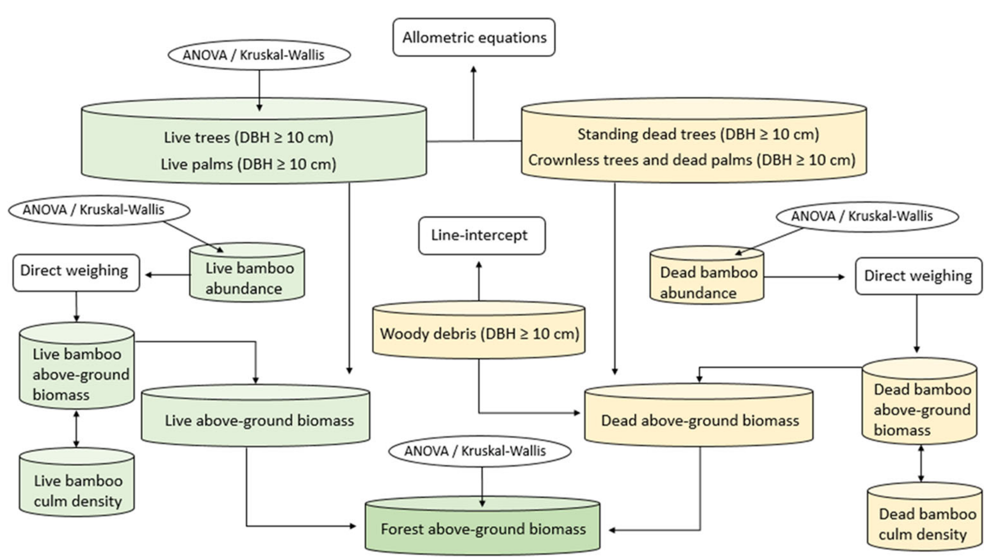

Fig. 3 Schematic of the conceptual framework of the study. Cylinders represent the sampled variables. Rounded rectangles represent the methodological approach and oval frames represent the analytical steps. Double arrows show the application of a linear regression model to observe the relationship between the two abundance variables for *Guadua* spp. (aboveground biomass and culm density). Color figure available in online version

Table 2 Aboveground biomass (live + dead) of trees, palms, bamboo, and forest per hectare in the different treatments

	Parameter	Control	Fire	Fire + logging	*p*
Trees	Mean (Mg ha^{-1})	215.0^{a}	105.4^{b}	122.3^{b}	ANOVA 0.012*
	CV (%)	40.9	39.5	63.1	
	CI	141. 4–288.7	70.7–140.3	57.7–186.8	
Palms	Mean (Mg ha^{-1})	4.3	14.2	0.5	Kruskal-Wallis 0.197
	CV (%)	84.3	253.5	116.3	
	CI	1.2–7.3	0–44.2	0.01–1.1	
	Mean (Mg ha^{-1})	219.3^{a}	119.7^{b}	122.8^{b}	ANOVA
Trees + palms	CV (%)	41.3	36.7	63.1	
	CI	143.6–295.0	86.0–156,3	58.1–187.6	0.019*
	Mean (Mg ha^{-1})	38.26	48.66	41.91	ANOVA
Bamboo	CV (%)	44.2	33.2	52.7	
	CI	24.12–52.40	35.16–62.17	23.44–60.38	0.534
	Mean (Mg ha^{-1})	259.97a	171.96b	167.34b	ANOVA
Forest	CV (%)	36.6	24.2	51.1	
	CI	180.3–339.6	137.0–206.9	95.8–238.8	0.045*

Significant differences between treatments are indicated by different lower-case letters (*a* and *b*) beside the means; * = $p < 0.05$

CV coefficient of variation; *CI* confidence interval

As was observed in the case of aboveground biomass of bamboo, culm density per unit area was higher, on average, by 22% in the two treatments with fire compared to the control plots (Appendix, Table 5). Although an ecologically relevant difference between treatments has been found here, there is a high variability of aboveground biomass in this forest type.

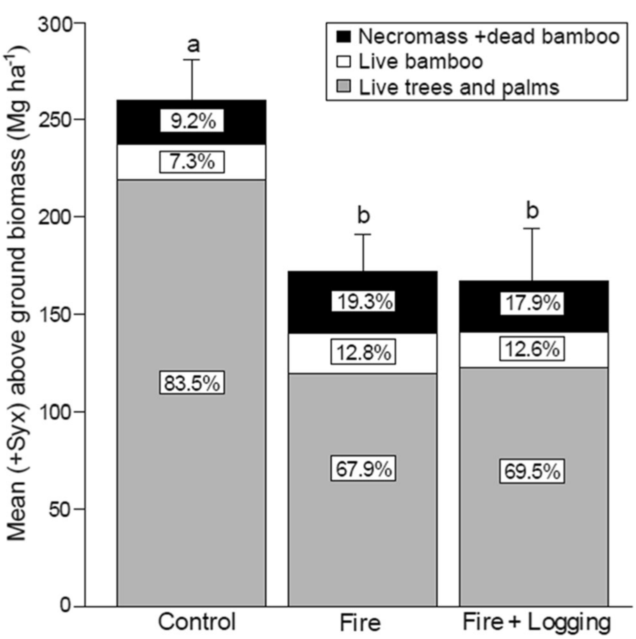

Fig. 5 Composition of the total (live + dead) aboveground biomass (Mg ha^{-1}) of the forest for each treatment

3.2 Forest biomass

In addition to necromass, we sampled 1111 live trees (DBH ≥ 10 cm), 105 live palms (DBH ≥ 10 cm), and 174 live and dead bamboos in the plots. The dry AGB (live + dead) of the forest was obtained by summing the values for all of the biomass classes sampled in the study. There was a significant difference ($p = 0.045$) between the control and the disturbed treatments (Table 2).

The classes that contributed most to the total amount of biomass (live + dead) were the live trees and palms, accounting for 83.5% of the total biomass in the control treatment. Considering all treatments, live trees and palms represented 77.1% of the total dry aboveground biomass of the forest (Fig. 5).

In terms of availability of combustible material, the largest amount of dead biomass was found in the treatment affected by fire, representing 17% of the total biomass in this treatment. Values for total dry aboveground biomass (live + dead) obtained in the control treatment (259.97 Mg ha^{-1}), intermediate-impact treatment (171.96 Mg ha^{-1}), and high-impact treatment (167.34 Mg ha^{-1}) were converted to equivalent carbon stock values of 129.87 Mg ha^{-1}, 85.76 Mg ha^{-1}, and 83.57 Mg ha^{-1}, respectively.

3.3 Biomass of live trees and palms

The values for live-tree biomass showed a significant difference ($p = 0.012$) between the control and fire treatments.

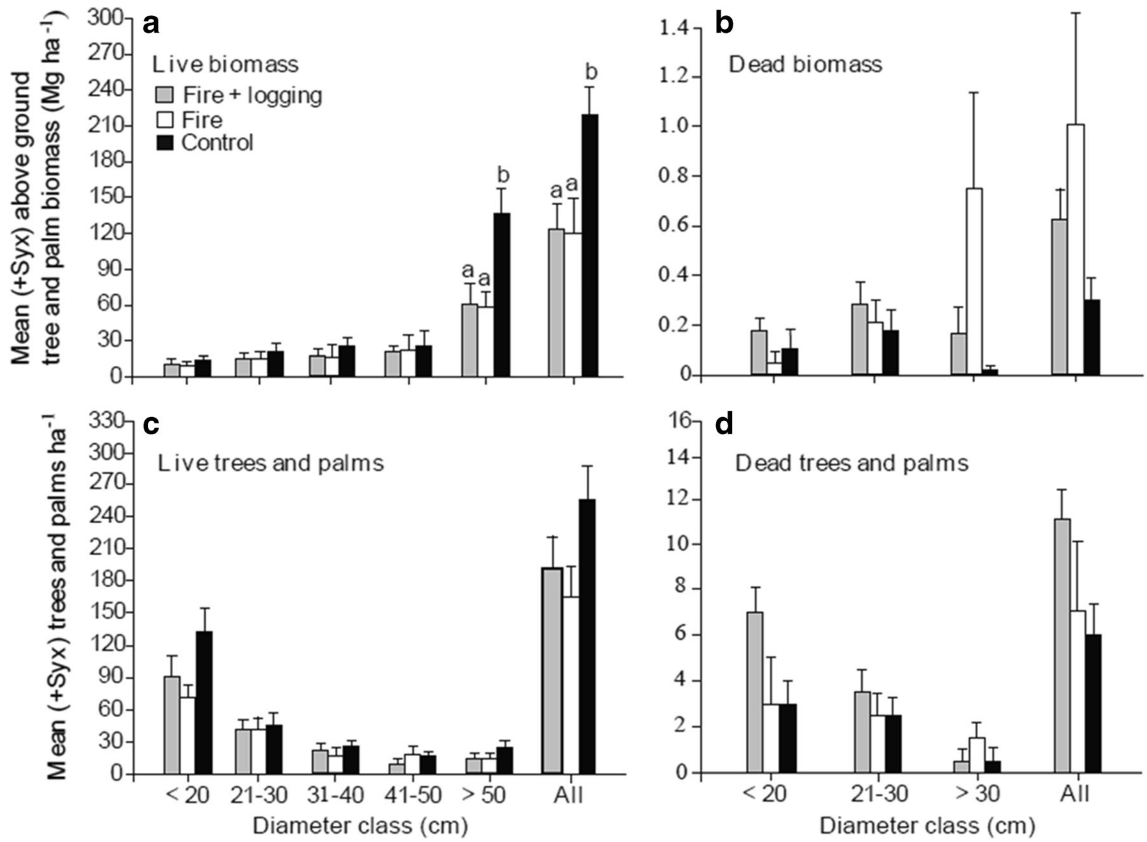

Fig. 6 Mean (+ S_{yx}) of the aboveground biomass in Mg ha^{-1} (**a**, **b**) and number (**c**, **d**) of live trees and palms per hectare by diameter class in the different treatments

This difference was detected from a Tukey test ($p < 0.05$) followed by application of ANOVA. In the case of biomass of live palms, absence of normality in the data, even after a logarithmic transformation, was shown by the Shapiro-Wilk test ($W = 0.83$, $p = 0.0001$). This made application of the Kruskal-Wallis test necessary (Table 2). Considering the group formed by live trees and palms, more than half of the aboveground biomass (53.7%) was composed of large individuals (DBH > 50 cm). Significant differences were observed for the aboveground biomass of live trees + palms ($p = 0.019$) and for the large individuals ($p = 0.049$). Using the Tukey test ($p < 0.05$) followed by ANOVA, differences were detected between the control and impact treatments (fire and fire + logging) (Fig. 6).

When considering the biomass of the group formed by live trees and palms, we observed proximity between the values obtained in the two treatments impacted by disturbances (Table 3).

Table 3 Mean (± standard deviation) aboveground biomass (Mg ha^{-1}) of live trees and palms

Diameter class (cm)	Control	Fire	Fire + logging	ANOVA *p*
≤ 20	13.35 ± 6.1	9.36 ± 3.32	9.97 ± 7.51	0.23**
21–30	20.05 ± 8.46	14.95 ± 3.58	15.3 ± 6.74	0.20*
31–40	25.13 ± 7.36	15.41 ± 9.76	16.45 ± 11.19	0.09*
41–50	25.36 ± 12.05	21.92 ± 18.09	20.68 ± 20.79	0.86*
> 50	135.43^{a} ± 85.85	58.04^{b} ± 38.53	60.40^{b} ± 57.48	0.049**
Total	219.3^{a} ± 90.54	119.7^{b} ± 44.86	122.8^{b} ± 72.29	0.019*

Significant differences between treatments are indicated by different lower-case letters (*a* and *b*) beside the means

*ANOVA & Tukey; ** Kruskal-Wallis & Mann-Whitney *U*-test

4 Discussion

4.1 Bamboo-dominated forest and disturbances

In this study, we show an increase in bamboo abundance, a significant decrease in large-tree aboveground biomass, and, consequently, in aboveground forest biomass following fire and post-burn logging. However, one must consider the high spatial variability in aboveground biomass and different potential responses of bamboo-dominated forests following anthropogenic disturbances. Fire occurrence in bamboo-dominated forests is 45% higher in dead than live bamboo populations during drought years, suggesting a potential process to the maintenance and expansion of bamboo in the forest (Dalagnol et al. 2018).

Considering the last 33 years (1984–2017), the years 2005, 2010, and 2016 had the highest frequencies and intensities of forest fires in the state of Acre, indicating a probable relation of these phenomena to the effects of a strong Atlantic dipole (2005), a strong Atlantic dipole together with a weak El Niño (2010), and a weak Atlantic dipole together with a strong El Niño (2016). Extreme events from both of these phenomena are increasing in frequency as a consequence of anthropogenic global warming (Meehl et al. 2007, p. 779; Cox et al. 2008; Evan et al. 2009).

In addition to climate change, direct human activities, such as logging, are also determinant factors for fire occurrence (Aragão et al. 2018). At least 46% of the total forest area impacted by forest fires in the state of Acre is located within settlement projects and at least 15% within government-created conservation units, where theoretically there should be low human pressure (da Silva 2017).

4.2 *Guadua* spp. abundance

Although the relationship between the two abundance variables for *Guadua* spp. (aboveground biomass and culm density) in the present study was positive and linear, it was not very strong ($R^2 = 0.34$). This relationship would be intuitive if all the ramets found in the sample units were fully sampled. However, the sampling method used the lateral extremities of the subplots as cutting limits of the culms in the biomass sampling.

Yavit (2017) found a nonlinear parabolic relationship between these two variables for *Guadua* spp. in southeastern Peru, where, after a certain point, further increase in bamboo density did not result in further increase in its biomass, instead leading to a reduction. One possible hypothesis that may explain this ecological mechanism is the lower density of trees in high bamboo density environments. In these scenarios, the culms lose their verticality, failing to access the forest canopy because they cannot rely on adjacent trees. Consequently, bamboos have their development limited by light, remaining thinner and shorter. However, the nonlinear pattern was not conclusive for our data set, where only one plot had high culm density with lower biomass, consistent with the nonlinear pattern (Appendix, Fig. 9).

Dead bamboo biomass was greater than live bamboo biomass for all treatments (Appendix, Fig. 7). A possible explanation for the large amount of dead biomass found in the current study may be tied to the end of the life cycle of the bamboo populations sampled. This condition was characterized in the field by the presence of abundant fruits (Appendix, Fig. 8), a condition that frequently precedes the periodic mass mortality event of bamboo populations (Janzen 1976; de Carvalho et al. 2013).

Biomass of *Guadua* spp. showed no significant difference between treatments. However, the intermediate-impact treatment (fire) had an average bamboo biomass more than 10 Mg ha^{-1} higher than the control treatment. In another area located 27 km from the city of Rio Branco and near the site of the current study, Torezan and Silveira (2000) reported only 10.2 Mg ha^{-1} of bamboo biomass, which is approximately 4 times lower than the mean value in the present study. In addition, the authors reported that the biomass of *Guadua* spp. represented 4.2% of the total forest biomass, while in the current study the corresponding value is 21.5%. Considering that the bamboo ramets sampled in both studies belonged to the same population and that the mass-flowering event was observed in 2016, a natural increase of bamboo biomass was expected due to ripening of culms and establishment of new ramets.

The mean value for aboveground biomass found by Yavit (2017) for *Guadua* spp. was 6.2 Mg ha^{-1} in areas located in the departments of Madre de Dios and Ucayali, Peru. This value was six times lower than the mean value of 38.26 Mg ha^{-1} for undisturbed plots in the current study.

Considering all treatments, the average biomass of *Guadua* spp. in our study (42.96 Mg ha^{-1}) represented 29.1% of the biomass of living trees (147.61 Mg ha^{-1}). The largest arboreal individual of the current study found in the control treatment was a *Calophyllum brasiliensis* (Guanandi) with 133.7 cm DBH. The biomass estimated for this single individual was 26.1 Mg, which represents more than half of the estimated mean biomass of *Guadua* spp. per hectare. This suggests high uncertainty for the tree component in the absence of a much larger sample size, and therefore also implies high uncertainty for values for bamboo when expressed as percentages of either tree or total biomass.

With respect to the dominance of bamboo, the mean values for the control treatment (2500 culms ha^{-1}), the intermediate-impact treatment (3400 culms ha^{-1}), and the high-impact treatment (2700 culms ha^{-1}) can all be considered high in relation to the values reported by Barlow et al. (2012) in Acre's Chico Mendes Extractive Reserve (RESEX), where there were 279.7 culms ha^{-1} in forest with no known impact and 282.2

culms ha^{-1} after forest-fire disturbance. The values in the present study were also higher than the 1420 culms ha^{-1} found by Torezan and Silveira (2000) in an area near our study site, and the 1350 culms ha^{-1} reported by Yavit (2017) in southeastern Peru. The bamboo densities that are closest to those found in this study were reported by Griscom and Ashton (2006) on the Tambopata River in Peru, with 3860 ± 265 culms ha^{-1} in forests dominated by *Guadua weberbaueri* and 2375 ± 618 culms ha^{-1} in forests dominated by *Guadua sacocarpa*.

4.3 Aboveground forest biomass

Since Amazon forest has great structural and floristic heterogeneity, a high variability in forest biomass is expected, even for plots in the same forest type (Fearnside 2018). Although the soils under forests in southwestern Amazonia have relatively high concentrations of phosphorus by Amazonian standards (Quesada et al. 2010), the biomass values can be considered low compared to values observed in other parts of the Brazilian Amazon (Nogueira et al. 2015). This can be explained by high tree turnover, which follows a decreasing gradient from west to east in the Amazon (Quesada et al. 2012) and implies high recruitment and mortality rates. A reduced residence time can be expected for carbon in the forests in the area of the present study.

The legacy left by impacts associated with these forests could be observed in our study more than 10 years after disturbance. The difference between the carbon stored in 1 ha of the control treatment and in the treatment with the highest impact was 46.3 Mg ha^{-1}. This amount is equivalent to the emissions from the annual consumption of goods and services by approximately 17 Brazilians, 19 Peruvians, or 25 Bolivians in 2015 (Le Quéré et al. 2015).

4.4 Biomass of live trees and palms

The biomass class of live trees and palms represented, on average, 74% of the total aboveground biomass (live + dead). Thus, the reduction of aboveground biomass value in the forest can be largely attributed to the reduction in the number of live trees and palms per hectare following disturbance (Fig. 5). A large part of the high aboveground biomass found in the undisturbed treatment can be attributed to the concentration of individuals in the highest diameter class (Fig. 6).

Although the treatment with the highest impact had more trees and palms per hectare than the treatment with intermediate impact, the latter had a larger number of individuals with DBH > 40 cm, which was reflected by a higher biomass value of live trees and palms (Fig. 6). The biomass of live trees and palms with DBH above 40 cm represented, on average, 70% of the biomass of live trees and palms in all diameter classes, and 54% of the total aboveground biomass of the forest (live + dead), indicating the great importance that maintaining these individuals has for the forest carbon stock.

Considering only live trees and palms with DBH > 50 cm, it was possible to observe a significant difference for biomass values between treatments ($p = 0.049$). The control treatment had a mean value 55.4% higher than the treatment with logging and fire and 57.1% higher than the treatment impacted only by fire (Table 3).

The values for biomass of live trees and palms (DBH > 10 cm) sampled by Barlow et al. (2012) 3 years after a fire in Acre were higher than those obtained in the present study for the forest without known impact (380 to 400 Mg ha^{-1}) and for the forest affected by fire (260 to 280 Mg ha^{-1}). There is evidence for a structural difference in the abundance of senescent large trees in the Amazon along a gradient from east to west, with older individuals being more abundant in the eastern Amazon region (Chao et al. 2008). In addition, studies also suggest a possible difference in the mortality dynamics of these large trees along this same gradient (Chao et al. 2008; Phillips et al. 2008). Large trees are also most sensitive to dry conditions from edge effects (Nascimento and Laurance 2004) and from experimental drought (Nepstad et al. 2007). Assuming that senescent large trees are more vulnerable to stress from drought (as well as disturbances from logging and fire) than are smaller trees, large trees in the southwestern Amazon would be more resistant to anthropogenic impacts than trees of similar diameter in eastern Amazonia because they are less senescent (Barlow et al. 2012). The data from the present study, however, reveal a high vulnerability of large trees to these disturbances, given the observation of a subtle reduction in the number of live trees and palms with DBH > 50 cm (Fig. 6), which represented a reduction of 45.4% in the biomass of the intermediate-impact treatment and 44.0% in the biomass of the treatment with the greatest impact (Table 3).

4.5 Bamboo-dominated forest, ecosystem services, and potential for management

The "cascade model" of ecosystem service generation presented in 2010 by Haines-Young and Potschin (2010) suggests a link between ecosystem services and human well-being. Despite the difficulty of defining and measuring ecosystem services, assigning a value to services provided by conserved forest is important for discussion and planning of public policies for conservation (Potschin and Haines-Young 2016), such as reducing emissions from deforestation and forest degradation (REDD+) (Fearnside 2012).

A complete cycle of generating and managing ecosystem services can be implemented by integrating public and private interests into planning and decision-making processes (Spangenberg et al. 2014). Because large trees are of central importance both for carbon stock and for the forest's value for timber management, the impact on these trees due to the increase of bamboo in conjunction with forest fires is both an environmental and a commercial concern.

5 Conclusions

This study suggests a downward trend in the aboveground carbon stock of the forest with increasing level of impact. Reduction in the aboveground biomass of live trees and palms, especially in the diameter class over 50 cm, is one of the main consequences related to disturbances in open forests dominated by bamboo. These individuals are of central importance for the carbon stock, and, from the economic point of view, decrease in their abundance leads to a loss of value of the standing forest, reducing the already-low potential of these forests for management.

The damage to Brazil's Amazon forest initiated by the 2005 drought, documented here, adds one more piece of evidence of the need to contain global climate change and of the logic for Brazil to assume a leading role in these efforts.

Acknowledgments We thank the National Institute for Research in Amazonia (INPA: PRJ15.125), the National Institute of Science and Technology for the Environmental Services of Amazonia (INCT-SERVAMB), the National Council for Scientific and Technological Development (CNPq/PCI Program Proc. 304130/2013-3 and 301183/2015-5; CNPq: Proc. 304020/2010-9; 573810/2008-7), and the Foundation for Support of Research in Amazonas State (FAPEAM: Proc. 708565) for logistical support. We owe personal thanks to Sebastião Mota, Evandro Ferreira, Marcos Viníces D'Oliveira, Aurora Miho Yanai, Jochen Schöngart, Reinaldo Imbrózio Barbosa, Nathan B. Gonçalves, and Bruce W. Nelson.

Statement on data availability The datasets generated and/or analyzed during the current study are available in the Zenodo repository (Ziccardi et al. 2019) at https://doi.org/10.5281/zenodo.3530726

Funding information This study received financial support from National Institute for Research in Amazonia (INPA: PRJ15.125), the National Institute of Science and Technology for the Environmental Services of Amazonia (INCT-SERVAMB), the National Council for Scientific and Technological Development (CNPq/PCI Program Proc. 304130/2013-3 and 301183/2015-5; CNPq: Proc. 304020/2010-9; 573810/2008-7), and the Foundation for Support of Research in Amazonas State (FAPEAM: Proc. 708565). This article is a contribution of the Brazilian Research Network on Global Climate Change, FINEP/Rede CLIMA Grant Number 01.13.0353-00.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Disclaimer The funding sponsors had no role in the design of the study, in the collection, analyses do, or interpretation of data, in the writing of the manuscript, and in the decision to publish the results.

Appendix

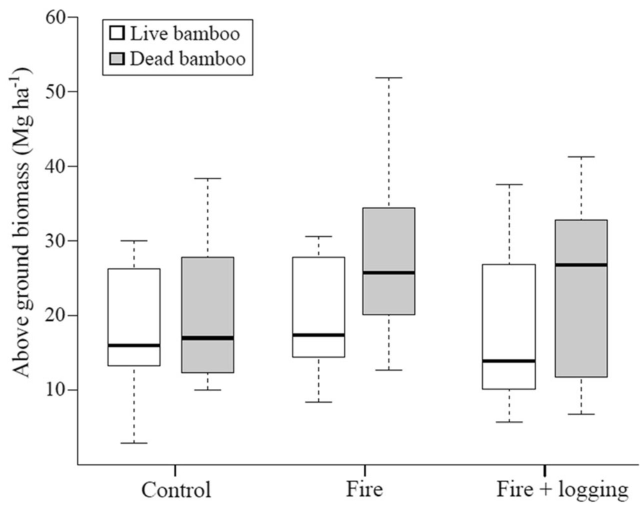

Fig. 7 Dry aboveground biomass of live and dead bamboo per hectare

Fig. 8 Abundance of fruits and seeds of *Guadua* spp. observed in the field, indicating a mass-flowering event

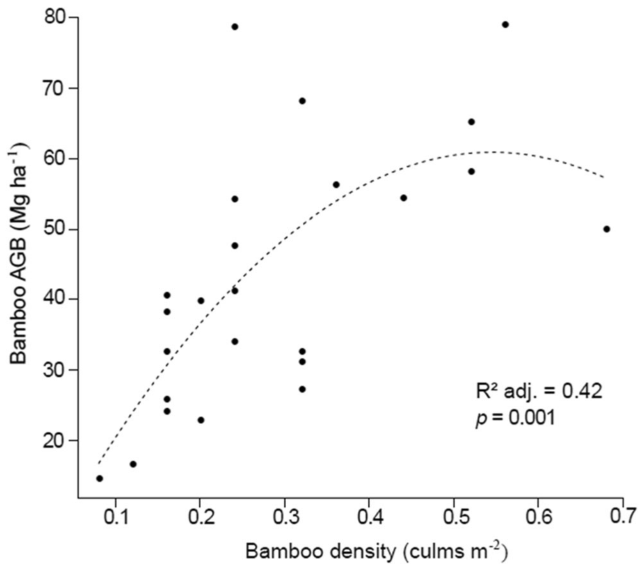

Fig. 9 Nonlinear regression between bamboo aboveground biomass (AGB) and bamboo density for all sample units

Table 4 Characteristic of woody debris related to the phases of wood decomposition

Phase of decomposition	Description of characteristics
C1	Woody debris without noticeable deterioration, recently fallen and resistant to attack by microorganisms
C2	Woody debris with few signs of fungal or insect attack, with initial deterioration
C3	Woody debris at an advanced stage of deterioration, easily breaking or cracking if touched

Table 5 *Guadua* spp. density in the different treatments

Treatment	Mean density (culms ha^{-1})	CV (%)	Percentage error (%)	*p* (ANOVA)
Control	2500	45.9	38.4	0.478
Fire	3400	50.3	42.1	
Fire + logging	2700	63.2	52.9	

CV coefficient of variation

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